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## ECTOTHERMY AND THE SUCCESS OF DINOSAURS

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Dinosaurs were the dominant terrestrial tetrapods of the Mesozoic and their ecological roles and biological impact are generally compared with those of mammals in the Cenozoic. This has led to the assumption that dinosaurs were endothermic also (Bakker, 1971, 1979) and there seems to be some evidence in support of this hypothesis. However, this evidence is not conclusive. Could it be that dinosaurs were in fact ectothermic and could their success be explained most simply in terms of a normal reptilian physiology?

In this paper I review the published evidence for and against dinosaur endothermy and attempt an assessment in terms of the thermoregulatory physiology of living animals, and I discuss the success and the extinction of dinosaurs in connection with published data on Mesozoic paleoclimatology. It is argued that endothermy in dinosaurs would have been energetically costly and yet there appears to have been no need for it. Ostrom (1979) complains that critics of dinosaur endothermy merely offer alternatives and do not disprove the arguments of their opponents. This paper attempts to show why dinosaurs (with the possible exception of some theropods) had to be ectothermic.

Before proceeding, the four basic descriptive terms used in thermoregulatory physiology should be defined accurately (Cowles, 1940, 1962; McNab, 1978). A *poikilothermic* animal has no control over body temperature, which follows external conditions, while a *homeothermic* animal has a constant body temperature. An *ectotherm* derives heat from external sources (generally solar radiation directly or indirectly) and an *endotherm* from internal sources (generally metabolic or muscular heat).

This paper was written before the

AAAS symposium published as Olson and Thomas (1979) and references to papers from this volume are, as a result, brief.

### DISCUSSION OF EVIDENCE FOR DINOSAUR ENDOTHERMY

Interest in the thermoregulatory physiology of dinosaurs has revived recently (Bakker, 1975a; Desmond, 1975; Gould, 1977; May, 1977; Marx, 1978; Olson and Thomas, 1979), although speculations have been made on this topic for at least 100 years. Audouin (1929) and Nopcsa (1934) suggested that dinosaur extinction might have been related to their ectothermy, but other later authors have suggested that it was connected with their endothermy (Wieland, 1942; Russell, 1965; Cloudsley-Thompson, 1971; Bakker, 1972, 1973).

Broili (1941) and Schuh (1951), extrapolating from finds in pterosaurs and synapsids, predicted that dinosaurs would be found with "hair," necessary insulation in an endotherm. However, others have related the large size and naked skin of dinosaurs to endothermy, arguing that the absence of small dinosaurs is connected with the problems of excessive heat loss by small uninsulated endotherms with a high surface/volume ratio (Bakker, 1971, 1972, 1973; Ricqlès, 1974). These latter interpretations were criticized by Thulborn (1973) and Feduccia (1973) who pointed out that young dinosaurs were small and naked and could only have avoided cooling stress problems if they were ectothermic.

The evidence most recently presented for dinosaur endothermy includes erect gait, paleoclimates and distribution, small agile dinosaurs, brain size, predator-prey ratios, bone histology, and the parietal-pineal complex.

*Erect gait.*—Dinosaurs had erect stance and advanced gait. Among living animals, only endotherms have erect gait; and it was suggested that this and the supposed ability of dinosaurs to achieve fast speeds indicated endothermy (Schuh, 1951; Ostrom, 1970, 1974; Bakker, 1971, 1972, 1973, 1974, 1975a; Dodson, 1974). However, this view has been widely criticized as a logical *non sequitur* (Thulborn, 1973; Bennett and Dalzell, 1973; Feduccia, 1973, 1974; Bennett, 1974; Halstead, 1976). The fact that the only living animals with erect gait are endotherms does not mean that every animal with erect gait is an endotherm—it should also be noted that many mammals and other endothermic animals (see below) have a sprawling gait (Jenkins, 1971). In addition, Alexander (1976) calculated speeds of only 1–3.6 ms<sup>-1</sup> from trackways of dinosaur footprints, although one hadrosaur trackway indicates a speed of 7.5 ms<sup>-1</sup> (Russell and Béland, 1976). Thus large dinosaurs, at least, may have moved relatively slowly and the erect stance may be no more than the most efficient way of supporting a heavy body (Bennett and Dalzell, 1973; Feduccia, 1973; Bennett, 1974; McNab, 1978).

*Paleoclimatology and distribution.*—Finds of dinosaurs within the Cretaceous Arctic Circle (Russell, 1973) have been thought to indicate endothermy also (Bakker, 1975a; Desmond, 1975), but precise data on Mesozoic climates are not given (Halstead, 1975b, 1976). There is no evidence of glaciation in the Mesozoic (Schwarzbach, 1963; Bakker, 1975b) and climates at these high latitudes need not have been cold. In general, Mesozoic climates were warmer than today (Dorf, 1970; see below).

*Small agile dinosaurs.*—Many smaller dinosaurs (especially lightly built theropods like *Compsognathus*, *Saurornithoides* and *Deinonychus*) were presumably agile and must have been able to move rapidly (Ostrom, 1978). At first sight, this is very different from many living lizards and might be thought to be good evidence for endothermy in dino-

sosaurs. However, this may be connected with gait rather than thermoregulation. Most living reptiles have a sprawling stance, whereas the agile theropods had an erect stance. The erect posture which supported the great weight of brontosaurus allowed agile motion in smaller dinosaurs. The generally warm Mesozoic climates (see below) may have maintained their body temperatures high enough during the day for activity and their carnivorous diet provided readily assimilable energy. After a cool night, body temperatures may have been increased by basking or uptake of heat from rocks in the early morning as in living reptiles. Ostrom (1978, 1979) suggests that the only possibly endothermic dinosaurs were these small theropods, particularly in view of their possible relationship to birds.

*Brain size.*—Feduccia (1973) suggested that the small lizard-like brain size of dinosaurs speaks for ectothermy, but finds of “ostrich dinosaurs” with large brains (Russell, 1972) were interpreted as evidence for endothermy (Dodson, 1974; Ricqlès, 1974; Bakker, 1974, 1975a). However, the large brains of these dinosaurs are associated with good eyesight and balance (Halstead, 1975b) and do not necessarily imply advanced mammal-like intelligence. In any case, internal thermoregulation requires a smaller mass of neural tissue than that required by ectotherms for the behavioral control of internal temperature (Jerison, 1973) and thus brain size may not be a reliable indicator of endothermy (cf. Robinson, 1971).

*Predator-prey ratios.*—Herbivores (whether endothermic or ectothermic) can support about 5% of their biomass of endothermic predators, and for ectothermic (reptile) carnivores, this predator-prey ratio is apparently nearer 30–50% (Bakker, 1972, 1975a, 1975b, 1979). Bakker (1972, 1973, 1974, 1975a, 1975b) calculated predator-prey ratios for certain fossil populations and used the values he obtained as indices of ectothermy or endothermy. He noted a drop from 50% in the Early Permian to 10% in the Late Permian and concluded that this repre-

sented the changeover from ectothermy to endothermy in populations of fossil reptiles.

Charig (1976) listed many possible sources of error in applying predator-prey ratios to fossil communities, such as collector bias, incompleteness of the fossil record, relative life spans, and interactions of other animals in food chains. I would add that some "prey" species (e.g., *Brontosaurus*) might have been unavailable for predation owing to very large size, although they could have been scavenged after they died, but their inclusion would greatly lower the apparent predator-prey ratio. The present-day elephants effectively have no natural predators because of their large size. Of course, the ratios can only indicate whether the predator is endothermic or ectothermic: the amount of prey required would be the same whatever its thermoregulatory state. If ectothermic tyrannosaurs ate their young or other carnivores, or if they were partly scavengers, the ratios could be explained readily (Tracy, 1976).

In fact, it seems that ratios of large ectothermic predators to prey closely approach those for endothermic predators, thus casting doubt on the value of this concept as a measure of the presence of endothermy in dinosaurs (Thulborn, 1973; Farlow, 1979; Russell and Béland, 1979). Halstead (1976) suggested that ratios vary with the size of the animals involved, and not with thermoregulatory state.

Bakker apparently used unspecified "corrections" in some calculations of relative numbers of faunal elements and some of his assumptions about ingestion rates are not well founded (Farlow, 1976; Russell and Béland, 1979). His conclusions cannot be properly assessed until these corrections, assumptions, and his original data are published.

*Bone histology.*—In large mammals the regeneration and internal remodelling of bone involves the development of Haversian systems (Enlow, 1962). Haversian bone and good vascularization are associated with the freeing and fixing of phos-

phocalcic salts, and they develop especially in rapid growth (Ricqlès, 1974). The idea has arisen that these Haversian systems indicate endothermy (Enlow and Brown, 1957; Currey, 1962; Ricqlès, 1969, 1972a, 1972b, 1974, 1976; Bakker, 1972, 1974, 1975a; Dodson, 1974).

Large mammals, most birds, advanced synapsids and dinosaurs have extensive Haversian systems, and tunas, turtles and crocodiles have them less developed. They are not present in small mammals, passerine birds, lizards, snakes or primitive reptiles (Enlow, 1969; Ricqlès, 1974, 1976). The first two in this list are the "most" endothermic vertebrates (i.e., they have the highest rates of mass-specific metabolism), and they might be expected to have such structures most highly developed (McNab, 1978). Thus, Haversian systems are present in most living endotherms and some living ectotherms and tend to be associated with large size (Halstead, 1976). Bouvier (1977) lists animals with secondary Haversian systems and shows that their presence is not correlated with endothermy. The correlation seems instead to be with homeothermy (McNab, 1978).

Dinosaurs were large, and yet their eggs were mechanically limited in size; the hatchlings often being only 1–2% of the weight of their parents (Colbert, 1961). A vulnerable young dinosaur may have had to grow fast in order to achieve its adult size and this would have involve continuous bone remodelling. The presence of Haversian systems in these forms is probably explained by their large size and rapid growth.

*Parietal-pineal complex.*—Living reptiles may control their body temperature by behavioral means to within a very narrow range. This control is effected in response to information from the pineal gland and parietal eye, and these structures tend to disappear in the fossil record as animals become endothermic. Certain fossil amphibians and early fossil reptiles (e.g., batrachosaurs, cotylosaurs, pelycosaurs: Olson, 1976) show large parietal

openings, whereas dinosaurs do not. This might be taken as evidence of endothermy, but there is no pineal in crocodiles. The loss of the parietal-pineal complex may be related to the fact that both groups of reptiles live in warm climates and do not need such a precise regulator (Roth, 1979).

#### LARGE SIZE OF DINOSAURS AND INERTIAL HOMEOTHERMY

Studies of large living reptiles (alligators: Colbert et al., 1946, 1947; Galápagos tortoise: Mackay, 1964; Komodo monitor: McNab and Auffenberg, 1976) have shown that rates of internal temperature change are very slow during normal subtropical diurnal temperature fluctuations. By extrapolation, temperatures of medium to large dinosaurs living in similar climatic conditions would remain constant to within 1 or 2 C inertially without internal heat production (Colbert et al., 1946, 1947; Spotila et al., 1973; McNab and Auffenberg, 1976; McNab, 1978; Spotila, 1979). However, Gunn (1943) speculated that dinosaurs would have displayed diurnal cycles of body temperature fluctuation only somewhat more out of phase with external temperature changes than in smaller reptiles. Working from data on recent reptiles, he assumed that basal heat production was constant for a given surface area and that large reptiles thus produced less heat per gram body weight. However, metabolism in reptiles is not directly proportional to body weight or surface area (Bennett and Dawson, 1976), and these speculations cannot be regarded as valid. Thus dinosaurs achieved thermal constancy by large size (Cloudsley-Thompson, 1972; Halstead, 1975a, 1975b, 1976). High metabolic rates may have been produced by activity metabolism and large size rather than thermoregulation (Bennett and Dawson, 1976). Thus it seems that dinosaurs could have been ectothermic inertial homeotherms; indeed, if they had been endotherms, large dinosaurs would have suffered overheating (McNab and Auffenberg, 1976; McNab, 1978).

Spotila et al. (1973) modelled an inertially homeothermic dinosaur maintaining its internal temperature at 30 C, but Bakker (1975b) suggested that 38 C+ would be a more likely temperature because of its "high activity." Ignoring the circular logic here, 38 C is the normal body temperature of a eutherian mammal, and many highly active reptiles and non-eutherian mammals normally operate at lower temperatures (Schmidt-Nielsen, 1975). The alleged "high activity" of large dinosaurs still remains highly speculative and indeed Spotila (1979) suggests that a "very active . . . lifestyle is entirely compatible with the thermoregulatory status as ectothermic homeotherms."

#### HEAT-EXCHANGE STRUCTURES AND THERMOREGULATION

Several early reptiles displayed sail-like structures which have been interpreted variously as defensive, display, camouflage, or temperature-control organs. The Early Permian pelycosaur *Edaphosaurus* and *Dimetrodon* in particular had large dorsal "sails," produced by elongation of the neural spines, which are usually supposed to be involved in temperature regulation (Rodbard, 1949; Romer, 1966; Olson, 1971; Bramwell and Felgett, 1973; Halstead, 1975a). The large herbivorous dinosaur *Ouranosaurus* and the carnivore *Spinosaurus* from the Cretaceous of North Africa both had dorsal sails formed similarly from elongated neural spines. These are proposed as structures to increase heat-loss during vigorous exercise in a hot environment (Halstead, 1975a). Recent work on *Stegosaurus* (Farlow et al., 1976) has suggested that its apparently well-vascularized dorsal plates could have acted as efficient forced heat convection "fins" in a dry, hot environment. Cooling structures are seen, for example, in present-day African elephants which extend their large well-vascularized ears in order to lose excess heat (Sikes, 1971).

Small animals with large expanses of membrane or expanded ribs associated with gliding or flight (e.g., bats, pterosaurs, the supposed Triassic archosaurs

*Podopteryx* and *Longisquama*, *Kuehneosaurus* and other gliding lizards) would also experience an increase in heat-loss or uptake via these structures. This would probably be an incidental effect and "sail" or membrane structures have different basic functions and origins in large and small animals.

In a medium or large ectotherm, a basking structure would increase considerably the rate of morning heating when the animal stood broadside to the sun, and daytime cooling could be effected if the animal faced the sun with the minimum area of sail presented to it. However, this additional vascularized area would also increase rates of evening cooling if there was a sudden drop in temperature at sunset. Probably blood vessels in the "sail" could also dilate and constrict in order to assist the regulation of heat loss and gain. Early Permian pelycosaurs are generally assumed to have been ectothermic (Bakker, 1975a, 1975b; Olson, 1976; Ricqlès, 1976), and in general only the larger genera have sails (Halstead, 1975a), but the largest pelycosaur, the ½-ton *Cotylorhynchus* (Romer, 1966), a possible inertial homeotherm, had no sail. However, no small genus had a sail and this may confirm the function to increase the rate of body heating in the morning in a large ectotherm (Bramwell and Fellgett, 1973). Bakker (1971, p. 652) argued for a non-thermoregulatory display function for the pelycosaur sail, comparing it with that found in the living lizards *Basiliscus* and *Hydrosaurus*. However, only the males of *Basiliscus* possess crests (Pope, 1957) and males of *Hydrosaurus* have larger crests than females (Schmidt and Inger, 1957), and there is little evidence of such sexual dimorphism in pelycosaurs (Romer and Price, 1940, p. 171-172).

The dorsal sails of the Cretaceous dinosaurs *Ouranosaurus* and *Spinosaurus* and the plates of the Jurassic *Stegosaurus* could be heat-loss convectors in an ectothermic or endothermic model. In a hot environment, an endotherm would have greater need of them because of its smaller

range of internal temperature tolerance, but the absence of such structures in most contemporaneous dinosaurs could suggest one of the following: cooler Mesozoic climates elsewhere, other heat-loss adaptations in other dinosaurs, a misinterpretation of the function of "sails" or that heat-loss problems were not generally acute. Thus, although "sails" were probably basking structures involved in thermoregulation, they do not seem to offer information on thermoregulatory physiology. It may be of importance to note that sails have evolved in parallel in a herbivore and presumably coexisting carnivore in the cases of both *Edaphosaurus* and *Dimetrodon*, and *Ouranosaurus* and *Spinosaurus*.

#### EVOLUTION OF ENDOTHERMY

It is important to remember that the difference between an endotherm and an ectotherm need not be too great. The only basic change necessary in the evolution of endothermy was an increase in the concentration of mitochondria (Bennett and Dawson, 1976). Other changes, some or all of which may occur over a period, are new neural circuitry, development of involuntary responses like shivering, panting or sweating, regulation of peripheral circulation, insulating layer of fur, feathers or fat (Satinoff, 1978). Heath (1968) suggested that endothermy arose in mammal-like reptiles in response to the acquisition of an erect stance which was supposed to involve increased muscular tension. However, this idea is probably not tenable since body temperature in mammals is maintained without muscular contractions and all the cells, not just skeletal muscle, are involved (Janský, 1973). The cell membrane sodium pump, controlled by thyroxine, produces heat and stimulation of this mechanism may have been the step involved in the evolution of mammalian endothermy (Edelman and Ismail-Beigi, 1971; Stevens, 1973).

Heinrich (1977) proposed that endothermy arose in vertebrates and insects in order to permit high levels of activity for

extended periods. High temperature set points (40 C or more) may have evolved from an inability to dissipate rapidly all of the heat produced as a result of high activity rates. Constant high body temperatures involved changes in biochemistry resulting in more rapid substrate turnover by enzymes.

Endothermy is not an all or nothing thing. "Primitive" living mammals (monotremes, didelphid marsupials, tenrecs, *Solenodon*, certain hedgehogs) regulate their body temperatures at relatively low levels (27–33 C) which are far below normal levels in placentals (37–38 C) (Bakker, 1971; Crompton et al., 1978). Many so-called "cold-blooded" animals are, in fact, endotherms which generate heat by muscular activity (Indian python: Hutchinson et al., 1966; lizards: Bartholomew and Tucker, 1964; Leatherback turtle: Frair et al., 1972; tuna: Carey, 1973; Carey and Teal, 1969b; Mako and Porbeagle sharks: Carey, 1973; Carey and Teal, 1969a; many large flying insects [moths, butterflies, bees, beetles, locusts, dragonflies]: Heinrich, 1974). Different forms of endothermy have arisen independently several times. There is no clear dividing line between ectotherms and endotherms either today or presumably also in the past, and thus attempts to reclassify vertebrates on the basis of endothermy alone (Bakker and Galton, 1974; Bakker, 1975a) hardly seem justified (cf. Charig, 1976).

Present evidence seems to suggest that dinosaurs were ectothermic, the larger ones being inertial homeotherms. Mammal-like reptiles (therapsids) were dominant on land in the Late Permian and they were replaced gradually in most medium-large terrestrial niches by archosaurs throughout the increasingly arid Triassic. An attempt is made here to explain the replacement of mammal-like reptiles by dinosaurs in terms of the advantage of ectothermy in an arid environment. Thus, we must first consider Mesozoic paleoclimatology and then compare the relative efficiency of ectotherms and endotherms in arid conditions.

## MESOZOIC PALEOCLIMATOLOGY

The climate represented by the Late Permian reptile beds appears to have been largely equable with some swampy and arid conditions (Cox, 1967; Olson and Vaughan, 1970; Robinson, 1971; Bakker, 1975b). Recovery from the Late Carboniferous glaciation of southern Gondwanaland may have produced generally cool conditions in some areas (King, 1961). Arid areas appear to have become more extensive during the Triassic (King, 1961; Cox, 1967; Dunbar and Waage, 1969; Robinson, 1971) and the Upper Triassic Red Bed environment of certain early ornithischian dinosaurs was hot and seasonally arid (Thulborn, 1978).

When dinosaurs were most widespread, in the Jurassic and Cretaceous, climates were generally hot or warm and equable (Colbert, 1953, 1964; King, 1961; Schwarzbach, 1961, 1963; Vakhrameev, 1964; Berlin et al., 1966; Bowen, 1966; Axelrod and Bailey, 1968; Volkheimer, 1969, 1972; Dunbar and Waage, 1969; Montford, 1970; Barnard, 1973; Spotila et al., 1973; Ricqlès, 1974; Hallam, 1975). Temperatures were more uniform globally (Lowenstam, 1964; Dunbar and Waage, 1969; Hallam, 1975; Dott and Batten, 1976; Donn and Shaw, 1977) and latitudinal temperature gradients were less steep than today (Bowen, 1966; Donn and Shaw, 1977). There is no evidence of glaciation in the Mesozoic (Schwarzbach, 1963; Bakker, 1975b) and tropical or temperate floras have been found in the Jurassic of the Arctic (Vasilevskaya, 1973) and Antarctic (Barghoorn, 1953). However, there were apparently some temperature fluctuations during and at the end of the Cretaceous (Lowenstam and Epstein, 1959; Lowenstam, 1964; Smiley, 1966; Krassilov, 1973, 1975; Vakhrameev, 1975; Van Valen and Sloan, 1977; McLean, 1978). Seasonal conditions have been recorded from the Jurassic (Bowen, 1966; Dawson, 1970) and Cretaceous (Dodson, 1971). Dorf (1970, p. 345) summarizes Mesozoic climates, as interpreted

TABLE 1. *Characters of typical ectotherm (reptile) and endotherm (mammal).*

	Ectotherm	Endotherm
Internal regulation of body temperature	no	yes
Basal metabolic rate	low	high
Food supply required	small	large
Range of preferred body temperatures	wide	narrow
Water loss	reduced (uricotelic)	may be high (ureotelic)

from paleobotanical evidence, as follows: "Evidence suggests that the Triassic, Jurassic and Early Cretaceous climates were more uniform and warmer than at present with minor reversals toward cooler and drier conditions." Bakker (1975*b*) suggested that Jurassic and Cretaceous climates may not have been so warm as has been assumed, but the evidence indicates only limited cool periods.

Paleoclimatic data are derived from studies of sedimentology, paleobotany (whole plants and pollen and spores), invertebrate paleontology (e.g., coral reefs) and oxygen isotope ratios and other geophysical methods (Bowen, 1966). Dinosaurs have been used as evidence for warm Mesozoic climates (e.g., Colbert, 1953, 1964; Schwarzbach, 1963; Volkheimer, 1969, 1972), but this is best avoided for the present study (Ostrom, 1970).

#### THERMOREGULATORY PHYSIOLOGY IN ARID REGIONS

The apparent gradually increasing aridity of the Triassic would favor animals which did not rely on an abundant food supply and which could tolerate high temperatures and conserve water. These are the characters typical of an ectotherm (Table 1). Ancestral archosaurs (thecondontians) were probably ectotherms, whereas late therapsids were probably partially endothermic (i.e., regulating their internal temperatures at a lower level than eutherians, say 30 C, and still relying on behavioral responses for part of the control [Brink, 1956; Hopson, 1973; Bakker, 1975*a*; Olson 1976]). McNab (1978) postulates that the reduction in size of mammal-like reptiles at the end of the Permian

and the development of a secondary palate correlated with the evolution of endothermy in cynodonts and bauriamorphs and evidence from bone structure supports this (Ricqlès, 1974). Thus endothermy preceded the evolution of mammals by 25 million years. However, Crompton et al. (1978) believe that endothermy (they call it homeothermy) arose only later, in small nocturnal Mesozoic mammals, and that mammal-like reptiles were still ectothermic.

Present-day arid regions may experience diurnal cycles of temperature with cold nights, and seasonal cycles of aridity, with wet seasons. However, the survival of an animal depends on how well it can survive the worst conditions. Animals may either tolerate or avoid the heat and aridity of a desert.

Endotherms (birds and mammals) cope with desert life chiefly by avoiding the worst conditions. Birds require water and seek shade or pant in order to lose heat (Dawson and Hudson, 1970). Large desert mammals (camels, antelope, etc.) have evolved many special adaptations such as the ability to store heat during the day and lose it overnight, shade-seeking, reflective and insulating pelage and seasonal migrations to avoid arid conditions. However, most desert mammals weigh less than 250 g, and many weigh less than 50 g (Bartholomew and Dawson, 1968). These small mammals largely avoid desert conditions by being nocturnal and/or burrowing.

Sustained endothermy requires constant high levels of food which may not be available in either very hot arid regions or seasons (metabolic rates of endotherms are



5–7 times those of ectotherms of the same weight [Bennett and Dawson, 1976] and 80–90% of the oxidative energy of an endotherm is used to maintain its body temperature [Bartholomew, 1968]. Also, in hot arid environments, the water needed to dissipate heat may be in short supply [Bligh, 1972, 1976].

These problems may be reduced, in part, by being ectothermic. Reptiles are “apparently well adapted for life in arid regions” (Cloudsley-Thompson and Chadwick, 1964, p. 160). In present-day desert regions the most abundant vertebrates are lizards (Mayhew, 1968; Templeton, 1972). Lethal body temperatures for lizards are around 49–50 C and for snakes, 43–44 C (Mayhew, 1968), while normal tolerated body temperature ranges can approach 20 C (e.g., *Dipsosaurus dorsalis*, the desert iguana, tolerates 29–47 C [Templeton, 1970]), whereas most birds and mammals tolerate a range of only about 2 C and the camel can only tolerate 34–40 C (Schmidt-Nielsen et al., 1957). Desert reptiles lose less water than endotherms of the same weight (Chew and Dammonn, 1961; Schmidt-Nielsen and Dawson, 1964; Cloudsley-Thompson, 1971).

It is interesting to note that the only large desert animals at present are mammals. But, of course, most large animals in any terrestrial environment today are mammals, presumably because of their rapid adaptive radiation at the beginning of the Tertiary and the specialized nature of the surviving reptile groups which were apparently not preadapted to compete successfully and evolve into large herbivores or carnivores on land. Most large reptiles today are carnivores (Crocodylia, Komodo monitor, snakes) and herbivory is less common (Porter, 1972). In the Early Triassic, when mammals were absent, medium-large herbivorous reptiles were abundant and, with increasing aridity throughout that period, it seems reasonable to assume that the successful ones (archosaurs) were still ectothermic. Any advantages that endothermy may have had for the Late Permian and Early Triassic therapsids in the wetter, more equable

conditions of those times (Bakker, 1975*b*) would not apply to archosaurs in the hot, seasonally arid Late Triassic. Conditions were such that early dinosaurs may have had to aestivate to survive over the dry season (Thulborn, 1978). However, endothermy would have been of value to small insulated animals that had a large surface/volume ratio and were either nocturnal (e.g., early mammals), or required large amounts of energy for flight (e.g., birds, pterosaurs) (Bakker, 1971; Ostrom, 1974; Desmond, 1975). Bakker (1975*b*, p. 392) argues that endothermy is superior to ectothermy in wet, tropical conditions. He suggests that a particularly cold night might lower the body temperature of a reptile by 10 C or so and it would be unable to recover. However, if estimates of rates of diurnal cooling and heating in dinosaurs (Colbert et al., 1946, 1947; Spotila et al., 1973; Halstead, 1975*a*; McNab and Auffenberg, 1976) are correct, a fall of 10 C in a large dinosaur would require excessively cold conditions for a considerable period of time. Also, this argument only applies to wet tropical conditions which were restricted in extent in the Late Triassic when dinosaurs were establishing themselves.

#### REPLACEMENT OF THERAPSID BY ARCHOSAURS

Late Permian and Early Triassic thecodontians may be divided into two groups on the basis of presumed lifestyle. First, there were the medium-large freshwater predators (Proterosuchidae and Erythrosuchidae) which occupied the “crocodile niche” (Reig, 1970; Charig and Sues, 1976). Water tends to buffer ambient temperature fluctuations and hence endothermy is unnecessary for animals living in relatively warm water. The second thecodontian group (Euparkeriidae) were medium-sized predators of arid uplands and lowlands (Ewer, 1965).

These two groups comprise the first (admittedly not very abundant) wave of archosaur radiation, the replacement of mammal-like reptiles in many carnivorous niches. Both groups appear to owe this

success to the improvement of gait and jaw action (Romer, 1966) and to ectothermy.

During the Middle and Late Triassic, herbivorous therapsids also were replaced progressively by thecodontians and early dinosaurs. With increasing aridity, the areas of lush lowland vegetation were reduced, and those animals that could survive at higher temperatures on less plant food and lower water availability would be favored. Again, ectotherms had the advantage, and the second wave of archosaur radiation also may be attributed to their ectothermy. These, and other important ecological replacements of the Mesozoic are discussed in Benton (1979).

#### DINOSAUR SUCCESS

The success and extinction of the dinosaurs presents a paradox. Archosaurs replaced therapsids in nearly all major terrestrial niches causing the virtual extinction of the latter. The tiny descendants of the therapsids, the early mammals, continued throughout the Mesozoic as a relatively insignificant group of small insectivores but replaced the dinosaurs in nearly all their niches at the end of the Mesozoic. Note that the replacement of therapsids by dinosaurs apparently occurred by gradual processes of competition, whereas the adaptive radiation of Tertiary mammals occurred only after the sudden extinction of dinosaurs. The success of dinosaurs has been ascribed to many factors, such as insect-eating among diapsids (Watson, 1957), advanced gait (Bakker, 1968; Thulborn, 1975), endothermy (Cox, 1967; Bakker, 1971, 1972, 1973, 1975*a*, 1979), ectothermy and inertial homeothermy (Colbert et al., 1947), and uricotelism (Robinson, 1971).

Robinson (1971), assuming that both archosaurs and synapsids were ectothermic, suggested that the former were distinguished by uricotelism alone (note that Reig, 1970, p. 265, suggested that both mammals and archosaurs excreted urea rather than uric acid). However, if mammal-like reptiles were endothermic, dinosaur ectothermy (including uricotelism, but also the need for less food and toler-

ance of a wider range of temperatures than endotherms) would have been advantageous in arid Late Triassic environments. The development of large body size, and thus inertial homeothermy, in the less arid Jurassic and Cretaceous assured the continued success of dinosaurs (Colbert et al., 1946, 1947; Spotila et al., 1973). It cannot be assumed that endothermy is always selectively more advantageous than ectothermy.

#### DINOSAUR EXTINCTION

Dinosaur extinction has been explained in terms of a temperature drop at the end of the Cretaceous associated with ectothermy (Audouin, 1929; Nopcsa, 1934), a temperature rise at the end of the Cretaceous and endothermy (Wieland, 1942), a temperature drop and endothermy (Russell, 1965, 1966, 1967; Cloudsley-Thompson, 1971; Bakker, 1972, 1975*a*), a temperature drop and inertial homeothermy (Axelrod and Bailey, 1968; Halstead, 1975*a*), or a temperature rise and endothermy or ectothermy (McLean, 1978), among many other hypotheses.

Certain isotopic, micropaleontological and paleobotanical evidence seems to indicate a temperature drop at the end of the Cretaceous (Lowenstam and Epstein, 1959; Lowenstam, 1964; Russell, 1965, 1966; Hall and Norton, 1967; Worsley, 1971; Krassilov, 1975; Percival and Fischer, 1977; Van Valen and Sloan, 1977), but McLean (1978) gives evidence of a temperature drop followed by a rise at this time. Russell (1965, 1966) suggested that floras became more temperate in nature at the end of the Cretaceous and that this was associated with greater climatic seasonality. Axelrod and Bailey (1968) also postulated that reduced equability in the Late Cretaceous (indicated by floral changes) could have given diurnal temperature fluctuations that were too great for the inertially homeothermic dinosaurs to tolerate.

If the climate became cooler, the body temperatures of dinosaurs would fall gradually as night-time cooling came to exceed day-time heat absorption. When

body temperatures reached a dangerously low level, the animals would have become torpid and died since they lacked dermal insulation and the ability to hibernate, being generally too large to find suitable hibernation sites (Cys, 1967). However, this might not apply to smaller dinosaurs (Russell, 1967). Russell (1965, 1966) and Bakker (1972, 1975a) argued similarly, but assumed that dinosaurs were endothermic (note that Russell used the term "homiothermy," but he applied it to mammals and birds and almost certainly meant endothermy). The effects of colder climates would probably be greater on a large naked ectotherm than on an endotherm. Present-day naked endotherms such as elephants can survive for fairly long periods in extreme cold (Sikes, 1971), while cetaceans may live continuously in water at or near freezing point. The latter have thick blubber layers and heat conduction through the blubber is very slow (Vaughan, 1972) so that body core temperatures may be maintained at a high level. Thus, large naked endotherms at present can survive extreme cold and there is no reason to suppose that dinosaurs could not have done the same if they had been endothermic. However, if they were ectothermic, as I suggest, colder seasonal climates could have contributed to their extinction.

The reptiles which survived into the Tertiary were either small (lizards, snakes, land turtles) or aquatic (marine turtles, crocodilians). Small reptiles could maintain body temperatures by behavioral means, or hibernate during particularly cold seasons and, for aquatic reptiles, temperature fluctuations would be partially buffered by the water and they could hibernate by burrowing in the mud (Cys, 1967).

It should, however, be noted that dinosaur extinction was probably the result of a combination of causes, including climatic change, vegetation change and others (Halstead, 1969). Van Valen and Sloan (1977), in a detailed study of local dinosaur extinction, suggest that it was a gradual process of ecological replacement by

mammals produced by the cumulative effects of decreasing temperatures and changing vegetation.

#### SUMMARY

The evidence for dinosaur endothermy is partly inconclusive, partly spurious and, of course, its interpretation is totally speculative. Extrapolations from studies of thermoregulatory physiology of living reptiles suggest that ectothermic dinosaurs could have achieved homeothermy inertially simply by being large. Endothermy is a costly attribute and it is argued that it would have been distinctly disadvantageous, as well as unnecessary, in dinosaurs (with the possible exception of small theropods).

Mesozoic climates were generally warmer than at present and largely arid during the Late Triassic. It is suggested that ectothermy could have proved advantageous to archosaurs in the Late Triassic and may have contributed to the success of their replacement of the possibly endothermic mammal-like reptiles. Constant body temperatures without the necessity of consuming large quantities of food as in endotherms may have assured the continued success and diversification of dinosaurs in the warm Jurassic and Cretaceous.

A possible temperature drop towards the end of the Cretaceous, together with increasing seasonality of climates and the introduction of temperate floras, in conjunction with the large size, naked skin and inertial homeothermy of dinosaurs, may have contributed to their extinction.

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#### ADDENDUM

Several recent papers amplify the views expressed in this paper: Reid (1978) points out various discrepancies in the evidence for endothermy; Budyko (1978) argues for inertial homeothermy in terms of heat balance equations (cf. Spotila et al., 1973); Béland and Russell (1978, 1979) show that dinosaur predator/prey ratios do not indicate endothermic tyrannosaurs; and Kremp (1977) shows, from paleobotanical and palynological data, that the late Triassic reptile beds of North America, Europe, South America, and India all lay within the extensive arid zone of that time.

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