Dinosaur body temperatures: the occurrence of endothermy and ectothermy

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Abstract.—Despite numerous studies, the thermal physiology of dinosaurs remains unresolved. Thus, perhaps the commonly asked question whether dinosaurs were ectotherms or endotherms is inappropriate, and it is more constructive to ask which dinosaurs were likely to have been endothermic and which ones ectothermic. Field data from crocodiles over a large size range show that body temperature fluctuations decrease with increasing body mass, and that average daily body temperatures increase with increasing mass. A biophysical model, the biological relevance of which was tested against field data, was used to predict body temperatures of dinosaurs. However, rather than predicting thermal relations of a hypothetical dinosaur, the model considered correct paleogeographical distribution and climate to predict the thermal relations of a large number of dinosaurs known from the fossil record (>700). Many dinosaurs could have had ''high'' (≥30°C) and stable (daily amplitude ≤2°C) body temperatures without metabolic heat production even in winter, so it is unlikely that selection pressure would have favored the evolution of elevated resting metabolic rates in those species. Recent evidence of ontogenetic growth rates indicates that even the juveniles of large species (3000–4000 kg) could have had biologically functional body temperature ranges during early development. Smaller dinosaurs (<100 kg) at mid to high latitudes (>45°) could not have had high and stable body temperatures without metabolic heat production. However, elevated metabolic rates were unlikely to have provided selective advantage in the absence of some form of insulation, so probably insulation was present before endothermy evolved, or else it coevolved with elevated metabolic rates. Superimposing these findings onto a phylogeny of the Dinosauria suggests that endothermy most likely evolved among the Coelurosauria and, to a lesser extent, among the Hypsilophodontidae, but not among the Stegosauridae, Nodosauridae, Ankylosauridae, Hadrosauridae, Ceratopsidae, Prosauropoda, and Sauropoda.

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Introduction

The thermal physiology of dinosaurs has been the subject of much discussion for decades (Colbert et al. 1946; Bakker 1972; Farlow 1990; Seebacher et al. 1999; O'Connor and Dodson 1999). Much of the debate has focused on the question of whether dinosaurs were endotherms or ectotherms. This, however, is not the appropriate question to ask. Given the enormous diversity of the Dinosauria, both in space and time, all dinosaurs are unlikely to have possessed the same physiological make-up. Hence, it is more constructive to ask which dinosaurs would have gained a selective advantage from elevated metabolic rate and its attendant heat production, and which dinosaurs would have benefited more from ectothermy?

Past research on dinosaur thermal physiology has used biophysical modeling (Spotila et al. 1973; Dunham et al. 1989; O'Connor and Dodson 1999) and comparisons with extant species (Paladino et al. 1990, 1997) to learn about dinosaur body temperatures (T_b). Heat transfer relations between animals and their environment are extremely complex, and the exact value of some parameters, such as convection coefficients, can only be determined empirically, as their complexity precludes theoretical derivation (Mitchell 1976; Incropera and DeWitt 1996). Hence, biophysical modeling of T_b in relation to environmental conditions requires a number of simplifying assumptions and approximations (O'Connor and Spotila 1992). Predictions from theoretical models, therefore, are informative only if their underlying assumptions are valid in the biological context under consideration, and the only way to test the validity of theoretical models is to compare their predictions against empirical data. A major limitation of most biophysical studies of dinosaur T_b is that the relevance of their predictions has not been tested,

so that the results must be treated as speculative.

Comparisons with extant species are potentially useful, but the value of such comparisons depends to a large extent on the choice of the model species, because no modern animals are quite like dinosaurs. Elephants, which have been considered an endothermic model for dinosaurs (Paladino et al. 1997), can reach body mass comparable to medium-sized dinosaurs, so studying elephants can reveal some of the challenges that large terrestrial animals must have faced. However, elephants do not represent ''typical'' endotherms. Their great mass places elephants at one extreme of endothermic radiation, and their morphological and behavioral features that have evolved in order to dissipate heat (Wright 1984; Williams 1990) bear testimony that endothermy in large terrestrial animals is the exception rather than the rule. Because they reveal that it was of selective advantage for large endotherms to evolve heat-dissipating mechanisms, elephants are interesting, but it would be illogical to use an endothermic exception to establish a rule for dinosaurs.

Similarly, marine turtles (Paladino et al. 1990) are atypical reptiles because they are wholly aquatic and the selection pressures that acted to produce modern turtle species must have been quite different from those that acted on terrestrial species. Nonetheless, the fact that leatherback turtles are able to maintain T_b elevated above water temperatures (Paladino et al. 1990) is of interest and bears testimony to the diversity of thermal relations among reptiles.

Several authors have used crocodilians as models to learn about dinosaur thermal relations (Colbert et al. 1946; Spotila et al. 1973; Seebacher et al. 1999). Crocodiles are probably the most appropriate models for dinosaurs because they are the last living non-avian archosaurs and are likely to be similar to the type of basal archosaur from which dinosaurs evolved (Parrish 1997). In addition, crocodilians are the largest extant reptiles with an enormous ontogenetic size range. However, this is not to say that crocodilians are the only useful model. Crocodilians may be the single most useful model, but a synthesis of knowledge gained from other animals, such as turtles and elephants, will be the best approach to advance knowledge in this field.

It was the aim of this study to explore body temperatures (T_b) of a large sample of dinosaurs represented in the fossil record under the conditions prevalent at the time and place where they lived, in order to identify those groups in which selection pressures favoring endothermy would have been greatest or least. The study uses crocodiles as a ''null-model,'' and crocodiles are assumed to represent the simplest physiological and behavioral configuration possible for dinosaurs. The hypothesis tested here is that as crocodile-like ectotherms that thermoregulated behaviorally by moving between heating and cooling environments (Seebacher and Grigg 1997; Grigg et al. 1998; Seebacher 1999) dinosaurs could have had high and stable T_b (see below for definitions). Testing this hypothesis will reveal which dinosaurs, living at a particular place and time, may have had high and stable T_b with an ectothermic physiological make-up, so that selection pressures favoring endothermy would have been comparatively weak in those species, and, vice versa, which dinosaurs were unlikely to have been simple ectotherms.

Endothermy may not have evolved as a result of selection pressures acting directly on thermoregulatory ability. Rather, it has been suggested that selection pressures favored high levels of activity (Bennett and Ruben 1979; Hayes and Garland 1995) or increased capability for parental care (Farmer 2000; Koteja 2000). In either scenario, high maximal aerobic metabolic rates would have been selected for and the increase in resting metabolic rate, which characterizes endothermy, would have been a correlated response. However, aerobic metabolic rates are dependent on the thermal sensitivity of underlying biochemical processes (Crawford et al. 1999; St. Pierre et al. 1998), so thermoregulation and high aerobic metabolic rates cannot be viewed in isolation. Moreover, animals that are ''warm'' without possessing metabolic rates typical of modern endotherms could also maximize aerobic metabolic rates, because their T_b ranges would be optimal for related biochemical processes. Hence, it would be wrong to view endothermy

as ''superior'' to ectothermy, because both have their advantages and disadvantages (Pough 1980); in addition, selection pressures favoring endothermy would be relatively weak in animals that could be ''warm'' without incurring the high energetic cost of elevated, endothermic metabolic rates.

In many respects endothermy and ectothermy differ in degree rather than in kind, because all animals produce metabolic heat, and the mechanisms responsible for metabolic heat production are similar in all animals (except for brown fat in some hibernating mammals). Endotherms, however, have an increased capacity for metabolic heat production as a result of, for example, increased relative organ mass, increased density and complexity of mitochondria, and increased activity of ion pumps in their cell membranes (Else and Hulbert 1981, 1987). Moreover, mechanisms of heat transfer between animals and their environment are identical regardless of metabolic rates, and the importance of metabolic heat in thermoregulation is meaningful only when interpreted in context of heat lost or gained from the environment. Hence, ''endothermy'' and ''ectothermy'' describe extreme expressions of the same mechanisms rather than different evolutionary ''inventions.'' It is conceivable, therefore, that during the evolution of endothermy there existed a continuum of physiological constitutions that were intermediate to those known from typical ectotherms and endotherms today (Reid 1997a; O'Connor and Dodson 1999). In the text below, ''ectothermy'' and ''endothermy'' are used to denote metabolic physiologies of modern reptiles, and of birds and mammals, respectively.

Dinosaur T_b were calculated with a heat transfer model the predictive validity of which was tested extensively against a large set of field data from crocodiles (*Crocodylus porosus* and *C. johnstoni*) ranging in mass from 2.5 to 1010 kg (Seebacher 1999; Seebacher et al. 1999). This approach differs from previous studies, because the theory and its underlying assumptions have been validated against field data and because an attempt is made to consider ''real'' dinosaurs in their appropriate paleoenvironment.

Materials and Methods

Crocodile Field Data.—Field data and sampling methods were reported previously (Seebacher and Grigg 1997; Grigg et al. 1998). Briefly, 11 free-ranging crocodiles (*Crocodylus porosus*; 32–1010 kg) were studied in both winter and summer under seminatural conditions at Edward River Crocodile Farm on Cape York Peninsula, Australia (14°55′S,141°35′E). T_b was measured with calibrated temperature-sensitive radio transmitters (Sirtrack, Havelock North, New Zealand) that crocodiles swallowed and retained as pseudogastroliths in their stomachs. Each animal was sampled for 4–41 days.

In addition, data from two freshwater crocodiles (*Crocodylus johnstoni*; 2.5–3.6 kg) were used to validate predictions of the theoretical model (Seebacher and Grigg 1997; Seebacher et al. 1999). Wild *Crocodylus johnstoni* were sampled in the Lynd River, Cape York Peninsula, Australia (17°07′S,144°03′E), and T_b was recorded with temperature-sensitive transmitters that were surgically implanted into the abdominal body cavity.

Average daily T_b was calculated as the integral of continuous T_b measurements during the day divided by the period of integration. This is conceptually similar to an arithmetic mean, but it does not suffer from the non-independence of individual measurements.

The behavior of all study animals was recorded by scan sampling and direct observation during daylight hours.

Operative environmental temperatures (Bakken and Gates 1976; Tracy 1982; Seebacher 1999) were calculated from measurements of environmental parameters in the field. Shaded air temperatures, shallow and deep water temperatures, and ground temperatures were measured with temperature sensors (National Semiconductors LM335) connected to a data-logger (Data Electronics, Melbourne, Australia). Solar radiation was measured with a tube solarimeter (Irricrop Technologies, Narrabri, Australia) connected to the same data logger. Operative temperatures change with relative exposures of body surface area to different heat transfer mechanisms, so that different behavioral postures have different operative temperatures as-

sociated with them. Behavioral postures were incorporated into operative temperature calculations by changing relative contributions of heat transfer by conduction, convection in air and water and radiation as described by Grigg et al. (1998) and Seebacher (1999).

Calculations of Dinosaur T_b.—Dinosaurs included in this study and their paleogeographic distributions were taken from the catalog published by Weishampel (1990), as well as from the sources listed in the Appendix. In total, 701 dinosaurs from 321 genera were considered. Body mass of dinosaurs was calculated according to methods described by Seebacher (2001). Note that this method of mass calculation takes the different shapes of dinosaur groups into account, but possible shape-related modifications in heat transfer were not considered beyond the calculations of body mass. When a fossil did not allow an accurate determination of the animal's length (from which mass could be calculated [Seebacher 2001]), the mass of a closely related species was used instead. For example, Graham et al. (1997) describe the fossil of the right foot of a sauropod that was identified as belonging to the genus *Mamenchisaurus*, so the mass of this specimen was assumed to have been similar to that of *Mamenchisaurus hochuanensis*.

"Stable" T_b was defined as one fluctuating with an amplitude of 2°C or less, a definition drawn from the T_b fluctuations expected from endothermic mammals (Lovegrove et al. 1987), and one that has been used previously in relation to dinosaurs (Barrick and Showers 1994). "Warm" T_b was defined as 30°C or above. This is somewhat cooler than most modern birds and mammals (but not atypical for some [Lovegrove et al. 1987]), and it is typical for crocodilians (Seebacher and Grigg 1997; Grigg et al. 1998), which are assumed to be a model for ancestral archosaurs.

Heat conduction between the surface and the core of the animal was calculated for an animal consisting of two thermally distinct layers (Turner 1987; Seebacher et al. 1999): an outer layer made up of muscle and fat with a thickness of 0.15 total radius and an inner core consisting of bone, tissue and fat with 0.85 total radius. Applying Fourier's law to the tem-

perature distributions (Incropera and DeWitt 1996) of each layer gives the following conduction equations:

$$C_c dT_c/dt = -K_c(T_b - T_s) \tag{1}$$

$$C_s dT_s/dt = K_c(T_b - T_s) - K_s(T_s - T_e) \tag{2}$$

for the core (1) and outer layer (2), where C_c and C_s are the heat capacities (cM, where c = specific heat, and M = mass) for the core and outer layer, respectively; K_c and K_s represent kA/l, where k = conductivity, A = surface area, and l = thickness through the core and outer layer, respectively. T_c and T_s are the core and outer layer temperatures, respectively, and T_e is the operative environmental temperature. Substituting for T_s gives

$$(C_s C_c/K_c K_s)d^2 T_b/dt^2$$
$$+ (C_c/K_s + C_c/K_c)dT_b/dt + T_b$$
$$= T_e \tag{3}$$

The particular solution chosen for this second-order differential equation was a Fourier series to describe the slight asymmetry of the daily T_b and T_e fluctuations observed in the field (see "Results," below; also see Grigg et al. 1998; Seebacher et al. 1999):

$$T_b = T - A \sin((2Pt) + \varphi)$$
$$+ c_1 A \sin((4Pt) + \varphi)$$
$$- c_2 A \sin((6Pt) + \varphi) \tag{4}$$

where T = mean temperature, A = amplitude, P = period, t = time, φ = phase angle, and c_1 and c_2 are constants determining the "sawtooth" of the periodic motion (Halliday and Resnick 1978), which we determined empirically to be 0.305 and 0.109, respectively (Seebacher et al. 1999).

For investigations of the effect of insulation on T_b an extra body layer was added to the model above. Transient heat conduction through this insulation layer was calculated by nondimensional heat transfer analysis (Carslaw and Jaeger 1995; Incropera and DeWitt 1996):

$$\partial^2 \theta^*/\partial x^{*2} = \partial \theta/\partial Fo \tag{5}$$

where $\theta^* = (T - T_e)/(T_i - T_e)$, and T_i is the initial (skin) temperature; $x^* = x/L$ where L

= half thickness of the insulation; and Fo is the Fourier number. A first-order approximation of the infinite series solution to the above equation was used, where the midplane temperature

$$\theta^*_0 = C_1 e^\wedge(-\zeta_1^2 Fo) \qquad (6)$$

and C_1 is the coefficient for the solution of the first root (ζ_1) of $\zeta_n \tan \zeta_n = Bi$ where Bi is the Biot number. Conductivity of insulation was assumed to be the same as that of fur in modern mammals (Bowman et al. 1978).

In the analysis, dinosaurs were assumed to thermoregulate behaviorally by moving between sun and shade. Differential exposure to sun and shade changes operative environmental temperatures experienced by animals, which can be calculated (Seebacher 1999) and incorporated into the thermal model above.

Paleoclimate.—Estimates of paleoclimate were made from various lines of evidence in the literature (Vakhrameev 1991; Parrish 1993; Golonka et al. 1994; Sellwood et al. 1994; Tarduno et al. 1998). It was assumed that solar radiation throughout the Mesozoic was similar to present-day levels and that there was no sun in winter at latitudes higher than 70°.

It is generally agreed that the Mesozoic was warmer than the present (Barron 1983). The climate during the Permian was temperate (Yemane 1993), and the Pangean megamonsoon was strongest during the following Triassic, after which it abated so that the climate became drier during the Jurassic (Parrish 1993). This drying was accompanied by climatic cooling during the Triassic and Jurassic period (Bardossy 1996), but the climate was nonetheless "equable" (subtropical to warm-temperate) during the Jurassic (Vakhrameev 1991).

The Early Cretaceous and the early Late Cretaceous were very warm periods (Mayer and Appel 1999; Herman and Spicer 1996; Tarduno et al. 1998), but there also is good evidence that the climate cooled considerably during the Cnemonian–Turonian periods of the early Late Cretaceous (Sellwood et al. 1994; Barron 1995; Kuypers et al. 1999). Massive heat transport from the superheated Tropics toward the poles has been cited as at least part of the reason for the early Late Cretaceous cooling event (John-

son et al. 1996). Frakes et al. (1994) show a temperature increase (both oceanic and atmospheric) throughout the Early Cretaceous, which is followed by a sharp decline in temperature in the early Late Cretaceous leading to a distinct minimum in the Maastrichtian period in the late Late Cretaceous.

Paleoclimate estimates incorporated the patterns described above and were based on values collated from the various sources. Paleoclimate predictions vary in the literature, and the estimates presented here represent an attempt at a conservative consensus "model" that is warmer than the coolest prediction (sub-zero temperatures at high latitudes in the Early Cretaceous [Sloan and Barron 1990]) and cooler than the warmest prediction (mean annual polar temperatures exceeding 14°C in the Early Cretaceous [Tarduno et al. 1998]). More specifically, equatorial temperatures varied little throughout the Mesozoic and, judging from paleoclimate modeling maps, were estimated to range from 28.8°C in Early Jurassic winter to 30.5°C in Early Cretaceous summer (Golonka et al. 1994; Barron 1993; Frakes et al. 1994). Average latitudinal gradients in temperature were estimated to range from 0.27–0.31°C/1°lat in winter to 0.17–0.21°C/1°lat in summer (Barron 1983; Yemane 1993; Frakes et al. 1994; Francis 1994; Moore and Ross 1994; Huber et al. 1995; Huber and Hodell 1996). Equator-to-pole gradients were uneven, however, with a broader tropical region that peaked in extent in the late Early Cretaceous (Johnson et al. 1996) and, reflecting modern climate trends, the greatest decrease in temperature occurs at midlatitudes (Golonka et al. 1994). Daily variation in temperature was assumed to be similar to modern-day variation at the same latitude, and paleolatitudes were determined from maps of Smith et al. (1994).

Results and Discussion

Crocodile Field Data.—The T_b of crocodiles larger than 32 kg followed slightly asymmetric oscillations during the day (Fig. 1). The asymmetry, i.e., heating phase is shorter than the cooling phase and reflects the relatively short period during the 24-hour day when solar radiation can be absorbed. The amplitude
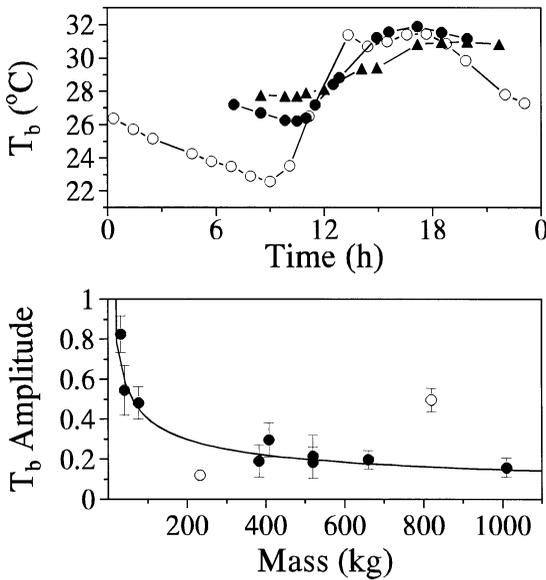
FIGURE 1. Upper panel, Examples of daily T_b fluctuations in crocodiles of different mass: 42 kg (open circles), 520 kg (solid circles), 1010 kg (triangles). Lower panel, Daily T_b amplitude decreased with mass; T_b amplitudes are dependent on fluctuations in operative temperature and are therefore expressed as the ratio of T_b to operative temperature amplitude. The two outliers (open circles) represent crocodiles that were subjected to constant aggression by dominant males. Redrawn from data of Seebacher et al. (1999).
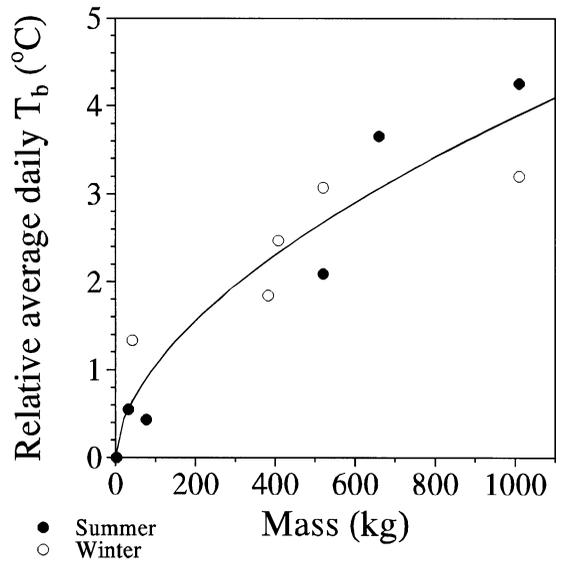

FIGURE 2. Average daily T_b of crocodiles increased with body mass. Taking small crocodiles as reference points (2.6 kg in winter and 3.5 kg in summer), average daily T_b increased by several degrees over a size range of 1000 kg. Redrawn from data of Seebacher et al. (1999).

of the daily T_b oscillations decreased with body mass, so that in winter T_b varied between 2° and 3°C during the day in a 1010-kg crocodile, compared with nearly 10°C in a 42-kg crocodile (Fig. 1). The T_b of two crocodiles did not follow the general pattern (Fig. 1, lower panel, 233 kg and 865 kg). Both these animals were the second largest males in their respective area and were therefore subjected to nearly constant aggression by the dominant males. The resulting altered behavior patterns explain the difference in T_b between these and the other crocodiles (Grigg et al. 1998). For this reason, data from these two animals have been omitted below.

As well as increasing in stability, T_b increased in magnitude with increasing mass (Fig. 2). This increase in T_b is the result of the decrease in convective heat transfer (i.e., the increase in boundary layer thickness) as crocodile length increases. Taking the average daily T_b of a 2.6-kg (winter) and a 3.5 kg (summer) crocodile as the reference points, T_b magnitude increased with mass ($T_b = 0.0775 Mass^{0.5664}$, r^2

= 0.88) so that a 1010-kg crocodile was on average 3–4°C warmer than the reference animals (Fig. 2).

To test the validity of the mathematical model in predicting T_b, all field data were also predicted mathematically, given the same environmental conditions measured in the field and the crocodiles' body mass (Fig. 3). Theory predicted measured T_b extremely well at any season and for any crocodile mass (Fig. 3). Overall, there were no significant differences between the predicted and the measured amplitudes of the daily T_b oscillations (t-test = −0.31, df = 8, $p = 0.76$).

Paleoclimate.—Air temperatures varied by up to 10°C between geological time periods, and there was a gradient between the equator and the poles of nearly 20°C in summer and 30°C in winter. The Early Jurassic and Late Cretaceous were the coolest periods, and the early Cretaceous was the warmest. Seasonal differences in mean daily air temperatures were most pronounced at high latitudes (up to 10°C difference between summer and winter at the poles), but differences in air temperature at the equator were negligible (Fig. 4).

Dinosaur T_b Patterns and Behavioral Thermoregulation.—Despite fluctuating environmen-
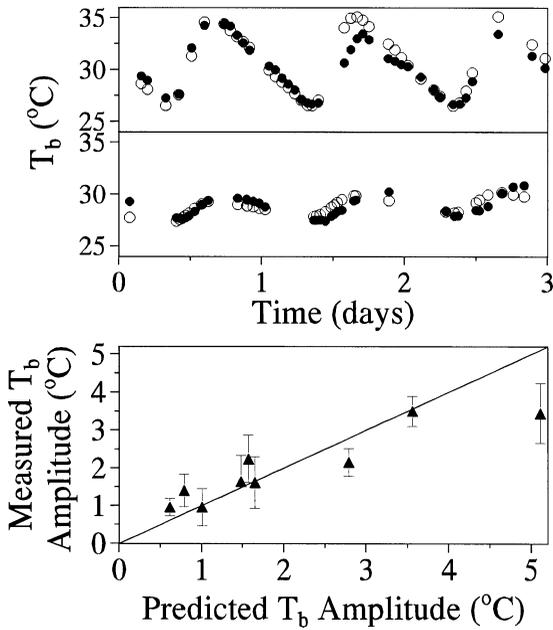
FIGURE 3. Theory predicted field data very well. Representative examples of measured (solid circles) and mathematically predicted (open circles) T_b are shown for a 32-kg crocodile in summer (top panel) and a 1010-kg crocodile in winter (middle panel). Overall, there were no significant differences between measured and predicted daily T_b amplitudes (bottom panel). Redrawn from data of Seebacher et al. (1999).
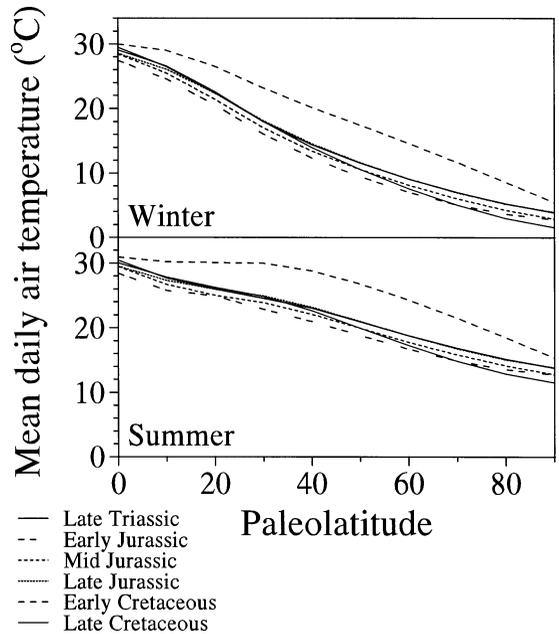

FIGURE 4. Paleoclimate estimates. Variation in mean daily air temperature in winter and summer during the different time periods of the Mesozoic.

tal temperatures, most dinosaurs could have had average daily T_b in winter of 30°C or greater at any time in the Mesozoic, even if they were crocodile-like ectotherms that thermoregulated by shuttling between sun and shade (Fig. 5).

In addition to being warm, most dinosaurs at low latitudes, and many at higher latitudes, could also have had stable T_b (Fig. 5). Daily T_b fluctuations in ectotherms depend upon ambient thermal conditions, expressed as operative environmental temperatures (Bakken and Gates 1976; Tracy 1982) to which the animal is exposed. The range of operative temperatures becomes greater with increased exposure to solar radiation, and it increases with increasing animal mass (Seebacher et al. 1999). Nonetheless, the analysis showed that winter T_b of medium sized, ectothermic dinosaurs (2000–3000 kg) that thermoregulated behaviorally by moving in and out of the sun would have been high (>30°C) and stable (±2°C or less) during any geological time period at latitudes up to 50–55° (Fig. 5).

The T_b of all dinosaurs could have exceeded 30°C in summer, and avoiding exposure to solar radiation rather than seeking heat would likely have been the thermoregulatory objective for large dinosaurs at low latitudes in summer (Fig. 6). A 5000-kg dinosaur (e.g., *Triceratops*, *Parasaurolophus*, or *Muttaburrasaurus*), the same mass as a large elephant, living at 0–10° latitude in the Early Cretaceous would have had to thermoregulate behaviorally to minimize irradiation at all times of the year in order to have T_b at or below 30°C. This may have been achieved by seeking shade during the day, and maybe by adopting a crepuscular habit. However, at midlatitudes (30–50°), the 5000-kg dinosaur would have had to seek the sun for at least part of the day even in summer, and it would have needed extended basking periods in winter at those latitudes to maintain a seasonally constant T_b (Fig. 6). For comparison with data shown in Figure 6, note that the sun exposure of a modern, thermoregulating heliothermic reptile, such as varanid lizards (Seebacher and Grigg 2001) or crocodiles (Seebacher and Grigg 1997; Grigg et al. 1998), would be less than half of the total available during a day. The transient nature of heat
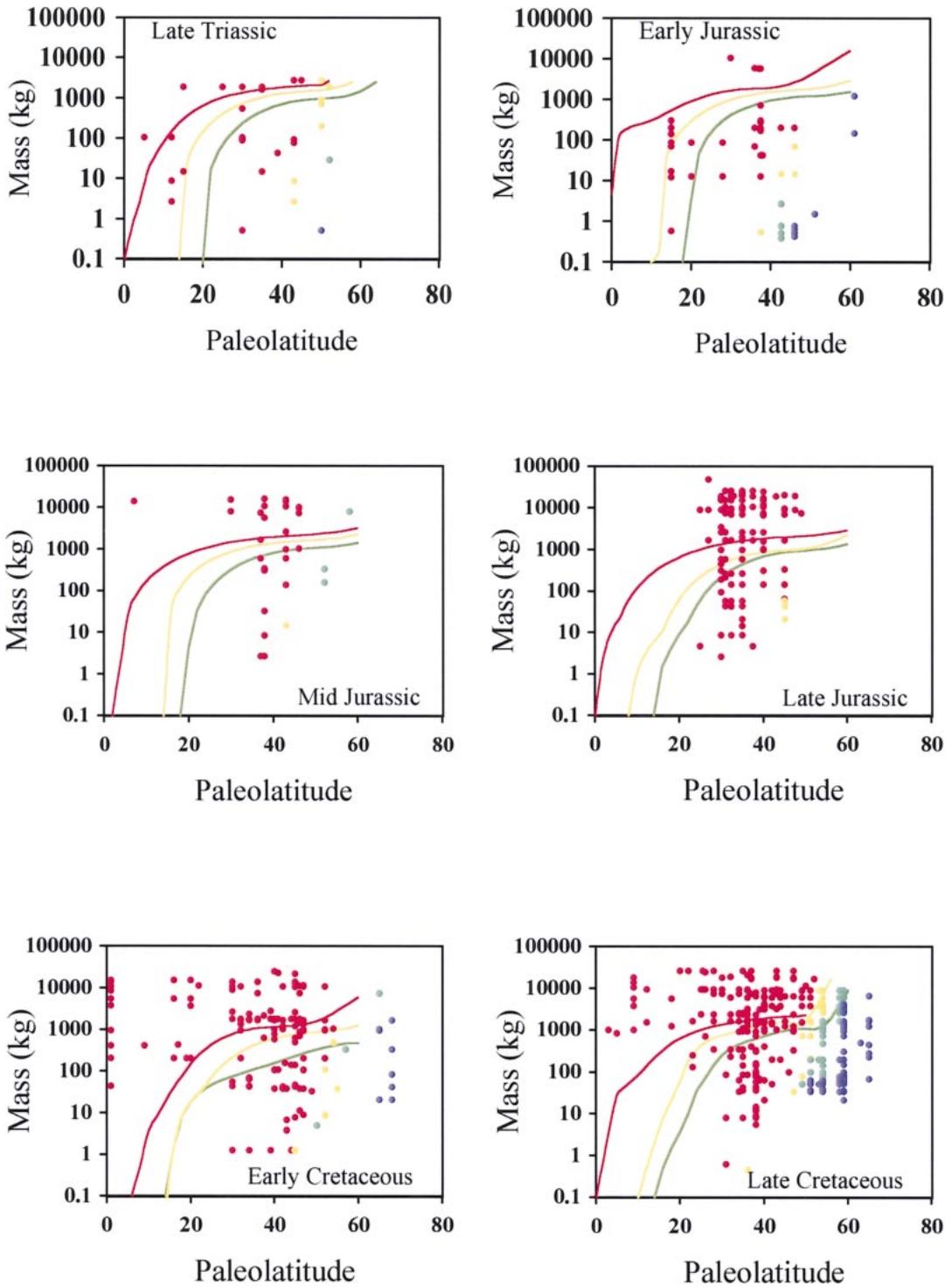
FIGURE 5. Body temperature of dinosaurs (703 fossils from 321 genera) in winter during different time periods. Most dinosaurs were warm (average $T_b > 30°C$, red circles), but average daily T_b decreased with decreasing mass and increasing paleolatitude (yellow circles = 25–30°C, green circles = 20–25°C, blue circles = <20°C). Lines indicate the combination of mass and paleolatitude at which daily T_b would have fluctuated with an amplitude of 2°C or less at different average T_b (colors as above). Note that dinosaurs exposed less to solar radiation would have been cooler, but their T_b would have been more stable.

transfer between an animal and its environment means that T_b is determined by the integrated environmental conditions over a given period of time, which increases with mass (Fig. 1) and which can be recognized by the lag in response of T_b relative to operative temperature oscillation. Hence, saying that a 5000-kg dinosaur has to avoid the sun means that it has to reduce radiative heat load during a whole solar day.

Selective advantages gained from high, endothermic metabolic rates would have been reduced in dinosaurs that could have had high and stable T_b without having to incur the high energetic cost of producing heat metabolically. The principal advantage of high and stable T_b lies in maintaining constant biochemical and physiological reaction rates near their optimum. Although an ectothermic physiology does not allow the same sustained levels of activity typical of many endotherms, the difference in physiological performance between warm ectotherms with stable T_b, such as many dinosaurs were (Fig. 5), and typical endotherms diminishes. In contrast, smaller animals at higher latitudes would have had variable and lower T_b (Fig. 5), so high metabolic heat production may have been of considerable advantage; if endothermy evolved among the Dinosauria, it most likely did in these latter species (see Fig. 5, and below). The conclusion that large ectotherms (see Fig. 5 for mass/latitude distributions) could have had stable T_b is in agreement with previous theoretical case studies (Spotila et al. 1973; Dunham et al. 1989; O'Connor and Dodson 1999). However, the crocodile data and the analysis above clearly show that it would be a mistake to equate stable T_b with endothermy (Barrick and Showers 1994). The present analysis complements previous work in explicitly showing the extent to which dinosaurs with an ectothermic metabolic make-up could have had warm and stable T_b with respect to body mass and paleolatitude (Fig. 5). It is clear that endothermy need not be evoked in order to explain apparently stable temperatures in medium-sized dinosaurs living at midlatitudes (Barrick et al. 1998).

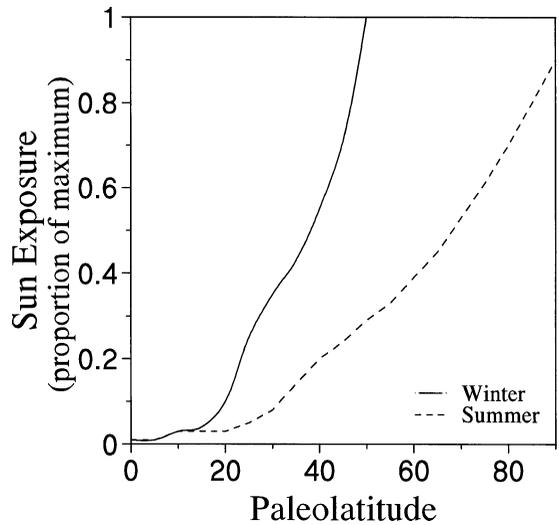Different lines of evidence indicate that endothermy as it is known from modern birds

FIGURE 6. Predicted seasonal behavior (expressed as % sun exposure) of a 5000-kg dinosaur living at different latitudes. To maintain high and stable T_b (amplitude = 2°C or less, average T_b = 30°C) between seasons the dinosaur would have had to change its thermoregulatory sun and shade-seeking behavior (0 = full shade, 1 = full sun) between seasons, and behavior would differ between animals living at different latitudes.

and mammals may not have been feasible for most, particularly larger, dinosaurs. The long necks of large dinosaurs, particularly sauropods, would have required the left ventricle to be impossibly large in order to maintain blood pressures in the head typical of modern endotherms (Seymour and Lillywhite 2000). In addition, the extremely long trachea of sauropods would have precluded lung ventilation rates necessary to sustain endothermic metabolic rates (Daniels and Pratt 1992). These results are consistent with the present, biophysically based analysis. There is some evidence that ventilation rates and respiration of even small theropods and early birds may have been inadequate to sustain high, endothermic metabolic rates. Lungs of theropods and early enantiornithine birds were simple bellows-like septate lungs with limited ventilation rates (Ruben et al. 1997), although it appears that one theropod dinosaur had a more sophisticated ventilation apparatus that allowed ventilation rates similar to those of mammals (Ruben et al. 1999). In addition, dinosaurs apparently did not possess respiratory turbinates (Ruben et al. 1996) which are considered a prerequisite for endothermic metabolic rates
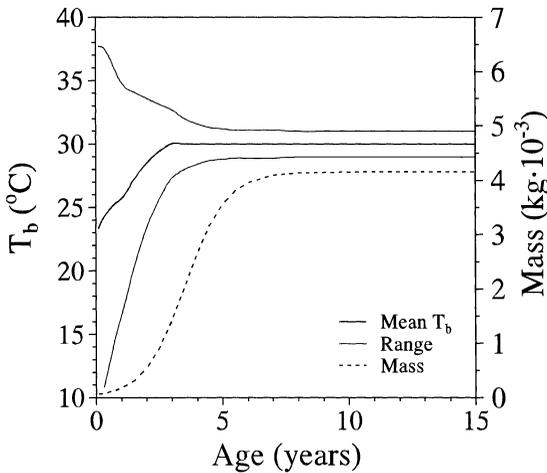
FIGURE 7. Average daily T_b (thick solid line) and T_b ranges (broken lines) of *Maiasaura peeblesorum* in winter at a latitude of 45° in the Late Cretaceous. The growth curve (mass; thin solid line) was based on data of Horner et al. (2000), who suggested that juvenile *M. peeblesorum* grew rapidly, reaching late juvenile size (3.5 m, 330.7 kg) within one to two years, and adult body size (7–9 m, 2090.3–4078.8 kg) within six to eight years. If hatching occurred in spring, juveniles would have been six to seven months old (232.6 kg) before experiencing their first winter.

(Hillenius 1992) because they dramatically reduce respiratory water loss; evidence for this (Ruben et al. 1996, 1997) is based on very few specimens, so caution should be exercised in applying the conclusions to dinosaurs in general. If it were true, however, that even small dinosaurs were unable to sustain endothermic metabolic rates, it would indicate that the ''cool'' dinosaurs in Figure 5 either underwent a period of dormancy during winter (as seen in many modern reptiles) or displayed remarkable physiological acclimatization to function normally at low T_b. Seasonal metabolic acclimatization is well known to occur in fish (e.g., St.-Pierre et al. 1998; Crawford et al. 1999), but little is known from reptiles.

Dinosaurs grew much larger than mammals, and large dinosaurs maintained relatively high population densities compared with real or projected population densities of similar-sized mammals (Farlow 1993; Farlow et al. 1995). This has been taken to indicate that dinosaurs may have had lower food consumption rates, i.e., lower metabolic rates than mammals (Farlow et al. 1995). Evidence from body size distributions and population den-

sities may therefore strengthen the argument made above that selection pressures did not favor high metabolic rates for most dinosaurs, at least for those that could have had high and stable T_b with an ectothermic metabolic make-up (Fig. 5).

Ontogeny.—The above predictions were made for adult dinosaurs but, as is the case in modern animals, thermal relations would have changed ontogenetically, particularly in species with large adult body sizes. The crocodile field data shown above provide a good example of such ontogenetic changes in T_b. Growth rates of dinosaurs are the subject of some debate (Reid 1997b), but recently it has been suggested that dinosaurs displayed a sigmoidal growth pattern, with rapid growth after hatching and slowed growth rates later in life (Padian et al. 2001; Erickson et al. 2001). This would indicate that growth patterns of dinosaurs were identical to those observed in wild American alligators (*A. mississippiensis*) (Rootes et al. 1991; Elsey et al. 1992, 2001)—a fact not appreciated by Padian et al. (2001). In a particular example based on an ontogenetic series of skeletal elements, Horner et al. (2000) suggested that the hadrosaur *Maiasaura peeblesorum* would have reached its adult size of 7–9 m in six to eight years. The nesting period of *M. peeblesorum* may have been as short as one to two months, and the animals would have reached a late juvenile size of 3.5 m after one to two years (Horner et al. 2000). Assuming that offspring hatched in spring, like modern crocodilians for example (Elsey et al. 2001; Webb and Manolis 1989), the juveniles would be at least six to seven months old before their first winter. Using Horner et al.'s (2000) growth estimate, their body mass (Seebacher 2001) would have been 120–150 kg at the beginning of winter and around 200 kg at the end of winter. Hence, in a Late Cretaceous climate at 45° latitude, the T_b of juvenile *M. peeblesorum* would have varied between 15.8°C and 35.2°C at the beginning of their first winter, and between 18.0°C and 34.4°C at the end of winter (Fig. 7). By modern reptilian standards, these T_b ranges are very typical (Seebacher and Grigg 1997, 2001; Grigg et al. 1998; Grigg and Seebacher, 1999). Moreover, T_b would have stabilized very quickly as the an-

imals grew older, so that average daily T_b of *M. peeblesorum* at 3 years of age would have been 30°C ($\pm$2.7°C) even in winter, and winter daily T_b of a 10 year old animal would have varied between 29.0°C and 31.0°C (Fig. 7). Note that in these predictions, as above, it was assumed that the animal thermoregulated behaviorally to attain average T_b of 30°C whenever possible.

The above example demonstrates that metabolic heat production is not a pre-requisite for juveniles of large dinosaurs to have T_b within a biologically functional range. It is debatable, however, whether dinosaurs with an ectothermic physiology could have achieved growth rates similar to those suggested for *M. peeblesorum*. Using crocodilians as comparison, Padian et al. (2001) argued that dinosaurs could not have achieved such fast growth rates as simple ectotherms. This conclusion must be treated with caution, however, because crocodilians can grow fast enough to form fibrolamellar bone (Reid 1997b), and Ruben (1995) demonstrated that growth rates of the small theropod *Troodon* were identical to those of alligators. Moreover, the presence of lines of arrested growth, which has been taken to indicate ectothermic metabolic rates resulting in pronounced seasonal fluctuations in T_b, do not provide conclusive evidence of metabolic status; a wide variety of endothermic and ectothermic animals including birds, dinosaurs, and crocodilians (Reid 1990; Chinsamy et al. 1994; Farlow et al. 1995; Rasch et al. 2001) show lines of arrested growth, and the stable T_b of large ectothermic animals (Fig. 5) may preclude formation of lines of arrested growth.

Insulation and Small Dinosaurs.—The T_b of small dinosaurs (<100 kg) and Avialae (e.g., *Hypsilophodon* [Galton 1974], *Sinosauropteryx* [Chen et al. 1998], *Beipiaosaurus* [Xu et al. 1999b], *Mononykus* [Perle et al. 1993]) that lived at mid latitudes (45–55°) or higher would have been well below 30°C in winter if they had been crocodile-like ectotherms (Fig. 5). It may be in this category that selection pressures for morphological and/or physiological thermoregulatory adaptations would have been strongest. The recent discoveries of integumentary structures on taxonomically di-
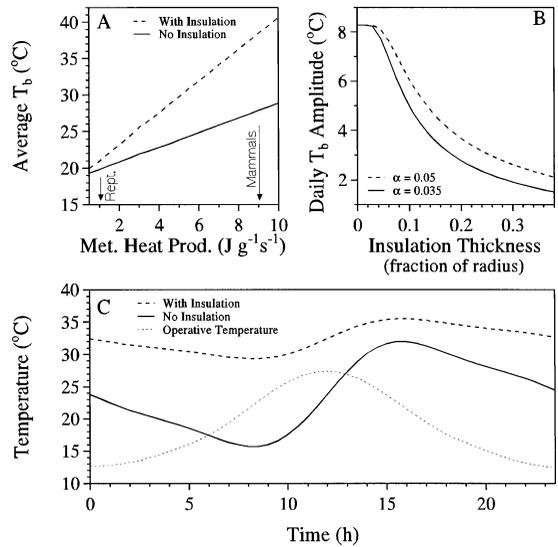

FIGURE 8. Average daily T_b increases with resting metabolic rate (averages for modern reptiles and mammals are indicated), but the increase in T_b would be far greater in animals possessing thermal insulation in the form of fur or feathers, for example (A). Daily T_b amplitudes decrease with the thickness and the quality of insulation (thermal diffusivity, α, range of 0.035–0.05 $\times$ 10^{-7} m^2 s^{-1}), and the biological relevance of these patterns can be observed in modern birds and mammals that change their fur or feather thickness between seasons and/or latitudes (B). Average daily T_b in winter of a small (3.8 kg) dinosaur, such as *Sinosauropteryx*, which lived at 50° latitude in the Early Cretaceous and had resting metabolic rates intermediate between those of modern ectotherms and endotherms (0.5 ml O$_2$ g^{-1} h^{-1}). T_b of an animal with insulation (of 20 mm thickness) would be much greater and would fluctuate far less than that of an uninsulated dinosaur. Operative temperatures are also shown.

verse coelurosaurs living at 45–50° paleolatitude in the Early Cretaceous (Chen et al. 1998; Xu et al. 1999a,b) may represent an example of such an adaptation.

Insulation dampens out responses to daily fluctuations in operative temperature and traps metabolically produced heat (Fig. 8). The difference in average daily T_b between an insulated and an uninsulated animal increases with increasing metabolic heat production, so average daily T_b of an insulated animal with mammal-like metabolic rates is nearly twice as high as that of an identical animal without insulation (Fig. 8A) (all predictions were made for a 3.8-kg animal living at 50° latitude in winter in the Early Cretaceous, and insulation thickness = 20 mm; see below). Moreover, quality and thickness of insulation

affect T_b fluctuations considerably (Fig. 8B). For example, an increase in insulation thickness from 10% of the body radius to 20% of body radius decreases daily T_b fluctuations by nearly one-half. The biological relevance of these changes in heat transfer is demonstrated in the seasonal changes of fur thickness seen in many mammals.

The T_b of *Sinosauropteryx* (body mass 3.8 kg), for example, living at 50° latitude in the Early Cretaceous would have fluctuated daily with an amplitude of 8.1°C; average T_b would have been 23.8°C in winter (Fig. 8C) if the animal had no insulation and a resting metabolic rate of two to three times that of a varanid lizard (0.5 ml O_2 g^{-1} h^{-1} [Thompson and Withers 1997]). If the integumentary structures (20 mm thickness [Chen et al. 1998]) provided featherlike insulation, however, winter daily T_b fluctuations would have been reduced to an amplitude of 3.1°C, and average T_b would have increased to 32.4°C (Fig. 7B), assuming that the thermal diffusivity of the integumentary structures was similar to that of feathers of modern birds (0.05. 10^{-7} m^2 s^{-1} [Bowman et al. 1978; Incropera and DeWitt 1996]). Hence, even with resting metabolic rates intermediate between that of typical reptiles and mammals (Reid 1997a; O'Connor and Dodson 1999), insulation has a striking effect on the magnitude and stability of T_b.

Selection for high and stable T_b must have been a necessary corollary in the evolution of high levels of activity or parental care. This means that, given the physiological and physical relationships shown in Figure 8, the selective advantages conferred by elevated metabolic rates on small dinosaurs would have been minimal in the absence of insulation; insulation such as may have been afforded by feathers or featherlike structures must therefore have been present already or must have coevolved with elevated metabolic rates.

Incidence of Endothermy and Ectothermy among Dinosaurs.—If one accepts ectothermy as the ancestral condition among archosaurs, endothermy must have evolved sometime between the early Late Triassic, when dinosaurs first appeared in the fossil record (Sereno 1999), and the evolution of modern birds whose ancestors probably appeared first in the early Late Jurassic (Dodson 2000; Sumida and Brochu 2000). Moreover, as outlined in the introduction, it is conceivable that an evolutionary trend toward endothermy was of selective advantage not only once but repeatedly, when lineages radiated into new environments, for example. From the analysis above, it is possible to speculate on the relative likelihood of an evolutionary trend towards endothermy among dinosaurian lineages (Fig. 9). Note, however, that this attempt at determining the phylogenetic distribution of endothermy is not meant to represent a final conclusion; rather, it was designed as a working hypothesis that will change as new insights from fossils are gained.

Because the strength of selection pressures favoring endothermy decreases with increasing body mass, it is therefore contradictory that endothermy coevolved with large body size. Thus endothermy is very unlikely to have evolved in lineages in which the most recent species are predominantly large, such as prosauropods, sauropods, stegosaurs, nodosaurs, ankylosaurs, and ceratopsids.

On the other hand, many coelurosaurs were comparatively small, reaching their greatest diversity in the Late Cretaceous. From this perspective, if endothermy did evolve among dinosaurs, it most likely evolved within this group. Note, however, that this is not to say that endothermy was obligatory for small gen-

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FIGURE 9. Speculated phylogenetic distribution of endothermy among the Dinosauria (cladogram redrawn from Sereno 1999). Endothermy must have evolved sometime in the lineage leading to modern birds (Ornithurae, very dark shading) and is likely to have occurred in coelurosaurs, among which the evolutionary trend was a decrease in body size, and which lived at mid to high paleolatitudes (dark shading). It is less likely that endothermy evolved among other theropods that showed an evolutionary trend toward large body size (light gray shading), or among any other group of dinosaurs in which the most recent members attained large body size (very light gray shading). Hypsilophodontids and heterodontosaurids remained small and occurred at mid to high latitudes, so endothermy may have been of selective advantage in those dinosaurs (gray shading).
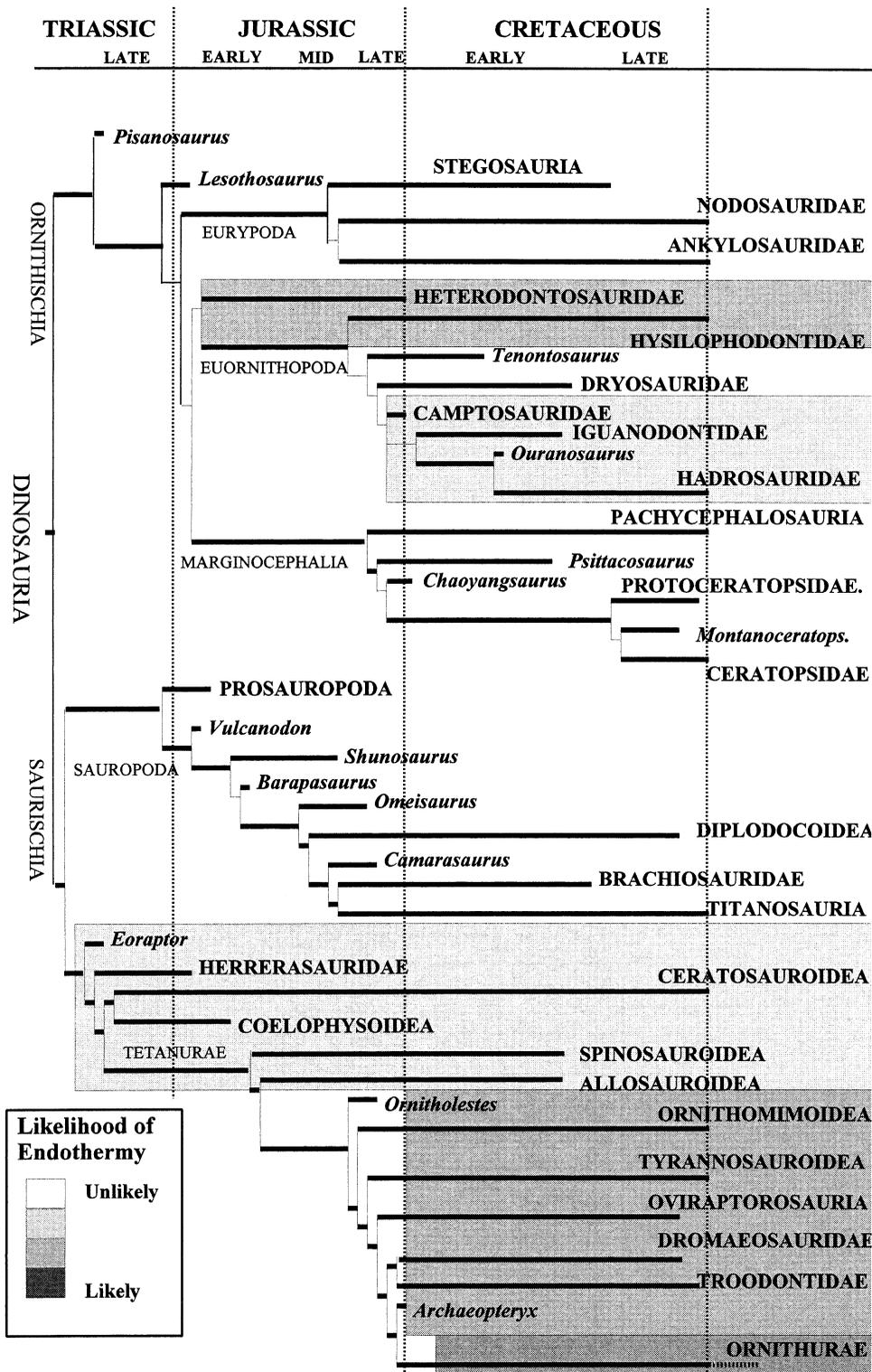
era; it was simply feasible. Similarly, among the Ornithopoda, the Heterodontosauridae and Hysilophodontidae remained small (<100 kg [Brett-Surman 1997; Seebacher 2001]) and relatively undiversified throughout their evolutionary history. Moreover, hypsilophodontids had a cosmopolitan distribution that reached into the high latitudes of Gondwana (Rich 1996). Hence, at least for hypsilophodontids living at mid to high latitude (>45°; see Fig. 5), endothermy may have been of selective advantage. The case for heterodontosaurids is more doubtful, as they were a very basal group of ornithopod that are known primarily from low to mid latitudes in the Early Jurassic, and the Late Jurassic fossil finds are fragmentary and uncertain (Weishampel 1990).

Morphological transformation was most sustained in the evolution of the Hadrosauridae within the Ornithopoda, and in the coelurosaurs within the Tetanurae (Sereno 1999). The evolution of skeletal diversity may indicate rapidly changing selection pressures as a result of radiation into new ecological niches. It is more likely, therefore, that endothermy evolved in lineages exposed to ''new'' selection pressures rather than in very conservative lineages, which changed little morphologically and, presumably, ecologically (Schluter 2001). Hadrosaurs are also distinguished in being the only other dinosaur lineage that contained members reaching body masses comparable to sauropods, so although hadrosaurs reached great diversity, it is doubtful that they evolved endothermy. Morphological diversification among coelurosaurs, on the other hand, lends support to the above speculation that endothermy may have evolved within that lineage.

Hypsilophodonts, on the other hand, were conservative lineages that changed little in their morphology over geological time, which may indicate that selection pressures remained relatively stable during their evolution; endothermy is thus less likely to have evolved in this group than in coelurosaurs.

The thermoregulatory advantages gained from elevated resting metabolic rates are doubtful in animals without insulation. The increase in energy demand associated with an increase in resting metabolic rates would proba-

bly have greatly reduced the selective advantage of the latter in uninsulated animals. Most skin impressions from dinosaurs indicate the presence of naked skin (Czerkas 1997; Sumida and Brochu 2000), except for integumentary structures in coelurosaurs that may have afforded thermal insulation (Chen et al. 1998). Although other dinosaurs may have possessed integumentary structures with insulatory qualities, present knowledge indicates that these evolved in the Coelurosauria only (this conclusion may change as new fossil evidence is discovered). The earliest known feathers stem from the Late Jurassic, so if those feathers possessed insulating qualities, endothermy may have evolved sometime after that.

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Appendix

Dinosaur taxa used in the analysis in addition to those listed by Weishampel (1990).

Species	Reference
Afrovenator abakensis	Sereno et al. 1994
Alxasaurus elesitaiensis	Russell and Dong 1993a
Andesaurus delgadoi	Calvo and Bonaparte 1991
Angaturama limai	Kellner and Campos 1996
Bactrosaurus johnsoni	Godefroit et al. 1998
Beipiaosaurus inexpectus	Xu et al. 1999b
Caenagnathus sp.	Currie et al. 1993
Carcharodontosaurus saharicus	Sereno et al. 1996
Caudipteryx zoui	Qiang et al. 1998
Ceratosauridae sp.	Tykoski 1997
Chirostenotes pergracilis	Sues 1997
Coelurosauria sp.	Zhao and Xu 1998
Cryolophosaurus ellioti	Hammer and Hickerson 1994
Deltadromeus agilis	Sereno et al. 1996
Diplodocidae sp.	Gabunia et al. 1998
Dromaeosauria sp.	Azuma and Currie 1995
Eoraptor lunensis	Sereno et al. 1993
Gargoyleosaurus parkpini	Carpenter et al. 1998
Gasparinisaura cincosaltensis	Coria and Salgado 1996
Giganotosaurus carolinii	Coria and Salgado 1995
Herrerasaurus ischigualastensis	Sereno and Novas 1992
Hypsolophodontidae sp.	Hilton et al. 1997
Leaellynasaura amicagraphica	Rich and Rich 1989
Majungasaurus crenatissimus	Sampson et al. 1996
Malawisaurus dixeyi	Jacobs et al. 1993
Mamenchisaurus sp.	Russell and Zheng 1993
Mamenchisaurus sp.	Graham et al. 1997
Megaraptor namunhuaiquii	Novas 1998
Monolophosaurus jiangi	Zhao and Currie 1993
Mononychus olecranus	Perle et al. 1993
Nodosauridae sp.	Gasparini et al. 1996
Ornithodesmus cluniculus	Howse and Milner 1993
Ornithopoda sp.	Milner and Hooker 1992
Ornithopoda sp.	Thulborn 1994
Patagonykus puertai	Novas 1997
Pelecanimimus polyodon	Perez-Moreno et al. 1994
Protoarchaeopteryx robusta	Qiang et al. 1998
Rhoetosaurus brownei	Rich 1996
Sauropoda sp.	Rauhut and Werner 1997
Sauropoda sp.	Molnar and Wiffen 1994
Scipionyx samniticus	Dal Sasso and Signore 1998
Seismosaurus halli	Gillette 1991
Shanxia tianzhenensis	Barrett et al. 1998
Shuvosaurus inexpectatus	Chatterjee 1993
Siamotyrannus isanensis	Buffetaut et al. 1996
Sinornithoides youngi	Russell and Dong 1993b
Sinornithosaurus millenii	Xu et al. 1999a
Sinosauropteryx prima	Chen et al. 1998
Sinraptor dongi	Currie and Zhao 1993
Suchomimus tenerensis	Sereno et al. 1998
Tenontosaurus dossi	Winkler et al. 1997
Thecodontosaurus antiqus	Benton et al. 2000
Theropoda sp.	Molnar and Wiffen 1994
Theropoda sp.	Heckert et al. 1994
Theropoda sp.	Coria and Currie 1997
Theropoda sp.	Benton et al. 1997
Titanosaurus colberti	Jain and Bandyopadhyay 1997
Unenlagia comahuensis	Novas and Puerta 1997
Velociraptor mongoliensis	Norell and Clark 1992
Wuerhosaurus ordosensis	Dong 1993