PHYSICAL REVIEW E **92**, 032706 (2015)

Metabolism of dinosaurs as determined from their growth

Scott A. Lee
Department of Physics and Astronomy, University of Toledo, Toledo, Ohio 43606, USA

(Received 25 May 2015; revised manuscript received 3 August 2015; published 14 September 2015)

A model based on cellular properties is used to analyze the mass growth curves of 20 dinosaurs. This analysis yields the first measurement of the average cellular metabolism of dinosaurs. The organismal metabolism is also determined. The cellular metabolism of dinosaurs is found to decrease with mass at a slower rate than is observed in extant animals. The organismal metabolism increases with the mass of the dinosaur. These results come from both the Saurischia and Ornithischia branches of Dinosauria, suggesting that the observed metabolic features were common to all dinosaurs. The results from dinosaurs are compared to data from extant placental and marsupial mammals, a monotreme, and altricial and precocial birds, reptiles, and fish. Dinosaurs had cellular and organismal metabolisms in the range observed in extant mesotherms.

DOI: 10.1103/PhysRevE.92.032706 PACS number(s): 87.19.−j

I. INTRODUCTION

As the dominant land animals of the Mesozoic Era, dinosaurs are important in the study of the history of life on Earth. The largest sauropod dinosaurs were the largest land-living animals that have ever existed on Earth and were about an order of magnitude larger in mass than the largest extant land animal (the African elephant, *Loxodonta africana*). How and why they attained such enormous size are issues of importance. Though the nonavian dinosaurs have been extinct since the end of the Cretaceous Period (about 65.5 million years ago), in this paper, mass growth rates of dinosaurs are analyzed with a model based on cellular properties to determine their cellular and organismal metabolisms. This is the first determination of the cellular metabolism of dinosaurs. Though other workers have used statistical models to evaluate the organismal metabolism of dinosaurs by comparisons to extant animals, this work is the first determination of the organismal metabolism via a model based on the cellular properties of the animal. The growth of a large number of extant animals is also analyzed in order to compare to our results of 20 dinosaurs.

Closely related to this work on metabolism is the issue of body temperature regulation in dinosaurs. In extant animals, two main thermal regulation strategies are observed: endothermy and ectothermy. In endotherms (mammals and birds), the body temperature T_B is maintained very close to a fixed value, such as 37 °C in humans. T_B is maintained mainly by internal mechanisms, such as an increased metabolism in cold environments and the existence of an insulating layer (e.g., fur, hair, feathers, or blubber). In contrast, the body temperature of ectothermic animals (including reptiles and fish) is highly variable and determined, essentially, by the temperature of the surrounding environment. Since the closest extant relatives of dinosaurs are reptiles and bird, it is unclear if dinosaurs were endotherms or ectotherms. It is also possible that they used neither of these two mechanisms.

A significant advantage of endothermy is the maintenance of a high T_B. Since the rate of all biochemical reactions is dependent on the temperature, having a high T_B means that the important processes of the endotherm happen at a high rate regardless of the temperature of the surrounding environment. This permits endotherms to be active throughout the year and to occupy virtually every part of the planet. However, endothermy has the cost of requiring the animal to eat relatively large amounts of food in order to maintain the high temperature via its metabolism.

Because an ectothermic animal does not use significant amounts of metabolically generated heat to maintain its body temperature, ectotherms have a lower metabolic rate. Consequently, ectotherms need less food than endotherms. However, extended periods of low temperatures will cause T_B to fall in ectotherms. This slows their metabolism and can cause them to fall into torpor. Under such conditions, ectotherms become vulnerable to predation by endotherms. Ectothermy also limits the animals to live in regions of the planet without extended periods of cold.

Not all extant animals are either endotherms or ectotherms. Mesothermy is a temperature regulation strategy intermediate between endothermy and ectothermy, as shown by the small number of extant mesotherms. The body temperature of the echidna, the egg-laying mammal *Tachyglossus aculeatus*, varies between 28° and 35 °C, a much larger range than observed in endotherms [1]. Leatherback turtles (*Dermochelys coriacea*) have T_B which is about 3 °C above the temperature of the surrounding environment [2]. Lamnid sharks and tuna have the ability to maintain their body temperature about 10 °C warmer than the environmental temperature [3–5]. All extant mesotherms have metabolic rates that are intermediate between that observed for extant endotherms and ectotherms [6].

Erickson *et al.* [7] first used mass growth rates to show that dinosaurs regulated their body temperature in a manner distinct from endothermy and ectothermy. These authors used a sigmoidal function (based on the work of Sussman [8]) to fit their mass growth data. Analysis of mass growth rates in extant animals by Case [9] had already showed that the maximum growth rate correlates with the thermal regulation strategy of the animal: Endothermic animals have a higher maximum growth rate than ectothermic animals. Based on these results, the work of Erickson *et al.* suggested that dinosaurs were mesotherms.

Grady *et al.* [10] have recently shown additional evidence that the metabolism of dinosaurs is most consistent with mesothermy. They determined the maximum growth rate by fitting the mass growth of a large number of extant animals as well as dinosaurs using (primarily) the Gompertz model [11].

Two other models were used in certain cases: the von Bertalanffy [12] and the logistic [13] models. All three of these models involve an exponential growth, although the forms of these models differ. It is important to note that these methods are not based on the cellular properties of the organism. Rather, these expressions were developed because of their statistical correlation with the data. The theoretical expressions from these models then allowed for the evaluation of the maximum growth rate of the animal which was related to its metabolism. Grady *et al.* [10] found that the organismal metabolism of dinosaurs was in the range observed in extant mesotherms, in agreement with the results of Erickson *et al.* [7].

Understanding the metabolism of extinct animals requires a careful study of the metabolism of extant animals. In early, pioneering work, Kleiber [14] and Brody [15] first showed that the organismal metabolic rate, B, is related to the mass of the adult animal, M, via a power law: $B = B_o M^{\alpha}$. Kleiber [14] and Brody [15] reported that α is $3/4$.

Nagy *et al.* [16] have measured the field metabolic rate (FMR) of a large number of extant free-ranging placental mammals, marsupials, birds, and reptiles. The FMR is a measure of the average metabolic rate of the wild animal measured over time periods ranging from days to weeks. Their data (shown in Fig. 1) reveal several interesting trends. For all masses, the FMR for endotherms is about an order (or one and half orders) of magnitude higher than it is for ectotherms. Within a given taxon, the spread in the FMR is about an order of magnitude at any mass. The FMR of birds is slightly higher than for mammals. For masses above about 2 kgs, the FMR of mammals and reptiles almost overlap in value. For a given taxon, the FMR is essentially a linear function of mass on this log-log plot, meaning that the FMR and mass are related by a power law, as shown earlier by Kleiber [14] and Brody [15].

The large spread in the FMR for a certain mass within a given taxon shows the variability of living organisms. This indicates that a similar variability and possible overlaps are to be expected in the results of the current work. With such variability, it is important to analyze as many animals as possible in order to be able to determine the average values with the minimum possible uncertainty.

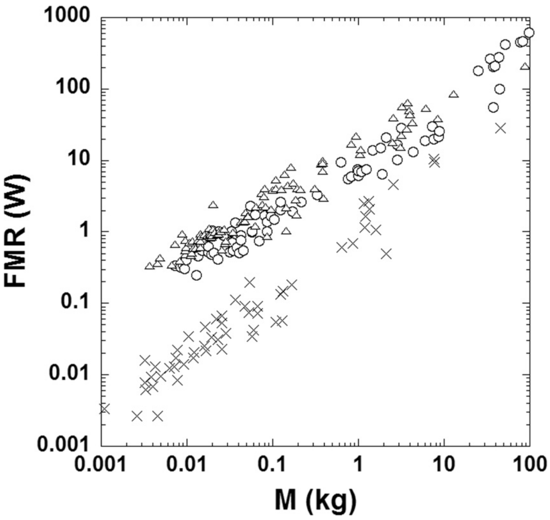

FIG. 1. Field metabolic rates of extant animals. The field metabolic rate (in watts) of extant birds (△), mammals (○), and reptiles (×) as a function of adult mass (in kilograms). The data are from Nagy *et al.* [16].

The data of Fig. 1 can be fit by a power law for each taxon. The exponent α is 0.681 ± 0.018 for birds, 0.734 ± 0.018 for mammals, and 0.888 ± 0.029 for reptiles. Nagy *et al.* [16] also found that α varies within a taxon. Placental mammals have a higher value of α than marsupial mammals. The exponent α of the FMR is also affected by diet. For instance, carnivorous mammals are found to have a higher value of α than insectivorous and herbivorous mammals.

It should also be noted that most metabolic studies on extant animals have been on animals with adult masses of 100 kg and less. Such animals are easier to handle and, for captive studies, have smaller needs of living space and food. However, a number of the dinosaurs of the current study had masses much larger than 100 kg. The sauropod dinosaurs had masses in excess of 20 000 kg.

The basal metabolic rate (BMR) is the minimum energy per unit time required to keep an animal alive. This is typically measured with the animal immobile, and, therefore, the BMR is less than the FMR. The BMR also depends on the adult mass via a power law but with a different exponent than the FMR. For placental mammals, Hayssen and Lacy [17] found α to be 0.696 for the BMR while Nagy *et al.* [16] found α to be 0.772 for the FMR.

The fact that the metabolism obeys a power-law relationship with the mass for all taxa shows the imprint of the underlying physical mechanism limiting the biological variability. Heat is lost by an animal through its skin and its exhaled breath. If the heat losses through breathing are insignificant, then simple dimensional analysis implies that the heat loss is proportional to $V^{2/3}$ where V is the total volume of the animal. This shows that the heat loss and the metabolism are proportional to $M^{2/3}$.

Alternatively, the organismal metabolism is affected by the fact that biological functions are limited by the rate at which the necessary resources (oxygen and nutrition) can be delivered to the cells. The size of the organism scales as the number of cells which scales as the mass or volume of the organism. For animals, the resources are delivered via fluid flow through the capillaries. These resources must flow through the surface of the capillaries in order to be delivered to the cells. Therefore, the rate at which resources are delivered to the cell scales as a surface area. The fact that the need scales as the volume (or, equivalently, mass) while the delivery scales as a surface area implies that the exponent of the metabolism-mass relationship is expected to be $2/3$.

West *et al.* [18,19] have argued that the exponent α is $3/4$, rather than $2/3$. Their reasoning is based on the same observation that the needed resources flow through the walls of the capillaries of the animal. However, West *et al.* [18,19] have argued that the exponent is $3/4$ due to the self-similar fractal nature of the arterial system.

Dodds *et al.* [20] have reviewed a number of studies of the relationship between the BMR and M and found significant empirical support for $\alpha = 2/3$.

Conservation of energy is one of the pillars of theoretical physics and this principle is applied to metabolism, the production of the energy necessary to sustain life, in this paper. Ricklefs [21] first developed this approach for a growing animal in 1969 and the approach was further developed by West *et al.* [22] in 2001 using $\alpha = 3/4$. Given the results of Dodds *et al.* [20], we develop a model using $B = B_o M^{2/3}$. This approach yields a theoretical expression of the mass growth of an animal in terms of fundamental cellular parameters of the animal, including B_c, the average cellular metabolism.

The growth of animals has long been the subject of intensive study and a variety of growth models were developed, including the Gompertz, [11] the von Bertalanffy [12], and the logistic [13] models mentioned above. Although these models are very useful in providing a framework to determine the maximum growth rate of an animal, they are not based on the fundamental parameters of the cell. Rather, their validity was justified solely on their ability to fit the data. The model developed in this paper relates the observed mass growth to the fundamental parameters of the living organism, as described in the next section. We will compare the results obtained from a large number of extant animals to the results of dinosaurs from the fossil record in order to address the issue of metabolism in dinosaurs.

Due to genetic and environmental differences, all animals show variety in their growth. Taking data from a large number of individuals for each species permits one to determine the average mass and its standard deviation as a function of age. As an example, the average mass of a nonpregnant adult female African elephant is 2658 ± 263 kg [23].

Determining the masses of extinct animals is even more difficult. The fossilized remains almost never contain any soft tissue. Furthermore, it is relatively rare to find the complete fossilized skeleton. For these growth studies, a series of complete fossilized skeletons for animals at different ages are needed in order to determine the mass as a function of age.

Reconstructing soft tissue on the fossilized skeleton of an extinct animal is subjective. The size of the points of attachments for tendons provides some guidance about the associated muscles when a comparison is made to extant animals. As noted earlier, sauropod dinosaurs were about an order of magnitude more massive than any extant animal living on the land, meaning that there are no extant animals of similar size.

Scale models have been used for estimating the volume of a dinosaur [24–26]. The volume can be converted to the mass via the density. Using the average density observed in extant animals would then yield the mass of the dinosaur. However, a number of dinosaurs display pneumaticity in which air spaces are found inside vertebrae of sauropods [27] and theropods [28]. Wedel [27] suggests that the masses of sauropods suggested by volume methods might need to be lowered by about 10% because their density has been overestimated by not accounting for the pneumaticity in the skeleton.

The availability of three-dimensional graphical computer programs has facilitated the determination of the volume of dinosaurs [29,30]. Gunga *et al.* [31] have pioneered the use of lasers to produce three-dimensional (3D) photogrammetry of actual skeletons. One significant advantage of using 3D graphical programs is that calculations can be easily done on different body parts, permitting for the quick exploration of the effects of different shapes on the body mass.

A biomechanical approach relates the dimensions of the long bones to the mass of the animal [32,33]. This technique has the advantage of providing the mass of dinosaurs for whom only one or more long bones have been recovered. However, the accuracy of its predicted masses can be very poor.

Hutchinson *et al.* [34] have used three-dimensional laser scanning of four articulated specimens of adult *Tyrannosaurus rex* in order to determine the mass of an adult *T. rex* as well as the variability of the mass. They found that the largest adult *T. rex* ("Sue," specimen FMNH PR 2081 of the Field Museum of Natural History in Chicago) had a mass of about 9500 kg. They determined that adult *T. rex* had body masses in the 6000- to 8000-kg range; that is, the adult mass was 7000 ± 1000 kg. This variation of 14% is consistent with the variation noted in extant *L. africana* and this percentage value will be used for the variation of the masses of the dinosaurs in this study.

The adult mass is necessary for our study but not sufficient. We also need the mass of the juvenile dinosaurs throughout their growth. Because of the rarity of complete skeletons of juveniles of the same dinosaur species, Erickson and Tumanova [35] developed a methodology to reconstruct the mass growth curve of the dinosaur based on the adult mass and dimensions of long bones (usually the femur) from juvenile specimens. Noting that the femoral length (L) scales as $M^{1/3}$ in extant archosaurs-crocodilians [36] and birds [37], they calculated L^3 for each femur and divided each value by L^3 for the longest femur (presumed to be from a fully grown adult) to determine the fraction of growth displayed by that individual. Multiplying each fraction by the adult mass then yields the mass of the juvenile dinosaur. Erickson and Tumanova performed these measurements and calculations on the length of femora from seven specimens of *Psittacosaurus mongoliensis* at different stages of development. This methodology has been widely adopted for determining the mass growth curves of dinosaurs.

The age of a dinosaur at different stages of growth can be determined by an examination of certain bones, particularly the long bones of the limbs, such as the femur and humerus. These bones of many (but not all) animals display lines of arrested growth (LAGs). Based on studies of extant vertebrates, LAGs represent annual fluctuations in growth rate. Therefore, counting the number of LAGs in a bone yields a minimum age [38].

The initial mass of the animal, m_o, at the time of hatching or birth is very important for an accurate determination of the mass growth curve. A direct measurement of m_o is not possible for many dinosaurs. However, Dolnik [39] has found that the egg mass, m_{egg} is related to the adult mass M of dinosaurs as

$$m_{\text{egg}} = 0.46\, M^{0.46}. \tag{1}$$

Deeming and Birchard [40] have found that the mass of a newly hatched bird is 70% of the egg mass. The mass of newly hatched dinosaurs can then be determined using Eq. (1) and assuming this ratio to be true for nonavian dinosaurs. The uncertainty in m_o is determined by propagating the uncertainty in the adult mass M in Eq. (1).

II. MODEL

The total metabolism, B, of the animal during growth provides the necessary power to its cells plus the power needed to create new cells. Each animal is composed of a variety of cells (muscle cells, nerve cells, cells of different organs, etc.):

$$B = \sum_{j=1}^{d} \left(N_{c,j} B_{c,j} + E_{c,j} \frac{dN_{c,j}}{dt} \right), \qquad (2)$$

where d is the number of different types of cells in the animal; $N_{c,j}$ is the number of cells of the jth type, $B_{c,j}$ is the cellular metabolism of the jth type of cell; and $E_{c,j}$ is the energy required to make a cell of the jth type.

Since individual cells are composed of soft tissue which does not usually leave any trace in the fossil record, our calculations will be unable to discern any differences between the types of cells. Rather we will be able to calculate average properties of a typical cell. In that case, Eq. (2) becomes:

$$B = N_c B_c + E_c \frac{dN_c}{dt}. \qquad (3)$$

B_c and E_c are the cellular metabolism of an average cell and the energy required to create an average cell, respectively, while N_c is the number of cells. The first term on the right-hand side of Eq. (3) is the metabolism necessary to maintain the living cells while the second term is the metabolism used to grow new cells.

E_c and B_c are assumed to remain unchanged throughout growth. Furthermore, the mass of an average cell, m_c, is assumed to be the same for all animals and to remain constant throughout growth. Bianconi *et al.* [41] determined the number of cells in a 70.0-kg human to be $(3.72 \pm 0.81) \times 10^{13}$, yielding $m_c = (1.88 \pm 0.41) \times 10^{-12}$ kg. Moses *et al.* [42] have determined that the energy required to produce one gram of biomass in all animals is 5774 ± 97 J, showing that E_c is the same for all animals. Combining these results yields $E_c = (1.09 \pm 0.24) \times 10^{-5}$ J.

The growth of the animal will be characterized by its total mass $m(t)$ at time t. Note that $N_c = m/m_c$ and, as discussed earlier, $B = B_o m^{2/3}$. Substituting and rearranging, Eq. (3) becomes

$$\frac{dm}{dt} = pm^{2/3} - qm, \qquad (4)$$

where $p = m_c B_o / E_c$ and $q = B_c / E_c$. The animal's mass at the time of hatching or birth is $m(t = 0) = m_o$ and its asymptotic mass $m(t = \infty) = M$.

While the animal is young and growing, the first term on the right-hand side of Eq. (4) is larger than the second term. Since the two terms have a different dependence on mass (one to the 2/3 power and the other to the first power), the right-hand side will become zero at the asymptotic mass M and the animal will stop growing:

$$0 = pM^{2/3} - qM \Rightarrow M = \left(\frac{p}{q}\right)^3 = \left(\frac{m_c B_o}{B_c}\right)^3. \qquad (5)$$

Such animals are said to have determinate growth since they attain a maximum size and do not grow any larger.

Because of their slow metabolism, ectothermic animals grow slowly. Such animals do not reach a maximum size during their lifetime since the right-hand side of Eq. (4) never becomes zero for them. These animals are said to display indeterminate growth since they continue to grow throughout their lives. However, the asymptotic mass M of these animals can be determined via Eq. (5). If they would live longer, they would reach their asymptotic mass M.

Equation (4) can be integrated by using a change of variables $[f = (m/M)^{1/3}]$ to yield:

$$m(t) = M\left\{1 - \left[1 - \left(\frac{m_o}{M}\right)^{1/3}\right] e^{-\frac{pt}{3M^{1/3}}}\right\}^3. \qquad (6)$$

Equation (6) is used to fit the experimentally determined mass growth curves (mass as a function of age). Because many data points are available for the mass growth curves of extant animals, the parameters m_o, M, and p are varied in a least-squares fit via the Levenberg-Marquardt algorithm. However, for dinosaurs, relatively few data points exist, and, as discussed later, the incompleteness of the dinosaur data sets can bias the results. To minimize this bias, the asymptotic mass M is determined by a careful survey of the refereed literature while the initial mass m_o is determined by using Eq. (1) to calculate the egg mass and then assuming that m_o is 70% the egg mass, as observed in extant birds. Consequently, the only free parameter in Eq. (6) for the dinosaur data is p. The metabolic prefactor B_o is then calculated by

$$B_o = \frac{pE_c}{m_c}. \qquad (7)$$

The cellular metabolism B_c is determined by

$$B_c = \frac{pE_c}{M^{1/3}}. \qquad (8)$$

Note that, in this methodology, both B_o and B_c are parameters which measure the metabolism of the animal on the time scale of its growth phase. Small animals can reach full size relatively quickly, but large animals take decades to fully mature.

In order to connect to the pioneering work of Erickson *et al.* [7] we also evaluate the maximum growth rate of the dinosaurs by finding the point of inflection of Eq. (6) and evaluating its first derivative at that point,

$$\left(\frac{dm}{dt}\right)_{\max} = \frac{4pM^{2/3}}{27}. \qquad (9)$$

The derivation of the $\alpha = 3/4$ model has been discussed by West and coworkers [18,19,22].

All dinosaurs, including the large sauropods, are believed to have laid eggs, as is the case with all extant birds and most extant reptiles [43–45]. Because of limitations of the surface area-to-volume ratio, the size of eggs is limited. Sauropod hatchlings from Argentina had a mass much less than 10 kg [46]. Since adult sauropods had masses on the order of 30 000 to 80 000 kg, these dinosaurs had to have a high growth rate in order to reach adult size within about 30 years.

All dinosaurs studied to date [43] have had large clutch sizes per litter, with about 20 eggs per litter. Though the parents might have been able to provide some care for such a large litter size, the young would have had to fend for themselves very quickly. The pressure of predation on such young animals would have selected for a high growth rate.

III. RESULTS AND DISCUSSION

Mass growth data from 35 placental and marsupial mammals [47–64], 1 monotreme [1], 30 birds [22,65–87], 15 fish [88–100], 7 reptiles [23,101–106], and 20 dinosaurs [7,23,35,107–119] were analyzed using Eq. (6).

Our results speak to the issue of the exponent α. As discussed earlier, the need for sustenance for the cells grows like the number of cells or, equivalently, the mass m of the animal. The ability of the body to deliver the sustenance to the cells is controlled by the capillary system and grows as m^{α}. Because of this difference in the power dependence of the mass, each cell in a small animal receives a relatively larger amount of nutrition and, therefore, can have a higher cellular metabolic rate. For larger animals, the metabolic rate of each cell is limited by the rate at which it receives nutrition. Therefore, the cellular metabolic rate B_c is expected to drop as $m^{-\beta}$ where $\beta = 1 - \alpha$. For $\alpha = 2/3$, the cellular metabolism is expected to scale as $m^{-1/3}$. If $\alpha = 3/4$, then the cellular metabolism should scale as $m^{-1/4}$.

To determine β, we analyze the mass growth curves of extant placental mammals, birds, reptiles, and fish using Eq. (6) and evaluate B_c for each animal, as shown in Fig. 2. Two analyses were performed for each animal: one using the $\alpha = 2/3$ model and the other using the $\alpha = 3/4$ model. The results for β are given in Table I. For the $\alpha = 2/3$ model, we see that β is within one standard deviation of the predicted value of $-1/3$ for both extant endothermic and ectothermic animals. That is, the data are consistent with the predictions of this model. For the $\alpha = 3/4$ model, the observed value of β is 3.5 standard deviations away from the prediction for extant endotherms and 1.6 standard deviations away from the prediction for extant ectotherms. Though not definitive, these results suggest that the $\alpha = 2/3$ model is a better representation of the metabolism and growth of extant animals than the $\alpha = 3/4$ model. Consequently, we use the $\alpha = 2/3$ model for our analysis of the mass growth of dinosaurs. This is the first such analysis of dinosaur growth using a model based on cellular properties and will yield important insights into dinosaur metabolism.

TABLE I. Cellular metabolism in extant endotherms and ectotherms. The predicted and observed values of β determined by analysis of extant endothermic and ectothermic animals for the $\alpha = 2/3$ and $\alpha = 3/4$ models.

	$\alpha = 2/3$		$\alpha = 3/4$	
	β_{pred}	β_{obs}	β_{pred}	β_{obs}
Extant Endotherms	$-1/3$	-0.349 ± 0.022	$-1/4$	-0.326 ± 0.022
Extant Ectotherms	$-1/3$	-0.289 ± 0.044	$-1/4$	-0.316 ± 0.041

The dinosaurs include 11 theropods (*T. rex, Daspletosaurus torosus, Gorgosaurus libratus, Allosaurus fragilis, Citipati, Deinonychus, Troodon, Oviraptor philoceratops, Coelophysis rhodesiensis, Shuvuuia deserti,* and *Archaeopteryx lithographica*), 3 sauropods (*Apatosaurus*, a mamenchisaurid, and *Alamosaurus sanjuanensis*), 2 prosauropods (*Massospondylus carinatus* and *Plateosaurus engelhardti*), 2 ornithopods (*Tenontosaurus tilletti* and *Dysalotosaurus lettowvorbecki*), a third ornithopod *Maiasaura peeblesorum* (a hadrosaur), and 1 ceratopsian (*P. mongoliensis*). These 20 dinosaurs include animals from both the Saurischian and Ornithischian branches of Dinosauria, as shown in Fig. 3 [120,121].

Figures 4 and 5 show the mass growth data and theoretical fits via Eq. (6) for the 20 dinosaurs of this study. The uncertainties in mass are taken to be 14% of the mass itself, as discussed earlier. It is possible that there is an undercounting error in the age of the dinosaur based on the number of LAGs since the earliest LAGs are sometimes lost to medullary cavity expansion and osteonal remodeling. Table II shows the parameters and fitting results for the dinosaurs.

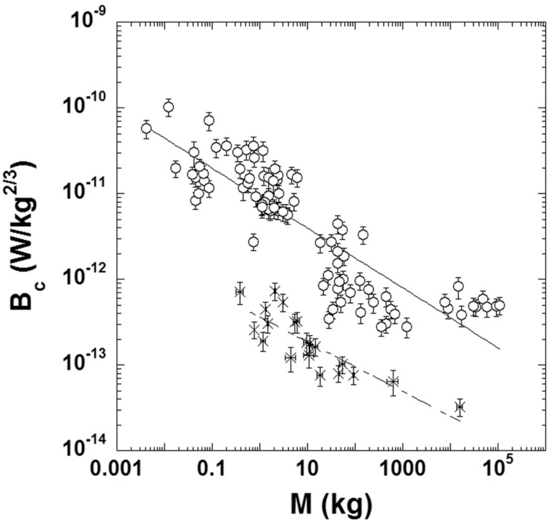

FIG. 2. Cellular metabolism B_c in extant endotherms and ectotherms. The cellular metabolism B_c (in W) as a function of the asymptotic mass M (in kg). The data for extant endothermic placental mammals and birds are shown by the open circles (o) and the data for extant ectothermic reptiles and fish are shown by the ×. The solid line shows the fit to the endothermic data and the dashed line shows the fit to the ectothermic data.

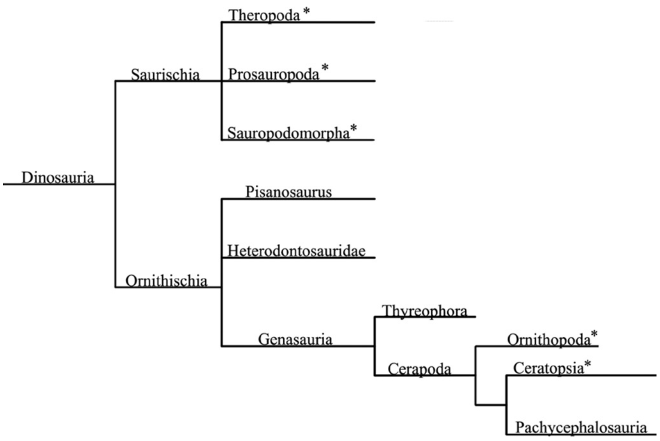

FIG. 3. Cladogram of Dinosauria. Cladogram of Dinosauria to show the relationships of the dinosaurs for whose growth data has been analyzed. The asterisks mark the clades from which the mass growth curves of dinosaurs have been analyzed. Note that animals from both the Saurischia and Ornithischia branches of Dinosauria have been studied.

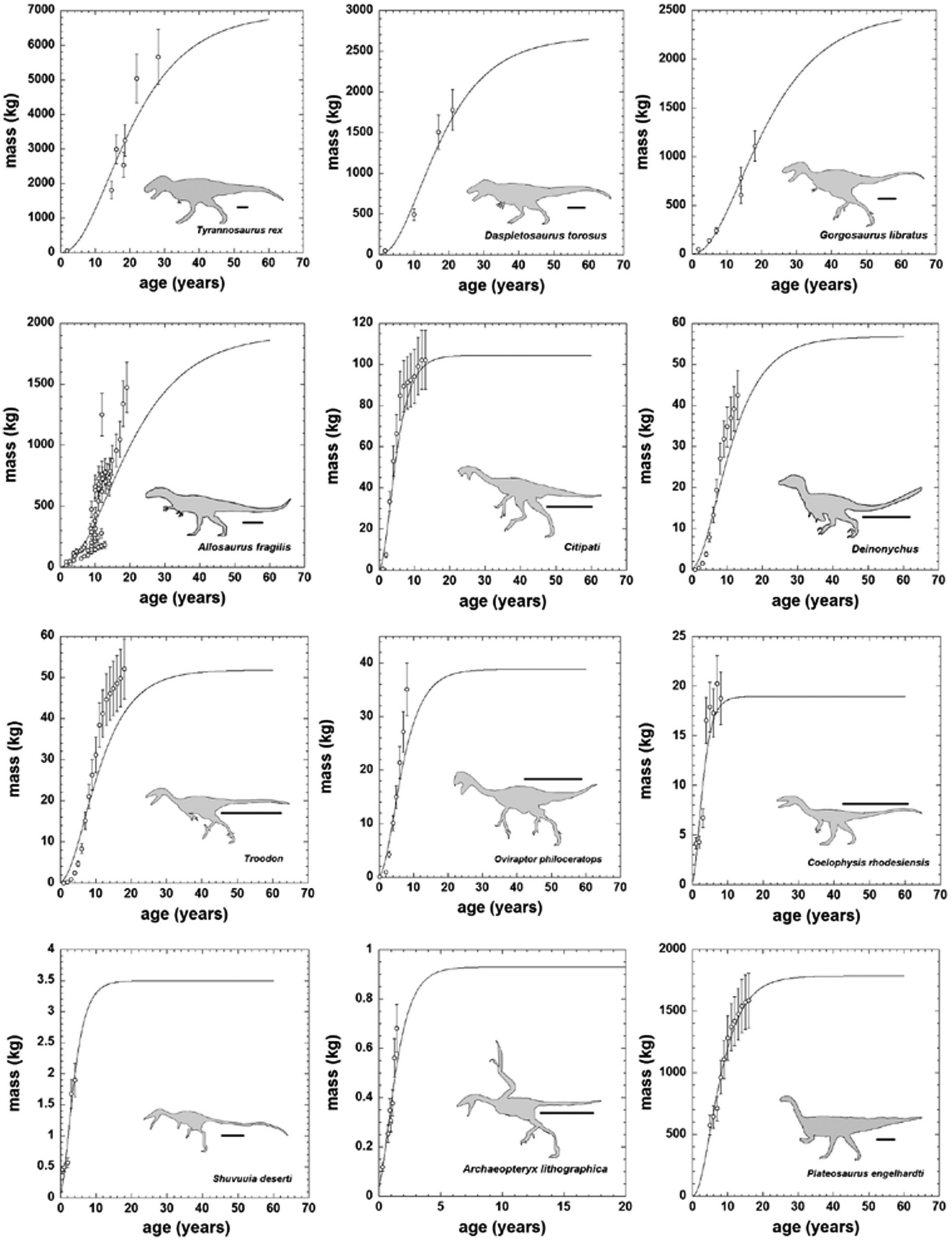

FIG. 4. Mass growth of dinosaurs I. Mass (in kilograms) of *T. rex, D. torosus, G. libratus, A. fragilis, Citipati, Deinonychus, Troodon, O. philoceratops, C. rhodesiensis, S. deserti, A. lithographica,* and *P. engelhardti* as a function of age (in years). The data are shown by the open circles (o) and the theoretical fits via Eq. (6) are shown by the solid line. The scale bar beside each dinosaur is 1 m long except for *S. deserti* and *A. lithographica*, whose scale bar is 0.1 m long.

Some of the dinosaur mass growth curves reported here were derived from a single specimen. A long bone (typically the femur) is sectioned and the LAGs are studied to determine the diameter of the bone at that particular age. Because the diameter of the bone is correlated to its length [122,123], the long bone length as a function of age could be determined

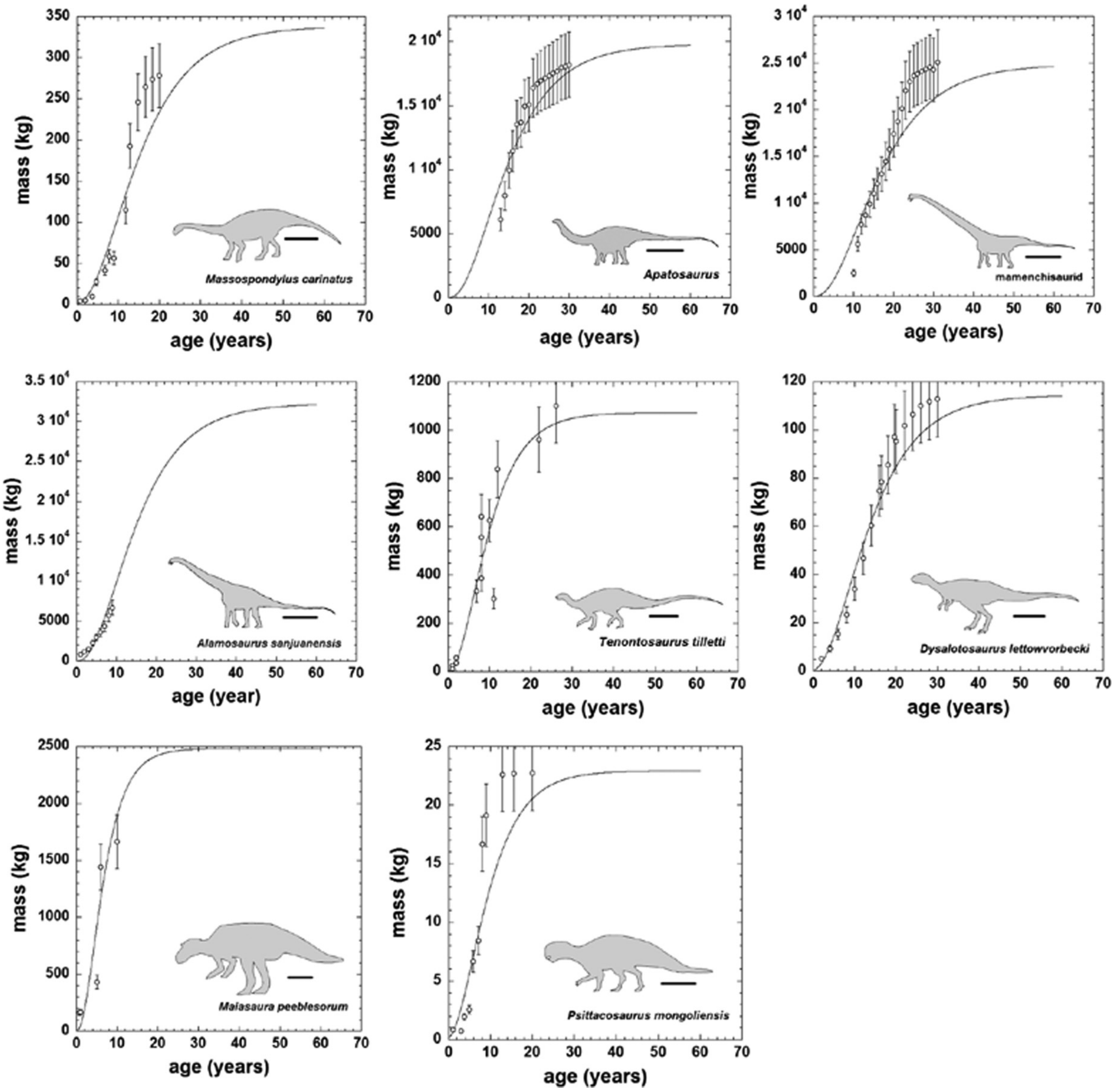

FIG. 5. Mass growth of dinosaurs II. Mass (in kilograms) of *M. carinatus, Apatosaurus,* a mamenchisaurid, *A. sanjuanensis, T. tilletti, D. lettowvorbecki, M. peeblesorum,* and *P. mongoliensis* as a function of age (in years). The data are shown by the open circles (o) and the theoretical fits via Eq. (6) are shown by the solid line. The scale bar beside each dinosaur is 1 m long except for *Apatosaurus*, the mamenchisaurid, and *A. sanjuanensis*, for whom the scale bar is 5 m long, and *P. mongoliensis*, for whom the scale bar is 0.3 m long.

from its diameter. Following the methodology of Erickson and Tumanova [35] and an independent estimate of the adult mass, the growth curve could be generated.

Using a bone from a single dinosaur has the obvious difficulty of a sample size of 1. It is not possible to know if the growth curve of that particular individual is a fair representation of the average mass growth curve for that species. It is possible that the individual dinosaur lived in a unique environment, either one with very plentiful resources that would facilitate growth or one with a paucity of resources that would limit the growth. It is also possible that the genetic makeup of that particular individual might predispose the animal to either particularly rapid or slow growth. The data from a single individual will not show any of the variability associated with either of these effects. Though it is not possible to account for the systematic bias of a single individual, an uncertainty of 14% will be given to each measurement. This uncertainty is propagated through the calculations and will help to yield reasonable uncertainties in the final results.

Figure 4 shows the 11 theropods and one of the prosauropods of this study. Note that the smallest dinosaur, *A. lithographica*, reaches its full adult size in the shortest time, about 4 years. Theropods with masses between about 1 and 105 kg (*Citipati, Deinonychus, Troodon, O. philoceratops, C. rhodesiensis,* and *S. deserti* reach their final adult size in about 10 years. The largest theropods (*T. rex, D. torosus, G. libratus,* and *A. fragilis*) with masses larger than about 1900 kg reach their full size in about 20 to 30 years.

It should be noted that the data for *A. fragilis* shows an unusual distribution. It is possible that more than one species

TABLE II. Mass and metabolic properties of dinosaurs. The asymptotic mass M, the initial mass m_o at time of hatching, the metabolic prefactor B_o, the cellular metabolic rate B_c, and the maximum mass gain rate $(dm/dt)_{\max}$ and their standard deviations for the dinosaurs of this study.

Species	M (kg)	m_o (kg)	B_o (W/kg$^{2/3}$)	B_c ($\times 10^{-14}$ W)	$(dm/dt)_{\max}$ (g/d)
Theropoda					
Tyrannosaurus rex	7000 ± 980	2.06 ± 0.13	0.808 ± 0.081	7.97 ± 1.60	649 ± 79
Daspletosaurus torosus	2700 ± 378	1.33 ± 0.09	0.678 ± 0.068	9.18 ± 2.25	289 ± 39
Gorgosaurus libratus	2500 ± 350	1.28 ± 0.08	0.554 ± 0.055	7.69 ± 1.84	224 ± 28
Allosaurus fragilis	1930 ± 270	1.17 ± 0.07	0.529 ± 0.053	8.01 ± 1.87	180 ± 20
Citipati	105 ± 15	0.298 ± 0.019	0.800 ± 0.085	31.9 ± 7.9	39.2 ± 5.5
Deinonychus	57.0 ± 8.0	0.225 ± 0.014	0.284 ± 0.031	13.9 ± 3.5	9.26 ± 1.32
Troodon	52.0 ± 7.3	0.215 ± 0.014	0.279 ± 0.032	14.1 ± 3.6	8.57 ± 1.26
Oviraptor philoceratops	39.0 ± 5.5	0.189 ± 0.012	0.405 ± 0.053	22.5 ± 5.8	10.3 ± 1.6
Coelophysis rhodesiensis	19.0 ± 2.7	0.136 ± 0.009	0.716 ± 0.094	50.5 ± 13.1	11.2 ± 1.8
Shuvuuia deserti	3.5 ± 0.5	0.0623 ± 0.0040	0.305 ± 0.048	37.8 ± 10.4	1.55 ± 0.28
Archaeopteryx lithographica	0.93 ± 0.13	0.0339 ± 0.0022	0.508 ± 0.051	97.8 ± 23.3	1.07 ± 0.13
Prosauropoda					
Plateosaurus engelhardti	1600 ± 224	1.04 ± 0.07	1.46 ± 0.15	23.5 ± 5.5	439 ± 48
Massospondylus carinatus	340 ± 48	0.511 ± 0.033	0.392 ± 0.039	10.6 ± 2.5	42.0 ± 5.2
Sauropoda					
Apatosaurus	20 000 ± 2800	3.33 ± 0.21	1.61 ± 0.16	11.2 ± 2.6	2600 ± 288
mamenchisaurid	25 100 ± 3500	3.70 ± 0.24	1.55 ± 0.16	9.99 ± 2.33	2915 ± 327
Alamosaurus sanjuanensis	32 600 ± 4600	4.17 ± 0.27	1.88 ± 0.19	11.1 ± 2.7	4201 ± 563
Ornithopoda					
Tenontosaurus tilletti	1080 ± 151	0.870 ± 0.056	0.903 ± 0.090	16.6 ± 4.0	209 ± 28
Dysalotosaurus lettowvorbecki	115 ± 16	0.310 ± 0.020	0.294 ± 0.029	11.4 ± 2.7	15.3 ± 1.7
Maiasaura peeblesorum	2500 ± 350	1.28 ± 0.08	1.77 ± 0.49	24.6 ± 8.7	715 ± 207
Ceratopsia					
Psittacosaurus mongoliensis	23.0 ± 3.2	0.148 ± 0.010	0.244 ± 0.035	16.2 ± 4.3	4.35 ± 0.74

(with different growth characteristics) have been assigned to *A. fragilis*. Another possibility is that sexual dimorphism might be present in this species.

The same basic growth patterns are noted in Fig. 5. Remarkably, even the large sauropods *Apatosaurus* and the mamenchisaurid, with asymptotic masses in the range of 20 000 kg, reach adult size in about 30 years. This is an even shorter amount of time than the about 40 years required for the African elephant to reach full size [23]. Recall that adult African elephants have masses in the range of 3000 (for females) and 5000 (for males) kg. The fact that the sauropods gained more than 7 times as much mass in only 3/4 of the time of African elephants shows that sauropod dinosaurs had a high growth rate which is an indication of a high metabolism.

Figure 6 shows the organismal metabolic prefactor B_o as a function of the asymptotic mass M. Figure 6(a) shows B_o for extant endothermic birds and placental mammals in the open symbols while B_o for extant ectotherms are shown by the open cross sign for reptiles and the "×" for fish. As the closest living relatives of dinosaurs, birds and reptiles are important animals for the study of the metabolism of dinosaurs. The polygon composed of the solid line encloses all of the endotherms (the birds and placental mammals) while the polygon composed of the dashed line encloses the ectotherms (the reptiles and birds). Note that all of these extant endotherms have a value of B_o that is greater than 1 W/kg$^{2/3}$. The maximum observed B_o for extant ectotherms is 0.50 W/kg$^{2/3}$.

Figure 6(b) shows B_o as a function of the asymptotic mass M for the same extant endotherms and ectotherms along with the results for four marsupial mammals (shown by open diamonds), four extant mesotherms (the echidna, the leatherback sea turtle, the Mako shark, and the tuna *Thunnus obesus*, all shown by solid triangles), and the same 20 species of dinosaurs (solid circles). Marsupials are known to have relatively low metabolic rates, as confirmed in Fig. 6(b), since their values of B_o are in the lower part of the endothermic polygon. Two marsupials, the female red kangaroo (*Macropus rufus*) and the female swamp wallaby (*Wallabia bicolor*), have a B_o of 0.558 and 0.767 W/kg$^{2/3}$, respectively, just below the endothermic polygon. Note that the data for B_o for the extant mesotherms lie mainly between the two polygons. The echidna (*Tachyglossus aculeatus*) has a B_o (0.513 W/kg$^{2/3}$) just bordering the ectothermic polygon. The leatherback turtle (*Dermochelys coriacea*) has a B_o (0.876 W/kg$^{2/3}$) just bordering the endothermic polygon.

Figure 6(b) shows that B_o for the dinosaurs of this study are mainly between the two polygons and overlap with the extant mesotherms. This is consistent with the results of Erickson *et al.* [7] and Grady *et al.* [10], who reported earlier that dinosaurs were mesotherms.

Figure 6(c) shows B_o as a function of the asymptotic mass M for the dinosaurs alone. The general trend seen in this figure is that the metabolic prefactor increases with mass. The dinosaurs with the largest values of B_o are the most massive ones. The saurischians are shown by the empty symbols

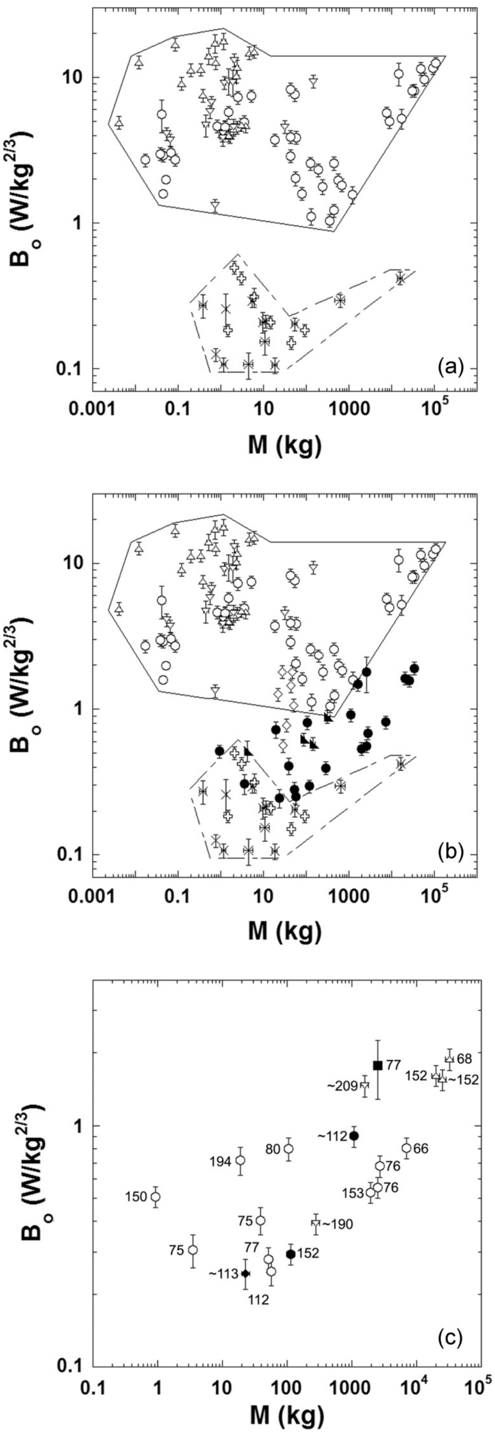

FIG. 6. Metabolic prefactor B_o. The metabolic prefactor B_o (in watts per kilograms$^{2/3}$) as a function of asymptotic mass M (in kilograms) for (a) placental mammals (○), altricial birds (△), precocial birds (▽), marsupial mammals (◇), reptiles (open cross), and fish (×); (b) placental mammals (○), altricial birds (△), precocial birds (▽), marsupial mammals (◇), reptiles (open cross), fish (×), extant mesotherms (solid triangle), and dinosaurs (●); and (c) theropods (○), sauropods (△), prosauropods (▽), ornithischians excluding the hadrosaurs and ceratopsians (●), a hadrosaur (solid square), and a ceratopsian (solid diamond). The polygon composed of solid lines encloses extant placental mammals and birds while the polygon composed of dashed lines encloses extant reptiles and fish. The times when the dinosaurs lived is marked on the figure in million years ago.

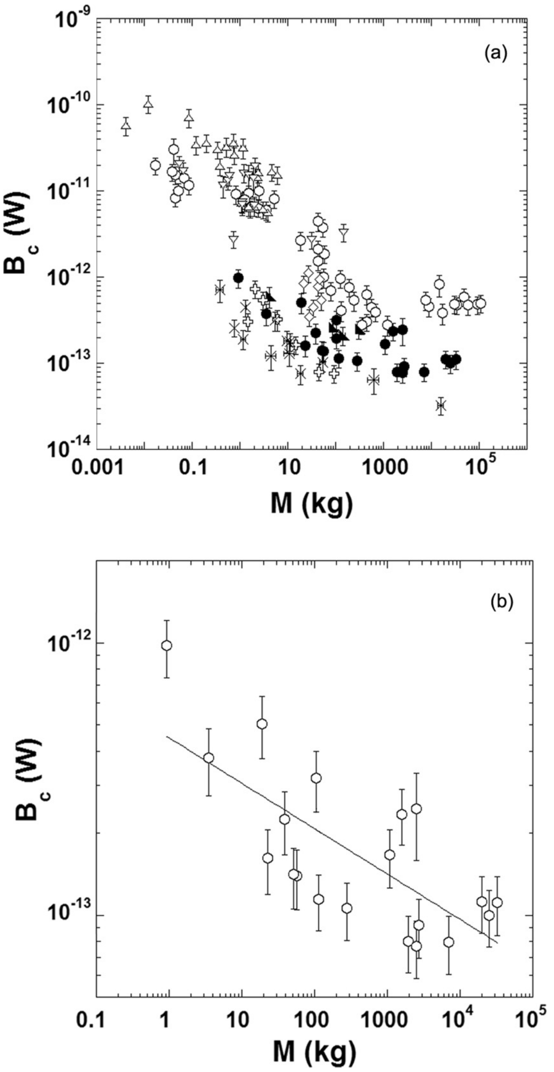

FIG. 7. Cellular metabolism B_c. The average cellular metabolism B_c (in watts) as a function of asymptotic mass M (in kilograms) for (a) placental mammals (○), altricial birds (△), precocial birds (▽), marsupial mammals (◇), reptiles (open cross), fish (×), extant mesotherms (solid diamond), and dinosaurs (●) and (b) dinosaurs. The solid line shows the fit to the data.

while the ornithischians are shown by the filled symbols. No significant difference is observed for these two branches of Dinosauria. More massive dinosaurs have larger values of B_o.

Figure 6(c) lists the times when the dinosaurs lived (listed in millions of year ago). The earliest dinosaur, *P. engelhardti*, lived between about 214 and 204 million years ago (MYA) and it had one of the largest values for B_o (1.46 W/kg$^{2/3}$). Similarly, one of the dinosaurs living between about 70 and 66 MYA (at the end of the Cretaceous Period) had a B_o of 1.88 W/kg$^{2/3}$. There are no observed trends with time of B_o for the dinosaurs.

Figure 7(a) shows the cellular metabolism B_c as a function of the asymptotic mass M for the same extant endotherms and ectotherms as in Fig. 2 along with the results for four marsupial mammals (open diamonds), four extant mesotherms (the echidna, the leatherback sea turtle, the Mako shark, and the tuna *T. obesus*, all shown by solid triangles), and 20 species of dinosaurs (solid circles). As in the case of B_o, we find that B_c for extant mesotherms and dinosaurs are intermediate between the values observed for the extant endotherms and ectotherms at all masses.

Figure 7(b) shows the cellular metabolism B_c for the dinosaurs as a function of the asymptotic mass M. The solid line shows the fit to this data in the form of a power law: $B_c = B_{c,o}M^{\beta}$. Our measured values for the dinosaurs are $B_{c,o} = (4.47 \pm 1.04) \times\ 10^{-13}$ W kg$^{0.167}$ and $\beta = -0.167 \pm 0.036$. Recall that β should be $-1/3$. Consequently, our measured value of β for the dinosaurs is 4.6 standard deviations different from the predicted value. This is a very strong indication that the dinosaur's cellular metabolism did not obey the expected mass dependence because it is not decreasing with mass as rapidly as it should. That is, the higher-mass dinosaurs have a cellular metabolism that is higher than expected.

Recall that Fig. 6(c) shows that the metabolic prefactor B_o increases with mass. The dinosaurs with the highest values of B_o are the most massive ones, particularly the sauropods. Therefore, we see that both the cellular metabolism B_c and the organismal metabolic prefactor B_o are larger for the largest dinosaurs than expected based on scaling arguments.

One important question from this work is how did the largest dinosaurs maintain such a high metabolism? As argued earlier, the cellular metabolism B_c should scale as $m^{-1/3}$ due to the $m^{2/3}$ relationship for the organismal metabolism. And this $m^{2/3}$ relationship is believed to have its origin in the fact that the need for nutrition to power the cellular metabolism scales as the mass m of the animal while the ability of the arterial system to deliver that nutrition is related to the surface area of the capillaries. However, since the cellular metabolism B_c is decreasing more slowly with mass than the prediction, the animals were somehow able to circumvent the limitation of cellular nutritional delivery due to the $m^{2/3}$ power law.

In the model used in this paper, the properties of an average cell have been calculated by assuming that all cells are the same with respect to their metabolism. However, it is known that, in adult humans, the brain receives 20% of the blood supply but accounts for only 2% of the mass of an adult [124]. Furthermore, the metabolism of a resting human brain is about 17 W [125,126], while the basal metabolic rate of a human is about 76 W [127]. In this manner we see that the brain produces about 20% of metabolism of a human even though it only accounts for 2% of the mass. Clearly, the brain is able to circumvent the $m^{2/3}$ law (which it accomplishes by having a greater density of blood vessels than normal tissue does) and more blood than expected is delivered to the brain.

Our growth analysis also reveals that brain tissue has a cellular metabolic rate about an order of magnitude greater than normal tissue. Herndon *et al.* [128] published postmortem data on brain and body masses of chimpanzees (*Pan troglodytes*). The growth analysis for the entire animal yields a cellular metabolism $B_c = 0.22$ pW while a growth analysis for just the brain yields a cellular metabolism $B_c = 2.1$ pW.

These results on human and chimpanzees brains show that growth in animals can exceed the predictions of the $m^{2/3}$ law. The fact that the large dinosaurs had a cellular metabolism larger than predicted by the $m^{2/3}$ law suggests that the dinosaurs, particularly the sauropods, grew in a manner which circumvented the $m^{2/3}$ law.

The sauropods were the largest land animals ever to live. They rivaled the largest extant cetaceans in mass and size. However, life in the sea differs substantially from life on land, making it unclear how relevant this comparison is. Also, all extant cetaceans are carnivorous while the sauropods were herbivorous. How and why sauropods attained such a large body size are issues of intensive research.

All herbivores face a significant challenge: extracting the nutritious contents of the plant cell through its tough cell wall. Plant cell walls contain a significant amount of cellulose which makes the cell wall very difficult to breach. All extant herbivores masticate their food very thoroughly to reduce the particle size and, more importantly, to disrupt the plant cell wall in order to make the nutritious cellular contents available for digestion by the herbivore. Extant herbivores have large batteries of teeth for grinding their food in a mortar-and-pestle fashion. In humans, these teeth are the molars.

Herbivores of progressively larger sizes must eat larger quantities of food. Masticating plant food properly takes a significant amount of time since each cell has to be trapped between the teeth and masticated. This means that larger herbivores spend a larger fraction of their waking time eating. The allometric relationship determined by Owen-Smith [129] reveals that herbivores using mastication with a mass of about 18 000 kg would spend 100% of their waking time for feeding. Since there were a substantial number of sauropods with masses greater than 18 000 kg, such sauropods must have used some other strategy for breaching the cell wall.

Figure 8 shows the skulls of two sauropods, [Fig. 8(a)] *Diplodocus* and [Fig. 8(b)] *Brachiosaurus* [130], and a [Fig. 8(c)] hadrosaur, *Edmontosaurus sasktachewanensis* [131]. Note the substantial dental battery of the hadrosaur. Clearly this was an animal well equipped for mastication. With a mass of about 3200 kg, its mass roughly matched that

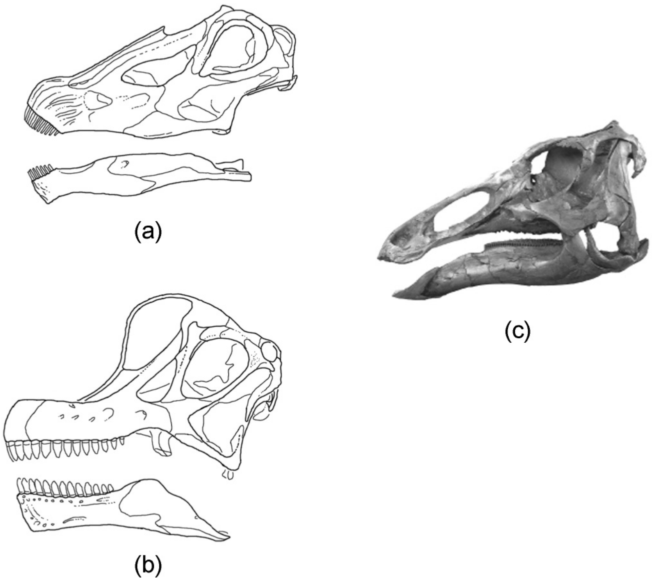

FIG. 8. The skulls of (a) *Diplodocus*, (b) *Brachiosaurus*, and (c) *E. sasktachewanensis*. These are not to scale. Panels (a) and (b) are modified from Ref. [130]. Panel (c) is from Ref. [131].

of female African elephants (*L. africana*). Like the African elephant, this animal would have been feeding for about 80% of its waking time [129].

Sauropods had no teeth that would be suitable for mastication. Diplodocoids and titanosaurs [represented by *Diplodocus* in Fig. 8(a)] had only pencil-like teeth near the front of their snout. Basal sauropods and macronarians [represented by *Brachiosaurus* in Fig. 8(b)] had spoon-shaped teeth. Since their teeth did not have the capability of mastication, the sauropods must have used some other strategy to extract the nutritious contents of the plant cells.

Over the years, a number of workers [132–134] have suggested that the sauropods had a muscular organ filled with rocks in the initial part of their digestive tract, equivalent to the gizzard found in birds. However, recent work with the gastroliths of ostriches suggests that the amounts of gastroliths recovered from sauropod dinosaurs were much too small to provide sufficient digestion for an animal the size of the sauropod [135]. The smooth stones recovered at sauropod fossil sites are believed to have been either accidentally swallowed by the animal or deliberately swallowed to gain needed minerals.

Hummel and Clauss [136] have recently articulated evidence that sauropods used gut bacteria to break down the tough plant cell walls in order to release the nutritious contents of the cell. In this manner, sauropods avoided mastication entirely and used their teeth solely to snip off plant parts for consumption. This plant material was then swallowed whole and the gut flora then proceeded to use their own enzymes to break down the cell walls for the mutual benefit of both dinosaur and bacteria.

This mechanism totally avoided the slow process of mastication and allowed the sauropod to consume enormous amounts of plant material in a relatively short time scale. The limit of about 18 000 kg imposed by mastication was removed and the animals grew to much larger masses (on the order of 80 000 kg).

The long necks of sauropods were an integral part of its foraging strategy. No longer limited by mastication, they used their long necks to reach large quantities of food while minimizing the motion of their large bodies. The necks could be used both vertically (like a giraffe) and horizontally.

Having developed an extremely efficient digestive system, sauropods successfully competed with all other herbivores, allowing them to grow to very large size.

Sauropods might have been driven to very large size by the pressure due to predators. Size affords protection to a herbivore since the blows that large herbivores can strike against a predator are sufficiently large to be lethal. An adult African elephant has no natural predators (except for humans) because of this very effect. A male African elephant has a mass of about 5000 kg while lions have a mass of less than 200 kg, meaning that the male African elephant is 25 times more massive than the lion.

During the Mesozoic Era, the predators had also evolved to very large sizes. Different species of *Allosaurus*, the apex predators of Late Jurassic Period North America, had masses on the order of 2500 kg [115]. Using the same scaling factor of 25 between predator and prey, this yields a mass of about 60 000 kg for large sauropods of the Late Jurassic. Intriguingly, this was the typical mass of such animals, as recently reported by Benson *et al.* [137] for one of the largest Late Jurassic Period sauropods: *Brachiosaurus altithorax* (56 000 kg).

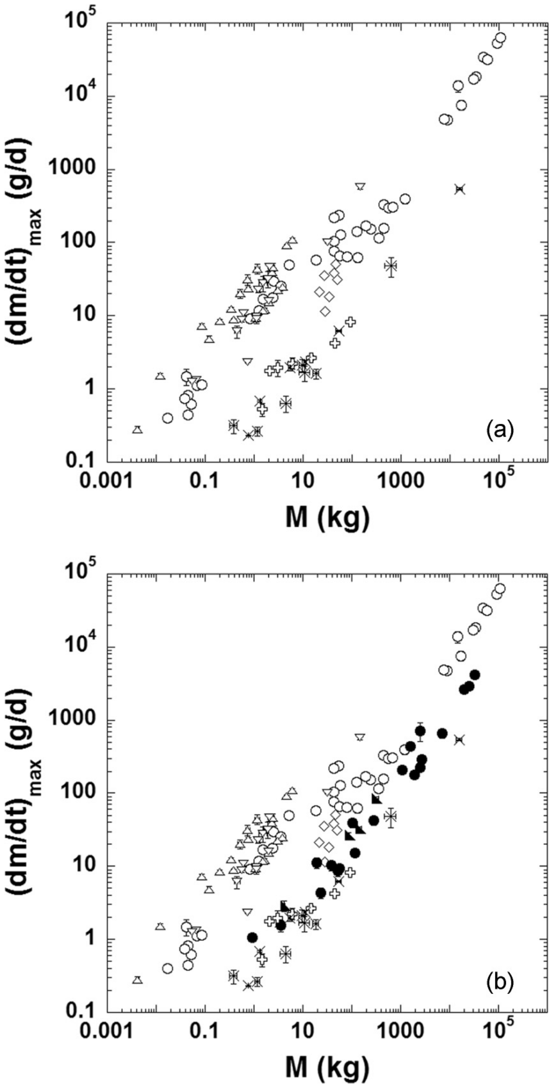

FIG. 9. Maximum growth rate. The maximum growth rate (in grams per day) as a function of asymptotic mass M (in kilograms) for (a) placental mammals (○), altricial birds (△), precocial birds (▽), marsupial mammals (◇), reptiles (open cross), and fish (×) and (b) placental mammals (○), altricial birds (△), precocial birds (▽), marsupial mammals (◇), reptiles (open cross), fish (×), extant mesotherms (solid triangle), and dinosaurs (●).

Finally, we turn to the issue of the maximum growth rate of the dinosaurs. Figure 9 shows the maximum growth rate as a function of asymptotic mass M. In Fig. 9(a) the maximum growth rate for the extant endotherms is seen to be roughly an order of magnitude greater than for extant ectotherms at all masses. This is consistent with the expectation that an animal with a higher metabolism grows at a faster rate. The marsupials, shown by the open diamonds (◇), show a slower maximum growth rate than the placental mammals and birds.

Figure 9(b) shows the maximum growth rate as a function of the asymptotic mass M for the same extant endotherms and ectotherms along with the results for four extant mesotherms (the echidna, the leatherback sea turtle, the Mako shark, and the tuna *Thunnus obesus*, all shown by solid triangles) and 20 species of dinosaurs (solid circles). We observe that the maximum growth rates of extant mesotherms and dinosaurs are between the observed maximum growth rates of extant endotherms and ectotherms. This result is the same as reported by Erickson *et al.* [7] and Grady *et al.* [10] and supports the idea that dinosaurs were mesotherms.

IV. SUMMARY

For the first time, the cellular metabolism of dinosaurs has been evaluated. The dinosaurs studied were *T. rex, D. torosus, G. libratus, A. fragilis, Citipati, Deinonychus, Troodon, O. philoceratops, C. rhodesiensis, S. deserti, A. lithographica, Apatosaurus,* a mamenchisaurid, *A. sanjuanensis, M. carinatus, P. engelhardti, T. tilletti, D. lettowvorbecki, M. peeblesorum,* and *P. mongoliensis*. The cellular metabolism for large dinosaurs is higher than expected on the basis of scaling arguments. This high metabolism suggests that the large dinosaurs were very efficient at deriving sustenance from their diet.

The organismal metabolic prefactor B_o of these dinosaurs is found to increase with size in the range observed in extant mesotherms, consistent with the results for the cellular metabolism.

The dinosaurs of this study came from both the Saurischia and Ornithischia branches of Dinosauria, arguing that the observed metabolic features were common to all dinosaurs.

The large sauropods are believed to have used gut bacteria for breaching the tough cell walls of the plants they consumed. Their small teeth were well equipped for biting off plant material which was then swallowed without mastication. Enzymatic action by their functional gut flora not only opened the individual plant cells but also fermented the less easily digested fiber. This "parallel processing" of their food allowed these animals to process enormous quantities of plant food quickly and efficiently. Their long neck also permitted very rapid browsing by being able to consume all food within reach without significant movement of their large bodies. By these mechanisms, the sauropods attained a high metabolism and rapid growth rate.

All other herbivorous dinosaurs had significant dental batteries for mastication of their plant diet. This is the same strategy observed in extant herbivores. Because of the constraint of having to masticate each parcel of food, this strategy limits the amount of food that such animals can consume in a day, and, therefore, ultimately limits the overall size of these dinosaurs. Their sizes fall within the range of the largest extant herbivores.

Though the results reported here are for the $\alpha = 2/3$ model, the same general trends are observed by using the $\alpha = 3/4$ model for these same animals: The large dinosaurs had high cellular and organismal metabolisms and all of the dinosaurs were mesotherms. However, the quality of the fits to the data are poorer for the $\alpha = 3/4$ model than for the $\alpha = 2/3$ model.

---

[1] S. Nicol and S. Andersen, Ecoscience **14**, 275 (2007).
[2] N. Mrosovsky and P. C. H. Pritchard, Copeia **1971**, 624 (1971).
[3] D. Barnal, K. Dickson, R. Shadwick, and J. Graham, Comp. Biochem. Physiol.ogy A **129**, 695 (2001).
[4] F. G. Carey and J. M. Teal, Comp. Biochem. Physiol. **28**, 199 (1969).
[5] F. G. Carey and J. M. Teal, Comp. Biochem. Physiol. **28**, 205 (1969).
[6] F. V. Paladino, M. P. OConnor, and J. R. Spotila, Nature **344**, 858 (1990).
[7] G. M. Erickson, K. C. Rogers, and S. A. Yerby, Nature **412**, 429 (2001).
[8] M. Sussman, *Growth and Development* (Prentice-Hall, New York, 1964).
[9] T. J. Case, Quart. Rev. Biol. **53**, 243 (1978).
[10] J. M. Grady, B. J. Enquist, E. Dettweiler-Robinson, N. A. Wright, and F. A. Smith, Science **344**, 1268 (2014).
[11] B. Gompertz, Philos. Trans. R. Soc. London **115**, 513 (1825).
[12] L. v. Bertalanffy, Arch. Entwicklungsmech **131**, 613 (1934).
[13] W. E. Ricker, Fish Physiol **8**, 677 (1979).
[14] M. Kleiber, Hilgardia **6**, 315 (1932).
[15] S. Brody, *Bioenergetics and Growth* (Reinhold, New York, 1945).
[16] K. A. Nagy, I. R. Girard, and T. K. Brown, Annu. Rev. Nutr. **19**, 247 (1999).
[17] V. Hayssen and R. C. Lacy, Comp. Biochem. Physiol. A **81**, 741 (1985).
[18] G. B. West, J. H. Brown, and B. J. Enquist, Science **276**, 122 (1997).
[19] G. B. West, J. H. Brown, and B. J. Enquist, in *Scaling in Biology*, edited by J. Brown and G. West (Oxford University Press, Oxford, 2000), pp. 87–122.
[20] P. S. Dodds, D. H. Rothman, and J. S. Weitz, J. Theor. Biol., **209**, 9 (2001).
[21] R. E. Ricklefs, Ecology **50**, 1031 (1969).
[22] G. B. West, J. H. Brown, and B. J. Enquist, Nature **413**, 628 (2001).
[23] A. H. Lee and S. Werning, Proc. Natl. Acad. Sci. USA **105**, 582 (2008).
[24] R. M. Alexander, *Dynamics of Dinosaurs and Other Extinct Giants* (Columbia University Press, New York, 1989).
[25] P. Christiansen, Gaia **14**, 45 (1997).
[26] P. Christiansen and R. A. Farina, Hist. Biol. **16**, 85 (2004).
[27] M. J. Wedel, *The Sauropods: Evolution and Paleobiology* (University of California Press, Berkeley, 2005), pp. 201–228.
[28] P. M. O'Connor, J. Morphol. **267**, 1199 (2006).
[29] D. M. Henderson, Paleobiology **25**, 88 (1999).
[30] F. Seebacher, J. Vertebr. Paleontol. **21**, 51 (2001).
[31] H. C. Gunga, K. Kirsch, J. Rittweger, L. Roecker, A. Clarke, J. Albertz, A. Wiedemann, S. Mokry, T. Suthau, A. Wehr, W. D. Heinrich, and H. P. Schultze., Mitteilungen aus dem Museum fur Naturkunde der Humboldt-Universitat Berlin, Geowissenschaftliche Reihe **2**, 91 (1999).
[32] J. F. Anderson, A. Hall-Martin, and D. A. Russell, J. Zool. (Lond.) **207**, 53 (1985).

[33] G. C. Cawley and G. J. Janacek, J. Zool. **280**, 355 (2010).

[34] J. R. Hutchinson, K. T. Bates, J. Molnar, V. Allen, and P. J. Makovicky, PLoS ONE **6**, e26037 (2011).

[35] G. M. Erickson and T. A. Tumanova, Zool. J. Linn. Soc.-Lond. **130**, 551 (2000).

[36] P. Dodson, J. Zool. Lond. **175**, 315 (1975).

[37] D. Carrier and L. R. Leon, J. Zool. Lond. **222**, 375 (1990).

[38] A. J. Martin, *Introduction to the Study of Dinosaurs*, 2nd ed. (Blackwell, Malden, MA, 2007).

[39] V. R. Dolnik, Zh. Obshch. Biol. **62**, 275 (2001).

[40] D. Deeming and G. Birchard, J. Zool. Lond. **271**, 78 (2007).

[41] E. Bianconi, A. Piovesan, F. Facchin, A. Beraudi, R. Casadei, F. Frabetti, L. Vitale, M. Pelleri, S. Tassani, S. Perez-Amodio, P. Strippoli, and S. Canaider, Ann. Hum. Biol. **40**, 463 (2013).

[42] M. E. Moses, C. Hou, W. H. Woodruff, G. B. West, J. C. Nekola, W. Zuo, and J. H. Brown, Am. Natur. **171**, 632 (2008).

[43] J. Werner and E. M. Griebeler, PLoS ONE **6** (2011), e28442.

[44] E. M. Griebeler and J. Werner, in *Biology of the Sauropod Dinosaurs: Understanding the Life of Giants*, edited by C. G. N. Klein, K. Remes and P. Sander (Indiana University Press, Bloomington, 2011), pp. 263–275.

[45] D. K. Zelenitsky, J. R. Horner, and F. Therrien, in *The Complete Dinosaur*, 2nd ed. (Indiana University Press, Bloomington, 2012), pp. 612–620.

[46] L. Chiappe, R. Coria, L. Dingus, F. Jackson, A. Chinsamy, and M. Fox, Nature **396**, 258 (1998).

[47] W. C. H. Green and A. Rothstein, Oecologia **86**, 521 (1991).

[48] R. M. Laws, East Afr. Wildlife J. **6**, 19 (1968).

[49] T. P. Jackson and R. J. van Aarde, J. Mammal. **84**, 851 (2003).

[50] A. Waldschmidt and E. Mueller, Comp. Biochem. Physiol. A **90**, 169 (1988).

[51] E. M. Derrickson, J. Mammal. **69**, 57 (1988).

[52] P. Jarman, Biol. Rev. Cambr. Philos. Soc. **58**, 485 (1983).

[53] W. L. Robinette, C. H. Baer, R. E. Pillmore, and C. E. Knittle, J. Wildlife Manag. **37**, 312 (1973).

[54] H. L. Anderson and P. C. Lent, J. Mammal. **58**, 53 (1977).

[55] G. L. Smuts, G. A. Robinson, and I. J. Whyte, J. Zool. Lond. **190**, 365 (1980).

[56] A. Vargas and S. H. Anderson, Am. Midl. Nat. **135**, 43 (1996).

[57] O. J. Rongstad, J. Wildlife Manag. **30**, 114 (1966).

[58] J. W. Laundre and L. Hernandez, J. Wildlife Manag. **66**, 849 (2002).

[59] J. Grobler, Koedoe, African Protected Area Conservation and Science **25**, 117 (1982).

[60] G. A. Heidt, M. K. Peterson, and G. L. Kirkland, J. Mammal. **49**, 413 (1968).

[61] S. G. Brown and C. H. Lockyer, *Antarctic Ecology* (Academic Press, London, 1984), Chap. 13, pp. 717–781.

[62] R. M. Laws, *Antarctic Ecology* (Academic Press, London, 1984), Chap. 12, pp. 621–715.

[63] P. Prestrud and K. Nilssen, J. Mammal. **76**, 522 (1995).

[64] H. C. Cheng and L. L. Lee, J. Mammal. **83**, 785 (2002).

[65] G. R. Bortolotti, Wilson Bull. **96**, 524 (1984).

[66] J. S. Coleman and J. D. Fraser, J. Field Ornithol. **60**, 197 (1989).

[67] G. H. F. Seixas and G. Mourao, Ornitol. Neotrop. **14**, 295 (2003).

[68] K. D. Whitmore and J. M. Marzluff, J. Wildlife Manag. **62**, 1460 (1998).

[69] R. Weaver, Auk **54**, 103 (1937).

[70] J. M. Starck and E. Sutter, J. Avian Biol. **31**, 527 (2000).

[71] R. M. Zink and J. T. Klicka, Wilson Bull. **102**, 514 (1990).

[72] S. E. Koenig, Bird Conserv. Int. **11**, 205 (2001).

[73] F. Fowler, Condor **33**, 193 (1931).

[74] K. A. Muller, Wilson Bull. **83**, 186 (1971).

[75] G. D. Constantz, Auk **97**, 622 (1980).

[76] B. Kessel, Am. Midl. Natur. **58**, 257 (1957).

[77] J. W. Parker, Condor **78**, 557 (1976).

[78] Y. Elhashmi, O. Arabi, T. Taha, and O. Eidam, Online J. Anim. Feed Res. **1**, 417 (2011).

[79] J. L. Navarro, P. E. Vignolo, M. R. Demaria, N. O. Maceira, and M. B. Martella, Arch. Gefluegelkd **69**, 90 (2005).

[80] P. Tholon and S. A. Queiroz, Rev. Bras. Cienc. Avic. **9**, 0 (2007).

[81] T. Pis, Comp. Biochem. Physiol. A **136**, 757 (2003).

[82] K. J. Reinecke, Auk **96**, 737 (1979).

[83] B. W. Cain, Condor **78**, 124 (1976).

[84] J. S. Sedinger, Condor **88**, 169 (1986).

[85] T. Pis and D. Lusnia, Comp. Biochem. Physiol. A **140**, 101 (2005).

[86] L. A. Bell, J. C. Pitman, M. A. Patton, D. H. Wolfe, S. K. Sherrod, and S. D. Fuhlendorf, Wilson J. Ornithol. **119**, 386 (2007).

[87] A. E. Aubin, E. H. Dunn, and C. D. MacInnes, Condor **88**, 365 (1986).

[88] M. C. Ribot-Carballal, F. Galvan-Magana, and C. Quinonez-Velaquez, Fish. Res. **76**, 14 (2005).

[89] J. H. Farley, N. P. Clear, B. Leroy, T. L. O. Davis, and G. McPherson, Marine. Freshwater Res. **57**, 713 (2006).

[90] K. M. Liu, M. L. Lee, S. J. Joung, and Y. C. Chang, Fish. Res. **95**, 154 (2009).

[91] C. M. Duarte and M. Alcaraz, Oecologia **80**, 401 (1989).

[92] S. J. Joung, Y. Y. Liao, and C. T. Chen, Fish. Res. **70**, 83 (2004).

[93] J. G. Pajuelo and J. M. Lorenzo, Fish. Res. **59**, 93 (2002).

[94] O. O. F. Weyl and A. J. Booth, Environ. Biol. **55**, 215 (1999).

[95] S. J. Newman, M. Cappo, and D. M. Williams, Fish. Res. **48**, 1 (2000).

[96] J. G. Diaz-Uribe, J. F. Elorduy-Garay, and M. T. Gonzalez-Valdovinos, Pacific Sci. **55**, 171 (2001).

[97] A. J. Booth, G. S. Merron, and C. D. Buxton, Environ. Biol. Fish. **43**, 171 (1995).

[98] S. P. Wintner, Environ. Biol. Fish. **59**, 441 (2000).

[99] I. Everson, *Antarctic Ecology* (Academic Press, London, 1984), Chap. 7, p. 491–532.

[100] D. B. Jepsen, K. O. Winemiller, D. C. Taphorn, and D. R. Olarte, J. Fish Biol. **55**, 433 (1999).

[101] R. J. Laver, D. Purwandana, A. Ariefiandy, J. Imansyah, D. Forsyth, C. Ciofi, and T. S. Jessop, PLoS ONE **7**, 0045398 (2012).

[102] S. J. Gorzula, Oecologia (Berl.) **35**, 21 (1978).

[103] V. de Buffrenil and G. Hemery, J. Herpetol. **36**, 419 (2002).

[104] T. Madsen and R. Shine, J. Anim. Ecol. **69**, 952 (2000).

[105] D. Wilson, R. Heinsohn, and J. Wood, J. Zool. **270**, 399 (2006).

[106] D. Frynta, P. Frydlova, J. Hnizdo, O. Simkova, V. Cikanova, and P. Velensky, Zool.al Sci. **27**, 917 (2010).

[107] G. M. Erickson, Trends Ecol. Evol. **20**, 677 (2005).

[108] G. M. Erickson, K. C. Rogers, D. J. Varricchio, M. A. Norrell, and X. Xu, Biol. Lett. **3**, 558 (2007).

[109] T. M. Lehman and H. N. Woodward, Paleobiology **34**, 264 (2008).

[110] G. M. Erickson, O. W. M. Rauhut, Z. Zhu, A. H. Turner, B. D. Inouye, D. Hu, and M. A. Norell, PLoS ONE **4**, 0007390 (2009).

[111] T. R. Hübner, PLoS ONE **7**, 0029958 (2012).

[112] E. M. Griebeler, N. Klien, and P. M. Sander, PLoS ONE **8**, 0067012 (2013).

[113] D. M. Henderson and E. Snively, Proc. Roy. Soc. Lond. B (Suppl.) **271**, S57 (2004).

[114] F. Therrien and D. M. Henderson, J. Vertebr. Paleontol. **27**, 108 (2007).

[115] G. S. Paul, *The Princeton Field Guide to Dinosaurs* (Princeton University Press, Princeton, NJ, 2010).

[116] H. C. Gunga, T. Suthau, A. Bellmann, A. Friedrich, T. Schwanebeck, S. Stoinski, T. Trippel, K. Kirsch, and O. Hellwich, Naturwissenschaften **94**, 623 (2007).

[117] D. J. Varricchio, J. R. Moore, G. M. Erickson, M. A. Norell, F. D. Jackson, and J. J. Borkowski, Science **322**, 1826 (2008).

[118] J. R. Spotila, M. P. OConnor, P. Dodson, and F. V. Paladino, Mod. Geol. **16**, 203 (1991).

[119] G. S. Paul, *Predatory Dinosaurs of the World* (Simon & Schuster, New York, 1988).

[120] R. J. Butler, J. Liyong, C. Jun, and P. Godefroit, Palaeontology **54**, 667 (2011).

[121] M. J. Benton, The Dinosauria*, 2nd.* (University of California Press, Berkeley, 2002), Chap. 1, p. 7–19.

[122] M. F. Bonnan, Paleobiology **30**, 444 (2004).

[123] B. M. Kilbourne and P. J. Makovicky, J. Anat. **217**, 135 (2010).

[124] M. Erecinska, S. Cherian, and I. A. Silver, Progr. Neurobiol. **73**, 397 (2004).

[125] R. F. Schmidt, *Integrative Functions of the Central Nervous System*, edited by R. F. Schmidt and G. Thews (Springer-Verlag, Berlin, 1989), pp. 124–165.

[126] J. Karbowski, BMC Biol. **5**, 18 (2007).

[127] G. A. Thibodeau, *Anthonys Textbook of Anatomy and Physiology*, 13th ed. (Mosby College, St. Louis, 1990), p. 616.

[128] J. G. Herndon, J. Tigges, D. C. Anderson, S. A. Klumpp, and H. M. McClure, Comp. **409**, 567 (1999).

[129] N. R. Owen-Smith, *Megaherbivores: The Influence of Very Large Body Size on Ecology* (Cambridge University Press, New York, 1988).

[130] J. A. Wilson and P. C. Sereno, Soc. Vertebr. Paleontol. Memoir **5**, 1 (1998).

[131] N. E. Campione and D. C. Evans, PLoS ONE **6**, 0025186 (2011).

[132] W. Janensch, Palaentogr. Suppl. **7**, 137 (1929).

[133] J. O. Farlow, Paleobiology **13**, 60 (1987).

[134] F. Sanders, K. Manley, and K. Carpenter, *Gastroliths from the Lower Cretaceous sauropod Cedarosaurus weiskofpae*, edited by D. H. Tanke and K. Carpenter (Indiana University Press, Bloomington, 2001), pp. 166–180.

[135] O. Wings and P. M. Sander, Proc. Roy. Soc. B: Biol. Sci. **274**, 635 (2007).

[136] J. Hummel and M. Clauss, *Biology of the Sauropod Dinosaurs: Understanding the Life of Giants*, edited by N. Klein, K. Remes, C. T. Gee, and P. M. Sander (Indiana University Press, Bloomington, 2011), 11–33.

[137] R. B. J. Benson, N. E. Campione, M. T. Carrano, P. D. Mannion, C. Sullivan, P. Upchurch, and D. C. Evans, PLoS Biol. **12**, 1001853 (2014).