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Embryonic metabolism of the ornithischian dinosaurs *Protoceratops andrewsi* and *Hypacrosaurus stebingeri* and implications for calculations of dinosaur egg incubation times

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The embryonic metabolisms of the ornithischian dinosaurs *Protoceratops andrewsi* and *Hypacrosaurus stebingeri* have been determined and are in the range observed in extant reptiles. The average value of the measured embryonic metabolic rates for *P. andrewsi* and *H. stebingeri* are then used to calculate the incubation times for 21 dinosaurs from both Sauischia and Ornithischia using a mass growth model based on conservation of energy. The calculated incubation times vary from about 70 days for *Archaeopteryx lithographica* to about 180 days for *Alamosaurus sanjuanensis*. Such long incubation times seem unlikely, particularly for the sauropods and large theropods. Incubation times are also predicted with the assumption that the saurischian dinosaurs had embryonic metabolisms in the range observed in extant birds.

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I. INTRODUCTION

Erickson *et al.* [1] have published the first direct measurement of the incubation time of nonavian dinosaur eggs by studying the daily growth of teeth in close to hatching fossilized dinosaur embryos. They found incubation times of 83 and 171 days for the ornithischian dinosaurs *Protoceratops andrewsi* and *Hypacrosaurus stebingeri*, respectively. Such long incubation times are in the range found for similarly sized eggs of extant reptiles rather than extant birds [2]. This result is surprising since a number of attributes related to avian reproduction have been observed in extinct dinosaurs [3], including asymmetric eggs [4–6], egg shell structure [7,8], brooding [9–14], and medullary bone [15]. These observations had led to the suggestion that the high embryonic metabolism of extant birds was present in nonavian dinosaurs. A close connection to extant birds is consistent with the fact that they are living dinosaurs [16,17]. The work of Erickson *et al.* [1] suggests that the extant sister taxon Crocodylia is a better model for embryonic development in ornithischian nonavian dinosaurs than extant birds.

The incubation times of extant reptiles are longer than observed in extant birds [2,18]. Twelve extant members of Crocodylia have an incubation time of 84.8 ± 9.1 days (mean and standard deviation) with a minimum of 68 and a maximum of 99 days [19–29]. Very long incubation times are present in species of *Varanus*. Their incubation time is 175.3 ± 55.6 days with a minimum of 98 and a maximum of 272 days [30–37]. However, the animals of *Varanus* have masses less than 100 kg and do not lay eggs in nesting colonies. Hiding their individual egg clutches lowers the probability of egg predation.

The degree of relevance of these ornithischian incubation times for the dinosaurs of Saurischia is unclear. The split between Ornithischia and Saurischia is believed to have happened between about 228 and 216.5 million years ago (Ma) [38]. Several lines of evidence suggest that postcranial pneumaticity and air sac lung function were primitive for Saurischia [39,40]. These are associated with a unidirectional breathing system which is highly efficient at extracting oxygen. Postcranial pneumaticity is not observed in any ornithischians. These results suggest that the metabolism of saurischians might have been different than ornithischians. It should also be noted that extant birds evolved from the theropod clade Paraves. The fact that birds (members of Avialae) first appeared about 165 Ma shows that at least some saurischians had elevated metabolisms perhaps as early as the Middle Jurassic [41,42].

Nesting colonies in extant birds provide mutual defense since multiple adults are surveying the surroundings at all times. Consequently, it is likely that any predator preying upon eggs would be detected and then pursued by adults. Nesting colonies have the disadvantage that they cannot be hidden and, therefore, attract predators. Also, since a large number of adults are restricted to the same general area, the area surrounding the colony will have to provide sustenance for all of the adults during the incubation of the eggs.

Dinosaur eggs have been the subject of many studies [1,43–55]. The rapid avian incubation has been assumed for nonavian dinosaurs [45,50,53,55], particularly for dinosaurs nesting in colonies such as the sauropod *Saltosaurus* [56]. The food requirements of the large sauropods would have placed a great stress on the surrounding area. Minimizing the incubation time by a high embryonic metabolism would have helped with the food requirement.

The incubation time of an egg is determined by the mass of the newly hatched animal and its embryonic metabolism. In an earlier work [55], a general model for the calculation of the incubation time of any egg based on conservation of energy was developed. Since no data existed for the embryonic metabolism of dinosaurs, an embryonic metabolic rate determined from extant birds was used. The embryonic metabolism of several species of Crocodylia were calculated and found to be much lower than observed in extant birds.

In this paper, the model of Ref. [55] is used to determine the embryonic metabolic rates of the dinosaurs *P. andrewsi* and *H. stebingeri* from the data of Erickson *et al.* [1]. These results are compared to the embryonic metabolic rates of extant birds and reptiles (including crocodylians).

The embryonic metabolic rates determined for *P. andrewsi* and *H. stebingeri* are then used to calculate the incubation times of the dinosaurs of Ref. [55]. These dinosaurs include animals from Theropoda, Prosauropoda, Sauropodomorpha, Ornithopoda, and Ceratopsia and come from both the

Saurischia and Ornithischia branches of Dinosauria. The resulting incubation times for the saurischians are found to be very long, particularly for the sauropods. Consequently, a higher metabolic rate for the saurischians is used to calculate their incubation times and the significance of these results are discussed.

Pioneering studies of metabolism were first reported by Kleiber [57] and Brody [58]. They showed that the organismal metabolic rate, B, for juveniles and adults in extant animals is related to the mass of the adult animal, M, via a power law:

$$B = B_o M^{\alpha}, \tag{1}$$

where B_o is the metabolic prefactor (units of W/kg^{α}) and they reported $\alpha = 3/4$. The fact that the metabolism is related to the mass for all taxa via a universal power law shows the imprint of the underlying physical mechanism limiting the biological variability.

Subsequent work has called the value of α into question [57–64]. Dodds *et al.* [63] reviewed a number of studies and found significant empirical support for $\alpha = 2/3$. West *et al.* [61,62] have argued that the exponent α is 3/4 due to the self-similar fractal nature of the arterial system.

In an earlier analysis of juvenile growth of dinosaurs [65], $\alpha = 2/3$ was used. However, Ref. [55] showed that $\alpha = 3/4$ yields a superior fit to the experimental data for embryonic growth in extant birds and reptiles. Consequently, in the current work, analysis will be performed using $\alpha = 3/4$.

Seymour *et al.* [64] recently reported that $\alpha = 0.83$ for specimens of *Crocodylus porosus* of different sizes. The masses of these animals ranged from 0.19 to 389 kg. However, their data indicated that α decreased for animals with masses between 291 and 389 kg. This calls into question the applicability of $\alpha = 0.83$ for animals with masses above 300 kg. Since these animals are members of Crocodylia, a taxon closely related to Dinosauria, our analysis will also be performed with $\alpha = 0.83$.

II. MODEL

Grady *et al.* [66] and Lee [65] developed models of the mass growth of animals based on conservation of energy in order to evaluate the metabolism of dinosaurs. Lee [55] extended that model to the growth of embryos. In this approach, the total metabolism, B, of the animal during growth is assumed to provide the necessary power to its cells plus the power needed to create new cells:

$$B = N_c B_c + E_c \frac{dN_c}{dt}. \tag{2}$$

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. (2) 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 the growth of the embryo. 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.* [67] 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.* [68] have determined that the energy required to produce 1 kg of biomass (E_c/m_c) is the same in all animals and is equal to $(5.774 \pm 0.097) \times 10^6$ J/kg. Combining these results yields $E_c = (1.09 \pm 0.24) \times 10^{-5}$ J.

The growth of the animal is characterized by its total mass $m(t)$ at time t. Note that $N_c = m/m_c$ and, as discussed earlier, $B = B_o m^{\alpha}$ with $\alpha = 3/4$ or 0.83.

The solution of Eq. (2) is discussed in Refs. [55,65]. The expression for the mass of the animal as a function of time t, $m(t)$ is given by

$$m(t) = M\left\{1 - \left[1 - \left(\frac{m_o}{M}\right)^{(1-\alpha)}\right] e^{-\frac{(1-\alpha)pt}{M^{(1-\alpha)}}}\right\}^{\left(\frac{1}{1-\alpha}\right)}, \tag{3}$$

where m_o is the initial mass of the animal [either the mass of the fertilized ovum (6.4 mg) [66] for an embryo or the hatchling/birth mass for a juvenile], M is the final adult mass and the metabolic mass gain parameter $p = m_c B_o/E_c$. In this manner, the metabolic prefactor B_o can be determined by fitting the mass growth data for either an embryo or a juvenile.

To determine the incubation time, Eq. (3) is solved for the hatching time t_h when the developing embryo has reached its hatching mass m_h. In this case, the initial mass m_o is the mass of a fertilized ovum (6.4 mg) and M is the final mass of the adult animal. Inverting Eq. (3) for the incubation time t_h yields

$$t_h = \frac{E_c M^{(1-\alpha)}}{(1-\alpha) m_c B_o} ln\left[\frac{1 - \left(\frac{m_o}{M}\right)^{(1-\alpha)}}{1 - \left(\frac{m_h}{M}\right)^{(1-\alpha)}}\right]. \tag{4}$$

Equation (4) can be solved for the metabolic prefactor B_o in order to determine the metabolism of an embryo based on its incubation time t_h, the initial mass of the fertilized ovum m_o, its mass at the time of hatching m_h, and its adult mass M:

$$B_o = \frac{E_c M^{(1-\alpha)}}{(1-\alpha) m_c t_h} ln\left[\frac{1 - \left(\frac{m_o}{M}\right)^{(1-\alpha)}}{1 - \left(\frac{m_h}{M}\right)^{(1-\alpha)}}\right]. \tag{5}$$

Equation (5) allows one to determine the embryonic prefactor B_o without the mass growth data.

TABLE I. Embryonic metabolism of *Protoceratops andrewsi* and *Hypacrosaurus stebingeri* for $\alpha = 3/4$. The species, the mass of the egg m_{egg} (measured in kg), the mass of the hatchling m_h (measured in kg), the adult mass M (measured in kg), the observed incubation period t_h^{obs} (measured in days), and the calculated metabolic prefactor B_o (measured in $W/kg^{3/4}$) are given. The mass of the eggs and the observed incubation times are from Ref. [1]. The adult masses M of *P. andrewsi* and *H. stebingeri* are from Refs. [164] and [165], respectively.

Species	m_{egg} (kg)	m_h (kg)	M (kg)	t_h^{obs}(d)	$B_o(W/kg^{3/4})$
Protoceratops andrewsi	0.194	0.136	180 ± 25	83	1.98 ± 0.10
Hypacrosaurus stebingeri	4.251	2.976	4000 ± 560	171	2.17 ± 0.11

TABLE II. Metabolisms of extant birds, extant reptiles and dinosaurs. The mean metabolic prefactor B_o (determined from mass growth data) and its standard deviation for different groups of animals are given. [a]The results for the embryonic metabolism of dinosaurs are derived from the data of Erickson *et al.* [1].

$\alpha = 3/4$ group	Juvenile $B_o(W/kg^{3/4})$	Embryonic $B_o(W/kg^{3/4})$
Extant birds	13.07 ± 6.96	4.82 ± 0.99
Extant reptiles	0.311 ± 0.149	1.69 ± 0.76
Extinct dinosaurs	0.642 ± 0.313	2.08 ± 0.13[a]
$\alpha = 0.83$ group	Juvenile $B_o(W/kg^{0.83})$	Embryonic $B_o(W/kg^{0.83})$
Extant crocodylians	0.339 ± 0.179	2.67 ± 0.19
Extinct dinosaurs	0.828 ± 0.636	3.18 ± 0.28[a]

III. RESULTS AND DISCUSSION

Erickson *et al.* [1] have reported incubation times of 83 and 171 days, respectively, for the ornithischian dinosaurs *P. andrewsi* and *H. stebingeri*. They also report the masses of the nearly hatched eggs to be 0.194 and 4.251 kg for *P. andrewsi* and *H. stebingeri*, respectively. Deeming and Birchard [69] have determined that the mass of a newly hatched bird, m_h, is 70% of the egg mass. We assume that this relationship is valid for nonavian dinosaurs also. Table I gives the data used for the calculation of the embryonic metabolisms of these two dinosaurs via Eq. (5) with $\alpha = 3/4$. The average metabolic prefactor B_o for *P. andrewsi* and *H. stebingeri* is 2.08 ± 0.13 $W/\text{kg}^{3/4}$.

Lee [55] showed that the embryonic metabolic prefactor B_o has a standard deviation of about 20% for extant birds and mammals. Greater variability should be expected for reptiles because of the larger temperature fluctuations. The fact that the two embryonic metabolisms derived for *P. andrewsi* and

TABLE III. Juvenile metabolism and predicted incubation times of dinosaurs. The adult mass M (in kg), the initial mass m_o at time of hatching (in kg), the metabolic prefactor B_o (in $W/\text{kg}^{3/4}$) for $\alpha = 3/4$ and the predicted incubation times t_h^{pre} (in days) for the dinosaurs of this study. The values of α are given for the relevant columns. [a]The average metabolic prefactor B_o of ornithischian dinosaurs *P. andrewsi* and *H. stebingeri* (2.08 $W/\text{kg}^{3/4}$) for $\alpha = 3/4$ was used to calculate the incubation times for all of the dinosaurs. [b]The average metabolic prefactor B_o of ornithischian dinosaurs *P. andrewsi* and *H. stebingeri* (3.18 $W/\text{kg}^{0.83}$) was used to calculate the incubation times for all of the dinosaurs for $\alpha = 0.83$. [c]For $\alpha = 3/4$, the average metabolic prefactor B_o of ornithischian dinosaurs *P. andrewsi* and *H. stebingeri* (2.08 $W/\text{kg}^{3/4}$) was used to calculate the incubation times for the ornithischian dinosaurs while a higher metabolic prefactor $B_o = 4.82$ $W/\text{kg}^{3/4}$ (the value observed in extant birds) was used to calculate the incubation times for the saurischian dinosaurs. [d]The hatchling mass m_h of *Rapetosaurus krausei* has been reported by Curry Rogers *et al.* [148]. The adult mass M of this sauropod was calculated by using the result of Deeming and Birchard [69] to relate the hatching mass m_h to the mass of the egg, m_{egg}, and then the result of Dolnik [166] was used to relate m_{egg} to the adult mass M.

Species	M (kg)	m_o (kg)	juvenile B_o ($W/\text{kg}^{3/4}$) $\alpha = 3/4$	t_h^{pre} (d) $\alpha = 3/4$ Ornith. ave.[a]	t_h^{pre} (d) $\alpha = 0.83$ Ornith. ave.[b]	t_h^{pre} (d) $\alpha = 3/4$ split[c]
Theropoda						
Tyrannosaurus rex	7000 ± 980	2.06 ± 0.13	0.612 ± 0.061	159 ± 39	144 ± 35	69 ± 17
Daspletosaurus torosus	2700 ± 378	1.33 ± 0.09	0.580 ± 0.070	144 ± 35	135 ± 33	62 ± 15
Gorgosaurus libratus	2500 ± 350	1.28 ± 0.08	0.449 ± 0.045	142 ± 35	134 ± 33	61 ± 15
Allosaurus fragilis	1930 ± 270	1.17 ± 0.07	0.388 ± 0.039	139 ± 34	132 ± 32	60 ± 14
Citipati osmolskae	105 ± 15	0.298 ± 0.019	0.713 ± 0.088	102 ± 25	109 ± 26	44 ± 11
Deinonychus antirrhopus	57.0 ± 8.0	0.225 ± 0.014	0.315 ± 0.056	96 ± 23	105 ± 25	41 ± 10
Troodon formosus	52.0 ± 7.3	0.215 ± 0.014	0.284 ± 0.030	95 ± 23	104 ± 25	41 ± 10
Oviraptor philoceratops	39.0 ± 5.5	0.189 ± 0.012	0.139 ± 0.026	92 ± 22	102 ± 25	40 ± 10
Coelophysis rhodesiensis	19.0 ± 2.7	0.136 ± 0.009	0.830 ± 0.101	86 ± 21	98 ± 24	37 ± 9
Shuvuuia deserti	3.5 ± 0.5	0.0623 ± 0.0040	0.364 ± 0.055	74 ± 18	90 ± 22	32 ± 8
Archaeopteryx lithographica	0.93 ± 0.13	0.0339 ± 0.0022	0.528 ± 0.060	66 ± 16	86 ± 21	29 ± 7
Prosauropoda						
Plateosaurus engelhardti	1600 ± 224	1.04 ± 0.07	3.74 ± 0.57	136 ± 33	130 ± 32	58 ± 14
Massospondylus carinatus	340 ± 48	0.511 ± 0.033	0.391 ± 0.039	115 ± 28	117 ± 28	50 ± 12
Sauropoda						
Alamosaurus sanjuanensis	32,600 ± 4,600	4.17 ± 0.27	1.34 ± 0.15	189 ± 46	161 ± 39	81 ± 20
mamenchisaurid	25,100 ± 3,500	3.70 ± 0.24	3.26 ± 0.32	183 ± 45	158 ± 38	79 ± 19
Rapetosaurus krausei[d]	20,500 ± 2,800	3.40 ± 0.21	-	180 ± 44	156 ± 38	77 ± 19
Apatosaurus	20,000 ± 2,800	3.33 ± 0.21	1.40 ± 0.22	179 ± 43	156 ± 38	77 ± 19
Ornithopoda						
Maiasaura peeblesorum	2500 ± 350	1.28 ± 0.08	1.36 ± 0.39	142 ± 35	134 ± 33	142 ± 35
Tenontosaurus tilletti	1080 ± 151	0.870 ± 0.056	0.678 ± 0.057	130 ± 32	127 ± 31	130 ± 32
Dysalotosaurus lettowvorbecki	115 ± 16	0.310 ± 0.020	0.270 ± 0.027	103 ± 25	109 ± 27	103 ± 25
Ceratopsia						
Psittacosaurus mongoliensis	23.0 ± 3.2	0.148 ± 0.010	0.282 ± 0.034	88 ± 21	100 ± 24	88 ± 21

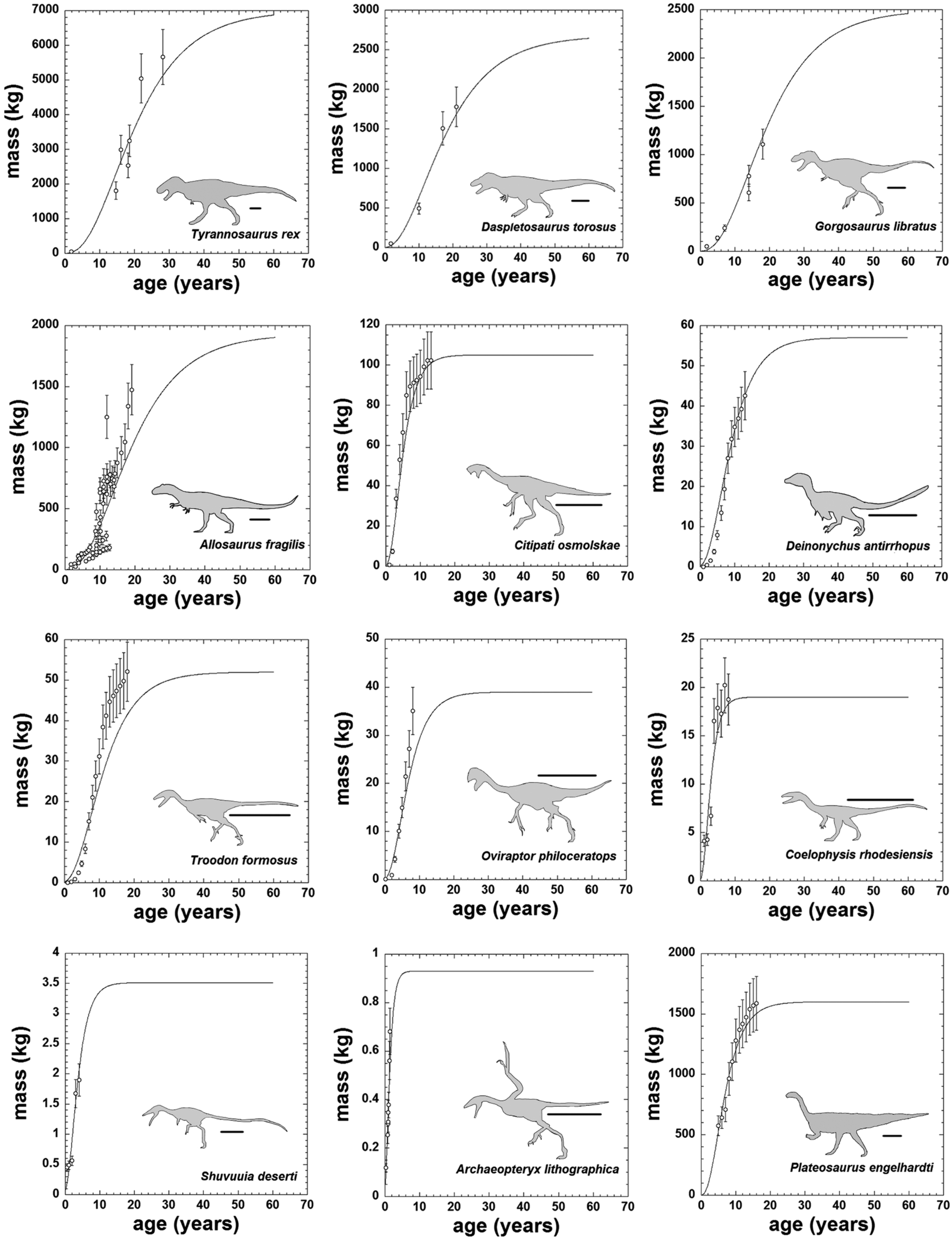

FIG. 1. Mass growth of dinosaurs I. Mass (in kilograms) as a function of age (in years). The data are shown by the open circles (o) and the theoretical fits via Eq. (3) are shown by the solid line. The scale bar beside each dinosaur is 1 m long except for *Shuvuuia deserti* and *Archaeopteryx lithographica* whose scale bar is 0.1 m long.

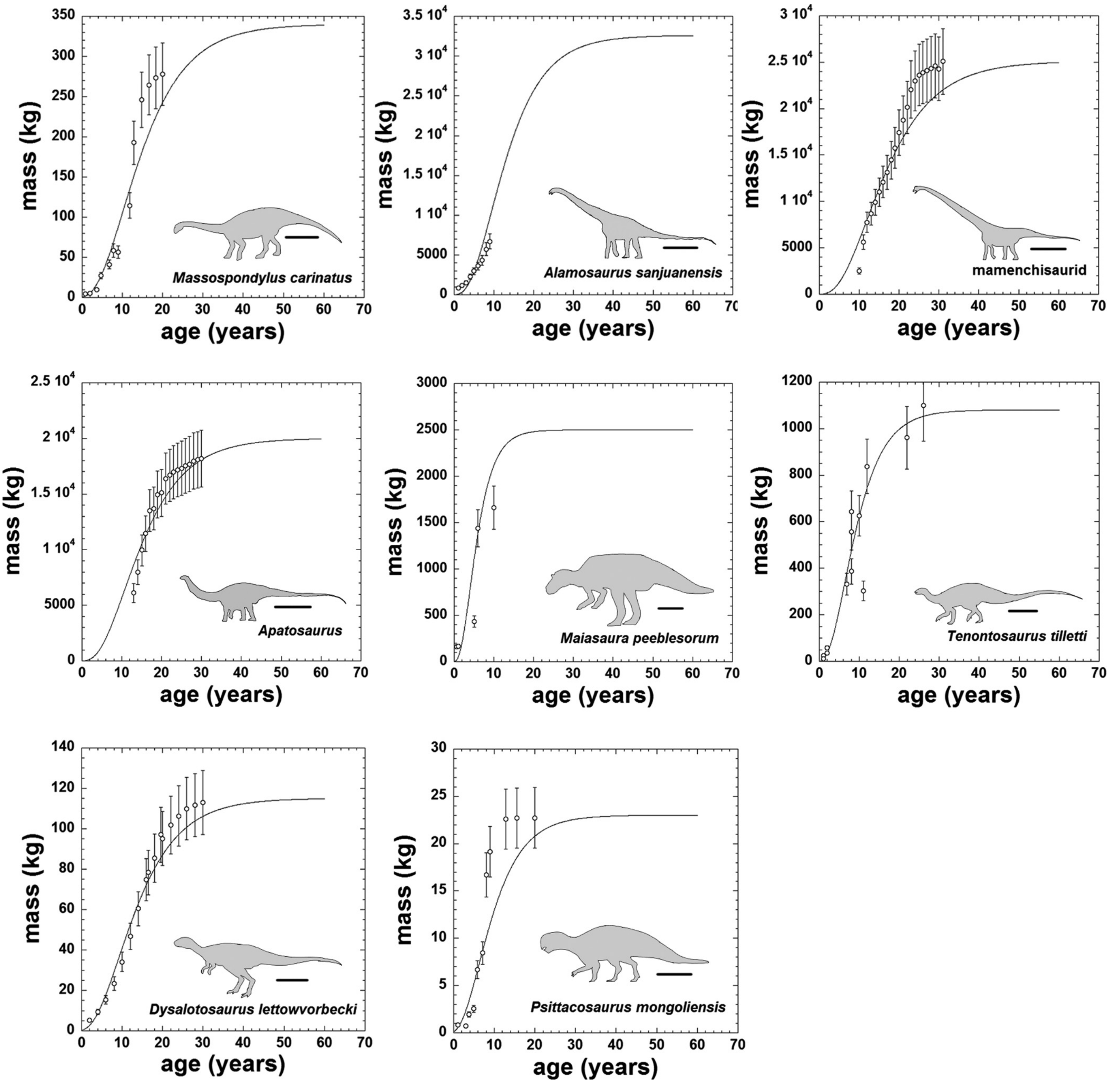

FIG. 2. Mass growth of dinosaurs II. Mass (in kilograms) as a function of age (in years). The data are shown by the open circles (o) and the theoretical fits via Eq. (3) are shown by the solid line. The scale bar beside each dinosaur is 1 m long except for *Apatosaurus*, the mamenchisaurid, and *Alamosaurus sanjuanensis* for whom the scale bar is 5 m long and *Psittacosaurus mongoliensis* for whom the scale bar is 0.3 m long.

H. stebingeri differ by only about 10 % is most likely a statistical fluctuation rather than evidence that all ornithischian dinosaurs had a B_o of about 2 $W/\mathrm{kg}^{3/4}$ while embryos.

Before discussing the significance of this measurement of embryonic metabolism in dinosaurs, let us examine the embryonic and juvenile metabolisms of extant birds and reptiles. Table I of Ref. [55] gives the embryonic metabolism of extant birds and crocodilians for $\alpha = 3/4$ and those results will be used in this analysis.

Mass growth data during the juvenile phase for 29 birds [70–92], 12 reptiles [93–102], and 20 dinosaurs [65] were analyzed [14,93,103–116] using Eq. (3) in order to determine their juvenile metabolic prefactor B_o. Mass growth data during the embryonic phase for 30 birds [117–130] and five reptiles [131–134] were analyzed using Eq. (3) in order to determine their embryonic metabolic prefactor B_o. The average results for these groups are given in Table II and the individual results for the dinosaurs are listed in Table III. Figures 1 and 2 show the mass growth data and fits with Eq. (3) using $\alpha = 3/4$ for the 20 juvenile dinosaurs of this study. The values of M and m_o were fixed and are listed in Table III.

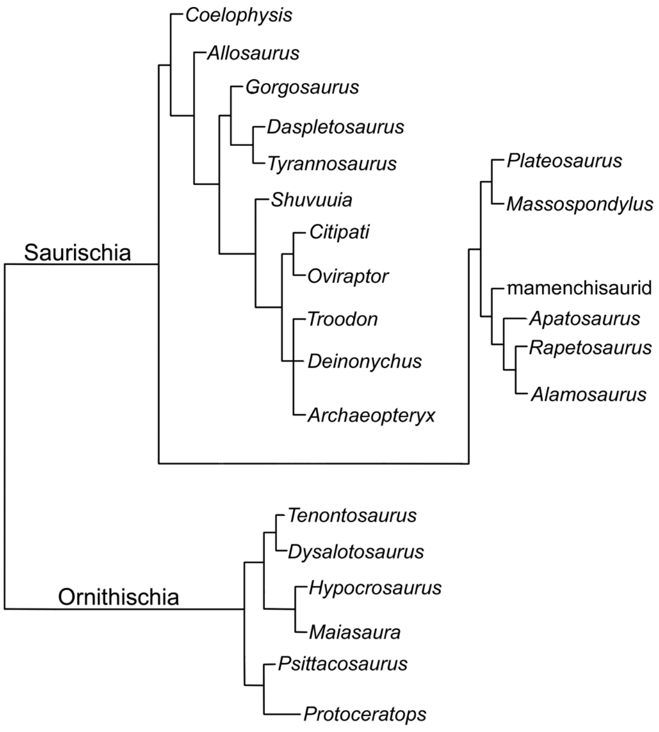

FIG. 3. Cladogram of the dinosaurs of Table III.

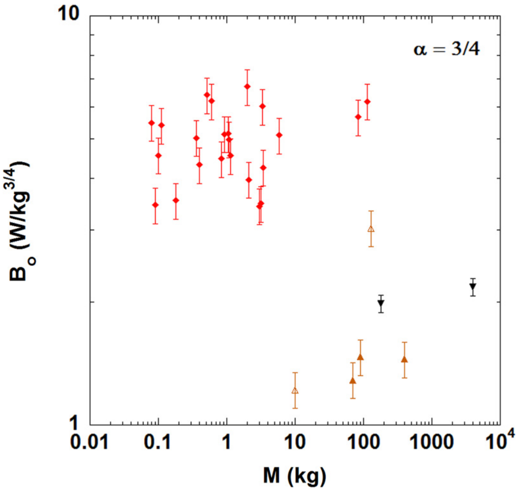

FIG. 4. Embryonic metabolism of the animals of this study for $\alpha = 3/4$. The embryonic metabolic prefactor B_o is shown as a function of the adult mass M of the animals. Birds are shown with the solid diamonds, members of Crocodylia are shown with the upward-pointing solid triangles, other reptiles by the upward-pointing open triangles and dinosaurs are shown with downward-pointing solid triangles. The results for the birds and reptiles were determined via Eq. (3) while the results for the dinosaurs (*Protoceratops andrewsi* and *Hypacrosaurus stebingeri*) were derived from the incubation times reported in Ref. [1].

The difficulties associated with determining the mass growth curves of extinct animals, including dinosaurs, have been discussed in Ref. [65]. These include the variability in growth due to genetic and environmental differences. For extant animals, data can be obtained from a large number of animals in order to obtain the average growth curve. Even with such data, the adult mass M of the animal will have significant uncertainty. For instance, the average mass of a nonpregnant adult female African elephant (*Loxodonta africana*) is 2658 ± 263 kg [93]. The fits for *Troodon* and *Oviraptor* would be improved if a higher adult mass M were used.

The scarcity of dinosaur fossils frequently limits the number of specimens, increasing the uncertainty in the mass measurements. Reconstructing the mass of a partial skeleton usually involves the assumption that the mass of the animal scales as the cube of the femoral length [103]. This assumption has been tested in only a limited number of extant animals [135,136].

The data for *Allosaurus* has the possible problem of being derived from more than one species, as described by Lee and Werning [93].

The age of the juvenile dinosaur is usually determined by counting the 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 [137]. However, in certain circumstances, resorption of bone can obliterate a LAG, giving an age which is too young.

The cladogram of the dinosaurs of this study is shown in Fig. 3 [38,138–147]. Note that there are no direct measures of the incubation times of any nonavian saurischians. In the absence of such data, the first approach will be to use average embryonic metabolism of the ornithischians *P. andrewsi* and *H. stebingeri* for the calculations of the incubation times of all the dinosaurs.

Embryos inside an egg cannot regulate their own body temperature. The average embryonic metabolic rate depends on the temperature: embryos kept at higher temperatures will have, on average, a faster metabolism. Most extant birds brood their eggs. Given the high body temperatures of birds, avian eggs are kept at relatively high temperatures. Most extant reptiles do not brood their eggs. Some reptiles (such as the crocodylians) cover their eggs with vegetation which provides an insulating layer for the eggs. The decay of this vegetation releases heat which raises the temperature of the eggs.

Figure 4 shows the embryonic metabolic prefactor B_o (for $\alpha = 3/4$) as a function of mass for the extant animals of this study and the ornithischian dinosaurs *P. andrewsi* and *H. stebingeri*. As expected, Fig. 4 shows that extant birds have a higher embryonic metabolism than extant reptiles. It is also observed that embryonic metabolism of *P. andrewsi* and *H. stebingeri* is lower than for extant birds and in the range observed for extant reptiles. This suggests that the embryonic metabolisms of these two dinosaurs were essentially the same as extant reptiles. These same results are evident in Table II.

Figure 5 shows comparisons of the juvenile and embryonic metabolisms (for $\alpha = 3/4$) for extant birds, extant reptiles and extinct dinosaurs. For extant birds, we see that embryonic metabolism is, on average, less than the juvenile metabolism. This is expected since the juvenile birds are fully endothermic and maintain, in general, very high body temperatures. In contrast, the bird embryo inside its egg is reliant on heat from its parent. On average, the temperature of the egg is lower than the body temperature of the adult bird, contributing to

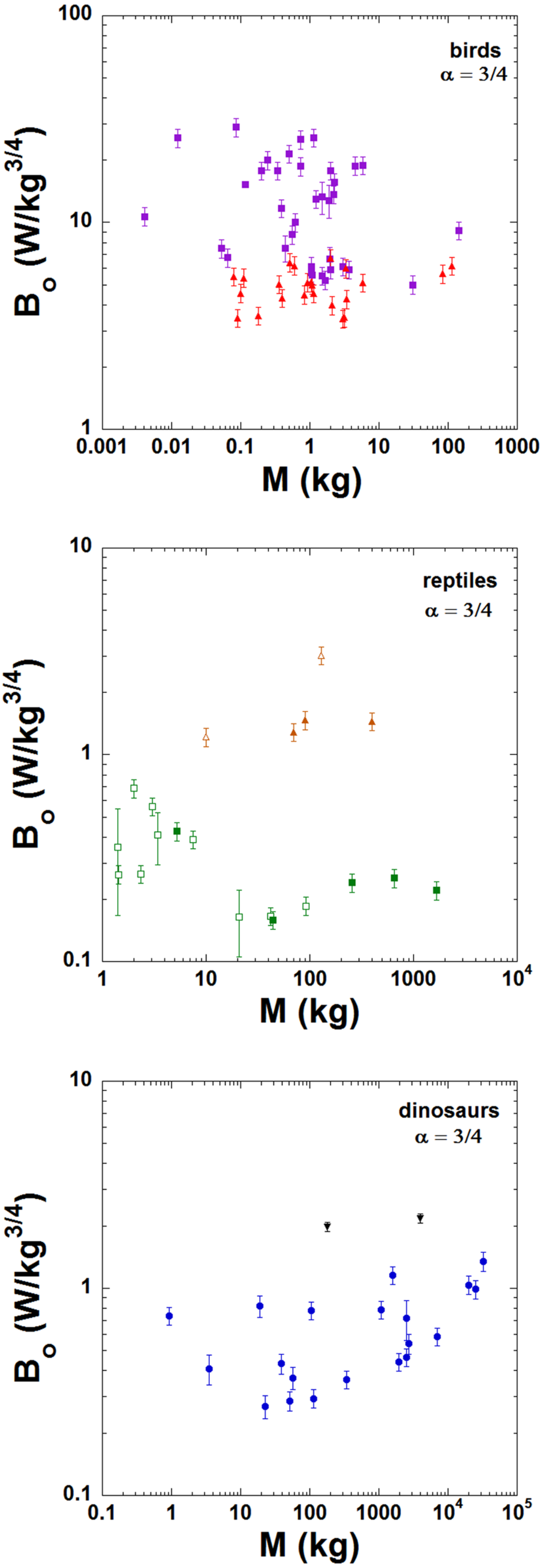

FIG. 5. Juvenile and embryonic metabolisms of the animals of this study for $\alpha = 3/4$. The metabolic prefactor B_o is shown as a function of the adult mass M of the animals. In the top panel, the data for birds are shown with solid squares for the juveniles

an embryonic metabolism which is lower than the juvenile metabolism.

Figure 6 shows the juvenile and embryonic metabolims for extant crocodylians and extinct dinosaurs for $\alpha = 0.83$. The same three trends are observed as for the $\alpha = 3/4$ case. First, the embyonic metabolism of *P. andrewsi* and *H. stebingeri* is in the same range as observed in extant crocodylians. Second, the ornithischian embryonic metabolism of the dinosaurs is slightly higher than their juvenile metabolism, on average. Third, the juvenile metabolism of dinosaurs is higher than the juvenile metabolism of crocodylians. Therefore, there is no significant difference between the results of the $\alpha = 3/4$ and $\alpha = 0.83$ models.

As ectotherms, extant reptiles have body temperatures greatly influenced by their environment. During the warm part of the day, the body temperature of reptiles can be as warm, or warmer, than that of an endothermic animal. At such peak temperatures, reptiles will metabolize faster than true endotherms, just not for as long. However, because the body temperature of a reptile is lower than an endotherm for the majority of the day, the overall effect is that the average juvenile metabolism of ectotherm is lower than for an endotherm. This effect is seen in Fig. 5 in which the juvenile metabolism of extant reptiles is seen to be more than an order of magnitude lower than the metabolism in extant birds.

The embyonic metabolism of extant reptiles is seen to be greater than in juvenile reptiles. Crocodylians do make insulating nests with decaying vegetation to provide heat. This environment is conducive to the increased embryonic metabolism observed in Figs. 5 and 6.

As first shown by Erickson *et al.* [104] and supported by Grady *et al.* [66], dinosaurs used mesothermy, a temperature regulation strategy that is intermediate to endothermy and ectothermy. Mesothermy permitted the dinosaurs to maintain an average body temperature higher than observed in extant ectotherms (including reptiles) but lower than in extant endotherms (including birds). Figure 5 shows that the embryonic metabolisms of *P. andrewsi* and *H. stebingeri* are greater than observed for the juvenile metabolism of twenty dinosaurs. However, the factor by which embryonic metabolism is higher than juvenile metabolism in dinosaurs is less than that factor in extant reptiles. Given that the embryonic metabolisms of these two groups are essentially the same, this difference is due to the fact that the juvenile metabolism is higher in mesothermic dinosaurs than in ectothermic extant reptiles.

In Ref. [55], the incubation times for the dinosaurs were calculated using Eq. (4) with the assumption that the

←

FIG. 5. (*Continued*) and upward-pointing triangles for the embryos. In the middle panel, the data for reptiles are shown with solid squares and solid upward-pointing triangles for juvenile and embryonic members of Crocodylia, respectively. For the other reptiles, the juveniles are shown with the open squares and the embryos are shown by the upward-pointing open triangles. In the bottom panel, the data for the dinosaurs is shown by the solid circles for juveniles and by downward-pointing triangles for the embryos. The data used to determine the embryonic metabolisms for the dinosaurs (*Protoceratops andrewsi* and *Hypacrosaurus stebingeri*) are from Ref. [1]

embryonic metabolic prefactor B_o for dinosaurs was the same as observed in extant birds. The current analysis of B_o based on the data of Erickson *et al.* [1] shows that the embryonic metabolism of (*P. andrewsi* and *H. stebingeri* was slower than in extant birds.

Using Eq. (4), we now calculate the incubation times of the twenty-one dinosaurs of this study. (Data [148] published for a 21st dinosaur, *Rapetosaurus krausei*, permits the evaluation of its embryonic metabolic prefactor also.) First, we use $\alpha = 3/4$ and assume that the average embryonic metabolism (2.08 $W/\text{kg}^{3/4}$) of *P. andrewsi* and *H. stebinderi* is valid for all dinosaurs. The results of this calculation are given in the fifth column of Table III . Since Seymour *et al.* [64] recently reported that $\alpha = 0.83$ for specimens of *Crocodylus porosus* of different sizes, we repeat our calculations with $\alpha = 0.83$. This analysis yields an average embryonic metabolism of 3.18 $W/\text{kg}^{0.83}$ for *P. andrewsi* and *H. stebinderi* which is then used to calculate the incubation times for all dinosaurs. The results of this calculation are given in the sixth column of Table III.

The predicted incubation times resulting from these two calculations are very long. *Archaeopteryx lithographica* has a predicted incubation time of 66 days in the $\alpha = 3/4$ model and 86 days in the $\alpha = 0.83$ model. *Alamosaurus sanjuanensis* has a predicted incubation time of 189 days in the $\alpha = 3/4$ model and 161 days in the $\alpha = 0.83$ model. The trends predicted by both values of α are essentially the same, showing no significant difference between the two models.

Dinosaurs that provide active care for their eggs and young would have been negatively impacted by long incubation times since the parents would have been restricted in their movements for significant periods of time. Large nesting colonies nests have been found for the sauropod titanosaurs [47,56,149]. The gregarious nature of their nesting behavior is shown by the close spacing of the clutches, the high density of the clutches and their continuity [47]. Such a large concentration of eggs would have attracted predators and, consequently, the parents presumably guarded the nesting colony until the eggs were hatched and the young were able to leave the area. The nests in these colonies are spaced about the length of an adult dinosaur, consistent with the adults laying their eggs at the same time. As shown in Table III, the incubation time was about 170 days, showing that these large sauropods were restricted in their movements for about 6 months a year. Given the large amount of food required by the adults, the vegetation of the neighboring areas must have been impacted negatively.

Sauropods are believed to have formed herds as indicated by trackway evidence [150–152]. Myers and Fiorillo reported age segregation within *Alamosaurus* on the basis of trackways [150]. The differences between fossil accumulations composed entirely of immature animals and mixed-age ichnological assemblages imply that herd composition was variable. The sauropod *R. krausei* has been shown to have been precocial [148]. Once the young were hatched, both the adults and young presumably left the nesting area fairly soon since the large number of adults would have depleted food resources near the nesting area during egg incubation.

The saurischian *Citipati, Deinonychus, Troodon*, and *Oviraptor* are all believed to have brooded their eggs [9–14].

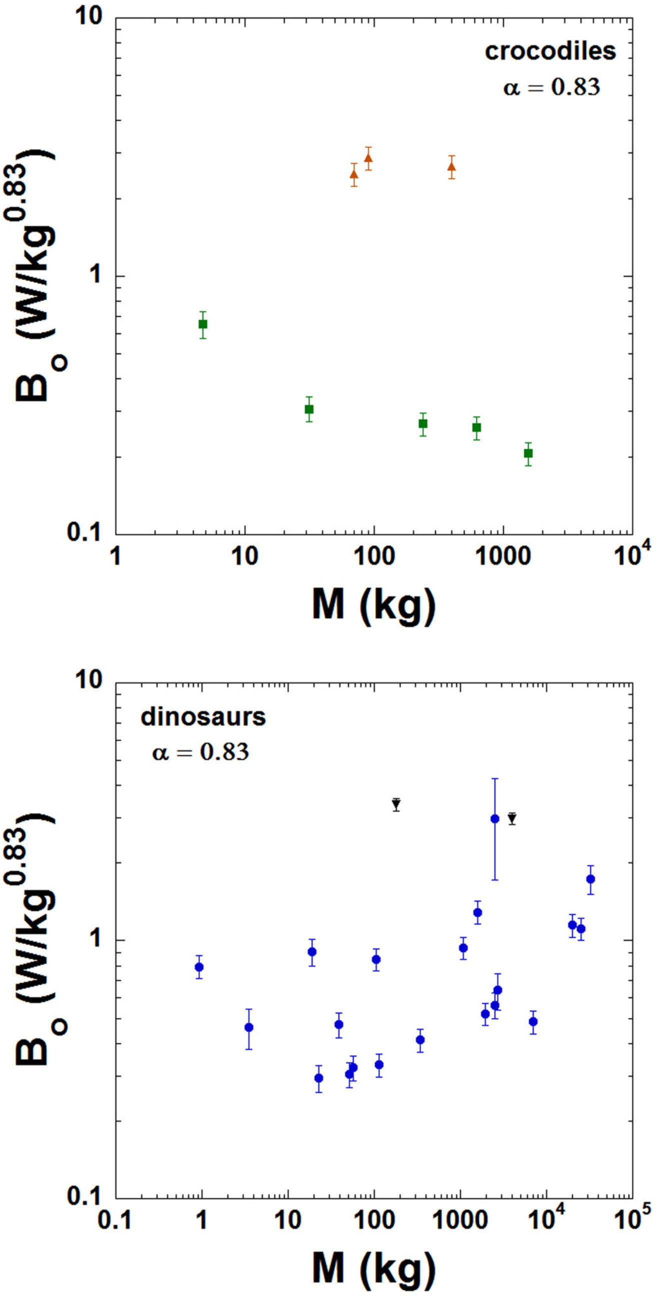

FIG. 6. Juvenile and embryonic metabolisms of the crocodylians and dinosaurs of this study for $\alpha = 0.83$. The metabolic prefactor B_o is shown as a function of the adult mass M of the animals. For crocodylians, the data for juvenile and embryos are shown are shown with solid squares and upward-pointing solid triangles, respectively. For the dinosaurs, the data for juveniles are shown with solid circles for the juveniles and downward-pointing triangles for the embryos. Recall that the results for the embryonic dinosaurs (*Protoceratops andrewsi* and *Hypacrosaurus stebingeri*) are derived from the data of Ref. [1]

It is likely, though not proven, that *Coelophysis, Shuvuuia*, and *Archaeopteryx* also sat on their eggs. These and other brooding dinosaurs would have to be on their nest for about 2 to 4 months, also exposing them to predation as well as restricting their ability to attain sustenance.

Trackway evidence suggests gregarious behavior in tyrannosaurs [153] and *Deinonychus*-sized theropods [154,155]. Though too large to brood their eggs, if the tyrannosaurs guarded their nests in order to protect the eggs and then provided care for their young (as done by extant crocodylians), the incubation times of 130–160 days would have exposed the adults to the difficulty of finding sustenance in the same area for roughly 5 months.

As discussed earlier, the postcranial pneumaticity and associated air sacs suggest a higher metabolism in sauropods and theropods. Also, the fact that birds (members of Saurischia) appear in the Middle Jurassic also supports the supposition that saurischians had a high metabolism. This high metabolism would presumably have been present in the embryonic stage also, as argued by the problem of egg predation. Consequently, for our third calculation of dinosaur incubation times, we assume that saurischians had a metabolism the same as observed in extent birds.

The average embryonic metabolic prefactor for extant birds of Fig. 4 is $B_o = 4.82 \pm\ 0.99\ W/\mathrm{kg}^{3/4}$. In seventh column (marked "split") of Table III, the incubation times of the saurischian dinosaurs are calculated using this value of the metabolic prefactor for $\alpha = 3/4$ while the ornithischian calculations are still performed with the average metabolism from *P. andrewsi* and *H. stebingeri*.

The incubation times for the saurischians reported in seventh column are about 40 % of the times reported in the fifth column. These new incubation times minimize the problems associated with the long incubation times predicted by the ornithischian metabolism. It should be noted that it is possible that some saurischians had the slow metabolism displayed by *P. andrewsi* and *H. stebingeri*. However, it seems likely that the largest saurischians (the sauropods and the large theropods) had an avian embryonic metabolism.

In recent work on sauropod dinosaurs, Ruxton *et al.* [53] used allometric relationships from extant birds and crocodylians to estimate the incubation time for sauropod dinosaurs to have been 65–82 days. The predicted sauropod incubation times of the seventh column are consistent with the result of Ruxton *et al.*

In the seventh column of Table III, it is assumed that the saurischian *Massospondylus carinatus* and *Plateosaurus engelhardti* had the avian metabolism during incubation.

There is evidence that the young of *M. carinatus* remained in their nests for a period of couple months after hatching [156–158]. This suggests that their young were altricial and that the parents actively cared for the young. Using the ornithischian embryonic metabolism results in a predicted incubation time of about 115 days. Since the young were not ready to leave the nesting area for a couple of months, the parents had to spend about 6 to 7 months each year guarding their nest and caring for their young. With the higher avian embryonic metabolism, the parents would have spent about 3 to 4 months caring for their eggs and young.

Noting that the ornithischians never had postcranial pneumaticity nor air sacs, it is likely that all ornithischians had a slow embyonic metabolism of roughly $2\ W/\mathrm{kg}^{3/4}$. However, some of them might have had a slightly higher embryonic metabolism. *Maiasaura peeblesorum* nested in colonies and cared for their young in their nests for a period of several months [159,160]. With a calculated incubation time of about 140 days, *Maiasaura* would have been restricted to the nesting area for more than half a year (roughly 200 days). Suggestions [161–163] that large ornithischian dinosaurs made migrations of about 3,000 km from lower latitude nesting sites to higher latitude feeding areas in polar regions might be inconsistent with the long incubation times predicted in this study. Having to spend so long at the nesting site might not leave sufficient time for the long trip during the remainder of the year.

IV. SUMMARY

The embryonic metabolisms of the ornithischian dinosaurs *P. andrewsi* and *H. stebingeri* have been determined to be in the range observed in extant reptiles. This average embryonic metabolism was then used to calculate the incubation times for twenty-one dinosaurs from both Sauischia and Ornithischia. The calculated incubation times vary from about 70 days for *A. lithographica* to about 180 days for *A. sanjuanensis*. Such long incubation times, particularly for the sauropods who nested in colonies, seem unlikely. Incubation times were calculated for the saurischian dinosaurs with the assumption that their embryonic metabolism was the same as in extant birds.

It is hoped that new studies of embryonic tooth development in close to hatching embryos of other dinosaur species will soon be published. It is important to obtain data from as many different dinosaurs as possible. It would be particularly useful to have such data from members of Saurischia. Further progress in determining the embryonic metabolism of nonavian dinosaurs will be possible with the publication of such data.

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