Theropod dinosaurs had primate-like numbers of telencephalic neurons

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Understanding the neuronal composition of the brains of dinosaurs and other fossil amniotes would offer fundamental insight into their behavioral and cognitive capabilities, but brain tissue is not fossilized. However, when the bony brain case is preserved, the volume and therefore mass of the brain can be estimated with computer tomography; and if the scaling relationship between brain mass and numbers of neurons for the clade is known, that relationship can be applied to estimate the neuronal composition of the brain. Using a recently published database of numbers of neurons in the telencephalon of extant bird and non-avian reptiles, here I show that the neuronal scaling rules that apply to these animals can be used to infer the numbers of neurons that composed the telencephalon of dinosaur, pterosaur and other fossil reptile species, after using the relationship between brain and body mass to determine whether bird-like (endothermic) or non-avian reptile-like (ectothermic) rules apply to each fossil species. This procedure indicates that theropods such as *Tyrannosaurus rex* and *Allosaurus* had monkey-like numbers of telencephalic neurons, which would make these animals not only giant but also long-lived and endowed with flexible cognition, and thus even more magnificent predators than previously thought.

The mammal and bird-rich modern amniote fauna arose from the opportunity created by the demise, in a catastrophic astronomical event, of the giant archosaur species that dominated the Earth during the Mesozoic[1-3]. Understanding how that event changed animal diversity has been a key goal of evolutionary biology, with two predominant lines of inquiry. On the one hand, there has been much interest in how mammals ascended to the modern range of diversity, coming to constitute the largest animals in both body and brain size[4,5], whereas birds became smaller compared to their ancestors[6]. On the other, a still growing number of studies focus on establishing whether dinosaurs were ectotherms, mesotherms, or had the high metabolic rates

characteristic of modern warm-blooded animals, and the fast-paced behavior that comes with it[7-9]. Both lines of inquiry rely on fossilized bones, which inform about the size of brain and body. Because brain tissue is not preserved in the fossil record, inferences about the behavioral and cognitive capabilities of prehistoric amniotes have necessarily been made on the sole basis of brain size, usually "adjusted" for body size[4,6,10,11] under the assumption that there is a mandatory, universal allometric relationship between brain and body size, the only expedient that makes the human brain appear to be an outlier amongst mammals[11,12]. Whenever such allometric scaling rules also apply to the relationship between brain (or brain structure) size and the number of neurons that composes it, brain size serves as a proxy for its numbers of signal processing units, which should constitute a primary determinant of signal processing capacity[13,14]. We have thus been able to infer the numbers of neurons that composed the brain of prehistoric hominin species[15] and fossil mammals[16,17].

Because neuronal scaling rules differ across clades, it is numbers of neurons, rather than brain size, that constitute a direct proxy for cognitive capabilities[14,18]. That behavioral and cognitive capabilities cannot be inferred universally from absolute or relative brain size has been recently demonstrated independently in at least two ways. Analysis of larger datasets shows that brain and body size evolve separately in both mammalian[5] and bird[6] evolution, making body size an unreliable universal predictor of brain mass. In an independent line of investigation, the advent of a new non-stereological method to count brain cells, the isotropic fractionator[19], allowed the realization that there is no mandatory, universal relationship between brain structure size and its numbers of neurons, with different scaling relationships applying to different clades of mammals and birds[20, 21]. As a result, simple, absolute numbers of neurons in the pallium (organized as a cortex in mammals), which endows vertebrates with complex, flexible cognition, are a much better proxy for cognitive abilities than brain or pallial size, whatever the size of the body[14]. It thus follows that understanding the capability for behavioral and cognitive flexibility of the extinct species that once dominated the Earth's fauna requires going beyond the veil of brain and body size and gaining direct understanding of the numbers of neurons that composed the pallium of those animals.

The isotropic fractionator, which consists of turning brains or brain structures into a homogeneous soup of floating cell nuclei that allows the fast, unbiased, and reproducible estimation of how many neuronal and non-neuronal cells composed those structures, has by now been applied to over 200 species of mammals, birds, and non-avian reptiles[22]. While the resulting dataset did not separate the pallial from the subpallial structures that together compose the telencephalon of reptiles, it did establish that the vast majority of telencephalic neurons are found in the pallium of non-avian reptiles and basal birds; thus, numbers of telencephalic neurons in the dataset offer a good approximation for the number of pallial neurons (though the subpallium also contributes to flexible behavior[23]). In contrast to the recent initial analysis of the full dataset which focused on relationships between numbers of neurons and body mass[22], here I concentrate on the clade-specific relationships between telencephalic and brain mass and numbers of telencephalic neurons in the different clades of living avian- and non-avian reptiles in search of establishing what relationships putatively applied to prehistoric species, which I then use to estimate numbers of telencephalic neurons in select species with known brain volume and mass.

Figure 1a shows that the neuronal scaling rules that apply to the telencephalon of avian and non-avian reptiles are clearly distinct. For a similar telencephalic mass (which occurs in the largest reptiles and the smallest birds), basal bird clades in the dataset (Palaeognathae, Galliformes, Anseriformes, and also Columbiformes, in red), which arose before the K-Pg border[24], have ca. 5 times as many telencephalic neurons as non-avian reptiles (in green), and the post-K-Pg-derived Passariformes, Psittaciformes and Strigiformes clades have even more telencephalic neurons (in black). For instance, the zebra finch has 55 million telencephalic neurons whereas the Sudan plated lizard has only 14 million, though both have a telencephalon of ca. 0.3 g. Strikingly, there is very little overlap in numbers of telencephalic neurons between birds and non-avian reptiles, a distinction that I have hypothesized to result from the increased oxidative rates that make endothermy possible in birds compared to other reptiles[25] (rather than from endothermy itself[22,26]). Figure 1b shows that endothermic reptiles (i.e., birds) do have larger brains compared to ectothermic reptiles of a similar body mass, but again in a clade-specific

manner, such that bird species belonging to later-derived clades (songbirds, parrots, and owls) have even larger brain mass for a similar body mass.

Together, the distinction between bird clades in Figures 1a and 1b shows that the shift to endothermy cannot be the sole cause of increased brain mass and numbers of telencephalic neurons in birds relative to body mass[26,27]. Importantly, these findings establish that comparisons across species and clades for where brain scaling is involved cannot treat "birds" as a single entity, as has been standard in the field[10]. However, amongst non-avian reptilian clades, neuronal scaling rules are much more uniform[26], and for the purposes of this study, all extant reptiles in the dataset can be considered to share the scaling rules of interest, which are clearly distinct from the scaling rules that apply to extant basal birds (Figure 1a).

While brain size should be considered a developmental consequence, not a cause, of numbers of neurons in any brain region[20], expressing the number of telencephalic neurons in the brain as a function of brain mass shows that brain mass has strongly predictive power to arrive at estimates of numbers of telencephalic neurons in a brain of known mass, once the neuronal scaling rules that presumably apply are known. Figure 1c shows that clearly different predictive scaling rules apply to extant basal birds and non-avian reptiles, with non-overlapping 95% prediction intervals across the entire range of bird-like brain sizes. Specifically, these distinct power laws are such that over 80% of the variation in numbers of telencephalic neurons in non-avian reptile species, and over 90% in basal birds, can be accounted for by the variation in brain mass, if clade identity is respected.

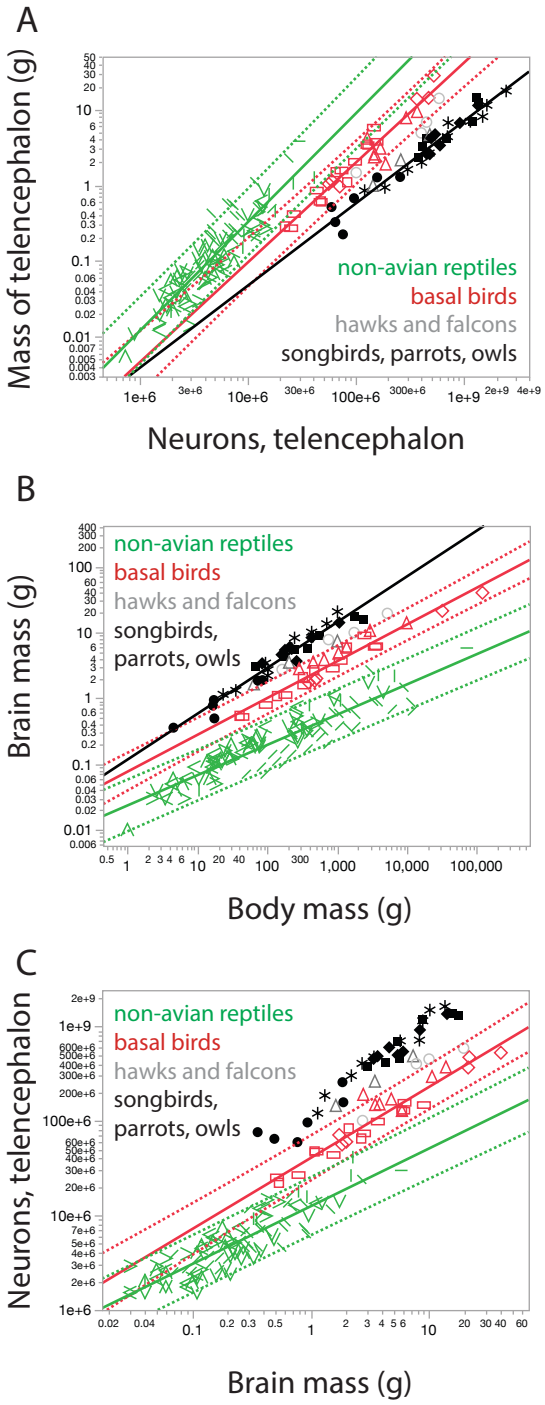

Figure 1. Scaling relationships that apply to extant avian and non-avian reptile species. A, clade-specific scaling of telencephalic mass with numbers of telencephalic neurons distinguishes basal (early-derived) bird clades (Palaeognathae, Galliforms, Anseriformes, Columbiformes) from other, later-derived bird clades (Falconiformes and Accipitriformes; and Passeriformes, Psittaciformes, and Strigiformes) and

reptiles. Power functions are $M_{tel} = e^{-24.284\pm0.988} N_{tel}^{1.437\pm0.064}$ (non-avian reptiles; r^2=0.826, p<0.0001, n=108 species, plotted in green), $M_{tel} = e^{-23.611\pm1.306} N_{tel}^{1.319\pm0.071}$ (basal birds; r^2=0.933, p<0.0001, n=27 species, plotted in red), $M_{tel} = e^{-20.567\pm0.934} N_{tel}^{1.086\pm0.047}$ (Passeriformes, Psittaciformes and Strigiformes; r^2=0.949, p<0.0001, n=31 species, plotted in black), and $M_{tel} = e^{-23.387\pm5.032} N_{tel}^{1.264\pm0.258}$ (Accipitriformes and Falconiformes; r^2=0.828, p=0.0045, n=7 species, fit not plotted). **B**, clade-specific scaling of brain mass with body mass similarly distinguishes basal (early-derived) bird clades (Palaeognathae, Galliforms, Columbiformes, Anseriformes) from other, later-derived bird clades (Falconiformes and Accipitriformes; and Passeriformes, Psittaciformes, and Strigiformes), and reptiles. Power functions are $M_{br} = e^{-3.749\pm0.104} M_{bd}^{0.460\pm0.019}$ (non-avian reptiles; r^2=0.842, p<0.0001, n=108 species, plotted in green), $M_{br} = e^{-2.565\pm0.188} M_{bd}^{0.560\pm0.026}$ (basal birds; r^2=0.948, p<0.0001, n=27 species, plotted in red), $M_{br} = e^{-2.141\pm0.166} M_{bd}^{0.696\pm0.032}$ (Passeriformes, Psittaciformes and Strigiformes; r^2=0.944, p<0.0001, n=31 species, plotted in black), and $M_{br} = e^{-1.771\pm0.159} M_{bd}^{0.554\pm0.025}$ (Accipitriformes and Falconiformes; r^2=0.990, p<0.0001, n=7 species; fit not plotted). **C**, clade-specific predictive relationships for estimating numbers of telencephalic neurons from brain mass for basal birds and non-avian reptiles. Power functions are $N_{tel} = e^{17.518\pm0.076} M_{br}^{0.753\pm0.045}$ (basal birds; r^2=0.918, p<0.0001, n=27 species, plotted in red) and $N_{tel} = e^{16.342\pm0.057} M_{br}^{0.612\pm0.031}$ (non-avian reptiles; r^2=0.791, p<0.0001, n=108 species, plotted in green). All data from [22].

Pterosaurs and dinosaurs are archosaurs, the sister clade to modern non-avian reptiles whose sole survivors are birds (Figure 2), and it is thus likely that their brains were either composed like non-avian reptile brains, or had already shifted to the composition of modern basal bird brains. Given that brain mass can be estimated accurately with micro-CT of extant or fossilized skulls[10,28,29], the predictive equations plotted in Figure 1c can be used to infer the numbers of telencephalic neurons that composed the brains of dinosaur, pterosaur, and other fossil reptilian species provided that these species are found to conform to the scaling rules that apply to either modern basal birds or non-avian reptiles (Table S1). Figure 2, using data compiled from the literature[10,28,29], shows that the scaling of brain mass with body mass can indeed provide a distinguishing criterion across dinosaur species. Standard practice in the field has been to assume that a single scaling relationship applies homogeneously across mixed dinosaur clades[8,10,11]. Figure 2a confirms that a highly significant single scaling relationship can be fit to the ensemble of the fossil species sampled, with a 95% prediction interval that includes all but one species (Figure 2a), with an exponent of 0.460±0.031 (r^2=0.839, p<0.0001) that is similar to the

exponent that applies to extant non-avian reptiles only (0.460±0.019, r^2=0.842 in Figure 1b) but with a significantly larger intercept of $e^{-2.467\pm0.373}$ compared to the $e^{-3.749\pm0.104}$ of modern non-avian reptiles. If this joint scaling relationship intermediate between living reptiles and birds truly applied across all dinosaurs, as calculated previously[10], and these diverse species shared a single scaling relationship between brain and body mass (for example, if they were "mesothermic", as once suggested by a similar expedient of analyzing dinosaur species together regardless of clade[8]), then it would not be justified to apply the neuronal scaling rules of either modern birds or non-avian reptiles to these fossil species.

In contrast, Figure 2b shows that different dinosaurs and pterosaurs clearly conform to either reptile-like or basal bird-like brain x body scaling rules. Both *Archaeopteryx*, the earliest avian species of known brain and body mass, and a non-identified protoavis[28] (filled red circles) conform to the scaling relationship that applies to modern basally-derived birds, which originated within Jurassic theropods[24], with brains significantly larger than expected for a modern reptile of similar body mass. Likewise, the majority of theropod dinosaur species of known brain and body mass (filled pink circles) conform to the brain vs body mass relationship that applies to modern basal birds, with the exception of *Shuvuuia desertii* (with brain mass just below the prediction interval for basal birds) and the oviraptors *Tsaagan mangas* and *Zanabazar junior*[10] (with the brain mass expected for a modern non-avian reptile of similar body mass; unfilled pink circles). Conversely, most sauropod dinosaurs in the dataset had the brain mass expected for a modern non-avian reptile of their body mass (unfilled green circles), with the exception of *Protoceratops* (filled green circle), which approached the distribution of modern basal birds. Ornithischian (blue circles) and pterosaur species (black circles), in turn, align either with modern avian (filled circles) or non-avian reptile species (unfilled circles) in their brain vs body mass relationship, depending on the species (Figure 2b, Table S1). Thus, the comparison of the brain vs body mass relationships of the sampled fossil species with those of modern basal birds and non-avian reptiles suggests that the neuronal scaling rules shared by modern non-avian reptilian species also applied to the telencephalon of all non-theropod fossil species of reptiles, with the exception of some pterosaur and ornithischian species (filled data points in Figure 2b), whereas theropods as a whole already

had neuronal scaling rules similar to those of modern basal birds, according to the cladogram in Figure 2d.

The finding of distinct brain x body scaling relationship in different dinosaur and pterosaur clades and even species supports the conclusion of a recent analysis of fossil metabolites that showed that many, but not all, dinosaur species had high metabolic rates compatible with endothermy[7]. Specifically, while most theropods and the single sauropod (*Diplodocus*) tested had advanced lipoxidation end-products accumulated in quantities indicative of high metabolic rates, different ornithischian and pterosaur species showed concentrations compatible with either high or low metabolic rates[7]. Such clustered diversity amongst dinosaurs and pterosaurs in both metabolism[7] and brain x body scaling (Figure 2b) warrants discontinuation of the practice of treating these species as a mixed bag in scaling studies. Instead of using all-encompassing scaling rules such as the power function shown in Figure 2c, clade-specific analyses and scaling rules should be employed, informed by other features such as analysis of metabolites[7], which suggests the cladogram in Figure 2c, or by the scaling relationship between brain and body mass, which suggests the cladogram in Figure 2d.

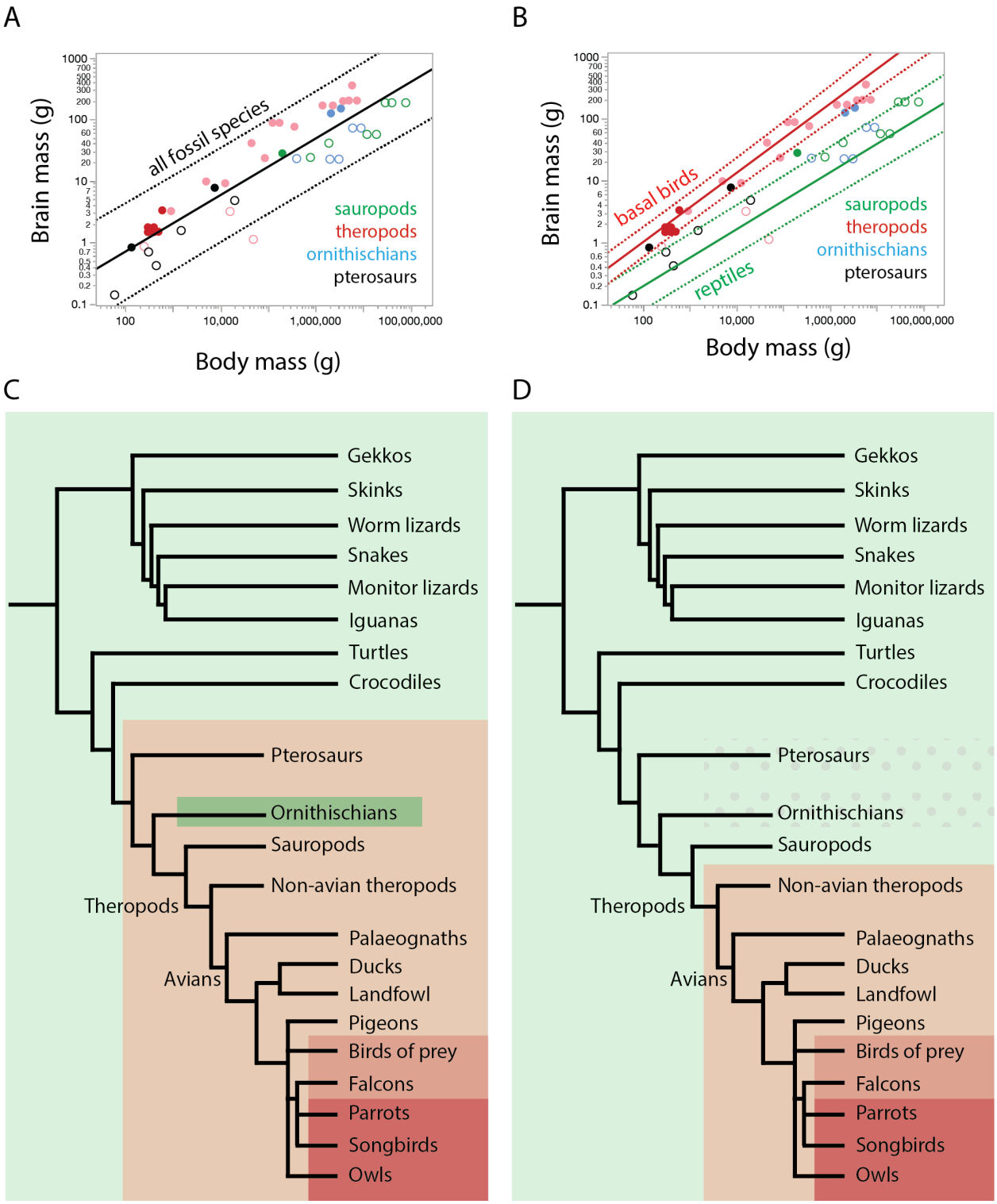

Figure 2. Dinosaur and pterosaur species vary in conforming to either modern basal bird (endothermic) or non-avian reptile (ectothermic) scaling relationships between brain and body mass. A, A single power function $M_{br} = e^{-3.749\pm0.104} M_{bd}^{0.460\pm0.031}$ (r^2=0.839, p<0.0001) can be fit to the relationship between brain and body mass (M_{br} and M_{bd}, respectively) across all the species in the dataset (Table S1). However, most

theropod species (shades of red) have larger brain mass than predicted for their body mass, whereas sauropods (green) and most pterosaur species (black) have smaller brain mass than predicted by this joint scaling function, which is consistent with a better account of the distribution by two separate functions. **B,** Data points for fossil species in Table S1 plotted into the fitted power functions that describe the brain x body mass relationship in modern basal birds and non-avian reptiles (Figure 1b) show that most theropods and early avians in the dataset have the brain mass expected for a generic basal modern bird that had their body mass, whereas most sauropods and pterosaurs have brain mass within the range expected for a generic non-avian modern reptile of their brain mass. Different ornithischian species conform to one of the other scaling relationship. Power functions, plotted with 95% prediction intervals, are the same as in Figure 1b. **C, D,** schematics of alternate proposals for the evolution of brain vs body mass relationships that are characteristic of ectothermic (green) or endothermic (shades of red) modern amniotes. **C,** metabolite-based analysis predicts that a brain x body scaling relationship similar to that characteristic of modern endothermic basal birds applied broadly across dinosaur and pterosaur species, but not in ornithischians. **D**, present brain x body scaling relationships shown in **B** predicts that endothermy was widespread in theropods but only occasional in pterosaurs and ornithischians.

Given the striking distinction in brain x body scaling between extant avian and non-avian reptiles shown in Figure 1, most likely associated with the distinction between endothermy and ectothermy[22,26], and the similar segregation of fossil dinosaur and pterosaur species shown in Figure 2, here I take the approach of hypothesizing that the neuronal scaling rules calculated for the telencephalon of endothermic or ectothermic modern species already applied to the brains of fossil species of matching brain vs body scaling relationship. Thus, considering that most fossil theropods had brains of the mass expected for a modern bird of theropod-like body mass (Figure 2a), the predictive neuronal scaling rule calculated for modern basal birds will also estimate the numbers of telencephalic neurons in fossil theropod species of known brain mass.

Using the published values of brain mass estimated from micro-CT analysis[10,28,29] (Table S1) plotted in Figure 2, I find that theropods had primate-like numbers of telencephalic neurons (Figure 3, Table S1), from just over 1 billion telencephalic neurons in the 76 g brain of *Alioramus*, comparable to a capuchin monkey, to over 3 billion telencephalic neurons in a 355 g brain of *Tyrannosaurus rex*, which is more telencephalic neurons than found in a baboon[30]. In comparison, scaling with non-avian reptile-like rules, *Triceratops*, with a 72 g brain similar in size

to *Alioramus*, presumably had only around 172 million telencephalic neurons – fewer than the 306 million neurons found in the cerebral cortex of a capybara[30]. Importantly, the use of endotherm (avian) scaling rules to estimate numbers of telencephalic neurons in theropods versus ectotherm (non-avian reptile) scaling rules in ornithischians is supported by recent metabolite findings in these species[7]. The distinction is highly consequential: if the *Tyrannosaurus* brain scaled like a non-avian reptilian ectotherm brain, it would have an estimated 455 million telencephalic neurons – still as many as in a large dog, but less than 15% of the baboon-like 3.4 billion telencephalic neurons estimated if basal bird-like scaling rules applied (Table S1).

In pterosaurs, the brain x body relationship in Figure 2b supports the metabolic finding consistent with endothermy in *Rhamphorhynchus muensteri* (though not in *R. gemmingi*; Table S1), but is consistent with ectothermy in *Pteranodon*[7]. Assuming basal bird-like scaling rules, the 8 kg pterosaur *Anhanguera* had an estimated 189 million telencephalic neurons, fewer than in a marmoset, in a brain of 8 g, which is almost 4 times as many telencephalic neurons as estimated in the small brain of *Archaeopteryx* (Figure 3). In contrast, assuming reptile-like scaling rules, a 450 g *Pterodactylus* animal had only an estimated 7 million telencephalic neurons, fewer than found in a mouse, in its 0.4 g brain (Table S1).

Comparing the present dataset with the species analyzed in that study of fossil metabolites, the only disagreement regards *Diplodocus*, the only sauropod tested in that study, suggested to have elevated oxidative metabolic rates consistent with endothermy but found here to conform to the brain x body scaling relationship of modern, ectothermic non-avian reptiles. Employing the latter, according to Figure 2b, sauropods such as *Brachiosaurus* and *Diplodocus* had only marmoset-like numbers of telencephalic neurons in their brains, even though these had mass that was similar in range to the brains of theropods that had estimated monkey-like numbers of telencephalic neurons (Figure 3, bottom row). Thus, until the metabolite concentrations of sauropod species can be systematically analyzed in more species, the present data suggest that these large quadrupeds had telencephalons that were composed according to the neuronal scaling rules that still apply to modern non-avian reptiles.

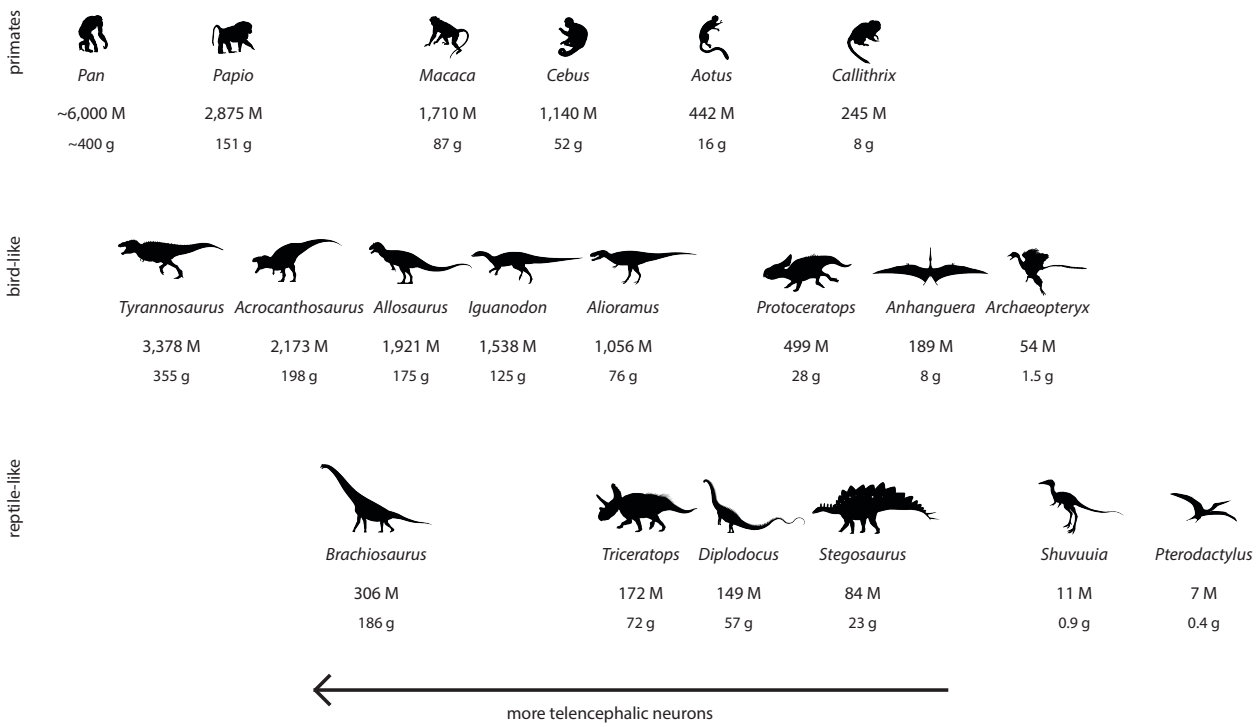

Figure 3. Estimates of numbers of telencephalic neurons in dinosaur and pterosaur species. Values below each image are numbers of telencephalic neurons (in millions, M) and brain mass (in grams). Select species from the dataset in Table S1 are depicted, ranked from left to right in decreasing order of numbers of telencephalic neurons and separated according to whether the species conforms to the brain vs body mass relationship of modern (endothermic) basal birds (center row) or of modern non-avian (ectothermic) reptilian species (bottom row). For comparison, select primate species of similar numbers of pallial neurons are shown in the top row. All images from phylopic.org**.**

The present findings on the diverse scaling of brain x body mass across dinosaur clades, which are compatible with endothermy in some and ectothermy in other species, add to the still-going debate about the metabolic condition of fossil dinosaurs by disputing the claim of homogeneous mesothermy across species[8] in favor of much larger diversity than previously suspected, supporting the finding that higher metabolic rates appeared in some but not all dinosaur clades[7]. As modeling techniques based on micro-CT data improve and allow the volume of other brain structures to be estimated, more evidence should help distinguish which dinosaur and pterosaur species were ecto- or endothermic. The cerebellum, for example, is decisively larger in extant endothermic species compared to ectothermic species of similar body mass[22];

thus, the size of the cerebellum relative to the mass of the telencephalon[26] and of the body may serve as a new diagnostic criterion to infer the metabolic status of species of the prehistoric fauna. Absent volumetric analyses of the cerebellum, simply determining whether the brain vs body mass relationship clusters with basal birds or with non-avian reptiles, as more fossil species have their brain and body masses estimated, should already provide diagnostic evidence of the metabolic status of those species.

Estimating the numbers of neurons in the telencephalon, whose main component is the pallium, a major contributor to behavioral flexibility, is obviously consequential for inferring the cognitive capabilities of dinosaur species. The present estimates showing that apex predators such as *Tyrannosaurus* had the numbers of telencephalic neurons found in modern medium-sized primates of impressive cognitive abilities adds a new dimension to how dinosaurs are pictured; an elephant-sized but agile carnivoran biped endowed with baboon-like cognition must have been an extremely competent predator indeed. But additionally, I showed recently that the number of neurons in the pallium is a true and reliable predictor of age at sexual maturity and maximal longevity in warm-blooded animals[31], such that 74% of variation in these life-history variables can be predicted in mammals and birds alike simply by the absolute number of neurons in the cerebral cortex, whereas body mass is irrelevant once numbers of cortical neurons are accounted for[31]. Using the reported equations $L = e^{-4.939} N_{cx}^{0.402}$ and $S = e^{-2.858} N_{cx}^{0.471}$ that relate maximal longevity (L) and age at female sexual maturity (S), respectively, to numbers of cortical neurons (N_{cx})[31], and assuming that most telencephalic neurons in reptiles are pallial[22], I can predict that a warm-blooded *Tyrannosaurus* of 2.2-3.4 billion telencephalic neurons would take 4-5 years to reach sexual maturity, and have an estimated maximal longevity of 42-49 years, similar to baboons, whereas *Archaeopteryx* should reach sexual maturity in ca. 8 months, and have a maximal lifespan of 10 years, similar to flycatchers and other songbirds[31]. In support of this estimate based on extant warm-blooded species, the survivorship pattern of tyrannosaurs is similar to that seen in long-lived, mammals and birds[32]. The predicted sexual maturity of *Tyrannosaurus* at age 5 years, like in modern warm-blooded amniotes of similar numbers of cortical neurons, anticipates by a full decade the previous demonstration that this species was sexually mature at 18 years of age (although that was admittedly an upper bound)[33]. While the

largest and oldest known *T. rex* lived an estimated 28 years, well under the predicted maximal longevity, the finding that only 2% of the population lived long enough to attain maximal size and age for the species[32] makes the estimate of a maximal lifespan of just over 40 years compatible with the oldest known fossil. Being able to infer what existed inside the brains of dinosaurs thus expands in several directions our knowledge of what life was like in the pre-asteroid, Mesozoic world.

Methods

All data on numbers of telencephalic neurons, brain and telencephalic mass, and body mass for 174 extant reptilian species (avian and non-avian) used to calculate the scaling relationships in Figure 1 were taken from Kverkova et al.[22]. All power functions were calculated using least-squares regression of log-transformed values in JMP 16 (Carey, NC). Brain mass and body mass values in fossil pterosaur and dinosaur species shown in Figure 2 were collected from three studies that compiled estimates from micro-CT studies[10,28,29]. Where more than one estimate was available for a species, all values are plotted so as to allow the evaluation of the impact of specimen and methodological variability.

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Acknowledgements

Thanks to Vanderbilt University for generous start-up funds, and to Pavel Nemec and collaborators who collected the reptilian data that made this study possible.

Competing interests: None.

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Table S1. Dataset and numbers of telencephalic neurons (N_{tel}) in dinosaur and pterosaur species predicted from brain mass (M_{br}) estimates reported in the literature. For the sake of clarity and reproducibility, all data compiled are listed, instead of calculating averages for each species, and are plotted in Figure 2a,b. For each species, estimated N_{tel} (in millions, M) are shown calculated according to the scaling relationships $N_{tel} = e^{17.518} M_{br}^{0.753}$ (for endothermic, basal birds) and $N_{tel} = e^{16.342} M_{br}^{0.612}$ (for ectothermic, non-avian reptiles; Figure 1c). M_{bd}, body mass in grams; M_{br}, brain mass in grams, converted from estimated brain volume in cm3 using 1 cm^3 = 1 g. Source of M_{bd} and M_{br} data is indicated next to each species. Values of N_{tel} in bold are the predictions according to Figure 2b.

Species	M_{bd}, g	M_{br}, g	N_{tel} if ectothermic	N_{tel} if endothermic	S (days), endothermic	L_{max} (years), endothermic
Pterosaurs						
Anhanguera piscator[29]	7,600	7.720	43.7 M	**188.9 M**	454	16
Pterodactylus kochi[28]	450	0.420	**7.4 M**	21.1 M	162	7
Pterodactylus elegans[28]	60	0.140	**3.8 M**	9.2 M	109	5
Pteranodon[28]	20,000	4.800	**32.7 M**	132 M	383	14
Rhamphorynchus gemmingi[28]	310	0.700	**10.0 M**	31.0 M	194	8
Rhamphorynchus muensteri[29]	136	0.830	11.2 M	**35.2 M**	206	8
Scaphognathus purdoni[28]	1,500	1.560	**16.4 M**	56.7 M	257	10
Ornithischians						
Anatosaurus[28]	3,400,000	150.0	268.5 M	**1,764 M**	1,300	38
Camptosaurus[28]	400,000	23.0	**85.2 M**	429.9 M	668	22
Euoplocephalus[28]	1,900,000	41.0	**121.4 M**	664.4 M	821	26
Iguanodon[28]	2,100,000	125.0	240.2 M	**1,538 M**	1,219	36
Kentrosaurus[28]	780,000	24.0	**87.5 M**	443.9 M	679	22
Protoceratops[28]	200,000	28.0	**96.1 M**	498.5 M	717	23
Stegosaurus[28]	3,100,000	22.5	**84.1 M**	422.8 M	663	22
Stegosaurus[28]	2,000,000	22.5	**84.1 M**	422.8 M	663	22
Triceratops[28]	9,000,000	72.2	**171.7 M**	1,017 M	1,003	31
Triceratops[28]	6,000,000	72.2	**171.7 M**	1,017 M	1,003	31
Sauropods						
Brachiosaurus[28]	78,300,000	186.0	**306.3 M**	2,075 M	1,403	41
Brachiosaurus[28]	40,000,000	186.0	**306.3 M**	2,075 M	1,403	41

Brachiosaurus[28]	29,000,000	186.0	**306.3 M**	2,075 M	1,403	41
Diplodocus[28]	19,000,000	57.0	**148.5 M**	851.4 M	922	29
Diplodocus[28]	12,000,000	57.0	**148.5 M**	851.4 M	922	29
Theropods						
Acrocanthosaurus atokensis[10]	3,770,000	197.876	318.2 M	**2,173 M**	1,434	42
Alioramus[10]	359,000	75.866	176.9 M	**1,056 M**	1,021	31
Allosaurus[28]	2,300,000	168.0	287.8 M	**1,921 M**	1,353	40
Allosaurus[28]	1,400,000	168.0	287.8 M	**1,921 M**	1,353	40
Citipati osmolskae[10]	85,960	23.434	86.2 M	**436.0 M**	673	22
Conchoraptor gracilis[10]	5,020	9.780	50.5 M	**225.8 M**	494	17
Dromicioemimus[28]	175,000	87.85	193.6 M	**1,179 M**	1,075	33
Dromicioemimus[28]	125,000	87.85	193.6 M	**1,179 M**	1,075	33
Khaan mckennai[10]	12,610	9.148	48.5 M	**214.7 M**	482	17
Shuvuuia desertii[10]	250	0.860	**11.4 M**	36.2 M	208	8
Troodon[28]	45,000	41.0	121.4 M	**664.4 M**	821	26
Troodontid[10]	920	3.222	25.6 M	**97.9 M**	333	12
Tsaagan mangas[B]	15,950	3.181	**25.4 M**	96.9 M	331	12
Tyrannosaurus[H]	7,400,000	202.0	322.2 M	**2,207 M**	1,445	42
Tyrannosaurus[H]	5,000,000	202.0	322.2 M	**2,207 M**	1,445	42
Tyrannosaurus[B]	5,840,000	355.3	455.2 M	**3,378 M**	1,765	49
Zanabazar junior[B]	49,300	1.119	**13.4 M**	44.1 M	229	9
Aves						
Archaeopteryx[H]	400	1.470	15.8 M	**54.2 M**	252	10
Archaeopteryx[H]	300	1.470	15.8 M	**54.2 M**	252	10
Archaeopteryx[H]	400	1.760	17.7 M	**62.1 M**	269	10
Archaeopteryx[H]	300	1.760	17.7 M	**62.1 M**	269	10
Archaeopteryx lithographica[B]	500	1.492	16.0 M	**54.8 M**	253	10
Unnamed protoavis[H]	600	3.320	26.1 M	**100.1 M**	336	13