Theropod dinosaurs had primate-like numbers of telencephalic neurons

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Abstract

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 only rarely 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 sauropsids (birds, squamates and testudines), 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 sauropsid species. The key to inferring numbers of telencephalic neurons in these species is first using the relationship between their estimated brain and body mass to determine whether bird-like (endothermic) or squamate-like (ectothermic) rules apply to each fossil sauropsid species. This procedure shows that the notion of "mesothermy" in dinosaurs is an artifact due to the mixing of animals with bird-like and squamate-like scaling, and indicates that theropods such as *Tyrannosaurus* and *Allosaurus* were endotherms with baboon- and monkey-like numbers of telencephalic neurons, respectively, 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.

Introduction

The modern mammal and bird-rich 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 (Alvarez et al., 1980; Bininda-Emonds et al., 2007; Yu et al., 2021). Until then, sauropodmorphs (the long-necked, plant-eating, quadruped dinosaurs), theropods

(the bipedal, carnivorous dinosaurs) and ornithischians (the sometimes armored, plant-eating dinosaurs; Langer et al., 2017) were the largest animals on land. They also had the largest brains amongst land animals at the time, approaching 200 g (the size of a lion's brain) in sauropodmorphs like *Giraffatitan brancai* (*Brachiosaurus)* and surpassing that in theropods such as *Tyrannosaurus rex* (up to 343 g; Hurlburt, 1996; Balanoff et al., 2013; Table 1). However, the fact that dinosaurs were sometimes gigantic has been used to imply that their rather large brains were actually undersized for their bodies, giving those animals very low encephalization quotients (EQ) – the first metric to set humans apart from other species, above all others, with a much larger brain than expected for our body size (Jerison, 1973). With low EQs, large dinosaurs could presumably not be that cognitively competent (Jerison, 1973; Hopson, 1977; Knoll and Schwarz-Wings, 2009; Rowe et al., 2011; Ksepka et al., 2020; Balanoff et al., 2013). Rather, it was small theropods such as troodontids, with relatively larger brains and thus higher EQs, that were considered to be "smarter" (Jerison, 1973).

The EQ is the ratio between the actual brain volume (or mass; these variables are interchangeable, given the specific density of the brain of approximately 1.0 mg/ml) and the brain volume mathematically expected for a species of a given body mass (Jerison, 1973). Calculating the EQ for a species is done under the assumption that brain and body mass are universally correlated across a wide range of species; interpreting the EQ as informative of cognitive capacities, in turn, assumes that brain mass is a universal predictor of numbers of neurons in the brain, and in the pallium (cerebral cortex, in mammals) in particular, the brain structure that most decidedly confers flexibility and complexity to animal behavior (Jerison, 1973). The problem is that while those were reasonable assumptions until the 2000s, we now know that they are both incorrect.

Recent analyses of large datasets show that brain and body size evolve separately in both mammalian (Bertrand et al., 2022) and bird (Ksepka et al., 2020) evolution, making body size an unreliable universal predictor of brain mass. In parallel, a new line of investigation created in my lab based on an original non-stereological method to count brain cells, the isotropic fractionator (Herculano-Houzel and Lent, 2005), allowed the realization that there is no mandatory, universal relationship between body mass and numbers of brain neurons, not even in the brainstem

structures that operate the body (Herculano-Houzel et al., 2014, 2015a; Herculano-Houzel, 2017). Additionally, there is no universal relationship between the size of a brain structure and its numbers of neurons; different scaling relationships apply to different clades of mammals and birds (Herculano-Houzel et al., 2014; Herculano-Houzel, 2016), while scaling relationships are mostly shared across reptiles (Kverkova et al., 2022; Herculano-Houzel, 2022). As a result of the lack of a universal correlation between body mass and brain composition, when numbers of neurons (the signal processing units of circuits) should be the limiting factor that determines the computational capacity of a network (Williams and Herrup, 1980), bringing body mass into comparisons of brain size across species of different clades is more than uninformative; it muddles interpretation, by bringing a confounding factor into the mix.

Rather, simple, absolute numbers of neurons in the pallium (organized as a cortex in mammals) are a much better proxy for cognitive abilities than brain or pallial size, whatever the size of the body (Herculano-Houzel, 2017). These are the signal processing units that make behavior flexible and complex and should thus constitute a primary determinant of signal processing capacity (Williams and Herrup, 1980; Herculano-Houzel, 2017; Ströckens et al., 2022). Absolute numbers of pallial neurons are a better predictor of flexible cognitive control than brain mass or EQ across birds and primates alike (Herculano-Houzel, 2017), and, across bird species, they are a great predictor of innovation rate (Sol et al., 2022). 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. That understanding can be reached once the scaling relationship between brain size and numbers of neurons for species in a given clade is known, which makes brain size a reliable proxy of numbers of neurons in that clade. In particular, numbers of pallial, or telencephalic, neurons in extant species can be estimated from brain size by clade-specific allometric power functions with r^2 values of typically 0.9, that is, which provide estimates with about 90% reliability (Herculano-Houzel, 2019a). Using this expedient, we have previously been able to infer the numbers of neurons that composed the brain of prehistoric hominin species (Herculano-Houzel and Kaas, 2011) and fossil mammals (Herculano-Houzel et al., 2011).

How to determine the scaling relationships that applied to fossil species, when brain tissue is not preserved in the fossil record? Brain mass of dinosaur species can be estimated with CT or micro-CT of extant or fossilized skulls (Hulburt, 1996; Knoll et al., 1999; Witmer et al., 2003; Balanoff et al., 2013). In these cases, the numbers of neurons that composed their brains, and their telencephalon in particular, can be estimated if one can determine the applicable predictive equations relating numbers of neurons to brain mass. Dinosaurs and pterosaurs (together with turtles and crocodilians) were archosaurs, the sister clade to modern squamates, which are ectothermic sauropsids; but living birds, which are endothermic sauropsids, are surviving dinosaurs. Thus, the alternative hypotheses tested here are that pterosaur and dinosaur brains were either composed like ancestral, and modern, ectothermic sauropsid brains, or had already shifted to the composition of modern, endothermic, early-branching bird brains (Herculano-Houzel, 2022).

Here I determine whether ectothermic or endothermic sauropsid scaling rules most likely applied to different dinosaur (and pterosaur) species, and use the allometric scaling equations that apply to the brain structures of modern birds and non-avian sauropsids to predict the numbers of neurons that composed the brains of fossil dinosaurs and pterosaurs based on their brain volumes. These allometric scaling equations describe the relationship between brain structure mass and numbers of neurons, determined using the isotropic fractionator (Herculano-Houzel and Lent, 2005). This method, 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 (Herculano-Houzel et al., 2015b), has by now been applied to over 200 species of mammals, birds, and non-avian sauropsids (Kverkova et al., 2022). While the resulting dataset did not separate the pallial from the subpallial structures that together compose the telencephalon of non-avian sauropsids, it did establish that the vast majority of telencephalic neurons are found in the pallium of early-branching 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; Boot et al., 2017). In contrast to the recent initial analysis of the full dataset which focused on relationships between numbers of neurons and body mass (Kverkova et al.,

2022), 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 sauropsids in search of establishing what relationships putatively applied to fossil species, which I then use to estimate numbers of telencephalic neurons in select species with known brain volume and mass.

Methods

All data on numbers of telencephalic neurons, brain and telencephalic mass, and body mass for 174 extant sauropsid species (avian and non-avian) used to calculate the scaling relationships in Figure 1 were taken from Kverkova et al. (2022). All power functions were calculated using least-squares regression of log-transformed values using the JMP 16 software package (Carey, NC). Power functions were calculated separately for different groups of birds, as detailed in the results (Accipitriformes, n=4 species; Anseriformes, n= 7; Columbiformes, n=5; Falconiformes, n=3; Galliformes, n=9; Palaeognathae, n=6 species; Passeriformes, n=13; Psittaciformes, n=11; Strigiformes, n=7); and for all non-avian sauropsids in the dataset (88 squamates, 19 testudines and 1 crocodilian species; Kverkova et al., 2022). Particular emphasis was placed on the early-branching ("pre-K-Pg") bird species, which in this dataset belong to Palaeognathae, Galliformes, Anseriformes and Collumbiformes, which share scaling relationships (see Figure 1, and Herculano-Houzel, 2022). Thus, all scaling relationships reported pertain to a group of species that belong to closely related clades that share a scaling relationship amongst themselves. *Within* each group, I chose to not adjust the scaling exponent for phylogenetic relatedness in the dataset because the point of calculating these scaling relationships was not to study phylogeny, but to use the mathematical functions to make predictions from brain mass, in which case the desired scaling relationship is the one that applies to the raw data, with no modifications introduced that would distort the mathematical reality of the relationships between the physical entities (structure mass) and (number of neurons).

Absolute estimated brain mass (not simply endocranial volume) and body mass values in fossil pterosaur and dinosaur species shown in Figure 2 were collected from four studies that compiled estimates from CT studies of endocranial volume (Table 10 in Hulburt, 1996; Witmer et al., 2003; Hulburt et al., 2013; Balanoff et al., 2013). Different brain-to-endocast fractions by

definition will impact the estimated brain mass or volume (Knoll et al., 2022); thus, care was taken to use explicitly reported estimates for brain mass, whether or not that matched the endocranial volume. Estimates for theropod and pterosaur species consider that theropod and pterosaur brains filled the endocranial cavity (Balanoff et al., 2013; Witmer et al., 2003), whereas Hurlburt's estimates for all dinosaurs except small theropods considered that brain mass was half that of endocast volume (Hurlburt, 1996, p. 147). Where available, specimen numbers are provided in Table 1 (they were not reported in Hurlburt's 1996 dataset). 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, as well as the range of body and brain size combinations. I note that the taxonomy of several fossil species has been updated since Hurlburt's data compilations that I use in Table 1. For the sake of making the present dataset transparent and readily verifiable by other researchers and useful to them, and because I am not a paleontologist but a neuroscientist using paleontological data, I chose to preserve in Table 1 the original names under which the data were originally reported by the authors.

Results

Figure 1a shows that the neuronal scaling rules that apply to the telencephalon of modern birds and non-avian sauropsids are clearly distinct. For a similar telencephalic mass (which occurs in the largest non-avian sauropsids and the smallest birds), early-branching bird clades in the dataset (Palaeognathae, Galliformes, Anseriformes, and also Columbiformes, in red), which arose before the K-Pg boundary (henceforth, pre-K-Pg birds; Brusatte et al., 2015), have ca. 5 times as many telencephalic neurons as non-avian sauropsids (in green), and the post-K-Pg-branching Passeriformes, 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 sauropsids, a distinction that I have hypothesized to result from the increased oxidative rates that make endothermy possible in birds compared to other sauropsids (Bennett and Ruben,

178 1979) rather than from endothermy itself (Kverkova et al., 2022; Herculano-Houzel et al., 2022).
179 Figure 1b shows that endothermic sauropsids (i.e., birds) do have larger brains compared to
180 ectothermic sauropsids of a similar body mass, but again in a clade-specific manner, such that
181 bird species belonging to post-K-Pg clades (songbirds, parrots, and owls) have even larger brain
182 mass for a similar body mass.

183 Together, the distinction between bird clades in Figures 1a and 1b shows that a shift to
184 endothermy cannot be the sole cause of increased brain mass and numbers of telencephalic
185 neurons in birds relative to body mass (Herculano-Houzel, 2022; Gillooly and McCoy, 2014), since
186 brain mass increases further relative to body mass in the post-K-Pg songbirds, parrots and owls
187 compared to the pre-K-Pg birds. Importantly, these findings establish that comparisons across
188 species and clades for where brain scaling is involved cannot treat "birds" as a single entity, as
189 has been standard in the field (Balanoff et al., 2013). However, amongst non-avian sauropsid
190 clades, neuronal scaling rules are much more uniform (Herculano-Houzel, 2022), and for the
191 purposes of this study, all extant non-avian sauropsids in the dataset (88 squamates, 19
192 testudines and 1 crocodilian species) can be considered to share the scaling rules of interest,
193 which are clearly distinct from the scaling rules that apply to extant pre-K-Pg birds (Figure 1a).

194 Expressing the number of telencephalic neurons in the brain as a function of brain mass
195 shows that within a clade, brain mass has strongly predictive power to arrive at estimates of
196 numbers of telencephalic neurons in a brain of known mass, once the neuronal scaling rules that
197 presumably apply are known. Figure 1c shows that clearly different predictive scaling rules apply
198 to extant pre-K-Pg birds and to non-avian sauropsids, with non-overlapping 95% prediction
199 intervals across the entire range of bird-like brain sizes. Specifically, these distinct power laws are
200 such that over 80% of the variation in numbers of telencephalic neurons in non-avian sauropsid
201 species, and over 90% in pre-K-Pg birds, can be accounted for by the variation in brain mass, if
202 clade identity is respected.
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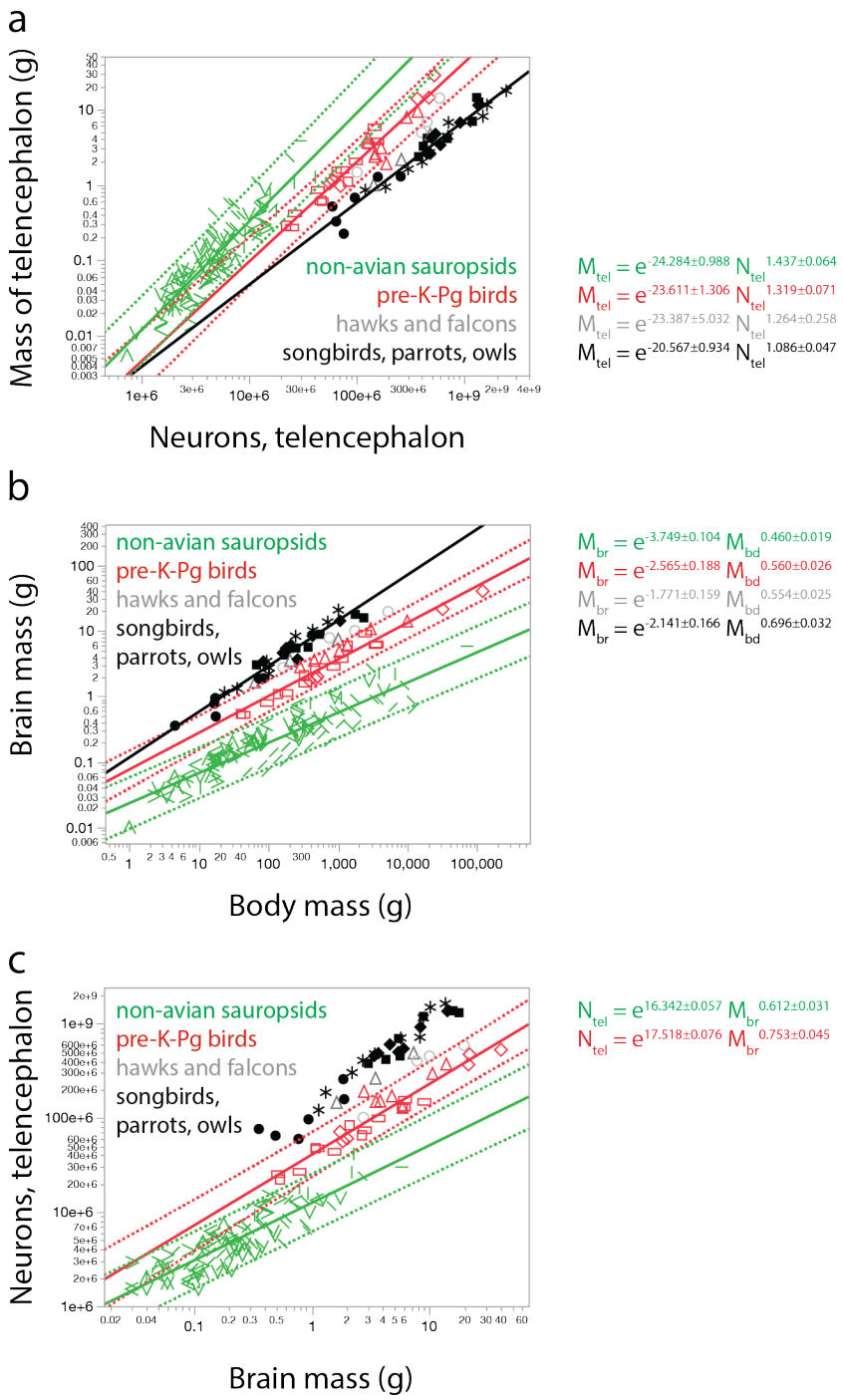


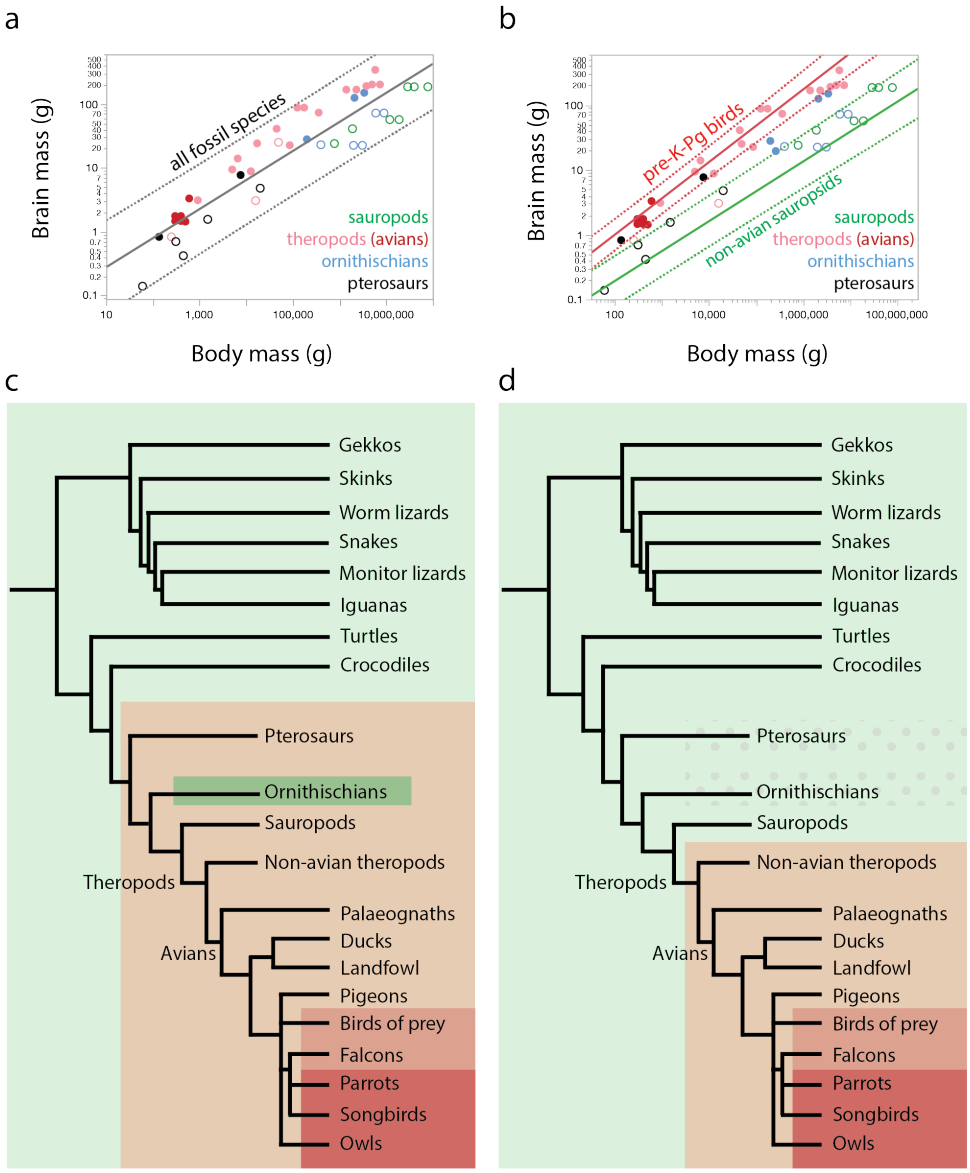
Figure 1. Scaling relationships that apply to extant avian and reptile species. A, clade-specific scaling of telencephalic mass (M_{tel}) with numbers of telencephalic neurons (N_{tel}) distinguishes pre-K-Pg bird clades (Palaeognathae, red lozangles; Galliforms, red rectangles; Anseriformes, red triangles; Columbiformes, red squares) from post-K-Pg bird clades (Falconiformes, grey triangles; and Accipitriformes, grey circles,

210 i.e. hawks and falcons; and Passeriformes, black circles; Psittaciformes, black asterisks; and Strigiformes,
211 black squares, i.e. songbirds, parrots, and owls; and non-avian sauropsids (including Testudines and
212 Crocodilia). Power functions are indicated next to the graph for each group (non-avian sauropsids in green,
213 with different symbols for the different clades in Kverková et al. (2022), r^2=0.826, p<0.0001, n=108; pre-
214 K-Pg birds in red, r^2=0.933, p<0.0001, n=27 species; Accipitriformes and Falconiformes, fit not plotted for
215 clarity, r^2=0.828, p=0.0045, n=7 species; Passeriformes, Psittaciformes and Strigiformes in black, r^2=0.949,
216 p<0.0001, n=31 species). **B**, clade-specific scaling of brain mass with body mass similarly distinguishes pre-
217 K-Pg bird clades (Palaeognathae, Galliforms, Columbiformes, Anseriformes) from other, later-branching
218 bird clades (Falconiformes and Accipitriformes; and Passeriformes, Psittaciformes, and Strigiformes), and
219 non-avian sauropsids. Power functions as in A: non-avian sauropsids plotted in green, r^2=0.842, p<0.0001,
220 n=108 species; pre-K-Pg birds plotted in red, r^2=0.948, p<0.0001, n=27 species; Accipitriformes and
221 Falconiformes, in grey, fit not plotted for clarity, r^2=0.990, p<0.0001, n=7 species; and Passeriformes,
222 Psittaciformes and Strigiformes plotted in black, r^2=0.944, p<0.0001, n=31 species. **C**, clade-specific
223 predictive relationships for estimating numbers of telencephalic neurons from brain mass for pre-K-Pg
224 birds and non-avian sauropsids. Power functions are indicated next to the graph for pre-K-Pg birds (in red;
225 r^2=0.918, p<0.0001, n=27 species) and for non-avian sauropsids (in green: r^2=0.791, p<0.0001, n=108
226 species). All data from Kverkova et al., 2022.
227
228 The predictive equations shown in Figure 1c can be used to infer the numbers of
229 telencephalic neurons that composed the brains of dinosaur, pterosaur, and other fossil
230 sauropsid species provided that these species are found to conform to the scaling rules that apply
231 to either modern pre-K-Pg birds or non-avian sauropsids. Figure 2, using data compiled from the
232 literature (Table 1), shows that the scaling of brain mass with body mass can indeed provide a
233 distinguishing criterion across dinosaur species. Standard practice in the field has been to assume
234 that a single scaling relationship applies homogeneously across mixed dinosaur clades (Jerison,
235 1973; Balanoff et al., 2013; Grady et al., 2014). Figure 2a confirms that a highly significant single
236 scaling relationship can indeed be fit to the ensemble of the fossil species sampled, with a 95%
237 prediction interval that includes all but one species (Figure 2a), with an exponent of 0.455±0.028
238 (r^2=0.857, p<0.0001) that is similar to the exponent that applies to extant non-avian sauropsids
239 only (0.460±0.019, r^2=0.842 in Figure 1b) but with a significantly larger intercept of $e^{-2.327\pm0.338}$
240 compared to the $e^{-3.749\pm0.104}$ of modern such species. If this joint scaling relationship intermediate

between living non-avian sauropsids and birds truly applied across all dinosaurs, as calculated previously (Balanoff et al., 2013), 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; Grady et al., 2014), then it would not be justified to apply the neuronal scaling rules of either modern birds or non-avian sauropsids to these fossil species.

In contrast, Figure 2b shows that individual dinosaur and pterosaur specimens clearly conform to the brain x body scaling rules that apply to either ectothermic or pre-K-Pg endothermic extant sauropsids. Both *Archaeopteryx*, the earliest avian species of known brain and body mass, and a non-identified "protoavis" (Hulburt, 1996; filled red circles) conform to the scaling relationship that applies to modern pre-K-Pg birds, which originated within Jurassic theropods (Brusatte et al., 2015), 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 pre-K-Pg birds, with the exception of *Shuvuuia deserti* (with brain mass just below the prediction interval for pre-K-Pg birds) and *Tsaagan mangas* (with the brain mass expected for a modern ectothermic sauropsid of similar body mass; unfilled pink circles). Conversely, most sauropodmorph dinosaurs in the dataset had the brain mass expected for a modern ectothermic sauropsid of their body mass (unfilled green circles). Ornithischian (blue circles) and pterosaur species (black circles), in turn, align either with endothermic pre-K-Pg birds (filled circles) or ectothermic sauropsids (unfilled circles) in their brain vs body mass relationship, depending on the species (Figure 2b, Table 1). *Protoceratops* (filled blue circle), in particular, approached the distribution of modern pre-K-Pg birds. Thus, the comparison of the brain vs body mass relationships of the sampled fossil species with those of modern ectothermic and endothermic pre-K-Pg sauropsids suggests that the neuronal scaling rules shared by modern ectothermic sauropsid species also applied to the telencephalon of all non-theropod fossil species of sauropsids, 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, endothermic pre-K-Pg sauropsids, according to the cladogram in Figure 2d. Figure 3a

shows how the brain x body mass relationship of fossil avian and non-avian theropods matches that of extant pre-K-Pg bird species (and, in comparison, primates have much larger brains for a similar body mass). Figure 3a also shows that despite the extreme difference in body size, the brain x body mass relationship of fossil sauropodmorphs, several pterosaurs and some ornithischians match the relationship that applies to extant non-avian sauropsids.



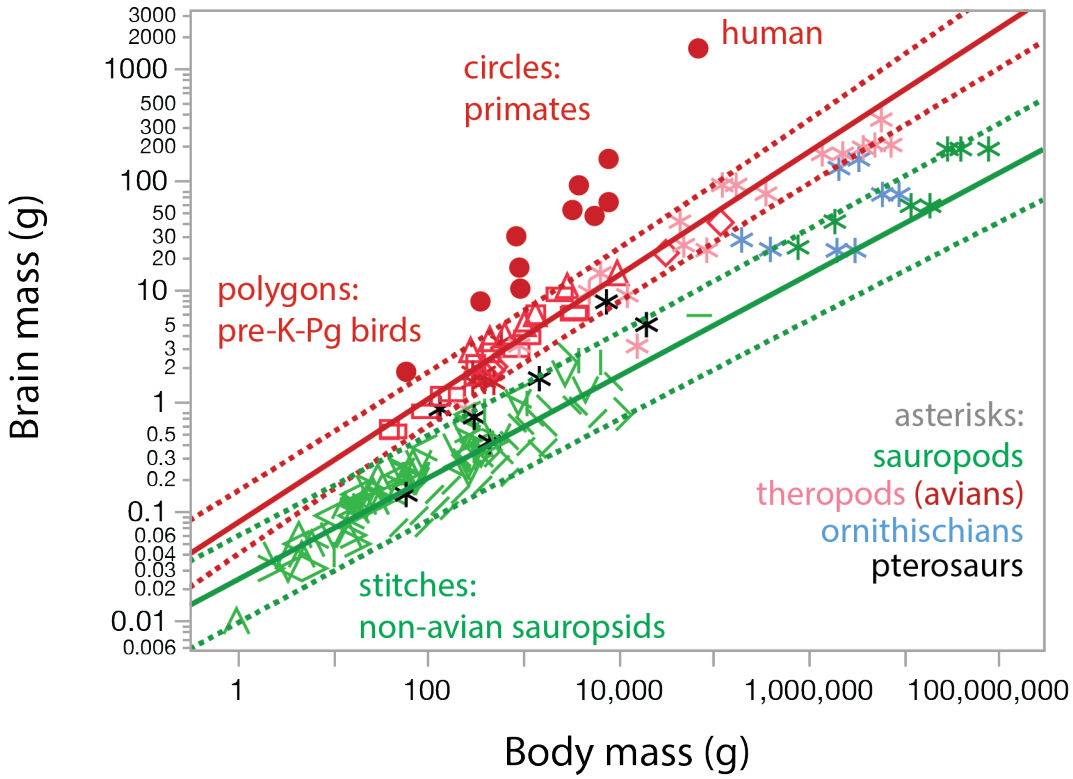
276

277 **Figure 2. Dinosaur and pterosaur species vary in conforming to either modern pre-K-Pg endothermic**

278 **(bird) or ectothermic (non-avian sauropsid) scaling relationships between brain and body mass. A,** A

single power function $M_{br} = e^{-2.327\pm0.338} M_{bd}^{0.455\pm0.028}$ (r^2=0.857, p<0.0001, plotted in grey) can be fit to the relationship between brain and body mass (M_{br} and M_{bd}, respectively) across all the fossil dinosaur and pterosaur species in the dataset (Table 1), color-coded as indicated in the key. However, most non-avian theropod species (pink) have larger brain mass than predicted for their body mass, whereas sauropodmorphs (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. Filled circles correspond to species that match brain x body mass scaling in pre-K-Pg birds; unfilled symbols denote species that match brain x body mass scaling in non-avian sauropsids, as in B. **B,** Data points for fossil species in Table 1 plotted onto the fitted power functions shown in Figure 1b that describe the brain x body mass relationship in modern ectothermic sauropsids and pre-K-Pg endothermic sauropsids show that most non-avian theropods (pink) and early avians in the dataset have the brain mass expected for a generic endothermic, pre-K-Pg modern bird that had their body mass, whereas most sauropodmorphs and pterosaurs have brain mass within the range expected for a modern generic ectothermic, non-avian sauropsid 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. Evolutionary trees based on Wiemann et al. (2022) and Kverkova et al. (2022). **C,** metabolite-based analysis (Wiemann et al., 2022) predicts that a brain x body scaling relationship similar to that characteristic of modern endothermic pre-K-Pg 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.

a


human
circles:
primates
polygons:
pre-K-Pg birds
stitches:
non-avian sauropsids
asterisks:
sauropods
theropods (avians)
ornithischians
pterosaurs
Brain mass (g)
Body mass (g)
3000
2000
1000
500
300
200
100
50
30
20
10
5
3
2
1
0.5
0.3
0.2
0.1
0.06
0.04
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0.02
0.01
0.006
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100
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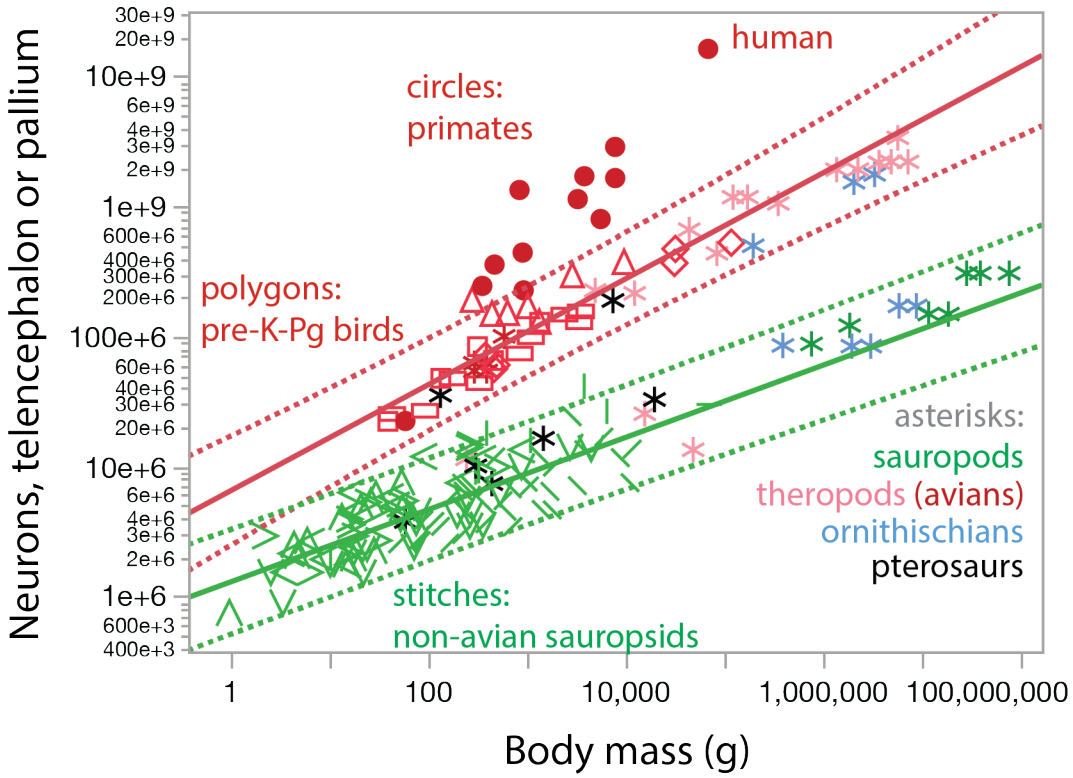
b


human
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pre-K-Pg birds
stitches:
non-avian sauropsids
asterisks:
sauropods
theropods (avians)
ornithischians
pterosaurs
Neurons, telencephalon or pallium
Body mass (g)
30e+9
20e+9
10e+9
6e+9
4e+9
3e+9
2e+9
1e+9
600e+6
400e+6
300e+6
200e+6
100e+6
60e+6
40e+6
30e+6
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10e+6
6e+6
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302

303 **Figure 3. Theropod dinosaurs overlap with modern pre-K-Pg endothermic sauropsids (birds) in their**
304 **brain x body mass scaling, which results in primate-like numbers of telencephalic neurons in theropods,**
305 **whereas most sauropodmorphs, pterosaurs and some ornithischians overlap with ectothermic non-**
306 **avian sauropsids. A,** Data points for fossil species in Table 1 (asterisks) as well as data points for extant
307 pre-K-Pg bird species (red polygons), extant non-avian sauropsids (green stitches) and primates (red
308 circles) plotted onto the fitted power functions shown in Figure 1b that describe the brain x body mass
309 relationship in modern ectothermic sauropsids and pre-K-Pg endothermic sauropsids. Power functions,
310 plotted with 95% prediction intervals, are the same as in Figure 1b. **B**, Same as in **A**, but showing measured
311 numbers of neurons in the mammalian cortex or in the telencephalon of extant sauropsids plotted
312 together with estimated numbers of neurons in the telencephalon of dinosaur and pterosaur species (bold
313 values in Table 1). Notice the similar numbers of neurons in the telencephalon of theropods and in the
314 cerebral cortex of primates despite much larger body masses in theropods.
315
316 Given the striking distinction in brain x body scaling between extant non-avian sauropsids
317 and pre-K-Pg birds shown in Figure 1, most likely associated with the distinction between
318 ectothermy and endothermy (Kverkova et al., 2022; Herculano-Houzel, 2022), and the similar
319 segregation of fossil dinosaur and pterosaur species shown in Figure 2, here I take the approach
320 of hypothesizing that the neuronal scaling rules calculated for the telencephalon of endothermic
321 or ectothermic modern species already applied to the brains of fossil species of matching brain
322 vs body scaling relationship. Thus, considering that most fossil theropods had brains of the mass
323 expected for a modern pre-K-Pg bird of theropod-like body mass (Figure 2b), the predictive
324 neuronal scaling rule calculated for modern pre-K-Pg birds will also estimate the numbers of
325 telencephalic neurons in fossil theropod species of known brain mass.
326 Using the published values of brain mass estimated from CT analysis (Table 1) plotted in
327 Figure 2, I find that theropods had primate-like numbers of telencephalic neurons (Figure 3B;
328 Table 1), although in bodies as much as 1,000 times larger than primates of similar numbers of
329 cortical neurons. As depicted in Figure 4, numbers of telencephalic neurons ranged from just over
330 1 billion telencephalic neurons in the 73 g brain of *Alioramus*, comparable to a capuchin monkey,
331 to over 3 billion telencephalic neurons in a 343 g brain of *Tyrannosaurus rex*, which is more
332 telencephalic neurons than found in a baboon (Herculano-Houzel et al., 2015a). In comparison,

333 scaling with ectothermic sauropsid rules, *Triceratops*, with a 72 g brain similar in size to
334 *Alioramus*, presumably had only around 172 million telencephalic neurons – fewer than the 306
335 million neurons found in the cerebral cortex of a capybara (Herculano-Houzel et al., 2015a).
336 Importantly, the use of endotherm (avian sauropsid) scaling rules to estimate numbers of
337 telencephalic neurons in theropods versus ectotherm (non-avian sauropsid) scaling rules in
338 ornithischians is supported by recent metabolite findings in these species (Wiemann et al., 2022).
339 The distinction is highly consequential: if the *Tyrannosaurus* brain scaled like a non-avian
340 ectothermic sauropsid brain, it would have an estimated 446 million telencephalic neurons – still
341 as many as in a large dog, but less than 15% of the baboon-like 3.3 billion telencephalic neurons
342 estimated if pre-K-Pg bird-like scaling rules applied (Table 1).

343 In pterosaurs, the brain x body relationship in Figure 2b supports the metabolic finding
344 consistent with endothermy in *Rhamphorhynchus muensteri* (though not in *R. gemmingi*; Table
345 1), but is consistent with ectothermy in *Pteranodon* (Wiemann et al., 2022). Assuming pre-K-Pg
346 endothermic sauropsid scaling rules, the 8 kg pterosaur *Anhanguera* had an estimated 189
347 million telencephalic neurons, fewer than in a marmoset, in a brain of 8 g, which is almost 4 times
348 as many telencephalic neurons as estimated in the small brain of *Archaeopteryx* (Figure 3). In
349 contrast, assuming ectothermic sauropsid scaling rules, a 450 g *Pterodactylus* animal had only an
350 estimated 7 million telencephalic neurons, fewer than found in a mouse, in its 0.4 g brain (Table
351 1).

352 Comparing the present dataset with the species analyzed in that study of fossil
353 metabolites (Wiemann et al., 2022), the only disagreement regards *Diplodocus*, the only
354 sauropodmorph tested in that study, suggested to have elevated oxidative metabolic rates
355 consistent with endothermy but found here to conform to the brain x body scaling relationship
356 of modern ectothermic sauropsids. Employing the latter, according to Figure 2b,
357 sauropodmorphs such as *Brachiosaurus* and *Diplodocus* had only marmoset-like numbers of
358 telencephalic neurons in their brains, even though these had mass that was similar in range to
359 the brains of theropods that had estimated monkey-like numbers of telencephalic neurons
360 (Figure 4, bottom row). Thus, until the metabolite concentrations of sauropodmorph species can
361 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 ectothermic sauropsids – which, incidentally, are the same that apply to modern non-primate mammals (Herculano-Houzel, 2022).

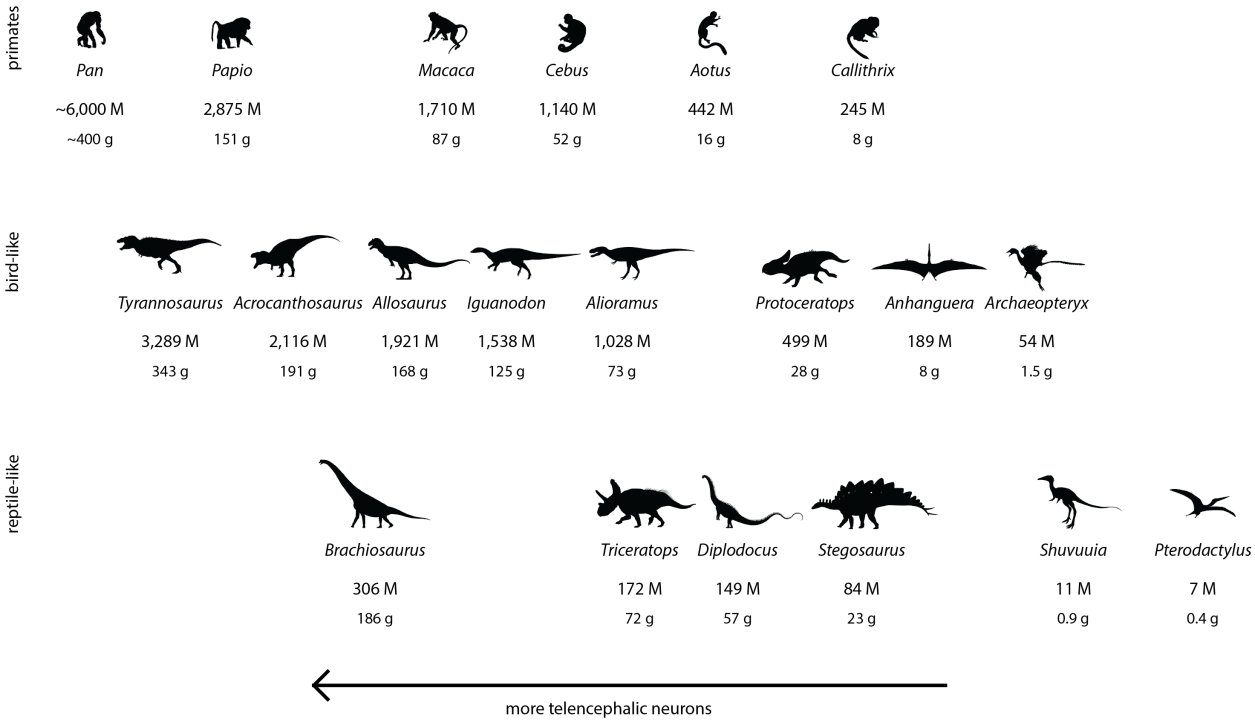

Figure 4. Estimates of numbers of telencephalic neurons in dinosaur and pterosaur species. Values below each image are numbers of telencephalic neurons (in millions, M) and brain mass (in grams). Select species from the dataset in Table 1 are depicted, ranked from left to right in decreasing order of numbers of telencephalic neurons and separated according to whether the species conforms to the brain vs body mass relationship of modern (endothermic) pre-K-Pg birds (center row) or of modern non-avian (ectothermic) sauropsid 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**.**

Discussion

Here I show that the scaling relationship between brain and body mass that applies to the moderately sized modern bird species originated in pre-K-Pg times still captures the scaling relationship that applied to relatively small as well as very large Mesozoic theropods, in an extreme example of how biological scaling can be very well described across several orders of

380 magnitude by power functions, which indicate the presence of scale-free, modular, self-
381 organizing principles at work (Herculano-Houzel et al., 2016; West, 2017). Importantly, the
382 overlap between extinct theropods and extant pre-K-Pg birds strongly suggests that theropods
383 were endothermic. Similarly, I find that the brain x body mass scaling relationship of most species
384 of sauropodmorph and ornithischian dinosaurs, as well as pterosaurs, is captured by the scaling
385 relationship that applies to modern ectothermic sauropsids, which suggests that those species of
386 dinosaurs were ectothermic, or if they were endothermic, they had not yet expressed the
387 enlarged brain mass that is presumably affordable by the increased oxidative capacity that
388 powers endothermy (Herculano-Houzel, 2022). However, it remains possible that the values
389 presented here for sauropodmorphs and ornithischians are underestimated, since they stem
390 from a dataset that considered that the brain of these species only filled 50% of the cranial cavity
391 (Hurlburt, 1996); likewise, it is possible that the values for theropods are slightly overestimated,
392 since they assume that in these species, the brain fills the cranial cavity (Balanoff et al., 2013;
393 Witmer et al., 2003).

394 On a related note, I acknowledge that the nomenclature and quite possibly some of the
395 data provided in Table 1 from the original data of Hurlburt (1996) are outdated, especially those
396 pertaining to sauropodmorphs and ornithischians. I provide those data as initial estimates for
397 non-Theropod species, and maintain the outdated names as in the original dataset, so that those
398 data can be easily located by future researchers, whom I hope will carry this study forward with
399 modern data.

400 Another methodological issue that will be disputed by some readers is that the scaling
401 relationships reported here are not "corrected" for phylogenetic relatedness, as detailed in the
402 Methods. The central issue of the present study, as in all my previous work, is the scaling
403 relationship between physical quantities such as brain structure mass and numbers of cells and
404 how one predicts the other in different ways in different clades. Whereas phylogenetic
405 comparative methods were initially introduced to alleviate issues with bias possibly introduced
406 by evolutionary relatedness in a sample, I have previously shown that any differences in the
407 scaling exponents calculated with and without accounting for phylogenetic relatedness differ by
408 only 1-2%, which is not a statistically significant difference, provided that there is no mixing in

409 the sample of species from clades already found to scale differently (Gabi et al., 2010; Herculano-
410 Houzel et al., 2011). Moreover, phylogenetic relationships are constantly being updated as
411 research progresses, which would affect the predictive scaling rules calculated if relatedness
412 within each clade were taken into consideration. This is another reason why I continue to prefer
413 to report only the scaling relationships that apply to the raw data (Herculano-Houzel et al.,
414 2015a). These mathematical functions will be readily useful to researchers interested in the
415 relationships between the physical entities involved; other researchers interested in the
416 phylogenetic signal possibly contained within the raw data provided are welcome to apply in their
417 own studies to further phylogenetic studies of evolution, which are not at all the focus of the
418 present work.

419 A still growing number of studies have focused on establishing whether dinosaurs were
420 ectotherms, mesotherms, or had the high metabolic rates characteristic of modern warm-
421 blooded animals, and the fast-paced behavior and life history that come with it (Werner and
422 Griebeler, 2014; Grady et al., 2014; Wiemann et al., 2022). The present findings on the diverse
423 scaling of brain x body mass across dinosaur clades, which are compatible with endothermy in
424 some and ectothermy in other species, add to the still-going debate about the metabolic
425 condition of fossil dinosaurs by disputing the claim of homogeneous mesothermy across species
426 (Grady et al., 2014) in favor of much larger diversity than previously suspected, supporting the
427 finding that higher metabolic rates appeared in some but not all dinosaur clades (Wiemann et
428 al., 2022). Specifically, while most theropods and the single sauropodmorph (*Diplodocus*) tested
429 had advanced lipoxidation end-products accumulated in quantities indicative of high metabolic
430 rates, different ornithischian and pterosaur species showed concentrations compatible with
431 either high or low metabolic rates (Wiemann et al., 2022). So much diversity amongst dinosaurs
432 and pterosaurs in both metabolism and brain x body scaling (Figure 2b) warrants discontinuation
433 of the practice of treating these species as a mixed bag in scaling studies. Instead of using all-
434 encompassing scaling rules such as the power function shown in Figure 2c, clade-specific analyses
435 and scaling rules should be employed, informed by other features such as analysis of metabolites
436 (Wiemann et al., 2022), which suggests the clustering indicated by the colors in Figure 2c, or by

437 the scaling relationship between brain and body mass, which suggests the clustering indicated
438 by the colors in Figure 2d.

439 As modeling techniques based on micro-CT data improve and allow the volume of other
440 brain structures to be estimated (Knoll et al., 2021), more evidence should help distinguish which
441 dinosaur and pterosaur species were ecto- or endothermic. The cerebellum, for example, is
442 decidedly larger in extant endothermic species compared to ectothermic species of similar body
443 mass (Kverkova et al., 2022); thus, the size of the cerebellum relative to the mass of the
444 telencephalon (Herculano-Houzel, 2022) and of the body may serve as a new diagnostic criterion
445 to infer the metabolic status of species of the prehistoric fauna. Importantly, this is not a
446 difference of 10-20%, but of 10-20 times in volume of the cerebellum relative to the brainstem
447 between living endothermic and ectothermic amniotes; therefore, models and simulations that
448 estimate the volume of the cerebellum in fossil animals of unknown metabolic status would
449 greatly contribute not only to understanding cerebellar evolution, but also to determining their
450 metabolic status. Still, absent volumetric analyses of the cerebellum, simply determining whether
451 the brain vs body mass relationship clusters with endothermic, pre-K-Pg birds or with
452 ectothermic sauropsids, as more fossil species have their brain and body masses estimated,
453 should already provide diagnostic evidence of the metabolic status of those species.

454 Estimating the numbers of neurons in the telencephalon, whose main component is the
455 pallium, a major contributor to behavioral flexibility, is obviously consequential for inferring the
456 cognitive capabilities of dinosaur species, whatever their body size (Herculano-Houzel, 2017). The
457 present estimates showing that apex predators such as *Tyrannosaurus* had the numbers of
458 telencephalic neurons found in modern medium-sized primates of impressive cognitive abilities
459 adds a new dimension to how dinosaurs are pictured; an elephant-sized but agile carnivoran
460 biped endowed with macaque- or baboon-like cognition must have been an extremely
461 competent predator indeed. But additionally, I showed recently that the number of neurons in
462 the pallium is a true and reliable predictor of age at sexual maturity and maximal longevity in
463 warm-blooded animals (Herculano-Houzel, 2019a), such that 74% of variation in these life-history
464 variables can be predicted in mammals and birds alike simply by the absolute number of neurons
465 in the cerebral cortex, whereas body mass is an irrelevant predictor once numbers of cortical

466 neurons are accounted for (Herculano-Houzel, 2019a). Using the reported equations $L = e^{-4.939}$
467 $N_{cx}^{0.402}$ and $S = e^{-2.858} N_{cx}^{0.471}$ that relate maximal longevity (L) and age at female sexual maturity
468 (S), respectively, to numbers of cortical neurons (N_{cx}; Herculano-Houzel, 2019), and assuming
469 that most telencephalic neurons in sauropsids are pallial (Kverkova et al., 2022), I can predict that
470 a warm-blooded *Tyrannosaurus* of 2.2-3.3 billion telencephalic neurons would take 4-5 years to
471 reach sexual maturity, and have an estimated maximal longevity of 42-49 years, similar to
472 baboons, whereas *Archaeopteryx* should reach sexual maturity in ca. 8 months, and have a
473 maximal lifespan of 10 years, similar to flycatchers and other songbirds (Herculano-Houzel,
474 2019). In support of this estimate based on extant warm-blooded species, the survivorship
475 pattern of tyrannosaurs is similar to that seen in long-lived, mammals and birds (Erickson et al.,
476 2006). The predicted sexual maturity of *Tyrannosaurus* at age 5 years, like in modern warm-
477 blooded amniotes of similar numbers of cortical neurons, anticipates by a full decade the
478 previous demonstration that, at 18 years of age, this species was sexually mature (although that
479 was admittedly an upper bound; Lee and Werning, 2008). While the largest and oldest known *T.*
480 *rex* lived an estimated 28 years, well under the predicted maximal longevity, the finding that only
481 2% of the population lived long enough to attain maximal size and age for the species (Erickson
482 et al., 2006) makes the estimate of a maximal lifespan of just over 40 years compatible with the
483 oldest known fossil.

484 Through their association with delayed sexual maturity and longer lifespans, larger
485 numbers of telencephalic neurons simultaneously endow brains with the cognitive flexibility that
486 can be construed as intelligence (Herculano-Houzel, 2017) and come with increased lifetime
487 opportunities to develop that increased biological signal processing capability into abilities such
488 as using and creating tools, and devising and perpetuating problem-solving processes
489 (Herculano-Houzel, 2019b). With enough pallial neurons and a long enough lifetime that comes
490 with it, generations overlap enough that developed abilities can be transmitted and perpetuated,
491 forming a body of technology and culture that characterizes populations (Herculano-Houzel,
492 2019b). The present findings invite the speculation that theropod dinosaurs such as *T. rex*, with
493 even more telencephalic neurons than modern tool-using and tool-making corvids (Olkowicz et
494 al., 2016), had the biological capability to use and craft tools, and develop a culture, like modern

birds and primates (Beck, 1974; Whiten et al., 1999; Sapolsky and Share, 2004; von Bayern et al.., 2018). Being able to infer what existed inside the brains of dinosaurs thus multiplies in several directions our knowledge of what life was like in the pre-asteroid, Mesozoic world, and places at least theropods, if not other dinosaurs as well, in the cognitive realm of tool-using and culture-building modern birds and primates.

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Acknowledgements

Thanks to Pavel Nemec and collaborators who collected the reptilian data that made this study possible, and to Fabien Knoll and another reviewer who remained anonymous for greatly improving this manuscript. This work was not supported by any type of funding.

Competing interests: None.

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Table 1. 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 reptiles; Figure 1c). M_{bd}, body mass in grams; M_{br}, brain mass in grams, converted from estimated brain volume in cm^3 using 1 cm^3 = 1 g. Source of M_{bd} and M_{br} data is indicated next to each species (*a*, Witmer et al., 2003; *b*, Hurlburt, 1996; *c*, Hurlburt et al., 2013; *d*, Balanoff et al., 2013). 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 (AMNH 25555) [a]	7,600	7.720	43.7 M	**188.9 M**	454	16
Pterodactylus kochi[b]	450	0.420	**7.4 M**	21.1 M	162	7
Pterodactylus elegans[b]	60	0.140	**3.8 M**	9.2 M	109	5
Pteranodon[b]	20,000	4.800	**32.7 M**	132 M	383	14
Rhamphorynchus gemmingi[b]	310	0.700	**10.0 M**	31.0 M	194	8

Rhamphorynchus muensteri (CM 11434)[a]	136	0.830	11.2 M	**35.2 M**	206	8
Scaphognathus purdoni[b]	1,500	1.560	**16.4 M**	56.7 M	257	10
Ornithischians						
Anatosaurus[b]	3,400,000	150.0	268.5 M	**1,764 M**	1,300	38
Camptosaurus[b]	400,000	23.0	**85.2 M**	429.9 M	668	22
Euoplocephalus[b]	1,900,000	41.0	**121.4 M**	664.4 M	821	26
Iguanodon[b]	2,100,000	125.0	240.2 M	**1,538 M**	1,219	36
Kentrosaurus[b]	780,000	24.0	**87.5 M**	443.9 M	679	22
Protoceratops[b]	200,000	28.0	**96.1 M**	498.5 M	717	23
Stegosaurus[b]	3,100,000	22.5	**84.1 M**	422.8 M	663	22
Stegosaurus[b]	2,000,000	22.5	**84.1 M**	422.8 M	663	22
Triceratops[b]	9,000,000	72.2	**171.7 M**	1,017 M	1,003	31
Triceratops[b]	6,000,000	72.2	**171.7 M**	1,017 M	1,003	31
Sauropodmorphs						
Brachiosaurus[b]	78,300,000	186.0	**306.3 M**	2,075 M	1,403	41
Brachiosaurus[b]	40,000,000	186.0	**306.3 M**	2,075 M	1,403	41
Brachiosaurus[b]	29,000,000	186.0	**306.3 M**	2,075 M	1,403	41
Diplodocus[b]	19,000,000	57.0	**148.5 M**	851.4 M	922	29
Diplodocus[b]	12,000,000	57.0	**148.5 M**	851.4 M	922	29
Theropods						
Acrocanthosaurus atokensis (OMNH 10146)[d]	3,770,000	191.0	311.3 M	**2,116 M**	1,416	41
Alioramus altai (IGM 100/1184)[d]	359,000	73.2	173.2 M	**1,028 M**	1,008	31
Allosaurus[b]	2,300,000	168.0	287.8 M	**1,921 M**	1,353	40
Allosaurus[b]	1,400,000	168.0	287.8 M	**1,921 M**	1,353	40
Bambiraptor[c]	6,582	14.0	62.9 M	**295.8 M**	561	19
Citipati osmolskae (IGM 100/978)[d]	85,960	22.620	84.4 M	**424.5 M**	665	22
Conchoraptor gracilis (IGM 100/3006)[d]	5,020	9.440	49.4 M	**219.8 M**	487	17
Dromicioemimus[b]	175,000	87.85	193.6 M	**1,179 M**	1,075	33
Dromicioemimus[b]	125,000	87.85	193.6 M	**1,179 M**	1,075	33
Khaan mckennai (IGM 100/973)[d]	12,610	8.830	47.4 M	**209.1 M**	476	17
Shuvuuia deserti (IGM 100/977)[d]	250	0.830	**11.2 M**	35.2 M	206	8
Troodon[b]	45,000	41.0	121.4 M	**664.4 M**	821	26

Troodontid (IGM 100/1126)[d]	920	3.110	25.1 M	**95.3 M**	329	12
Tsaagan mangas (IGM 100/1015)[d]	15,950	3.070	**24.9 M**	94.4 M	327	12
Tyrannosaurus[b]	7,400,000	202.0	322.2 M	**2,207 M**	1,445	42
Tyrannosaurus[b]	5,000,000	202.0	322.2 M	**2,207 M**	1,445	42
Tyrannosaurus rex (AMNH 5029)[d]	5,840,000	343	445.5 M	**3,289 M**	1,743	49
Zanabazar junior (IGM 100/1)[d]	49,300	25.14	90.0 M	**459.7 M**	690	23
Aves						
Archaeopteryx[b]	400	1.470	15.8 M	**54.2 M**	252	10
Archaeopteryx[b]	300	1.470	15.8 M	**54.2 M**	252	10
Archaeopteryx[b]	400	1.760	17.7 M	**62.1 M**	269	10
Archaeopteryx[b]	300	1.760	17.7 M	**62.1 M**	269	10
Archaeopteryx lithographica (BMNH 37001)[d]	500	1.440	15.6 M	**53.4 M**	250	10
Unnamed protoavis[b]	600	3.320	26.1 M	**100.1 M**	336	13

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