Mammals, birds and reptiles evolved with signature proportions of numbers of neurons across their brain structures

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Running title: Signature neuron ratios in amniote brains

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Abstract

Modern mammals, birds, and "reptiles" (squamates, turtles and crocodiles) share their developmental and evolutionary origins in the ancestral, stem amniotes of 300 million years ago. This study explores how the brains of amniotes diverged in their neuronal composition. The systematic analysis of a large dataset on the cellular composition of the major parts of the brain of 242 amniote species shows that it is not the case that a general theme in amniote evolution is the proportional expansion of the telencephalon or pallium, for such expansion only happened in owls, in primates, and in the largest mammalian species. Instead, the brains of extant mammalian, avian, and reptile species are characterized by signature proportions of numbers of neurons across the brain divisions. Reptile brains, with few exceptions, are characterized by having fewer than 10 million neurons in each brain division, with about 1.5 neurons in the telencephalon and 0.5 neuron in the cerebellum to every neuron in the rest of brain. In contrast, the brains of the closely related birds are characterized by much larger numbers of neurons that occur at a higher, fixed proportion of 4.5 neurons in the cerebellum to every neuron in the rest of brain, with variable ratios of pallial neurons. The brains of mammalian species, in turn, are characterized by larger numbers of neurons that occur at an average 4 neurons in the cerebellum to every neuron in the pallium regardless of numbers of neurons in the rest of brain. There is a striking continuity in the scaling of the pallium (or telencephalon) of extant mammalian and squamate brains that argues for a quantitative continuum between the two groups and dispels the mistaken notion that mammalian brains evolved with a qualitative change or an "addition" of structures to the "reptilian brain". The shared scaling rules between mammalian and squamate brain structures also allow for predicting the composition of early synapsid brains in amniote evolution.

Keywords: brain evolution, amniotes, numbers of neurons, brain size, endothermy

Introduction

Extant mammals (synapsids) and sauropsids (birds, squamates, turtles and crocodiles), which together constitute the amniotes amongst animals, are markedly different in appearance, body size, and life histories. Yet, they derive from common stem amniote ancestors that lived ca. 300 million years ago (Kemp, 2006), and their brains still share a common developmental program (Puelles et al., 2013). The largest amniote brains are all mammalian, but mammalian brains can be as small as those of some lizards; modern bird brains, in turn, are larger than most squamate brains, but not larger than those of dog-sized mammals (Kverkova et al., 2022). How did so much diversity in brain size arise, how come the different ranges, and how do they compare in terms of numbers of neurons?

Understanding the evolutionary history of modern amniote brains – those of mammals, birds, squamates, turtles and crocodiles – is an enterprise that is necessarily built on the comparative study of these extant brains in order to infer how they arose from evolutionary changes over time in their respective developmental programs. Until the advent of the isotropic fractionator, a method to reliably and rapidly count the neuronal and non-neuronal cells that compose brains without having to painstakingly cut them into thin sections for histological processing, microscopy and stereological analysis (Herculano-Houzel and Lent, 2005; Herculano-Houzel et al., 2015a), comparative studies of vertebrate brains were necessarily focused on the available data on structure size. While any data were better than no data, the limitation to data on structure size posed a number of problems. First, the interpretation of comparative studies of brain structure volume required the tacit assumption that the underlying scaling rules governing the cellular composition of brain tissues were shared across species and clades, or any results would be meaningless. Data obtained during the early 2000s using the isotropic fractionator rapidly proved this assumption to be invalid, for the relationship between the size of a brain or brain structure and its number of neurons is clade-specific such that structures of a similar size can have numbers of neurons that vary by a factor of up to 10-fold across species of different clades (Herculano-Houzel et al., 2006, 2007). Of note, the human cerebral cortex would indeed appear to be an outlier in its number of neurons, with ten times the number of neurons expected for a rodent cerebral cortex of similar mass – but its average of 16 billion neurons matches the prediction for a generic primate cortex of its mass (Azevedo et al., 2009). Second, absolute and

relative measurements of brain structure size often yielded conflicting interpretations (for instance, see Clark et al., 2001 and Sultan, 2002), for their meaning depends additionally on whether or not the size of the whole brain is a relevant reference and normalizer for brain structures. This, in turn, depends on whether the relative size of a brain structure accurately reflects the relative number of brain neurons located in that structure – which, it turns out, it does not (Herculano-Houzel, 2010; Herculano-Houzel et al., 2014a). For instance, the number of neurons in the mammalian cerebellum closely accompanies the number of neurons in the cerebral cortex across species such that an average rate of four neurons in the former for every neuron in the latter applies to the majority of mammals, even though the relative size of the cerebellum becomes smaller as the relative size of the cerebral cortex increases in larger species (Herculano-Houzel, 2010).

An even more problematic complication is the use of normalization of brain or brain structure size to body mass for comparisons across species, an expedient that became popular once it finally succeeded in setting humans apart from other species (Jerison, 1973). The problem with using body mass as a normalizer is that it assumes a mandatory and universal relationship between body mass and the numbers of neurons, and the mass of the brain structures housing those neurons, that operate the body (Jerison, 1973). In contrast, we have observed repeatedly that body size is largely free to vary across individuals and species without mandatory consequences for the numbers of neurons that compose brain structures or spinal cord (Burish et al., 2010; Herculano-Houzel et al., 2015b, 2015c). Put another way, bodies of a similar size occur with up to 50-fold different numbers of neurons in the spinal cord and brainstem across mammalian species. To understand evolutionary changes in brain composition, then, one must look at exactly that: variations in the numbers of neurons that compose the brain, regardless of variations in body mass.

Using the isotropic fractionator, my colleagues and I generated a body of data on the numbers of neuronal and non-neuronal cells that compose the major brain structures of 75 mammalian, 28 bird species, and the Nile crocodile (Herculano-Houzel et al., 2015b; Ngwenya et al., 2016; Olkowicz et al., 2016; Dos Santos et al., 2017; Jardim-Messeder et al., 2017). Those data showed that while similar scaling relationships for each of the major brain parts applied to many

mammalian (with the exception of primates) and bird species, there were obviously higher neuronal densities in the telencephalon of songbirds and parrots – even higher than in primates (Olkowicz et al., 2016). While those findings provided an answer to the question of how some birds can be as cognitively capable as primates (answer: because their small brains harbor primate-like numbers of pallial, and particularly associative pallial, neurons; Ströckens et al., 2022, Sol et al., 2022), addressing the question of how bird brain composition came to differ from mammalian brain composition required obtaining data on the third group of amniotes that links them together: extant ectothermic sauropsids. That is because while birds are a derived group amongst sauropsids, appearing within theropod dinosaurs during the Jurassic (Norell and Xu, 2005), modern squamates, which are ectothermic Sauropsids, are a sister group to mammals, with whom they share common ancestors that lived ca. 300 Mya (Kemp, 2006). Thus, comparison of the neuronal scaling rules between squamates and mammals might reveal the scaling rules that applied to the brains of ancestral amniotes.

That required dataset, with the numbers of neurons that compose the brains of 107 ectothermic sauropsid species in 6 major clades and an additional 37 endothermic sauropsid species covering a total of 9 avian (hereafter "bird") clades, was published recently (Kverkova et al., 2022). In this dataset, sauropsid brains were divided into telencephalon/cerebellum/rest of brain, in which case the subpallium is included in the telencephalon, and "rest of brain" is the brainstem plus diencephalon. In birds, numbers of cells were also available for the two parts of the telencephalon: the pallium (directly equivalent and indeed homologous to the mammalian cerebral cortex; Puelles et al., 2013) and subpallium (Olkowicz et al., 2016; Kverkova et al., 2022). By moving numbers for the subpallium into the "rest of brain", the bird data can be compared directly with the published data for mammals, in which the brain is subdivided into cortex/cerebellum/rest of brain, and the latter also includes the subpallium. While it is unfortunate that the subpallium was not separated from the pallium in the telencephalon of the ectothermic sauropsids examined, the total number of neurons in their telencephalon is small compared to the "rest of brain" in these species (Kverkova et al., 2022). With these caveats in mind, the combined dataset allows for the comparison of numbers of cells in the ectothermic sauropsid telencephalon/bird pallium/mammalian cerebral cortex, cerebellum, and the "rest of

133 brain" (hindbrain to diencephalon in ectothermic sauropsids, hindbrain to subpallium in birds
134 and mammals). For the sake of simplicity, and absent a better word to describe the ensemble of
135 ectothermic Sauropsids (that is, the ensemble of Archosauria that includes squamates, turtles
136 and crocodiles but excludes birds), I will heretofore refer to the ectothermic Sauropsids as
137 "reptiles".

138 The study that originally reported the reptile and extended bird dataset (Kverkova et al.,
139 2022) focused on describing the grade shifts in the relationship between brain and body mass
140 that characterize amniote evolution, but did not address a number of fundamental issues in
141 amniote brain evolution, starting with the neuronal scaling rules that apply to each clade
142 specifically whose systematic comparison is necessary to shed light on the evolution of the
143 amniote brain. Further, anchoring interpretations of brain evolution on relationships to body
144 mass is a flawed expedient that assumes a mandatory and universal relationship between brain
145 and body mass that is not there, as attested recently by studies on bird and mammalian brain
146 evolution (Ksepka et al., 2020; Bertrand et al., 2022) and our demonstrations that there is no
147 mandatory, much less a universal, scaling relationship between numbers of brain neurons and
148 body mass across species (Herculano-Houzel et al., 2015b,c; Ngwenya et al., 2016). Additionally,
149 studies of brain scaling often resort to "correcting" for phylogenetic relationships in the dataset
150 (as done in Kverkova et al., 2022), a procedure that aspires to eliminate sampling bias but glosses
151 over differences in scaling relationships across clades, and contaminates scaling relationships in
152 the raw data with inferences about phylogenetic relations that may or may not be correct. Since
153 the point of the present analysis is understanding the mathematics of the relationship between
154 the size of the brain and of how many cells brain tissue is made across different animal clades, I
155 focus the analysis on the scaling relationships that apply to the raw data; the only phylogenetic
156 information taken into consideration is that pertaining to the nested clades that each animal
157 belongs to. Indeed, the expedient of analyzing scaling relationships separately per clade achieves
158 on its own the most important type of "correcting" for phylogenetic relationships, which is
159 exactly the possibility that clade-specific scaling relationships exist.

160 Here I use the combined dataset of 242 amniote species to determine, regardless of body
161 mass, the cellular scaling relationships that apply to each clade among the three groups of

amniote animals – reptiles, mammals, and birds – to then address the following questions. First, is the relationship between brain structure mass and number of non-neuronal cells (the so-called non-neuronal scaling rule) that applies universally to mammals (Herculano-Houzel and Dos Santos, 2018) extensive to reptiles and birds? Non-neuronal cells in the brain include the endothelial cells that compose the brain vasculature, which may or may not scale similarly across endothermic and ectothermic species. Is the scaling of non-neuronal cells shared at least by all sauropsids (ectothermic reptiles and endothermic birds), or by all endothermic species? Second, are the main brain structures of amniotes fundamentally different in their neuronal composition, or do they form a continuum along a single scaling relationship across reptiles, birds and mammals, at least across the more closely related clades of reptiles and birds? Third, if there are such continuums, can the scaling rules that applied to the main divisions of the brain of ancestral amniote species be inferred? In that case, can amniote brain diversity be understood as a simple evolutionary story of continuity with occasional deviations, without major grade shifts, or are there major grade shifts to be accounted for – for example, associated with the independent evolution of endothermy in birds and mammals (Nespolo et al., 2011)?

The findings below are based exclusively on directly comparable data on numbers of neurons and mass of the telencephalon, cerebellum and rest of brain obtained with the isotropic fractionator for 242 species of reptiles, mammals and birds, compiled in Kverkova et al. (2022). For consistency, the olfactory bulbs, which are often not collected whole in brain dissections, are not included in any structure. All power functions were calculated using least-squares regression of log-transformed values in JMP 16 (Carey, NC).

Relationships of brain mass to body mass

Any systematic examination of how the neuronal composition of the brain evolved amongst amniotes must begin with laying down the basic aspects of how those brains have changed, and that starts with the relationship between the size of the brain and the size of the body. Across the 242 species of reptiles, mammals, and birds in the combined dataset, whole brain mass varies almost 500,000-fold, from 0.01 g in the Algerian sand gecko to 4,618.62 g in the African elephant, whereas body mass varies ten times as much, by a factor of 5 million, from

192 1 g to 5 Tons in the same species (Figure 1A). As a whole, larger species have larger brains, but in
193 a clade-specific manner. The power functions that describe the scaling of body mass with brain
194 mass across species of each clade amongst the three groups of amniotes in the dataset are
195 provided in Table 1. Importantly, within each group – reptiles, birds, and mammals –, a number
196 of clades share scaling rules, which is key to inferring what was once the scaling rule that applied
197 to ancestral animals in each group. The power functions that apply for each clade, and to groups
198 of clades that share scaling rules, are documented in Table 1.

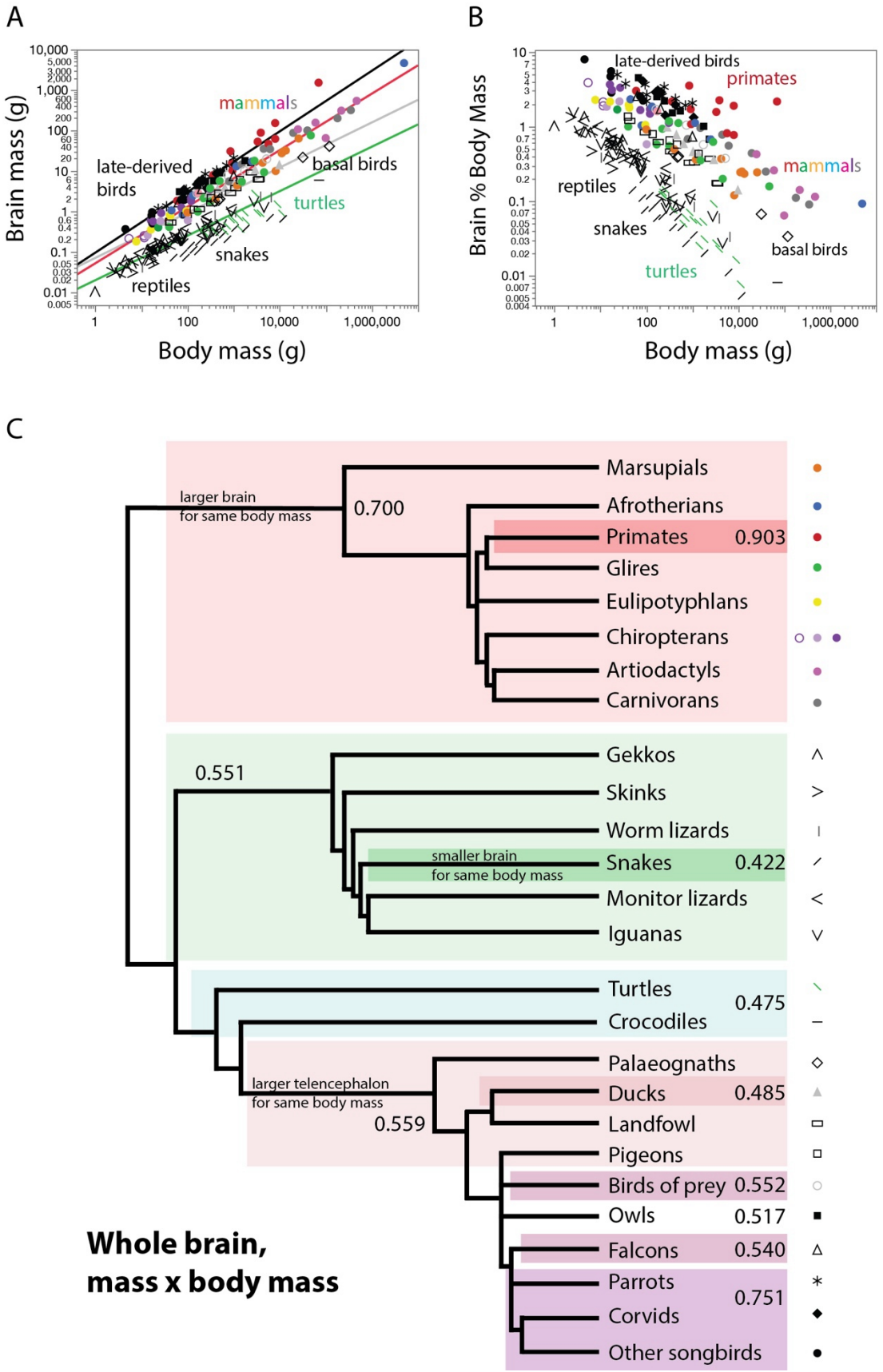
199 The wealth of data in the combined dataset can be summarized as follows. First: In every
200 clade, brain mass scales with brain mass raised to an exponent that is smaller than unity. This
201 means that while larger animals have larger brains, the brain does not increase in mass as rapidly
202 as the body does. The consequence is that larger animals have *relatively smaller* brains, as shown
203 in Figure 1B. The range of variation is enormous: amniote evolution has resulted in brains that
204 represent as little as 0.005% (in the snake *Boa constrictor*) and as much as 8% of body mass (in
205 the songbird *Regulus regulus*).

206 Second: As has been well established, and as Figures 1A and B illustrate, reptiles (the
207 ectothermic Sauropsids) have systematically smaller brains for their body sizes compared to birds
208 and mammals (Jerison, 1973), such that all data points for reptile species fall well below the data
209 points for the endothermic species (Figure 1A,B). The advent of endothermy was thus
210 accompanied by a step increase in the relative size of the brain (Jerison, 1973). Importantly,
211 however, similar step-like changes apply amongst birds and mammals. Amongst the former,
212 "basal birds" – Palaeognaths, Galliformes and Columbiformes, in particular – have much smaller
213 brains than "late-derived birds" – Passeriformes and Psittaciformes – of similar body mass.
214 Amongst mammals, it is primates that have larger brains than other species of similar body mass
215 (Figure 1B).

216 Third: As mentioned above, there is variation across clades within each of the three
217 groups of amniotes in the scaling of brain mass with body mass. The schematic in Figure 1C
218 captures the main differences. Most reptiles share the scaling of brain mass with body mass
219 raised to an exponent of 0.551±0.019, but snakes, and turtles and crocodiles, stand out with not
220 only relatively smaller brains but also smaller scaling exponents (Table 1). Interestingly, the

221 scaling exponent that applies to basal birds, of 0.559±0.021, is not significantly different from the
222 exponent that applies to most reptiles – although, as mentioned above, basal birds have brains
223 that are roughly 3.6x as large as reptiles of a similar body mass. The similar scaling exponent with
224 a shifted intercept (Table 1) indicates that birds arose with a step change towards a relatively
225 larger brain size – which, mechanistically, could result both from the enlargement of the brain
226 for a given body mass, and from the shrinking of the body that forms around the brain. Mammals,
227 in contrast, show both the step increase in relative brain size and a significantly different scaling
228 exponent for brain mass with body mass, of 0.700±0.017 across non-primate species (Figure 1C,
229 Table 1).

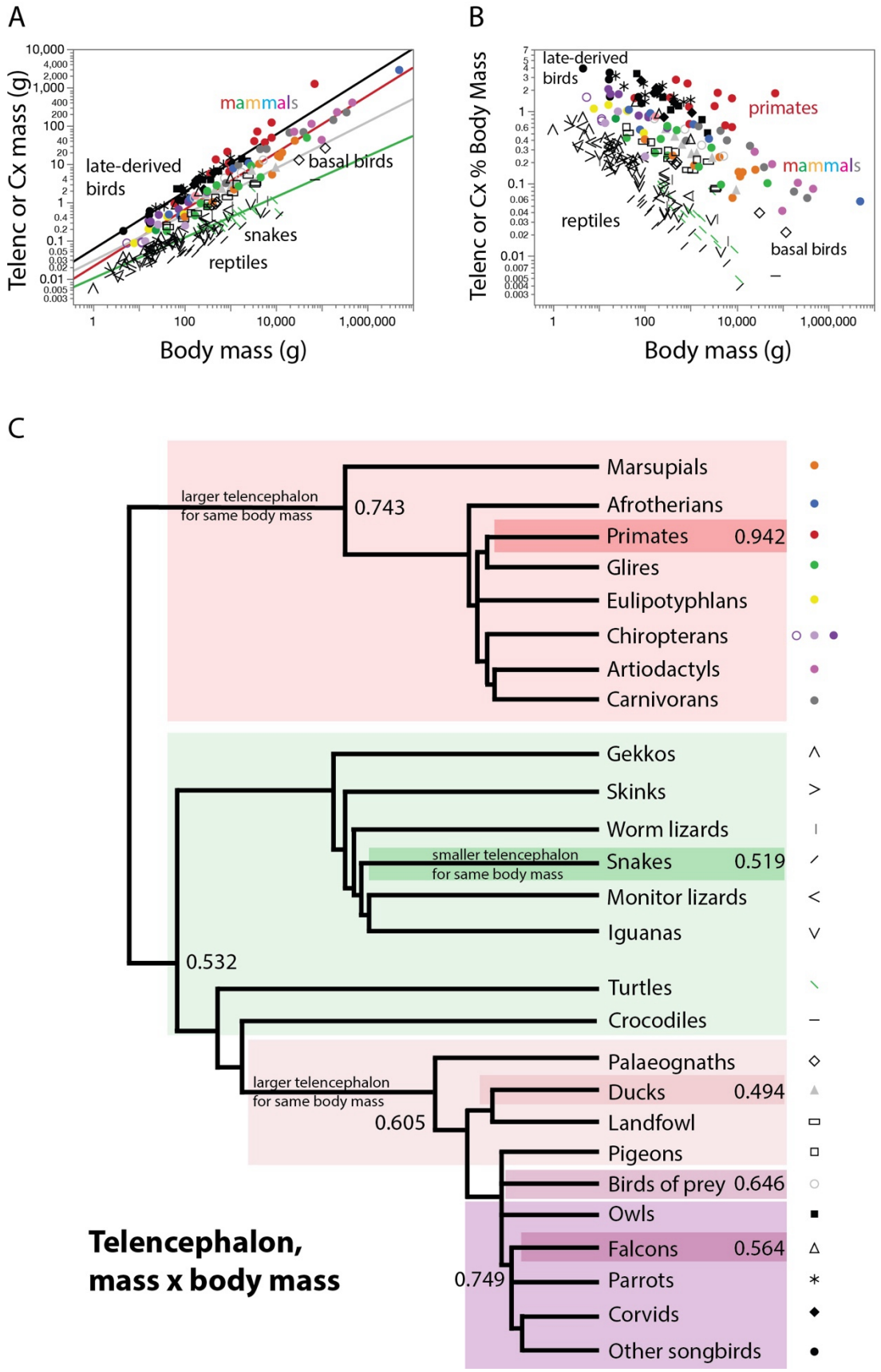
230 These major differences in the scaling of brain mass with body mass within and across
231 reptiles, birds and mammals, depicted schematically in Figure 1C, show that a change in relative
232 brain size did occur twice independently, first at the origin of mammals (assuming that ancestral
233 amniotes were ectothermic, as modern reptiles remain; see Nespolo et al., 2011), and later again
234 at the origin of birds. However, similar step changes apparently happened anew at the origin of
235 Strigiformes; at the origin of Passeriformes and Psittaciformes; and at the origin of Primates. This
236 indicates that there are mechanisms other than whatever caused endothermy that may lead to
237 a relative enlargement of the amniote brain.


A
Brain mass (g)
Body mass (g)
mammals
late-derived birds
basal birds
turtles
snakes
reptiles
B
Brain % Body Mass
Body mass (g)
late-derived birds
primates
mammals
reptiles
snakes
basal birds
turtles
C
larger brain for same body mass
0.700
Marsupials
Afrotherians
Primates 0.903
Glires
Eulipotyphlans
Chiropterans
Artiodactyls
Carnivorans
0.551
Gekkos
Skinks
Worm lizards
smaller brain for same body mass
Snakes 0.422
Monitor lizards
Iguanas
Turtles
Crocodiles
0.475
larger telencephalon for same body mass
0.559
Palaeognaths
Ducks 0.485
Landfowl
Pigeons
Birds of prey 0.552
Owls 0.517
Falcons 0.540
Parrots
Corvids
0.751
Other songbirds
Whole brain, mass x body mass

238

Figure 1. Larger amniotes have larger brains, but relatively smaller brains, in a clade-specific manner. **A**, absolute brain mass increases as different power functions of body mass across reptiles (minus snakes, turtles and crocodiles; plotted in green), basal birds (plotted in grey), late-derived birds (plotted in black), and mammals (minus primates; plotted in red). **B**, relative brain mass decreases with increasing body mass. For the sake of clarity, power functions are not plotted here. **C**, evolutionary tree showing the clades that share similar scaling exponents, which are shown where applicable. Power functions are listed in Table 1. Each data point corresponds to one species. The key used to depict each clade, employed throughout this chapter, is shown to the right.

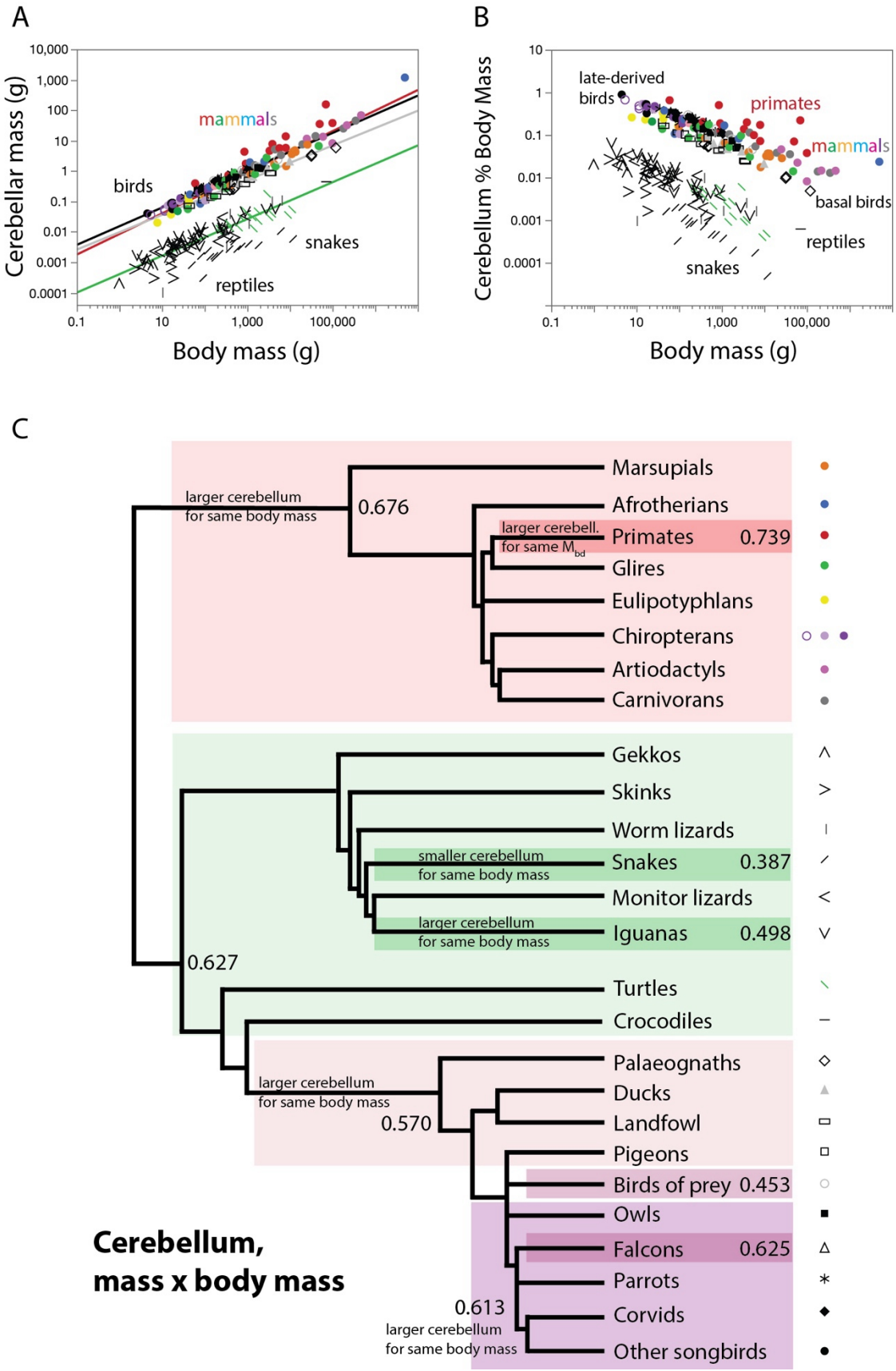
The three fundamental observations regarding the scaling of brain mass with body mass in amniotes – namely, the scaling exponents smaller than unity, the step change with the advent of endothermy, and the clade-specific scaling – also apply to each of the three main subdivisions of the brain: the telencephalon/pallium (which also describes the mammalian cerebral cortex), the cerebellum, and the "rest of brain". Figure 2 shows the scaling of the reptilian telencephalon, and the pallium of birds and mammals, where it is apparent that larger animals have an absolutely larger but also relatively smaller pallium; that birds and mammals have a larger pallium than reptiles of a similar body mass; and that clade-specific scaling rules apply. Most reptiles share the increase in mass of the telencephalon with body mass raised to the power of 0.532±0.018; interestingly, amongst reptiles of a given body mass, snakes have a relatively smaller telencephalon (expressed as a percentage of body mass, not of brain mass), although the scaling exponent remains similar (0.519±0.051). In both mammals and basal birds, there is a shift towards a relatively larger pallium compared to the body – which, again, could be the result of enlargement of the pallium or of a reduction in the size of the body –, and both within mammals and birds, there are some clades that have a particularly enlarged pallium for a given body mass (namely, primates, songbirds, parrots, and owls).


A
Telenc or Cx mass (g)
Body mass (g)
mammals
late-derived birds
basal birds
snakes
reptiles
B
Telenc or Cx % Body Mass
Body mass (g)
late-derived birds
primates
mammals
reptiles
basal birds
C
larger telencephalon for same body mass
0.743
Marsupials
Afrotherians
Primates 0.942
Glires
Eulipotyphlans
Chiropterans
Artiodactyls
Carnivorans
Gekkos
Skinks
Worm lizards
smaller telencephalon for same body mass
Snakes 0.519
Monitor lizards
Iguanas
0.532
Turtles
Crocodiles
larger telencephalon for same body mass
0.605
Palaeognaths
Ducks 0.494
Landfowl
Pigeons
Birds of prey 0.646
Owls
Falcons 0.564
0.749
Parrots
Corvids
Other songbirds
Telencephalon, mass x body mass

264

Figure 2. Larger amniotes have a larger pallium (or telencephalon) that is also relatively smaller, in a clade-specific manner. **A**, absolute cortical/pallial/telencephalic mass (in mammals, birds, and reptiles, respectively) increases as different power functions of body mass across reptiles (minus snakes; plotted in green), basal birds (plotted in grey), late-derived birds (plotted in black), and mammals (minus primates; plotted in red). **B**, relative cortical/pallial/telencephalic mass, expressed as a percentage of body mass, decreases with increasing body mass. For the sake of clarity, power functions are not plotted here. **C**, evolutionary tree showing the clades that share similar scaling exponents, which are shown where applicable. Power functions are listed in Table 1. Each data point corresponds to one species. The key used to depict each clade is shown to the right.

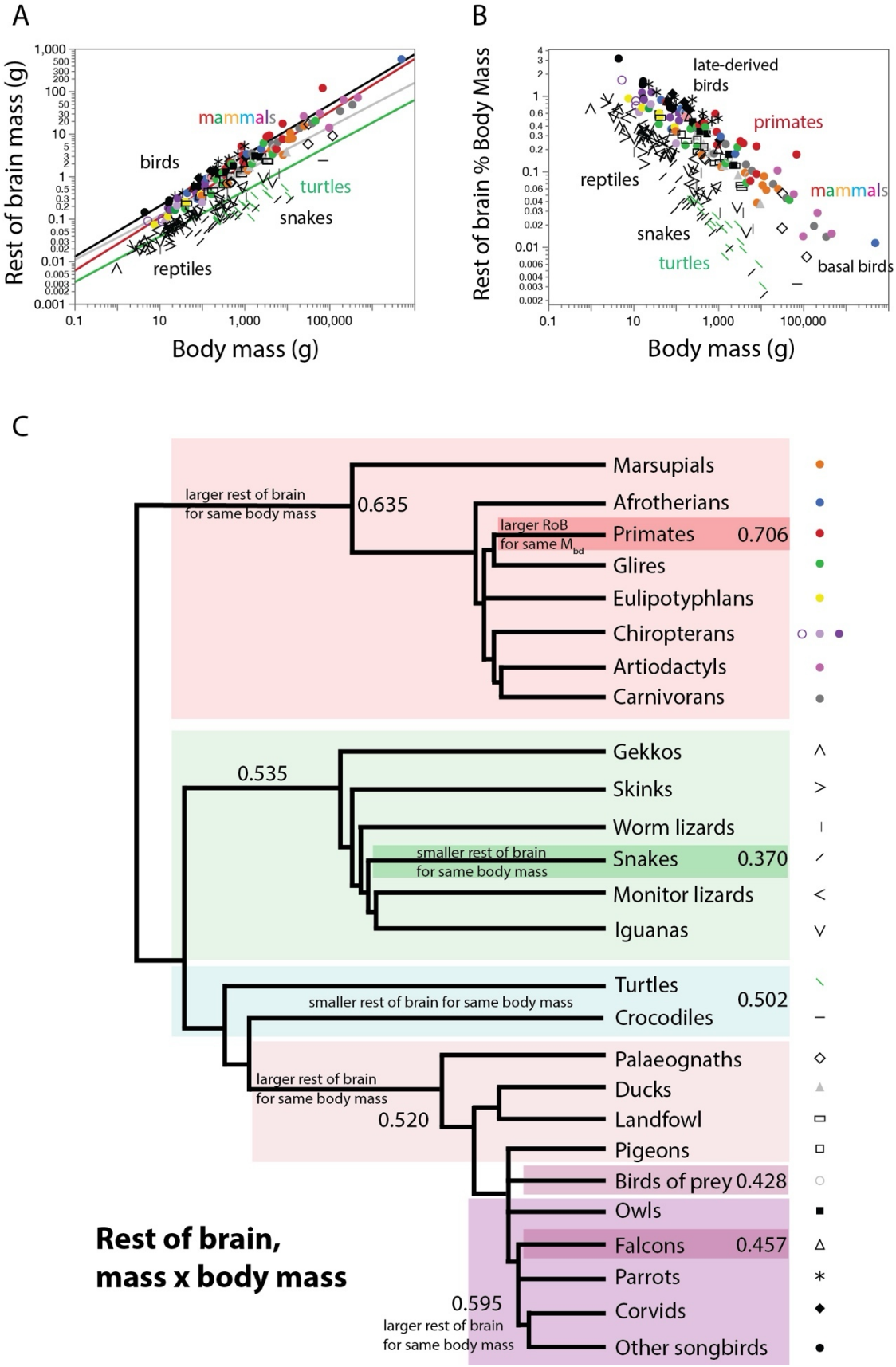
Similarly, Figure 3 shows the scaling of the amniote cerebellum, where it is again apparent that larger animals have an absolutely larger but also relatively smaller cerebellum (expressed as a fraction of body mass, not brain mass); that birds and mammals have a larger cerebellum than reptiles of a similar body mass; and that clade-specific scaling rules apply. Most reptiles, with the exception of snakes and iguanas, share an increase in mass of the cerebellum with body mass raised to the power of 0.627±0.034; interestingly, for a given body mass, snakes have a relatively smaller cerebellum compared to the size of the body, and iguanas have a relatively larger cerebellum, with scaling exponents that also veer away from the exponent shared by other clades (Figure 3C). In both mammals and basal birds, there is a shift towards a relatively larger cerebellum compared to the body, with a notable difference to the pallium: endothermic clades have a cerebellum that appears to be truly enlarged, with very little overlap with reptiles in absolute cerebellar mass (Figure 3A). Additionally, there is far less spread amongst endothermic species and clades in the scaling of cerebellar mass compared to the pallium (Figure 2). These key differences and their implications for understanding how brain evolution changed together with endothermy are explored in detail in a separate chapter (Herculano-Houzel, 2025).


A
Cerebellar mass (g)
10,000
1,000
100
10
1
0.1
0.01
0.001
0.0001
mammals
birds
snakes
reptiles
0.1
10
1,000
100,000
Body mass (g)
B
Cerebellum % Body Mass
10
1
0.1
0.01
0.001
0.0001
late-derived
birds
primates
mammals
basal birds
reptiles
snakes
0.1
10
1,000
100,000
Body mass (g)
C
larger cerebellum
for same body mass
0.676
larger cerebell.
for same M_{bd}
Marsupials
Afrotherians
Primates 0.739
Glires
Eulipotyphlans
Chiropterans
Artiodactyls
Carnivorans
Gekkos
Skinks
Worm lizards
smaller cerebellum
for same body mass
Snakes 0.387
Monitor lizards
larger cerebellum
for same body mass
Iguanas 0.498
0.627
Turtles
Crocodiles
larger cerebellum
for same body mass
0.570
Palaeognaths
Ducks
Landfowl
Pigeons
Birds of prey 0.453
Owls
Falcons 0.625
Parrots
Corvids
Other songbirds
0.613
larger cerebellum
for same body mass
Cerebellum,
mass x body mass

290

Figure 3. Larger amniotes have a larger cerebellum that is also relatively smaller, in a clade-specific manner. **A**, the absolute mass of the cerebellum increases as different power functions of body mass across reptiles (minus snakes; plotted in green), basal birds (plotted in grey), late-derived birds (plotted in black), and mammals (minus primates; plotted in red). **B**, relative cerebellar mass, expressed as a percentage of body mass, decreases with increasing body mass. For the sake of clarity, power functions are not plotted here. **C**, evolutionary tree showing the clades that share similar scaling exponents, which are shown where applicable. Power functions are listed in Table 1. Each data point corresponds to one species. The key used to depict each clade is shown to the right.

Figure 4 shows the scaling of the amniote rest of brain, which once more is absolutely larger, but also relatively smaller (as a fraction of body mass, not brain mass), in larger species. Again, the rest of brain is larger in birds and mammals than in reptiles of a similar body mass; and clade-specific scaling rules apply. Snakes are once again an exception amongst reptiles in the scaling of brain structure mass with body mass, but here they are joined by turtles and crocodiles, all of which have a smaller rest of brain than other reptiles of a similar body mass, whether with a similar scaling exponent (turtles and crocodiles) or a different one (snakes; Figure 4C). As seen for the pallium, there are some clades within mammals and birds that have a particularly enlarged rest of brain for a given body mass (namely, primates, songbirds, parrots, and owls); and there is a shift in both mammals and basal birds towards a relatively larger rest of brain compared to the body – which, again, could be the result of enlargement of the rest of brain or of a reduction in the size of the body.


A
Rest of brain mass (g)
Body mass (g)
mammals
birds
turtles
snakes
reptiles
B
Rest of brain % Body Mass
Body mass (g)
late-derived birds
primates
reptiles
mammals
snakes
turtles
basal birds
C
larger rest of brain for same body mass
0.635
larger RoB for same M_{bd}
Marsupials
Afrotherians
Primates 0.706
Glires
Eulipotyphlans
Chiropterans
Artiodactyls
Carnivorans
0.535
Gekkos
Skinks
Worm lizards
smaller rest of brain for same body mass
Snakes 0.370
Monitor lizards
Iguanas
smaller rest of brain for same body mass
Turtles
Crocodiles
0.502
larger rest of brain for same body mass
0.520
Palaeognaths
Ducks
Landfowl
Pigeons
Birds of prey 0.428
Owls
Falcons 0.457
Parrots
Corvids
Other songbirds
0.595
larger rest of brain for same body mass
Rest of brain, mass x body mass

312

Figure 4. Larger amniotes have a larger rest of brain that is also relatively smaller, in a clade-specific manner. **A**, the absolute mass of the rest of brain increases as different power functions of body mass across reptiles (minus snakes, turtles, and crocodiles; plotted in green), basal birds (plotted in grey), late-derived birds (plotted in black), and mammals (minus primates; plotted in red). **B**, relative cerebellar mass, expressed as a percentage of body mass, decreases with increasing body mass. For the sake of clarity, power functions are not plotted here. **C**, evolutionary tree showing the clades that share similar scaling exponents, which are shown where applicable. Power functions are listed in Table 1. Each data point corresponds to one species. The key used to depict each clade is shown to the right.

Table 1. Scaling of mass of the different brain structures of reptiles, birds and mammals with varying body mass. Values correspond to the equation $M_{str} = e^{a \pm SE} M_{bd}^{b \pm SE}$, the p-values for a and b, and the r^2 for the power fit, where M_{str} is the mass of a given brain structure and M_{bd} is the average body mass for the species. * pig excluded. **capybara excluded.

M_{str} x M_{bd}	n	a in e^a	b in M_{bd}^b	p, a	p, b	r^2
Whole brain						
Reptiles						
All	108	-3.749±0.104	**0.460**±0.020	<0.0001	<0.0001	0.842
Anguimorpha	7	-4.643±0.376	**0.646**±0.057	<0.0001	<0.0001	0.962
Crocodilia	1					
Gekkota	14	-4.294±0.172	**0.695**±0.058	<0.0001	<0.0001	0.923
Iguania	20	-3.787±0.162	**0.505**±0.032	<0.0001	<0.0001	0.932
Lacertoidea	15	-3.847±0.176	**0.561**±0.045	<0.0001	<0.0001	0.924
Scincoidea	14	-4.178±0.231	**0.598**±0.061	<0.0001	<0.0001	0.891
Serpentes	18	-4.148±0.259	**0.422**±0.043	<0.0001	<0.0001	0.861
Testudines	19	-3.528±0.512	**0.422**±0.072	<0.0001	<0.0001	0.668
Testudines and Crocodilia	20	-3.877±0.420	**0.475**±0.057	<0.0001	<0.0001	0.793
All minus Serpentes, Testudines and Crocodilia	70	-3.946±0.083	**0.551**±0.019	<0.0001	<0.0001	0.927
Birds						
All	65	-1.424±0.241	**0.470**±0.039	<0.0001	<0.0001	0.701
Accipitriformes	4	-1.748±0.340	**0.552**±0.048	0.0359	0.0076	0.985
Anseriformes	7	-1.731±0.283	**0.485**±0.039	0.0017	<0.0001	0.968
Columbiformes	5	-3.189±0.142	**0.681**±0.025	0.0002	0.0001	0.996
Falconiformes	3	-1.710±0.290	**0.540**±0.052	0.1070	0.0611	0.991
Galliformes	9	-3.023±0.285	**0.612**±0.044	<0.0001	<0.0001	0.966
Palaeognathae	6	-2.814±0.080	**0.562**±0.009	<0.0001	<0.0001	0.999
Passeriformes	13	-2.269±0.239	**0.714**±0.051	<0.0001	<0.0001	0.946
Psittaciformes	11	-2.488±0.254	**0.785**±0.048	<0.0001	<0.0001	0.968

Strigiformes	7	-1.155±0.256	**0.517**±0.042	0.0063	<0.0001	0.969
Passeriformes, Psittaciformes	24	-2.376±0.174	**0.751**±0.035	<0.0001	<0.0001	0.954
Galliformes, Columbiformes, Palaeognathae	20	-2.674±0.146	**0.559**±0.021	<0.0001	<0.0001	0.976
Accipitriformes, Falconiformes	7	-1.771±0.159	**0.554**±0.025	0.0001	<0.0001	0.990
Mammals						
All	69	-2.983±0.183	**0.729**±0.024	<0.0001	<0.0001	0.931
All non-primates	57	-2.982±0.127	**0.700**±0.017	<0.0001	<0.0001	0.969
Afrotheria	6	-2.927±0.270	**0.740**±0.033	0.0004	<0.0001	0.992
Artiodactyla*	4	-0.939±0.445	**0.548**±0.038	0.1690	0.0048	0.990
Carnivora	8	-1.877±0.499	**0.609**±0.051	0.0094	<0.0001	0.959
Chiroptera	13	-2.856±0.340	**0.693**±0.092	<0.0001	<0.0001	0.838
Eulipotyphla	5	-3.112±0.329	**0.727**±0.094	0.0025	0.0045	0.952
Marsupialia	9	-3.680±0.510	**0.742**±0.061	0.0002	<0.0001	0.955
Primata	11	-3.323±0.645	**0.903**±0.082	0.0006	<0.0001	0.931
Glires	10	-3.287±0.489	**0.712**±0.071	0.0001	<0.0001	0.927
Scandentia	1					
Cortex/pallium/telencephalon						
Reptiles						
All	108	-4.586±0.110	**0.503**±0.021	<0.0001	<0.0001	0.850
Anguimorpha	7	-5.231±0.514	**0.651**±0.078	0.0002	0.0004	0.933
Crocodilia	1					
Gekkota	14	-4.851±0.219	**0.690**±0.074	<0.0001	<0.0001	0.880
Iguania	20	-4.793±0.165	**0.527**±0.033	<0.0001	<0.0001	0.934
Lacertoidea	15	-4.742±0.184	**0.616**±0.046	<0.0001	<0.0001	0.931
Scincoidea	14	-4.959±0.223	**0.640**±0.058	<0.0001	<0.0001	0.909
Serpentes	18	-5.326±0.309	**0.519**±0.051	<0.0001	<0.0001	0.867
Testudines	19	-3.845±0.585	**0.415**±0.083	<0.0001	0.0001	0.598
Testudines and Crocodilia	20	-4.179±0.474	**0.465**±0.065	<0.0001	<0.0001	0.742
All minus Serpentes	90	-4.593±0.092	**0.532**±0.018	<0.0001	<0.0001	0.912
Birds						
All	65	-2.029±0.299	**0.481**±0.048	<0.0001	<0.0001	0.614
Accipitriformes	4	-2.979±0.334	**0.646**±0.047	0.0124	0.0054	0.989

Anseriformes	7	-2.316±0.370	**0.494**±0.052	0.0015	0.0002	0.948
Columbiformes	5	-4.106±0.162	**0.708**±0.029	0.0001	0.0001	0.995
Falconiformes	3	-2.449±0.282	**0.564**±0.050	0.0729	0.0568	0.992
Galliformes	9	-3.997±0.334	**0.647**±0.051	<0.0001	<0.0001	0.958
Palaeognathae	6	-3.841±0.086	**0.611**±0.010	<0.0001	<0.0001	0.999
Passeriformes	13	-2.999±0.276	**0.771**±0.059	<0.0001	<0.0001	0.939
Psittaciformes	11	-3.118±0.277	**0.823**±0.052	<0.0001	<0.0001	0.965
Strigiformes	7	-1.573±0.315	**0.532**±0.051	0.0041	0.0001	0.956
Passeriformes, Psittaciformes, Strigiformes	31	-2.837±0.184	**0.749**±0.035	<0.0001	<0.0001	0.940
Galliformes, Columbiformes, Palaeognathae	20	-3.697±0.151	**0.605**±0.021	<0.0001	<0.0001	0.978
Accipitriformes, Falconiformes	7	-2.708±0.184	**0.608**±0.028	<0.0001	<0.0001	0.989
Mammals						
All	70	-3.837±0.220	**0.774**±0.029	<0.0001	<0.0001	0.912
All non-primates	57	-3.878±0.150	**0.743**±0.020	<0.0001	<0.0001	0.962
Afrotheria	6	-3.670±0.264	**0.761**±0.032	0.0002	<0.0001	0.993
Artiodactyla*	4	-1.759±0.334	**0.589**±0.029	0.0341	0.0023	0.995
Carnivora	8	-2.475±0.610	**0.631**±0.062	0.0067	<0.0001	0.945
Chiroptera	13	-3.856±0.454	**0.761**±0.123	<0.0001	<0.0001	0.777
Eulipotyphla	5	-3.758±0.476	**0.725**±0.137	0.0042	0.0131	0.904
Marsupialia	9	-4.728±0.584	**0.797**±0.070	<0.0001	<0.0001	0.949
Primata	12	-3.901±0.652	**0.942**±0.084	0.0001	<0.0001	0.926
Glires	10	-4.319±0.530	**0.760**±0.077	<0.0001	<0.0001	0.925
Scandentia	1					
Cerebellum						
Reptiles						
All	108	-7.731±0.213	**0.528**±0.040	<0.0001	<0.0001	0.625
Anguimorpha	7	-11.226±1.110	**1.081**±0.169	0.0002	0.0014	0.891
Crocodilia	1					
Gekkota	14	-8.310±0.234	**0.814**±0.079	<0.0001	<0.0001	0.900
Iguania	20	-6.926±0.196	**0.498**±0.039	<0.0001	<0.0001	0.901
Lacertoidea	15	-7.614±0.300	**0.568**±0.076	<0.0001	<0.0001	0.813
Scincoidea	14	-8.453±0.548	**0.673**±0.144	<0.0001	0.0005	0.646
Serpentes	18	-8.274±0.593	**0.387**±0.097	<0.0001	0.0011	0.496

Testudines	19	-6.785±0.748	**0.443**±0.105	<0.0001	0.0008	0.510
Testudines and Crocodilia	20	-7.408±0.624	**0.537**±0.085	<0.0001	<0.0001	0.690
All minus Serpentes	90	-7.814±0.159	**0.604**±0.030	<0.0001	<0.0001	0.818
All minus Iguania, Serpentes	70	-8.033±0.180	**0.627**±0.034	<0.0001	<0.0001	0.833
Birds						
All	65	-3.856±0.161	**0.507**±0.026	<0.0001	<0.0001	0.859
Accipitriformes	4	-3.014±0.155	**0.453**±0.022	0.0027	0.0024	0.995
Anseriformes	7	-4.263±0.328	**0.548**±0.046	<0.0001	<0.0001	0.966
Columbiformes	5	-5.264±0.274	**0.709**±0.048	0.0003	0.0007	0.986
Falconiformes	3	-4.104±0.321	**0.625**±0.057	0.0496	0.0583	0.992
Galliformes	9	-5.033±0.271	**0.614**±0.041	<0.0001	<0.0001	0.969
Palaeognathae	6	-4.890±0.122	**0.577**±0.014	<0.0001	<0.0001	0.998
Passeriformes	13	-4.327±0.163	**0.646**±0.035	<0.0001	<0.0001	0.969
Psittaciformes	11	-4.410±0.234	**0.667**±0.044	<0.0001	<0.0001	0.962
Strigiformes	7	-3.530±0.155	**0.490**±0.025	<0.0001	<0.0001	0.987
Passeriformes, Psittaciformes, Strigiformes	31	-4.184±0.119	**0.613**±0.023	<0.0001	<0.0001	0.962
Anseriformes, Galliformes, Columbiformes, Palaeognathae	27	-4.639±0.169	**0.570**±0.024	<0.0001	<0.0001	0.959
Accipitriformes, Falconiformes	7	-3.546±0.237	**0.527**±0.037	<0.0001	<0.0001	0.976
Mammals						
All	72	-4.803±0.168	**0.704**±0.022	<0.0001	<0.0001	0.937
All non-primates	58	-4.772±0.131	**0.676**±0.017	<0.0001	<0.0001	0.964
Afrotheria	6	-5.274±0.398	**0.798**±0.048	0.0002	<0.0001	0.986
Artiodactyla*	4	-3.940±1.228	**0.612**±0.105	0.0850	0.0282	0.944
Carnivora	8	-3.936±0.407	**0.606**±0.042	<0.0001	<0.0001	0.972
Chiroptera	13	-4.226±0.225	**0.578**±0.061	<0.0001	<0.0001	0.891
Eulipotyphla	5	-5.661±0.494	**0.887**±0.142	0.0014	0.0083	0.929
Marsupialia	10	-5.124±0.425	**0.684**±0.050	<0.0001	<0.0001	0.959
Primata	13	-4.321±0.631	**0.739**±0.074	<0.0001	<0.0001	0.900
Glires**	9	-5.370±0.691	**0.743**±0.109	0.0001	0.0002	0.869
Scandentia	1					

Rest of brain						
Reptiles						
All	108	-4.231±0.111	**0.411**±0.021	<0.0001	<0.0001	0.789
Anguimorpha	7	-5.384±0.422	**0.644**±0.064	<0.0001	0.0002	0.953
Crocodilia	1					
Gekkota	14	-4.847±0.141	**0.640**±0.047	<0.0001	<0.0001	0.938
Iguania	20	-4.319±0.176	**0.496**±0.035	<0.0001	<0.0001	0.918
Lacertoidea	15	-4.338±0.166	**0.533**±0.042	<0.0001	<0.0001	0.925
Scincoidea	14	-4.676±0.257	**0.564**±0.067	<0.0001	<0.0001	0.853
Serpentes	18	-4.521±0.294	**0.370**±0.048	<0.0001	<0.0001	0.786
Testudines	19	-4.751±0.427	**0.445**±0.060	<0.0001	<0.0001	0.762
Testudines and Crocodilia	20	-5.134±0.359	**0.502**±0.049	<0.0001	<0.0001	0.854
All minus Testudines, Crocodilia, Serpentes	70	-4.514±0.085	**0.535**±0.019	<0.0001	<0.0001	0.919
Birds						
All	65	-2.563±0.174	**0.457**±0.028	<0.0001	<0.0001	0.810
Accipitriformes	4	-2.114±0.490	**0.428**±0.069	0.0497	0.0254	0.950
Anseriformes	7	-2.650±0.187	**0.436**±0.026	<0.0001	<0.0001	0.982
Columbiformes	5	-3.852±0.163	**0.630**±0.029	0.0002	0.0002	0.994
Falconiformes	3	-2.431±0.297	**0.457**±0.053	0.0773	0.0737	0.987
Galliformes	9	-3.707±0.228	**0.570**±0.035	<0.0001	<0.0001	0.974
Palaeognathae	6	-3.543±0.753	**0.530**±0.086	0.0093	0.0035	0.906
Passeriformes	13	-3.110±0.203	**0.614**±0.044	<0.0001	<0.0001	0.948
Psittaciformes	11	-3.508±0.229	**0.728**±0.043	<0.0001	<0.0001	0.969
Strigiformes	7	-2.498±0.152	**0.470**±0.025	<0.0001	<0.0001	0.986
Passeriformes, Psittaciformes, Strigiformes	31	-3.003±0.176	**0.595**±0.033	<0.0001	<0.0001	0.916
Anseriformes, Galliformes, Columbiformes, Palaeognathae	27	-3.343±0.185	**0.520**±0.026	<0.0001	<0.0001	0.941
Accipitriformes, Falconiformes	7	-2.408±0.244	**0.464**±0.038	0.0002	<0.0001	0.968
Mammals						
All	70	-3.683±0.125	**0.635**±0.017	<0.0001	<0.0001	0.956

All non-primates	57	-3.697±0.105	**0.622**±0.014	<0.0001	<0.0001	0.973
Afrotheria	6	-3.508±0.277	**0.641**±0.034	0.0002	<0.0001	0.989
Artiodactyla*	4	-0.636±0.657	**0.378**±0.056	0.4352	0.0215	0.958
Carnivora	8	-2.914±0.341	**0.540**±0.035	0.0001	<0.0001	0.976
Chiroptera	13	-3.819±0.287	**0.668**±0.078	<0.0001	<0.0001	0.871
Eulipotyphla	5	-4.010±0.119	**0.673**±0.034	<0.0001	0.0003	0.992
Marsupialia	9	-4.376±0.457	**0.679**±0.055	<0.0001	<0.0001	0.957
Primata	12	-3.726±0.591	**0.706**±0.076	<0.0001	<0.0001	0.896
Glires**	9	-4.130±0.615	**0.689**±0.097	0.0003	0.0002	0.878
Scandentia	1					

Proportional size of brain structures

While the relative size of the brain and each of its major subdivisions expressed as a percentage of body mass decreases with increasing brain size, the relative proportions of the parts of the brain may or may not scale relative to each other. To avoid confusion, I refer to the latter as *proportional size*: the mass of a brain structure expressed as a percentage of the mass of the whole brain. Thus, whereas the relative size indicates how a part of the brain scales with the body, the proportional size indicates how it scales with the brain.

Figure 5 shows that there is extensive overlap in the proportional size of the pallium/cerebral cortex/telencephalon across reptiles, birds, and mammals; it is only the largest primates, carnivorans and artiodactyls among mammals, and owls and parrots among birds, that have a pallium of distinctively larger proportional size amongst amniotes. Strikingly, while the proportional size of the pallium/telencephalon can be described to slowly scale up together with body mass across all reptiles, and across all mammals in the dataset, close examination clade by clade reveals that the norm is that the proportional size of the pallium/cerebral cortex/telencephalon does *not* scale with body mass. Such scaling is only evident in primates, artiodactyls and carnivorans among mammals, and in parrots and songbirds among birds (Table 2). It is thus *not* the case that a general theme in amniote evolution is the proportional expansion of the telencephalon or pallium.

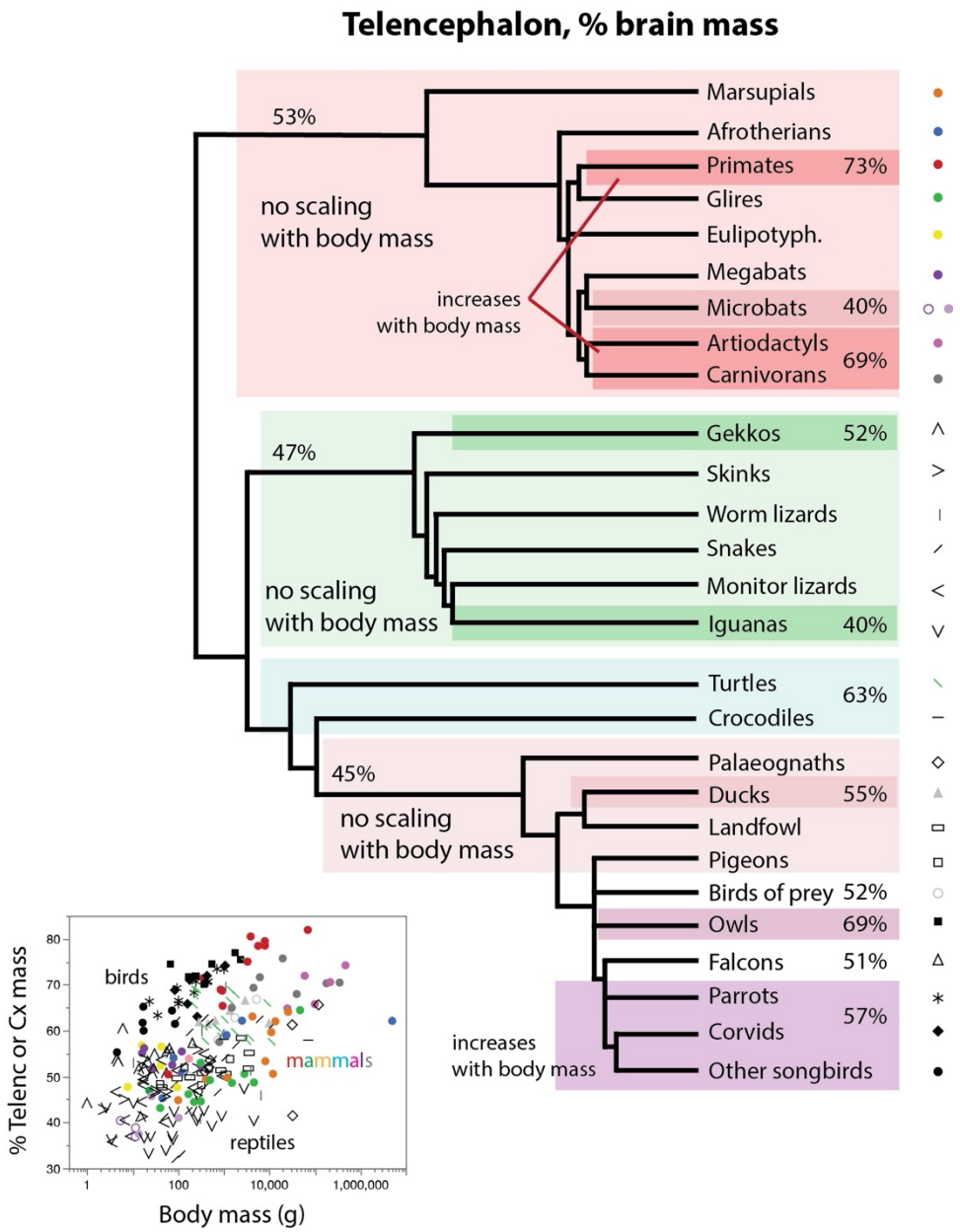


Figure 5. Amniotes have a telencephalon/pallium/cerebral cortex of mostly overlapping proportional size that, with few exceptions, does not scale with body mass. The evolutionary tree depicts the average proportional size of the telencephalon/pallium/cerebral cortex shared by clades in each rectangle. The graph shows the proportional size of the telencephalon/pallium/cerebral cortex plotted against the body mass of each species. For the sake of clarity, no power functions are plotted here, but note that the proportional size of this subdivision of the brain only scales with body mass in the few clades indicated in the schematic. Power functions are listed in Table 2. Each data point corresponds to one species. The key used to depict each clade is shown to the right.

Similarly, there is no systematic variation in the proportional size of the cerebellum with increasing body size in any clade of amniotes (Figure 6, Table 2). However, there is a striking difference in the proportional size of the cerebellum between ectothermic (reptiles) and

endothermic amniotes (birds and mammals), of 1-4% in the former, depending on the clade versus 8-13% in birds and 12-21% in mammals (average proportional cerebellar mass per clade; see Table 2). Amongst reptiles, the proportional mass of the cerebellum of snakes, iguanas, and turtles and crocodiles stands out from an otherwise shared average of ca. 2% (Figure 6). Amongst mammals, primates, artiodactyls and carnivorans have cerebellar of slightly smaller proportional size (ca. 12% on average, compared to a shared average of 14%), whereas microbats stand out with a proportionately larger cerebellum. Amongst birds, it is those species with the proportionately largest pallium (parrots, songbirds, and also owls) that have a proportionately smaller cerebellum. Additionally, it is only across the ensemble of Passeriformes and Psittaciformes that larger body mass is accompanied by a smaller proportional size of the cerebellum (Table 2).

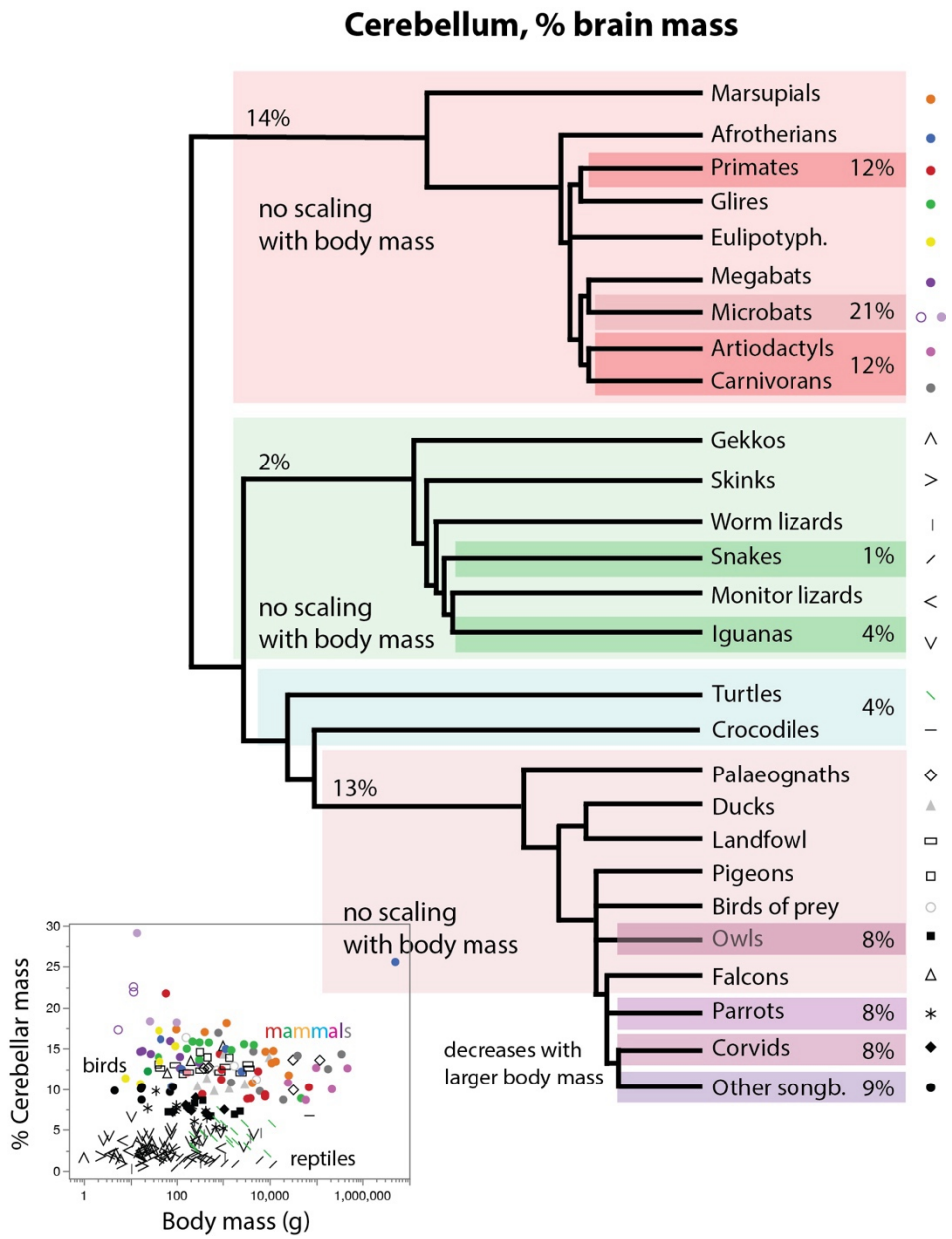


Figure 6. Endothermic amniotes have a proportionately larger cerebellum that does not scale with body mass. The evolutionary tree depicts the average proportional size of the cerebellum shared by clades in each rectangle. The graph shows the proportional size of the cerebellum plotted against the body mass of each species. The proportional size of this subdivision of the brain only scales with body mass (not plotted for clarity) in the ensemble of Passeriformes and Psittaciformes, as indicated in the schematic. Power functions are listed in Table 2. Each data point corresponds to one species. The key used to depict each clade is shown to the right.

As found for the pallium/telencephalon, there is no systematic decrease in the proportional size of the rest of brain across species with increasing body mass within each of the three groups of amniotes (Figure 7). Among mammals, such a decrease is only apparent when a

number of clades are pooled together, besides applying specifically within primates, carnivorans, and glires (Table 2). Within marsupials, the correlation is only significant when the largest species are considered. Among birds, there is no significant decrease in the proportional size of the rest of brain across the early-derived clades; the decrease appears later, within the later-derived clades, and even then, the scaling across clades (Figure 7, Table 2). Strikingly, however, there is a large decrease in the proportional size of the rest of brain between the ectothermic reptiles and the endothermic mammals and birds, an increase that parallels the large increase in the proportional size of the cerebellum (but not pallium) in the endothermic groups.

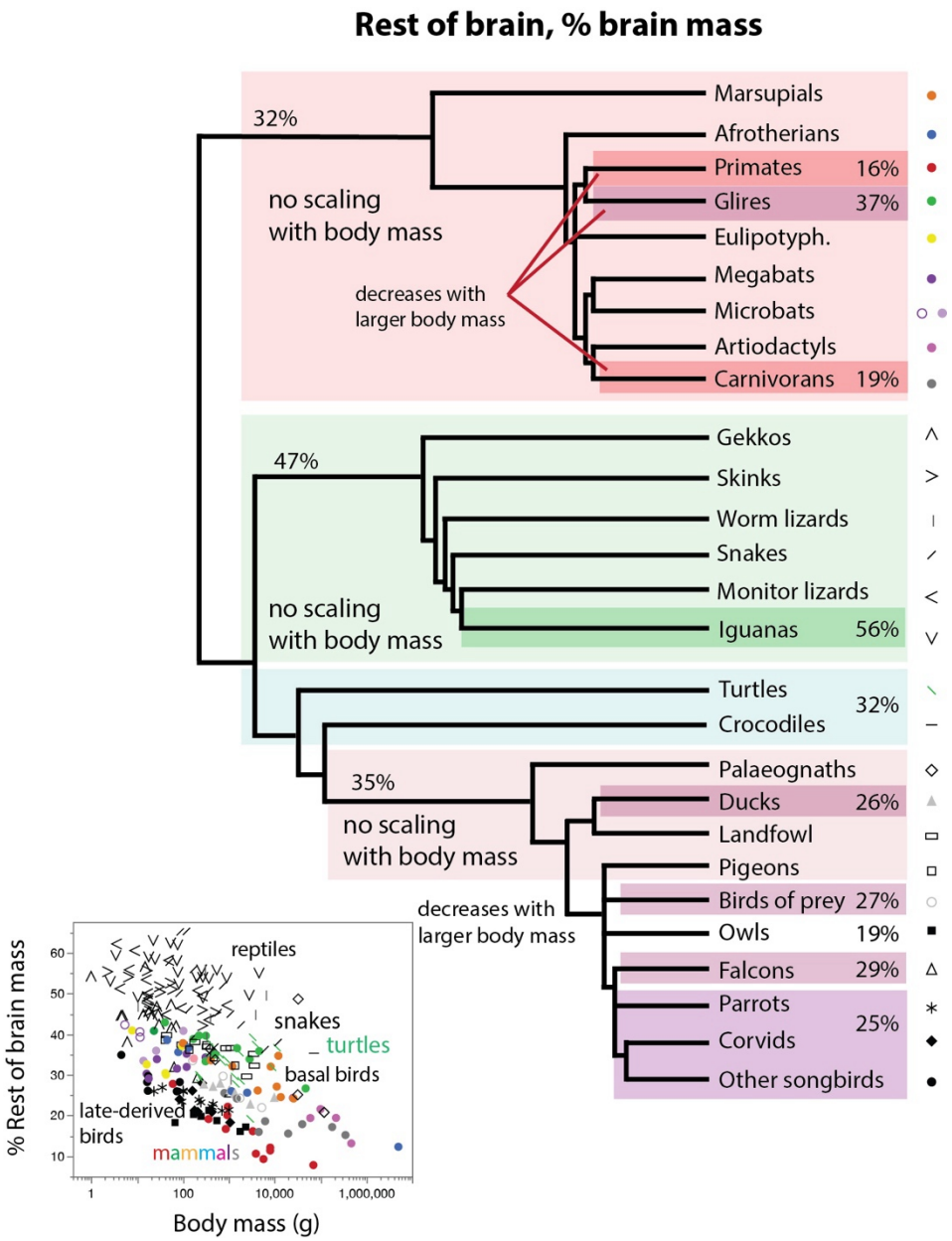


Figure 7. Endothermic amniotes have a rest of brain of decreased proportional mass compared to ectothermic reptiles, but the proportional size of the rest of brain only decreases with body mass within few clades. The evolutionary tree depicts the average proportional size of the rest of brain shared by clades in each rectangle. The graph shows the proportional size of the rest of brain plotted against the body mass of each species. For the sake of clarity, no power functions are plotted here, but note that the proportional size of this subdivision of the brain only scales with body mass in the few clades indicated in the schematic. Power functions are listed in Table 2. Each data point corresponds to one species. The key used to depict each clade is shown to the right.

Table 2. Scaling of the proportional mass of the different brain structures of reptiles, birds and mammals, expressed as % of total brain mass, as a function of body mass. Values correspond to the equation $\%M_{str} = e^{a\pm SE} M_{bd}^{b\pm SE}$, the p-values for a and b, and the r^2 for the power fit, where $\%M_{str}$ is the proportional mass of a given brain structure and M_{bd} is the average body mass for the species. Numbers in parentheses are the average relative structure mass ± SD for that clade. *pig excluded .**capybara excluded. ***elephant excluded.

$\%M_{str}$ x M_{bd}	**n**	**a in e^a**	**b in M_{bd}^b**	**p, a**	**p, b**	**r^2**
Cortex/pallium/telencephalon						
Reptiles						
All (50.67±9.61)	108	3.717±0.040	**0.039**±0.008	<0.0001	<0.0001	0.202
Anguimorpha (53.16±9.35)	7	3.992±0.240	**-0.005**±0.036	<0.0001	0.8961	0.004
Crocodilia (57.93)	1					
Gekkota (52.05±4.72)	14	3.886±0.066	**0.023**±0.022	<0.0001	0.3292	0.079
Iguania (40.06±3.83)	20	3.599±0.052	**0.019**±0.010	<0.0001	0.0879	0.153
Lacertoidea (46.38±5.77)	15	3.668±0.067	**0.045**±0.017	<0.0001	0.0207	0.348
Scincoidea (48.77±4.40)	14	3.751±0.054	**0.038**±0.014	<0.0001	0.0204	0.373
Serpentes (51.31±9.91)	18	3.467±0.178	**0.076**±0.029	<0.0001	0.0191	0.298
Testudines (63.71±5.08)	19	4.244±0.109	**-0.013**±0.015	<0.0001	0.4035	0.041
Testudines and Crocodilia (63.42±5.11)	20	4.266±0.087	**-0.017**±0.012	<0.0001	0.1758	0.099
All minus Testudines (46.87±7.07)	70	3.798±0.041	**0.009**±0.009	<0.0001	0.3145	0.015
Birds						
All (53.72±8.69)	65	3.930±0.068	**0.007**±0.011	<0.0001	0.5328	0.006
Accipitriformes (51.93±6.83)	4	3.312±0.025	**0.091**±0.003	<0.0001	0.0015	0.997
Anseriformes (54.59±1.95)	7	3.943±0.090	**0.008**±0.013	<0.0001	0.5524	0.075
Columbiformes (42.84±2.48)	5	3.583±0.099	**0.031**±0.017	<0.0001	0.724	0.515
Falconiformes (50.70±1.90)	3	3.778±0.005	**0.027**±0.001	0.0008	0.0212	0.999

Galliformes (43.78±3.11)	9	3.565±0.070	**0.033**±0.011	<0.0001	0.0165	0.584
Palaeognathae (47.97±8.36)	6	3.595±0.254	**0.031**±0.029	0.0001	0.3423	0.225
Passeriformes (56.71±6.38)	13	3.761±0.062	**0.061**±0.013	<0.0001	0.0008	0.656
Psittaciformes (57.67±2.53)	11	3.890±0.033	**0.032**±0.006	<0.0001	0.0007	0.740
Strigiformes (68.86±2.68)	7	4.132±0.072	**0.016**±0.012	<0.0001	0.2194	0.283
Passeriformes, Psittaciformes (57.15±4.92)	24	3.806±0.041	**0.050**±0.008	<0.0001	<0.0001	0.615
Galliformes, Columbiformes, Palaeognathae (44.80±5.33)	20	3.571±0.067	**0.033**±0.009	<0.0001	0.0023	0.413
Mammals						
All (58.02±11.72)	70	3.719±0.042	**0.047**±0.006	<0.0001	<0.0001	0.513
All non-primates (55.23±10.03)	57	3.711±0.036	**0.042**±0.005	<0.0001	<0.0001	0.580
Afrotheria (55.79±6.77)	6	3.859±0.083	**0.021**±0.010	<0.0001	0.1049	0.522
Artiodactyla* (70.41±3.99)	4	3.830±0.205	**0.036**±0.018	0.0029	0.1746	0.681
Carnivora (68.51±5.39)	8	4.008±0.120	**0.023**±0.012	<0.0001	0.1148	0.362
Chiroptera: Pteropodidae (53.47±2.07)	7	4.044±0.058	**-0.016**±0.014	<0.0001	0.2956	0.214
Chiroptera: Rhinolophoidea, Yangochiroptera (40.04±3.21)	6	3.604±0.108	**0.029**±0.036	<0.0001	0.4633	0.141
Eulipotyphla (52.21±4.48)	5	3.959±0.178	**-0.002**±0.051	0.0002	0.9708	0.001
Marsupialia (55.20±7.10)	9	3.557±0.135	**0.055**±0.016	<0.0001	0.0117	0.621
Primata (72.64±9.19)	12	3.775±0.094	**0.065**±0.012	<0.0001	0.0004	0.771

Glires** (47.61±3.23)	9	3.689±0.086	**0.028**±0.014	<0.0001	0.0809	0.372
Scandentia	1					
Afrotheria, Eulipotyphla, Glires, Marsupialia, Chiroptera (Pteropodidae) (52.96±5.94)	38	3.840±0.039	**0.020**±0.006	<0.0001	0.0013	0.251
Artiodactyla, Carnivora (68.88±4.75)	13	4.019±0.089	**0.020**±0.008	<0.0001	0.0344	0.346
Cerebellum						
Reptiles						
All (2.86±1.55)	108	0.572±0.143	**0.064**±0.027	0.0001	0.0176	0.052
Anguimorpha (2.75±1.77)	7	-2.003±0.842	**0.425**±0.128	0.0631	0.0210	0.688
Crocodilia (6.73)	1					
Gekkota (2.38±0.64)	14	0.428±0.157	**0.147**±0.053	0.0185	0.0166	0.392
Iguania (4.26±1.00)	20	1.466±0.159	**-0.010**±0.032	<0.0001	0.7505	0.006
Lacertoidea (2.27±0.68)	15	0.796±0.175	**-0.003**±0.044	0.0005	0.9397	0.000
Scincoidea (1.81±0.70)	14	0.256±0.330	**0.071**±0.087	0.4524	0.4313	0.052
Serpentes (1.31±0.54)	18	0.520±0.432	**-0.056**±0.071	0.2465	0.4419	0.037
Testudines (4.31±1.40)	19	1.303±0.468	**0.015**±0.066	0.0127	0.8206	0.003
Testudines and Crocodilia (4.43±1.47)	20	1.037±0.379	**0.055**±0.052	0.0136	0.2991	0.060
All minus Iguania, Testudines, Crocodilia, Serpentes (2.24±0.92)	50	0.406±0.155	**0.080**±0.037	0.0117	0.0370	0.088
Birds						

All (10.36±2.77)	65	2.103±0.115	**0.033**±0.018	<0.0001	0.0773	0.049
Accipitriformes (13.22±2.21)	4	3.277±0.200	**-0.102**±0.028	0.0037	0.0696	0.866
Anseriformes (11.51±1.86)	7	1.995±0.361	**0.062**±0.050	0.0027	0.2739	0.232
Columbiformes (13.49±1.03)	5	2.424±0.163	**0.032**±0.029	0.0007	0.3523	0.287
Falconiformes (13.60±1.67)	3	2.122±0.034	**0.088**±0.007	0.0102	0.0438	0.995
Galliformes (12.51±0.40)	9	2.528±0.049	**-0.000**±0.008	<0.0001	0.9726	0.002
Palaeognathae (12.51±1.36)	6	2.546±0.197	**-0.003**±0.022	0.0002	0.9023	0.004
Passeriformes (8.67±1.24)	13	2.434±0.095	**-0.064**±0.021	<0.0001	0.0095	0.472
Passeriformes: Corvids (7.70±0.65)	7	2.049±0.249	**-0.002**±0.045	0.0004	0.9654	0.000
Passeriformes: others (9.80±0.60)	6	2.251±0.093	**0.009**±0.028	<0.0001	0.7566	0.027
Psittaciformes (7.14±1.32)	11	2.598±0.164	**-0.125**±0.031	<0.0001	0.0028	0.647
Strigiformes (7.58±0.72)	7	2.175±0.194	**-0.025**±0.032	<0.0001	0.4568	0.115
Passeriformes, Psittaciformes (7.97±1.47)	24	2.526±0.097	**-0.098**±0.020	<0.0001	<0.0001	0.534
Galliformes, Columbiformes, Palaeognathae (12.76±0.98)	20	2.573±0.062	**-0.004**±0.009	<0.0001	0.6228	0.014
All minus Passeriformes, Psittaciformes, Strigiformes (12.63±1.48)	34	2.567±0.079	**-0.006**±0.011	<0.0001	0.6196	0.008
Mammals						
All (14.07±3.89)	69	2.815±0.071	**-0.030**±0.009	<0.0001	0.0024	0.130
All non-primates (14.58±3.81)	57	2.815±0.070	**-0.025**±0.009	<0.0001	0.0115	0.111

Afrotheria (15.29±5.44)	6	2.255±0.179	**0.058**±0.022	0.0002	0.0534	0.648
Artiodactyla* (10.52±1.65)	4	1.649±0.855	**0.060**±0.073	0.1935	0.5000	0.250
Carnivora (12.73±2.80)	8	2.547±0.418	**-0.003**±0.043	0.0009	0.9535	0.001
Chiroptera: Pteropodidae (14.22±1.07)	7	2.797±0.208	**-0.036**±0.026	<0.0001	0.2242	0.278
Chiroptera: Rhinolophoidea, Yangochiroptera (21.23±4.40)	6	3.155±0.283	**-0.041**±0.095	0.0004	0.6877	0.045
Eulipotyphla (13.60±2.72)	5	2.057±0.263	**0.159**±0.075	0.0043	0.1252	0.598
Marsupialia (14.56±2.56)	9	3.218±0.214	**-0.068**±0.026	<0.0001	0.0329	0.501
Primata (11.61±3.81)	11	3.144±0.290	**-0.095**±0.037	<0.0001	0.0293	0.427
Glires** (15.10±0.81)	9	2.618±0.080	**0.015**±0.013	<0.0001	0.2622	0.175
Scandentia	1					
Afrotheria***, Eulipotyphla, Glires, Marsupialia, Chiroptera (Pteropodidae) (14.15±2.13)	36	2.708±0.073	**-0.012**±0.011	<0.0001	0.3097	0.030
Artiodactyla, Carnivora (12.05±2.52)	13	2.603±0.320	**-0.013**±0.030	<0.0001	0.6760	0.016
Rest of brain						
Reptiles						
All (46.46±9.70)	108	4.071±0.046	**-0.052**±0.009	<0.0001	<0.0001	0.259
Anguimorpha (44.09±8.50)	7	3.838±0.291	**-0.011**±0.044	<0.0001	0.8125	0.012
Crocodilia (35.34)	1					
Gekkota (45.57±4.78)	14	3.890±0.069	**-0.028**±0.023	<0.0001	0.2603	0.104

Iguania (55.68±4.20)	20	4.073±0.042	**-0.012**±0.008	<0.0001	0.1651	0.104
Lacertoidea (51.35±5.62)	15	4.072±0.054	**-0.039**±0.014	<0.0001	0.0147	0.378
Scincoidea (49.42±4.19)	14	4.034±0.047	**-0.039**±0.012	<0.0001	0.0083	0.453
Serpentes (47.37±9.59)	18	4.273±0.168	**-0.073**±0.028	<0.0001	0.0170	0.307
Testudines (31.99±4.76)	19	3.338±0.230	**0.017**±0.033	<0.0001	0.6170	0.015
Testudines and Crocodilia (32.15±4.70)	20	3.312±0.182	**0.020**±0.025	<0.0001	0.4197	0.037
Anguimorpha, Gekkota, Scincoidea, Serpentes (47.00±7.20)	53	3.953±0.049	**-0.026**±0.010	<0.0001	0.0120	0.117
Iguania, Lacertoidea (53.82±5.26)	35	4.040±0.039	**-0.014**±0.009	<0.0001	0.1103	0.075
Birds						
All (27.79±6.73)	65	3.396±0.099	**-0.017**±0.016	<0.0001	0.2990	0.017
Accipitriformes (27.35±5.20)	4	4.177±0.137	**-0.127**±0.019	0.0011	0.0225	0.956
Anseriformes (25.97±1.88)	7	3.608±0.116	**-0.050**±0.016	<0.0001	0.0275	0.655
Columbiformes (35.73±2.47)	5	3.836±0.076	**-0.047**±0.013	<0.0001	0.0390	0.805
Falconiformes (28.92±3.14)	3	3.795±0.010	**-0.080**±0.002	0.0017	0.0146	0.999
Galliformes (35.81±3.11)	9	3.854±0.087	**-0.044**±0.013	<0.0001	0.0131	0.609
Palaeognathae (33.33±9.73)	6	3.893±0.453	**-0.050**±0.051	0.0010	0.3859	0.191
Passeriformes (25.59±4.48)	13	3.651±0.089	**-0.096**±0.019	<0.0001	0.0004	0.697
Psittaciformes (23.91±2.02)	11	3.500±0.052	**-0.063**±0.010	<0.0001	0.0001	0.821
Strigiformes (18.81±1.80)	7	3.207±0.170	**-0.046**±0.028	<0.0001	0.1581	0.355

Passeriformes, Psittaciformes (24.82±3.60)	24	3.602±0.057	**-0.084**±0.012	<0.0001	<0.0001	0.706
Galliformes, Columbiformes, Palaeognathae (35.05±5.62)	20	3.852±0.113	**-0.045**±0.016	<0.0001	0.0102	0.314
Mammals						
All (27.91±9.56)	69	3.897±0.086	**-0.093**±0.011	<0.0001	<0.0001	0.497
All non-primates (30.19±8.19)	57	3.892±0.056	**-0.078**±0.007	<0.0001	<0.0001	0.667
All minus primates, carnivorans, megabats (32.01±7.66)	42	3.919±0.054	**-0.074**±0.007	<0.0001	<0.0001	0.717
Afrotheria (29.13±9.93)	6	4.021±0.041	**-0.099**±0.005	<0.0001	<0.0001	0.990
Artiodactyla (19.58±4.12)	5	5.003±0.677	**-0.177**±0.058	0.0051	0.0560	0.755
Carnivora (18.76±3.94)	8	3.568±0.236	**-0.068**±0.024	<0.0001	0.0297	0.573
Chiroptera: Pteropodidae (32.31±2.23)	7	3.301±0.085	**0.042**±0.020	<0.0001	0.0907	0.467
Chiroptera: Rhinolophoidea, Yangochiroptera (38.73±3.36)	6	3.671±0.132	**-0.006**±0.044	<0.0001	0.8971	0.005
Eulipotyphla (34.19±4.67)	5	3.708±0.254	**-0.054**±0.073	0.0007	0.5113	0.155
Marsupialia (30.24±4.88)	9	3.909±0.191	**-0.063**±0.022	<0.0001	0.0289	0.518
Primata (15.75±6.17)	11	4.179±0.222	**-0.194**±0.028	<0.0001	<0.0001	0.841
Glires** (37.29±3.16)	9	3.858±0.097	**-0.039**±0.015	<0.0001	0.0367	0.468
Scandentia	1					

410

Scaling rules for non-neuronal cells are group-specific but not clade-specific

Across the brains of the 242 species of reptiles, mammals, and birds in the combined dataset, which vary in whole brain mass by almost 500,000-fold, the total number of non-neuronal cells varies over 100,000-fold, from just under 2 million in the Algerian sand gecko to 216 billion in the African elephant. At first sight, amniote brains as a whole vary in mass as an essentially linear power function of their numbers of non-neuronal cells (Figure 8A; power fit, exponent 0.992±0.010, r^2=0.978, p<0.0001; linear fit, r^2=0.993, p<0.0001). This means that a 1,000 times heavier amniote brain has approximately 1,000 times more non-neuronal cells, with roughly constant densities of non-neuronal cells.

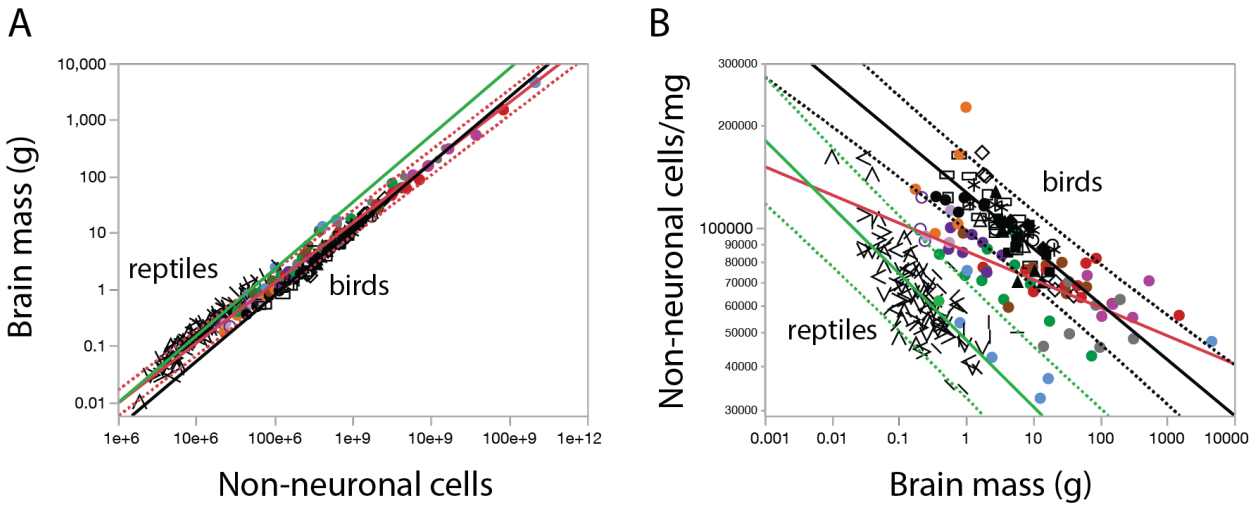


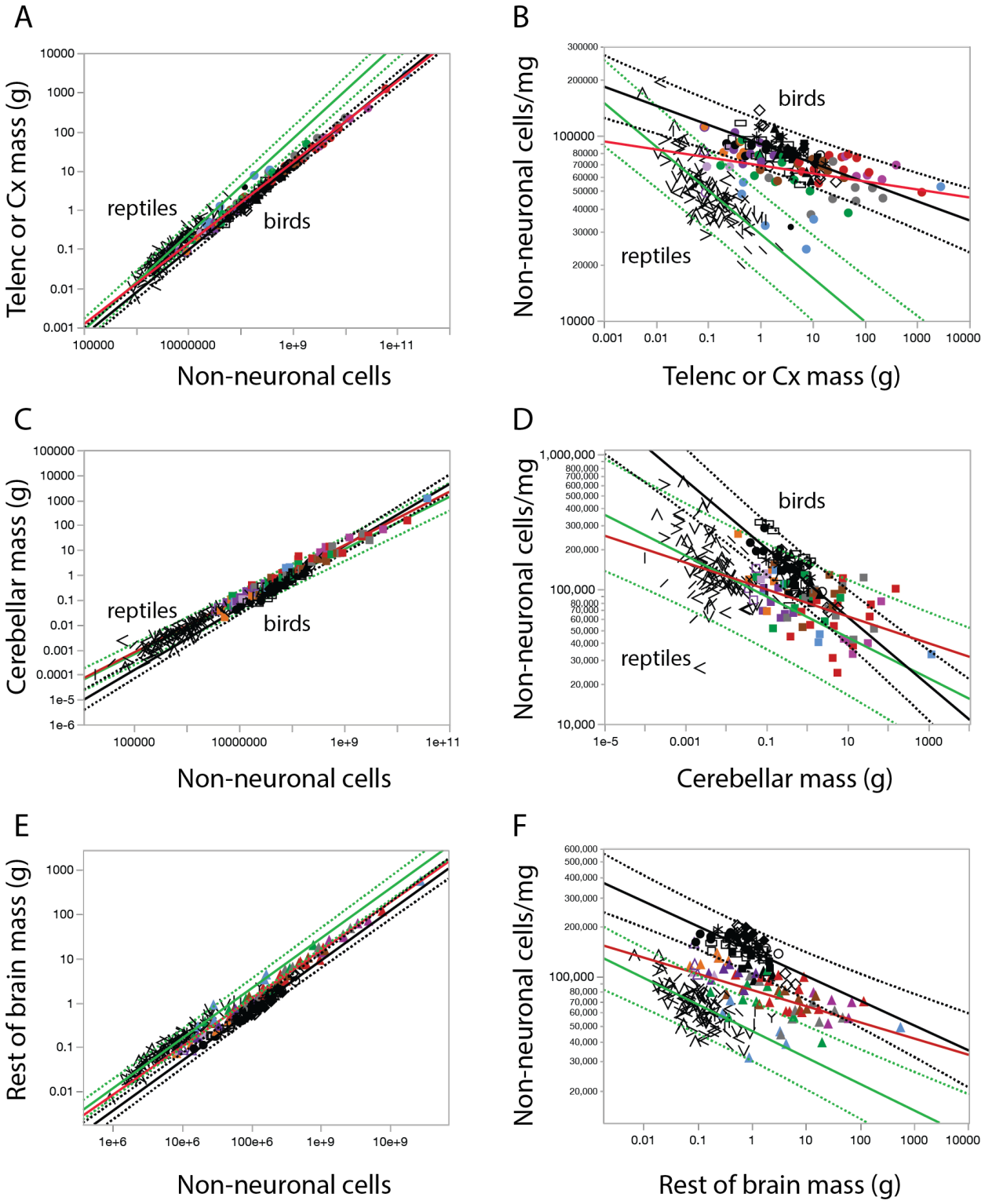
Figure 8. Birds, reptiles and mammals share a nearly linear relationship between brain mass and numbers of non-neuronal cells, although birds and mammals have significantly higher densities of non-neuronal cells than reptiles of similar brain mass. A, scaling of brain mass with non-neuronal cells across 108 species of reptiles, 69 species of mammals and 65 species of birds. Power functions are plotted for mammals (in red, with 95% prediction interval: exponent, 1.070±0.013, r^2=0.990, p<0.0001), reptiles (in green; exponent, 1.184±0.026, r^2=0.952, p<0.0001) and birds (in black; exponent, 1.170±0.020, r^2=0.982, p<0.0001). The power function fit across all 242 species has an exponent of 0.992±0.010 that is indistinguishable from linearity. **B**, closer inspection of the ratio between non-neuronal cells and brain mass, which is non-neuronal cell density, makes evident the small but highly significant decrease in non-neuronal cell density with increasing structure mass within each clade (power functions plotted), with exponents -0.081±0.014 (mammals, in red, r^2=0.354, p<0.0001), -0.192 (reptiles, in green, r^2=0.556, p<0.0001) and -0.161±0.015 (birds, in black, r^2=0.658, p<0.0001). Non-neuronal cell densities are overlapping between the larger bird and mammalian brains, but for brains around 1 g, birds have consistently higher non-neuronal cell densities than mammals, which are much higher than non-neuronal cell densities in reptiles. All scaling relationships are listed in Table 3. All symbols as in previous figures.

438 The power functions calculated separately for each of the three groups of amniotes
439 reveal, however, that each of them deviates significantly from linearity (Figure 8A). That non-
440 linearity is evidence in the scaling of overall non-neuronal cell density in the brain, which is the
441 ratio between numbers of non-neuronal cells and brain mass, shown in Figure 8B). Even more
442 importantly, examination of this ratio, as opposed to the two absolute values in the ratio, reveals
443 that the scaling of numbers of non-neuronal cells with brain mass is not even shared across
444 reptiles, birds, and mammals. The difference between Figures 8A and 8B highlights the need for
445 analyzing ratios (such as cell density) between variables that scale across several orders of
446 magnitude. For a given brain mass, there are more non-neuronal cells per gram of tissue in
447 mammals compared to reptiles, and even more so in birds compared to mammals (Figure 8B),
448 even though reptiles, birds and mammals share the same limited range of densities of non-
449 neuronal cells that vary mostly by ca. 3-fold, concentrated between 50,000 and 120,000 non-
450 neuronal cells/mg of brain (Figure 8B). Thus, the apparent shared and mathematically significant
451 linear scaling of numbers of non-neuronal cells with brain mass across all amniotes in the dataset
452 is not real, since densities of non-neuronal cells vary systematically with brain mass; and different
453 scaling relationships apply to each amniote clade, with higher densities of non-neuronal cells in
454 the brains of endothermic compared to ectothermic sauropsid species (birds, 104,237±21,850;
455 mammals, 77,068±28,861; reptiles, 66,439±21,903 non-neuronal cells/mg; Table 3).
456 Separate analysis of the scaling of non-neuronal cell density with the mass of each of the
457 three main subdivisions of the amniote brains in the dataset reveals that the pallium of mammals
458 and birds has up to twice higher densities of non-neuronal cells compared to reptilian
459 telencephalons of similar mass (Figure 9A,B). Non-neuronal densities in the pallium vary little but
460 decrease slowly with increasing structure mass across birds and mammals, with negative
461 exponents that are small but non-overlapping and significantly different from zero (-0.089±0.019
462 and -0.043±0.013, respectively; Figure 9B, Table 3). In contrast, densities of non-neuronal cells
463 drop rapidly in the telencephalon of reptiles as the mass of structure increases, with an exponent
464 of -0.236±0.020 (Figure 9B, Table 3).
465 In the cerebellum, birds and reptiles share similar non-neuronal cell densities that are also
466 higher than those found in most mammals (Figure 9D). As in the pallium/telencephalon, non-

467 neuronal cell densities scale differently with increasing cerebellar mass in each of the three
468 groups (Figure 9D, Table 3). In the rest of brain, like in the pallium/telencephalon, birds have
469 larger densities of non-neuronal cells than mammals, which in turn are larger than in reptiles,
470 and once more, neuronal cell densities scale differently with increasing rest of brain mass in each
471 of the three groups (Figure 9E,F; Table 3).

472 In contrast to the clade-specific scaling of absolute, relative and proportional brain
473 structure mass in amniotes, the scaling of numbers of non-neuronal cells with structure mass is
474 shared within each group of amniotes, with no systematic differences across clades.

475


A
Telenc or Cx mass (g)
Non-neuronal cells
reptiles
birds
B
Non-neuronal cells/mg
Telenc or Cx mass (g)
birds
reptiles
C
Cerebellar mass (g)
Non-neuronal cells
reptiles
birds
D
Non-neuronal cells/mg
Cerebellar mass (g)
birds
reptiles
E
Rest of brain mass (g)
Non-neuronal cells
F
Non-neuronal cells/mg
Rest of brain mass (g)

476

477

Figure 9. Scaling of density of non-neuronal cells with structure mass differs across brain structures and amniote clades. A, B, pallium/cerebral cortex/telencephalon; **C, D**, cerebellum; **E, F**, rest of brain. **A, C, E**: scaling of brain structure mass with number of non-neuronal cells in the structure. **B, D, F**: scaling of non-neuronal cell density with structure mass. Power functions with 95% prediction intervals are plotted for reptiles (green), birds (black), and mammals (red, without the prediction interval for clarity). All symbols as in previous figures. All power functions are listed in Table 3.

Table 3. Non-neuronal scaling rules for the telencephalon of reptiles and the pallium of birds and mammals; the cerebellum; and the rest of brain (hindbrain to diencephalon in reptiles and birds, hindbrain to striatum in mammals). Values correspond to the equations $M_{str} = e^{a\pm SE}\ O_{str}^{b\pm SE}$ and $O_{str}/M_{str} = e^{a\pm SE}\ M_{str}^{b\pm SE}$, the p-values for a and b, and the r^2 for the power fit, where M_{str} is structure mass, O_{str} is the number of non-neurons ("other cells") in the structure, and O_{str}/M_{str} is the density of non-neuronal (other) cells in the structure.

Whole brain						
M_{str} x O_{str}	**n**	**a in e^a**	**b in N_{str}^b**	**p, a**	**p, b**	**r^2**
All amniotes	242	-17.980±0.179	**0.992**±0.010	<0.0001	<0.0001	0.978
All reptiles	108	-20.989±0.424	**1.184**±0.026	<0.0001	<0.0001	0.952
All mammals	69	-19.499±0.264	**1.070**±0.013	<0.0001	<0.0001	0.990
All birds	65	-21.811±0.405	**1.170**±0.020	<0.0001	<0.0001	0.982
O_{str} /M_{str} x M_{str}	**n**	**a in e^a**	**b in N_{str}^b**	**p, a**	**p, b**	**r^2**
All reptiles (66,439±21,903)	108	10.772±0.031	**-0.192**±0.017	<0.0001	<0.0001	0.556
All mammals (77,068±28,861)	68	11.362±0.042	**-0.081**±0.014	<0.0001	<0.0001	0.354
All birds (104,237±21,850)	65	11.754±0.025	**-0.161**±0.015	<0.0001	<0.0001	0.658
Telencephalon or cortex						
M_{str} x O_{str}	**n**	**a in e^a**	**b in N_{str}^b**	**p, a**	**p, b**	**r^2**
All amniotes	242	-17.331±0.175	**0.967**±0.010	<0.0001	<0.0001	0.976
All reptiles	108	-21.137±0.500	**1.221**±0.032	<0.0001	<0.0001	0.932
All mammals	70	-18.617±0.268	**1.033**±0.014	<0.0001	<0.0001	0.988
All birds	65	-19.531±0.424	**1.069**±0.022	<0.0001	<0.0001	0.973
All mammals and birds	135	-18.950±0.232	**1.044**±0.012	<0.0001	<0.0001	0.983
O_{str} /M_{str} x M_{str}	**n**	**a in e^a**	**b in N_{str}^b**	**p, a**	**p, b**	**r^2**
All reptiles (52,454±25,334)	108	10.286±0.049	**-0.236**±0.020	<0.0001	<0.0001	0.566

All mammals (66,931±17,592)	70	11.137±0.037	**-0.043**±0.013	<0.0001	0.0011	0.145
All birds (83,690±17,249)	65	11.388±0.027	**-0.089**±0.019	<0.0001	<0.0001	0.259
Cerebellum						
M_{str} x O_{str}	**n**	**a in e^a**	**b in N_{str}^b**	**p, a**	**p, b**	**r^2**
All amniotes	245	-19.728±0.184	**1.072**±0.011	<0.0001	<0.0001	0.974
All reptiles	108	-20.990±0.424	**1.184**±0.026	<0.0001	<0.0001	0.952
All mammals	72	-19.501±0.444	**1.073**±0.024	<0.0001	<0.0001	0.966
All birds	65	-23.076±0.790	**1.242**±0.044	<0.0001	<0.0001	0.927
All mammals and reptiles	180	-20.053±0.193	**1.100**±0.012	<0.0001	<0.0001	0.978
O_{str} /M_{str} x M_{str}	**n**	**a in e^a**	**b in N_{str}^b**	**p, a**	**p, b**	**r^2**
All reptiles (156,454±98,672)	108	11.042±0.156	**-0.152**±0.029	<0.0001	<0.0001	0.205
All mammals (86,037±37,832)	72	11.281±0.046	**-0.100**±0.020	<0.0001	<0.0001	0.262
All birds (146,992±52,510)	65	11.627±0.035	**-0.254**±0.027	<0.0001	<0.0001	0.592
Rest of brain						
M_{str} x O_{str}	**n**	**a in e^a**	**b in N_{str}^b**	**p, a**	**p, b**	**r^2**
All amniotes	242	-17.980±0.179	**0.992**±0.010	<0.0001	<0.0001	0.978
All reptiles	108	-20.050±0.415	**1.129**±0.026	<0.0001	<0.0001	0.946
All mammals	70	-19.804±0.360	**1.087**±0.019	<0.0001	<0.0001	0.980
All birds	65	-21.227±0.546	**1.130**±0.029	<0.0001	<0.0001	0.959
O_{str} /M_{str} x M_{str}	**n**	**a in e^a**	**b in N_{str}^b**	**p, a**	**p, b**	**r^2**
All reptiles (68,583±18,770)	108	10.742±0.048	**-0.162**±0.019	<0.0001	<0.0001	0.394
All mammals (81,222±26,324)	70	11.318±0.034	**-0.099**±0.016	<0.0001	<0.0001	0.364
All birds (127,807±32,384)	64	11.778±0.024	**-0.189**±0.025	<0.0001	<0.0001	0.488
All structures						
M_{str} x O_{str}	**n**	**a in e^a**	**b in N_{str}^b**	**p, a**	**p, b**	**r^2**
All amniotes	242	-17.980±0.179	**0.992**±0.010	<0.0001	<0.0001	0.978
All reptiles	108	-20.050±0.415	**1.129**±0.026	<0.0001	<0.0001	0.946
All mammals	212	-19.318±0.207	**1.064**±0.011	<0.0001	<0.0001	0.978
All birds	194	-22.124±0.391	**1.193**±0.021	<0.0001	<0.0001	0.944

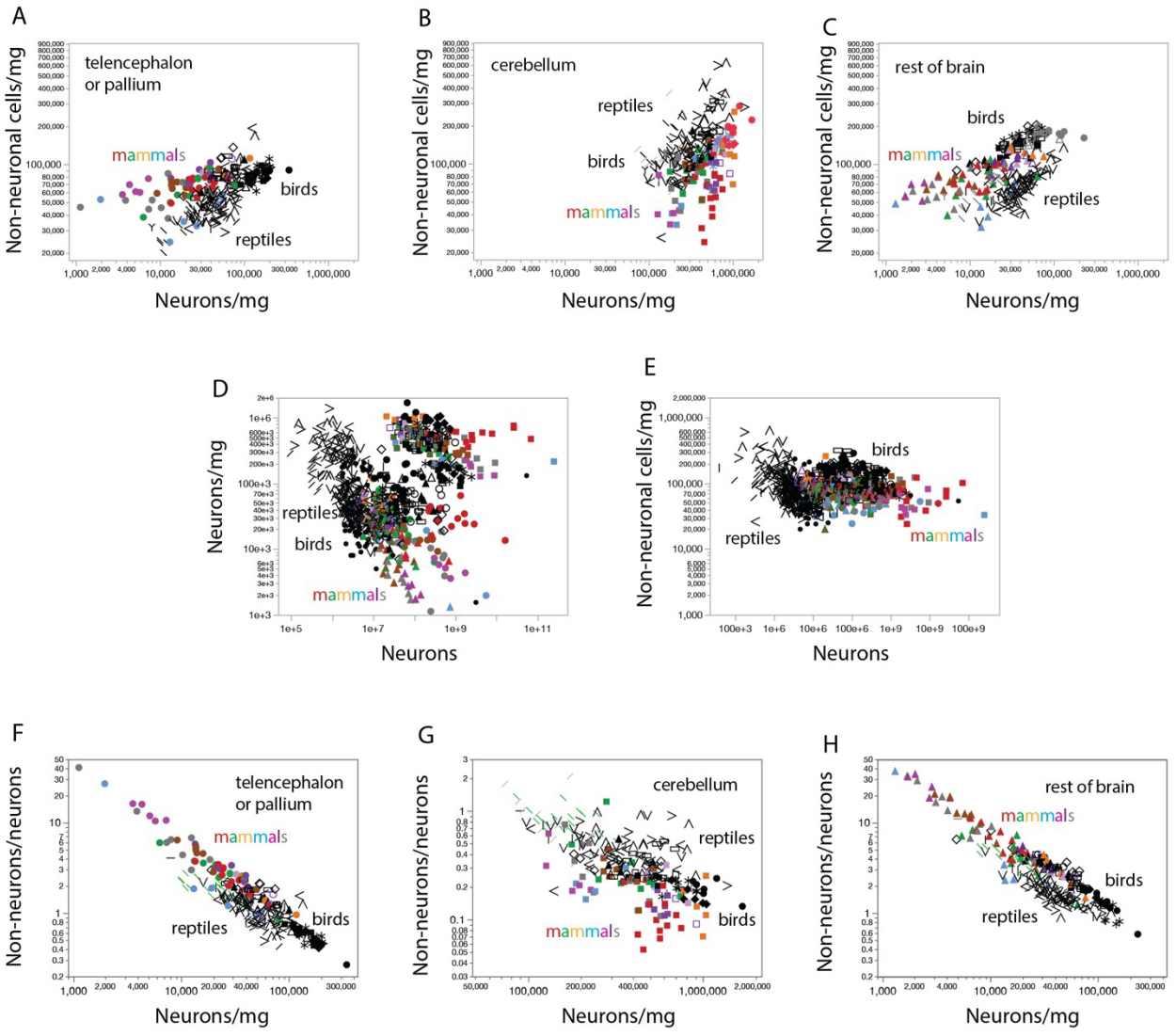
O_{str} /M_{str} x M_{str}	**n**	**a in e^a**	**b in N_{str}^b**	**p, a**	**p, b**	**r^2**
All reptiles (92,497±75,164)	324	10.460±0.039	**-0.246**±0.011	<0.0001	<0.0001	0.626
All mammals (78,139±29,589)	212	11.259±0.023	**-0.081**±0.009	<0.0001	<0.0001	0.261
All birds (119,496±45,385)	194	11.644±0.017	**-0.209**±0.014	<0.0001	<0.0001	0.538

Ratios of non-neuronal to neuronal cells are shared between birds and mammals

Across the 242 amniote species in the dataset, the total number of brain neurons varies over 100,000 fold, from just under 2 million in the Algerian sand gecko (Kverkova et al., 2022) to 257 billion in the African elephant (Herculano-Houzel et al., 2014b), which is a similar range as the variation of total numbers of non-neuronal cells. However, neuronal densities vary by over 1,000 times across brain structures and species, whereas non-neuronal densities vary by less than a factor of 10 (Figure 10). As numbers of neurons in the three brain subdivisions increase across species, there is an overall tendency for increasing numbers of neurons to be accompanied by decreasing neuronal densities spanning three orders of magnitude (and, conversely, by average neuronal cell size that increases by the same amount; Mota and Herculano-Houzel, 2014; Figure 10D), while variation in non-neuronal cell densities remains contained within one order of magnitude (Figure 10E).

As noted above, birds have higher densities of non-neuronal cells in the pallium and rest of brain compared to mammalian structures of similar mass (Figure 9), which raises the possibility that densities of glial cells and/or capillary cells have become distinctively higher in the brains of birds. However, the ratio of non-neuronal cells per neuron scales in a similar fashion across birds and mammals (Figure 10F-H). The perfect overlap and continuity in this relationship across the two groups indicates that densities of non-neuronal cells are higher for a same structure mass of

515 the pallium and rest of brain of birds compared to mammals for the simple reason that neuronal
516 densities are higher in birds compared to mammals (Figure 10A,C). Reptiles, in contrast, have
517 consistently lower ratios of non-neuronal cells per neuron for similar neuronal densities in the
518 telencephalon (Figure 10F) and rest of brain (Figure 10H) compared to both birds and mammals,
519 which indicates that the higher ratios of non-neuronal cells per neuron in birds and mammals are
520 associated with the evolution of endothermy, and occurred twice, independently, in each of
521 these two groups.
522



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524

Figure 10. Neuronal cell densities vary 1,000-fold across species and structures, while non-neuronal cell densities vary only ca. 10-fold, but with a relationship that is shared between mammals and birds. A-C, comparison of non-neuronal and neuronal cell densities in the telencephalon or pallium (cerebral cortex; **A**), cerebellum (**B**) and rest of brain (**C**). **D, E**, combined dataset contrasting the enormous variation in neuronal densities across species and structures of variable numbers of neurons (**D**) with the small variation in non-neuronal cell densities in the same structures and species (**E**). **F-H**, the scaling of the ratio between numbers of non-neuronal and neuronal cells is shared between mammals and birds in all three brain divisions: pallium (**F**), cerebellum (**G**) and rest of brain (**H**). All symbols as in previous figures.

Neuronal scaling rules are structure- and clade-specific

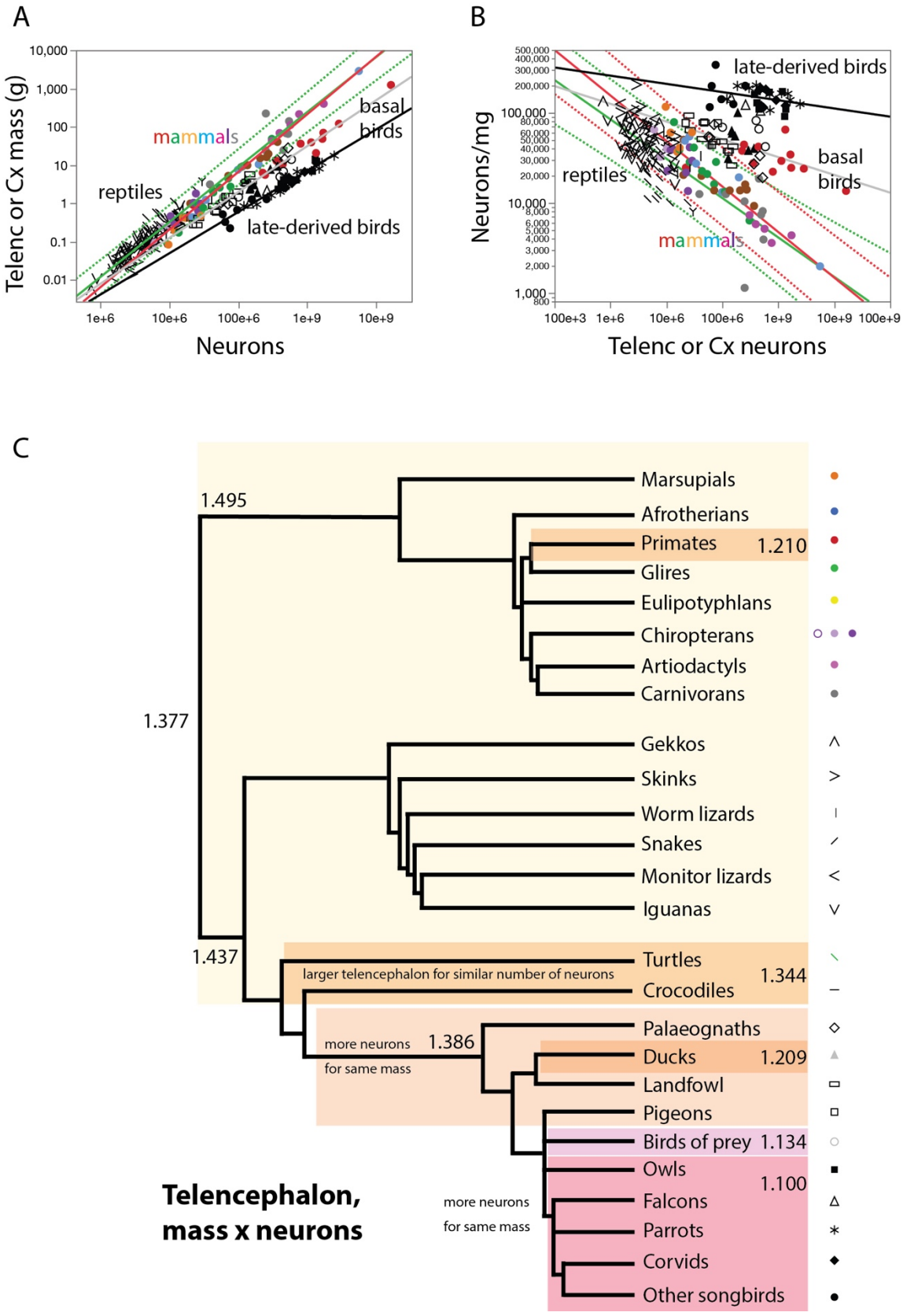
The neuronal composition of each of the three brain divisions scales very differently depending on the structure, and also depending on animal clade amongst each group of amniotes, as will be shown in the following sections. Thus, there is no such thing as the neuronal scaling rules for "the brains of mammals" or "the brains of birds", much less for "the brains of amniotes". Rather, the neuronal scaling rules that apply to the brains of amniote must be determined separately per brain structure and per clade, as described next. I then devote special attention to the scaling of numbers of neurons *across* brain structures in the different mammalian clades, an important feature of quantitative brain anatomy that informs about the scaling of functional relationships between brain structures in evolution (Herculano-Houzel, 2010; Herculano-Houzel et al., 2014a).

Neuronal scaling rules for the telencephalon are shared between reptiles and non-primate mammals

It is unfortunate that the study describing the cellular composition of the brains of non-avian reptiles (Kverkova et al., 2022) failed to separate the telencephalon into pallial and subpallial structures, unlike for birds. However, considering that the subpallium contributes only a minority of telencephalic neurons in early derived Palaeognathes and ground-dwelling birds (between 7 and 15%; Olkowicz et al., 2016), and assuming that the same is the case for non-avian reptiles, the neuronal composition of the reptile telencephalon will be considered representative of the reptilian pallium for the purposes of the comparison of scaling rules across clades.

559 Direct investigation of the relationship between the numbers of neurons that compose
560 the reptilian telencephalon and the mammalian cerebral cortex and the mass of the structures
561 reveals remarkable continuity across all reptilian and mammalian species in the dataset. Reptile
562 telencephalons and non-primate mammalian cerebral cortices of similar mass (which is the case
563 of the smallest mammals in the dataset: eulipotyphlans and bats) are composed of similar
564 numbers of neurons (Figure 11A). The telencephalon/mammalian cerebral cortex scales in mass
565 as a power function of its number of neurons that has statistically indistinguishable exponents
566 between reptiles (1.437±0.064) and non-primate mammals (1.495±0.033; Table 4), and data
567 points for even the largest non-primate mammalian species fall well within the 95% prediction
568 interval for reptiles (Figure 11A). The continuity in neuronal scaling rules between reptiles and
569 mammals, with a combined exponent of 1.377±0.024 (Table 4), strongly indicates that these
570 shared scaling rules already applied to the shared common ancestor between the two clades
571 (Figure 11C).
572 The shared scaling relationship across reptiles and most mammals between numbers of
573 telencephalic neurons and telencephalic (or cerebral cortical) mass with an exponent of roughly
574 1.4 means that as the structure gains 10x more neurons, measured neuronal density drops and
575 its inverse, which is average neuronal size, increases by $10^{0.4}$ = 2.5-fold (Mota and Herculano-
576 Houzel, 2014) in a similar manner across reptiles and non-primate mammals (Figure 11B). The
577 mammalian species with the fewest cerebral cortical neurons, which are bats and eulipotyphlans,
578 have similar neuronal densities as many of the reptiles in the dataset with matching numbers of
579 telencephalic neurons; and as mammalian cortices gain more cortical neurons, their average
580 neuronal density decreases in a way that can be predicted equally well using the power function
581 calculated for non-primate mammals (exponent -0.495±0.033) or for the reptilian telencephalon
582 (exponent -0.438 ± 0.064; Figure 11B; Table 5). In contrast, Testudines and the Nile crocodile
583 have lower neuronal densities than predicted for reptilian telencephalons of their numbers of
584 neurons (Figure 12B).
585 Closer examination of each clade in separate reveals that the neuronal scaling rules for
586 the telencephalon are shared across all clades of reptiles examined, with the exception of the
587 Nile crocodile and the Testudines (Table 4), which have systematically larger telencephalons than

predicted for the number of telencephalic neurons in a reptile (Figure 12A). While the crocodile telencephalon lies outside the 95% prediction interval for reptilian species, it fits the scaling rules for Testudines (Figure 12A), a finding that is in line with the evolutionary relatedness of Crocodilia and Testudines (Figure 11C). Combining Testudines and the Nile crocodile yields a scaling relationship with exponent 1.344±0.186 (Table 4), with a scaling relationship for all other reptile telencephalons of exponent 1.309±0.056 (Table 4). The similarity between the exponents indicates a grade shift in the neuronal composition of the telencephalon between Crocodilia and Testudines on the one hand, and all other extant non-avian Sauropsids on the other.


A
Telenc or Cx mass (g)
Neurons
mammals
reptiles
basal birds
late-derived birds
B
Neurons/mg
Telenc or Cx neurons
late-derived birds
basal birds
reptiles
mammals
C
Marsupials
Afrotherians
Primates
1.210
Glires
Eulipotyphlans
Chiropterans
Artiodactyls
Carnivorans
1.495
1.377
Gekkos
Skinks
Worm lizards
Snakes
Monitor lizards
Iguanas
1.437
Turtles
Crocodiles
1.344
larger telencephalon for similar number of neurons
Palaeognaths
Ducks
1.209
Landfowl
Pigeons
Birds of prey
1.134
Owls
Falcons
Parrots
Corvids
Other songbirds
1.100
more neurons for same mass
1.386
more neurons for same mass
Telencephalon, mass x neurons

597

Figure 11. Reptiles and non-primate mammals share neuronal scaling rules for the telencephalon/pallium, while two different scaling rules apply across birds, and primates conform to one of them. A, scaling of mass of the telencephalon or pallium with numbers of neurons across non-primate mammals (in red, with 95% prediction interval: exponent, 1.495±0.033), all reptiles (in green; exponent, 1.437±0.064), early-derived birds (Galliformes, Palaeognathae, Columbiformes, in gray; exponent, 1.386±0.060), and late-derived birds (Falconiformes, Passeriformes, Psittaciformes, and Strigiformes, in black; exponent, 1.100±0.044). For the sake of clarity, the 95% prediction interval is only plotted for reptilian species. Note that non-primate mammalian species conform to the prediction interval for reptiles. All power functions are listed in Table 4. **B**, Neuronal density (the ratio between neurons and telencephalic or pallial mass) decreases steeply with increasing numbers of telencephalic or pallial neurons across reptilian and non-primate mammalian species alike, while early-derived birds have higher neuronal densities, even higher in late-derived birds. Power functions plotted have exponents -0.438±0.064 (reptiles, in green), -0.495±0.033 (non-primate mammals, in red), -0.388±0.061 (early-derived birds, in gray) and -0.100±0.044 (late-derived birds, in black). All power functions are listed in Table 5. **C**, Putative cladogram for the evolution of the exponent that describes the scaling relationship between telencephalic mass and number of neurons, showing a shared exponent across most extant reptilian and mammalian species that can be inferred to have applied to ancestral amniotic species. Colored rectangles indicate a shift towards more telencephalic neurons without a change in the scaling exponent at the origin of birds, followed by a shift in scaling exponent at the origin of the recently-derived Passeriformes, Psittaciformes, Falconiformes and Strigiformes. Power functions are listed in Table 4. Each data point corresponds to one species. The key used to depict each clade is shown to the right.

The bird telencephalon, in contrast, gains neurons in a clearly distinct manner from non-avian reptilians – but at least two groups are clearly recognizable (Figure 11). In the first, composed by Palaeognathae and Galliformes, which in this dataset are the earliest derived in avian evolution that arose prior to the K-Pg extinction event (Brusatte et al., 2015), the telencephalon gains neurons with a pronounced drop in neuronal density, similar to that observed in reptiles and most mammals, with an exponent of -0.386±0.061 (Figure 11B, Figure 12C,D; Table 5). This scaling relationship captures the later arising Columbiformes very well, such that addition of Columbiformes species leaves the scaling exponent virtually unchanged (-0.388±0.061; Figure 12C,D, Table 5). Remarkably, while the range of neuronal densities is shared with reptiles and mammals, the neuronal scaling rules for the pallium of these early-arising birds appear shifted to the right compared to Testudines and the Nile crocodile (Figure 12E), as if the same brain structure volume now simply accommodated increased numbers of neurons (that is, with increased neuronal density) while maintaining the same allometry across species. The second group of birds is formed by the later, post-K-Pg-derived Falconiformes, Strigiformes, Passeriformes (including Corvidea) and Psittaciformes. In this group, telencephalic neuronal densities are much higher than in the vast majority of reptiles and mammals (Figure 11B), and barely decrease with varying numbers of neurons (-0.100±0.044, p=0.0315; Figure 12D, Table 5). As a result of these clade- and group-specific scaling rules, early-derived birds have more neurons

636 in the telencephalon than reptiles or non-primate mammals of similar pallial or telencephalic
637 mass; and later-derived birds have even more neurons concentrated in structures of a same
638 mass. Anseriformes and Accipitriformes species lie in between the two clades (Figure 12D).
639 Mapping these scaling relationships onto the phylogenetic tree of all species in the
640 dataset strongly suggests that the telencephalic scaling rule shared by modern (non-avian)
641 reptiles and non-primate mammals already applied to their common ancestral species (Figure
642 11C). Birds could have arisen with an increase in numbers of neurons generated in the same
643 volume, causing a shift towards higher neuronal densities, that remains in Palaeognathes such as
644 the emu and ostrich, landfowl, and pigeons; and further later shifts towards even higher neuronal
645 densities at the more recent derivation of songbirds, hawks, owls and parrots (Figure 11C).
646

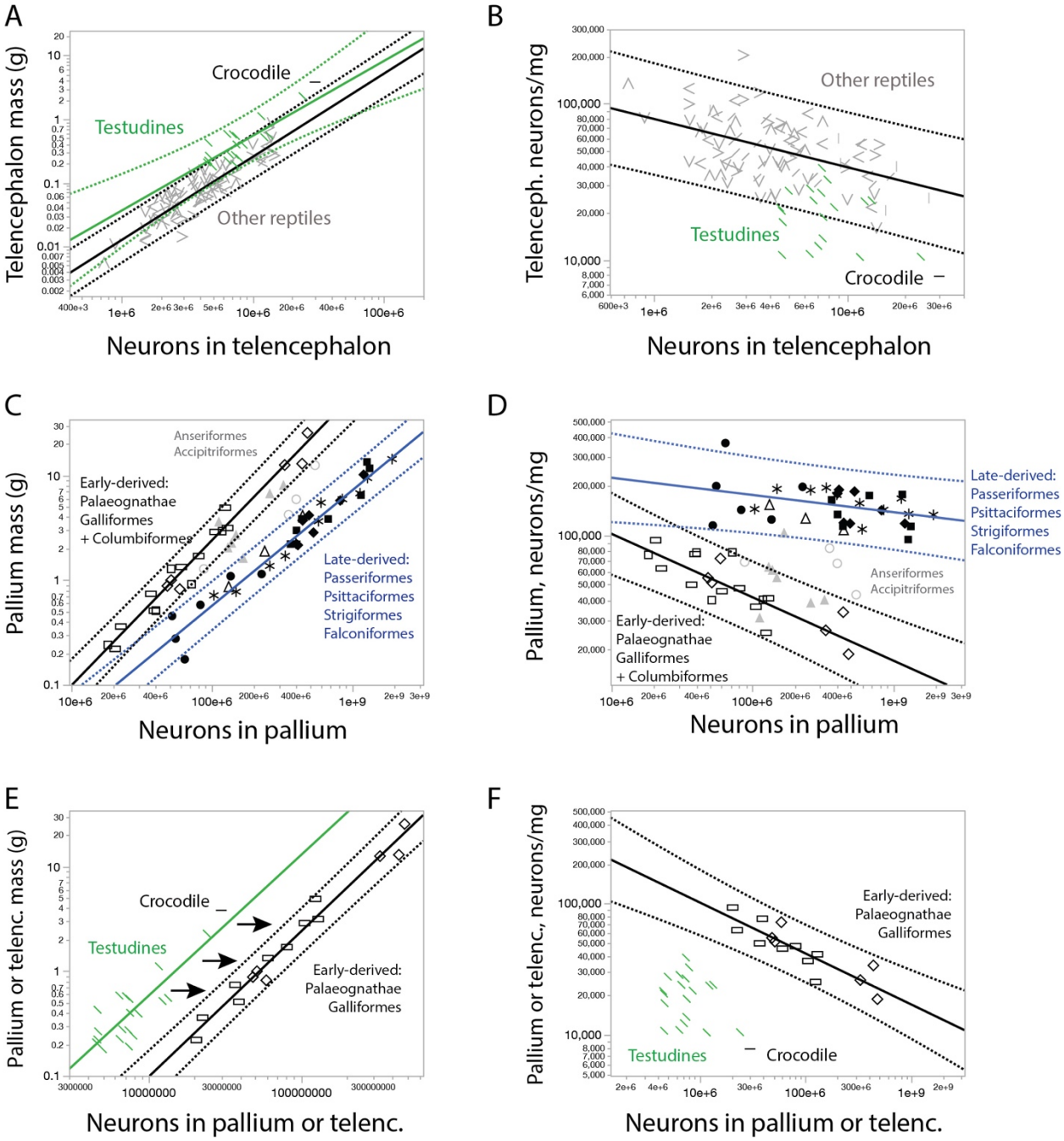

A
Telencephalon mass (g)
Crocodile
Testudines
Other reptiles
Neurons in telencephalon
B
Telenceph. neurons/mg
Other reptiles
Testudines
Crocodile
Neurons in telencephalon
C
Pallium mass (g)
Anseriformes
Accipitriformes
Early-derived:
Palaeognathae
Galliformes
+ Columbiformes
Late-derived:
Passeriformes
Psittaciformes
Strigiformes
Falconiformes
Neurons in pallium
D
Pallium, neurons/mg
Late-derived:
Passeriformes
Psittaciformes
Strigiformes
Falconiformes
Anseriformes
Accipitriformes
Early-derived:
Palaeognathae
Galliformes
+ Columbiformes
Neurons in pallium
E
Pallium or telenc. mass (g)
Crocodile
Testudines
Early-derived:
Palaeognathae
Galliformes
Neurons in pallium or telenc.
F
Pallium or telenc., neurons/mg
Early-derived:
Palaeognathae
Galliformes
Testudines
Crocodile
Neurons in pallium or telenc.

Figure 12. Neuronal scaling rules for the telencephalon of reptiles and birds. A, C, E, scaling of telencephalic mass with numbers of telencephalic neurons. **B, D, F,** scaling of neuronal density in the telencephalon with numbers of telencephalic neurons. **A, B,** Testudines and crocodile have larger telencephalons for their numbers of neurons, and thus lower neuronal densities, compared to other reptilian species. **C, D,** distinct neuronal scaling rules apply to the telencephalon of different bird clades, with higher neuronal densities and therefore more neurons in a telencephalon of similar mass in late-derived clades compared to early-derived clades. Anseriformes and Accipitriformes do not conform systematically to either scaling relationships. **E, F,** neuronal scaling rules that apply to the telencephalon of early-derived bird species and Testudines plus crocodile have similar exponents, indicative of a grade shift. All power functions are listed in Tables 4 and 5. Each data point corresponds to one species. Symbols as in all other figures.

Table 4. Neuronal scaling rules for the telencephalon of reptiles, and the pallium of birds and mammals. Values correspond to the equation $M_{str} = e^{a\pm SE} N_{str}^{b\pm SE}$, the p-values for a and b, and the r^2 for the power fit, where M_{str} is structure mass and N_{str} is the number of neurons in the structure.

M_{str} x N_{str}	n	a in e^a	b in N_{str}^b	p, a	p, b	r^2
Reptiles						
All	108	-24.284±0.988	**1.437**±0.064	<0.0001	<0.0001	0.827
Anguimorpha	7	-24.308±2.212	**1.417**±0.135	0.0001	0.0001	0.957
Crocodilia	1					
Gekkota	14	-21.361±2.904	**1.232**±0.194	<0.0001	<0.0001	0.770
Iguania	20	-24.553±1.196	**1.470**±0.079	<0.0001	<0.0001	0.950
Lacertoidea	15	-22.656±2.038	**1.312**±0.133	<0.0001	<0.0001	0.883
Scincoidea	14	-23.106±2.902	**1.332**±0.189	<0.0001	<0.0001	0.805
Serpentes	18	-22.199±1.749	**1.293**±0.113	<0.0001	<0.0001	0.891
Testudines	19	-19.585±3.618	**1.178**±0.228	<0.0001	<0.0001	0.610
Testudines and Crocodilia	20	-22.193±2.965	**1.344**±0.186	<0.0001	<0.0001	0.743
All minus Testudines and Crocodilia	88	-22.472±0.856	**1.309**±0.056	<0.0001	<0.0001	0.865
Birds						
All	65	-15.245±1.280	**0.840**±0.067	<0.0001	<0.0001	0.715
Accipitriformes	4	-20.574±4.346	**1.134**±0.223	0.0418	0.0366	0.928
Anseriformes	7	-21.727±8.597	**1.209**±0.453	0.0527	0.0446	0.587
Columbiformes	5	-22.941±4.428	**1.284**±0.250	0.0140	0.0142	0.898
Falconiformes	3	-24.320±0.355	**1.293**±0.018	0.0093	0.0090	0.999
Galliformes	9	-26.220±1.904	**1.476**±0.107	<0.0001	<0.0001	0.965
Palaeognathae	6	-25.004±1.876	**1.400**±0.100	0.0002	0.0001	0.980
Passeriformes	13	-20.890±1.692	**1.104**±0.088	<0.0001	<0.0001	0.935
Psittaciformes	11	-20.735±1.199	**1.093**±0.060	<0.0001	<0.0001	0.974
Strigiformes	7	-21.246±3.796	**1.124**±0.186	0.0025	0.0018	0.879

Galliformes, Palaeognathae	15	-24.694±1.111	**1.388**±0.061	<0.0001	<0.0001	0.976
Galliformes, Palaeognathae, Columbiformes	20	-24.679±1.087	**1.386**±0.060	<0.0001	<0.0001	0.967
Falconiformes, Passeriformes, Psittaciformes, Strigiformes	34	-20.799±0.879	**1.100**±0.044	<0.0001	<0.0001	0.950
Mammals						
All (minus bear)	68	-21.938±0.801	**1.275**±0.043	<0.0001	<0.0001	0.929
All non-primates	56	-25.702±0.598	**1.495**±0.033	<0.0001	<0.0001	0.974
Afrotheria	6	-27.188±1.319	**1.565**±0.071	<0.0001	<0.0001	0.992
Artiodactyla	5	-21.576±3.131	**1.303**±0.155	0.0063	0.0035	0.959
Carnivora (minus bear)	7	-20.273±3.869	**1.217**±0.200	0.0034	0.0017	0.882
Chiroptera	13	-26.777±2.641	**1.575**±0.162	<0.0001	<0.0001	0.895
Eulipotyphla	5	-26.451±9.222	**1.518**±0.557	0.0641	0.0721	0.713
Marsupialia	9	-22.703±1.796	**1.329**±0.097	<0.0001	<0.0001	0.964
Primata	12	-18.987±1.513	**1.087**±0.074	<0.0001	<0.0001	0.956
Glires	10	-29.369±1.702	**1.699**±0.096	<0.0001	<0.0001	0.975
Scandentia	1					
All non-primate mammals (minus bear), all reptiles	164	-23.441±0.390	**1.377**±0.024	<0.0001	<0.0001	0.954
All non-primate mammals (minus bear), all reptiles minus Testudines and Crocodilians	144	-23.780±0.334	**1.392**±0.020	<0.0001	<0.0001	0.971

Table 5. Scaling of neuronal density with varying numbers of neurons in the telencephalon of reptiles, and the pallium of birds and mammals. Values correspond to the equation $D_{Nstr} = e^{a\pm SE} N_{str}^{b\pm SE}$, the p-values for a and b, and the r^2 for the power fit, where DN_{str} is neuronal density (in neurons/mg) and N_{str} is the number of neurons in the structure.

D_{Nstr} x N_{str}	n	a in e^a	b in N_{str}^b	p, a	p, b	r^2
Reptiles						
All	108	17.390±0.990	**-0.438**±0.064	<0.0001	<0.0001	0.305
Anguimorpha	7	17.354±2.194	**-0.414**±0.134	0.0005	0.0273	0.656
Crocodilia	1					
Gekkota	14	14.423±2.902	**-0.230**±0.194	0.0003	0.2591	0.105
Iguania	20	17.756±1.203	**-0.478**±0.080	<0.0001	<0.0001	0.667
Lacertoidea	15	15.735±2.032	**-0.311**±0.132	<0.0001	0.0352	0.298
Scincoidea	14	16.201±2.905	**-0.332**±0.189	0.0001	0.1050	0.204
Serpentes	18	15.323±1.736	**-0.295**±0.112	<0.0001	0.0184	0.301
Testudines	19	13.104±3.686	**-0.204**±0.233	0.0024	0.3920	0.043
Testudines and Crocodilia	20	15.486±2.997	**-0.356**±0.188	<0.0001	0.0749	0.166
All minus Testudines and Crocodilia	88	15.563±0.858	**-0.309**±0.056	<0.0001	<0.0001	0.262
Birds						
All	65	8.003±1.273	**-0.179**±0.066	<0.0001	0.0089	0.104
Accipitriformes	4	13.794±4.346	**-0.140**±0.223	0.0866	0.5936	0.165
Anseriformes	7	14.721±8.597	**-0.203**±0.453	0.1475	0.6725	0.039
Columbiformes	5	16.826±4.617	**-0.330**±0.260	0.0356	0.2945	0.349
Falconiformes	3	17.404±0.513	**-0.292**±0.027	0.0188	0.0577	0.992
Galliformes	9	19.234±1.899	**-0.472**±0.106	<0.0001	0.0030	0.738
Palaeognathae	6	11.964±7.565	**-0.056**±0.402	0.1889	0.8952	0.005
Passeriformes	13	13.982±1.692	**-0.104**±0.088	<0.0001	0.2615	0.113
Psittaciformes	11	13.827±1.199	**-0.093**±0.060	<0.0001	0.1531	0.213
Strigiformes	7	14.327±3.804	**-0.123**±0.187	0.0131	0.5380	0.080
Galliformes, Palaeognathae	15	13.398±3.092	**-0.386**±0.061	<0.0001	<0.0001	0.755
Galliformes, Palaeognathae, Columbiformes	20	17.795±1.091	**-0.388**±0.061	<0.0001	<0.0001	0.697
Falconiformes, Passeriformes, Psittaciformes, Strigiformes	34	13.895±0.879	**-0.100**±0.044	<0.0001	0.0315	0.136
Mammals						
All (minus bear)	68	15.023±0.803	**-0.274**±0.044	<0.0001	<0.0001	0.375
All non-primates	56	18.793±0.600	**-0.495**±0.033	<0.0001	<0.0001	0.803

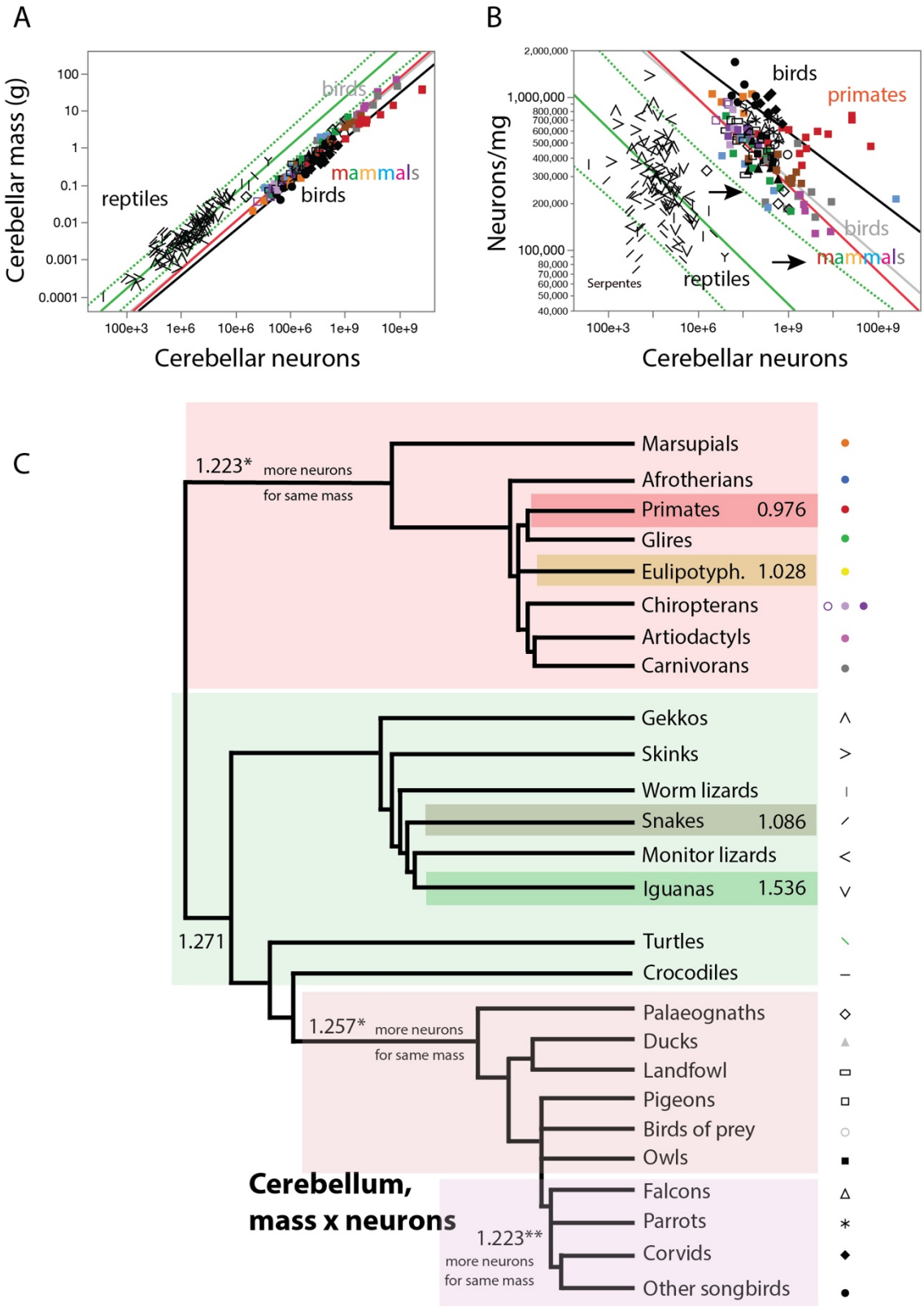
Afrotheria	6	20.260±1.332	**-0.564**±0.071	0.0001	0.0014	0.940
Artiodactyla	5	14.668±3.131	**-0.303**±0.155	0.0184	0.1447	0.562
Carnivora (minus bear)	7	13.365±3.870	**-0.217**±0.200	0.0182	0.3258	0.192
Chiroptera	13	19.803±2.656	**-0.571**±0.163	<0.0001	0.0050	0.526
Eulipotyphla	5	19.590±9.296	**-0.521**±0.561	0.1257	0.4217	0.223
Marsupialia	9	15.795±1.796	**-0.329**±0.097	<0.0001	0.0117	0.620
Primata	12	12.094±1.513	**-0.087**±0.074	<0.0001	0.2644	0.123
Glires	10	22.415±1.683	**-0.696**±0.095	<0.0001	<0.0001	0.870
Scandentia	1					
All non-primate mammals (minus bear), all reptiles	164	16.526±0.391	**-0.377**±0.024	<0.0001	<0.0001	0.605
All non-primate mammals, reptiles minus Testudines and Crocodilians	144	16.863±0.335	**-0.391**±0.020	<0.0001	<0.0001	0.722

Neuronal scaling rules for the cerebellum are shared across most endothermic species, with a step change from ectothermic reptiles

Differently from the telencephalon, the neuronal scaling rules that apply to the cerebellum are clearly distinct between reptiles and mammals, and overlap across most mammalian and the early-derived bird species (Figure 13). Amongst most reptiles, the cerebellum gains mass faster than it gains neurons, in a manner described by a power function of exponent 1.271±0.051 (Figure 13A, green; Table 6) from which snakes and iguanas are the only clear exceptions (Figure 14). Thus, across most reptilian species as a whole, more cerebellar neurons are also on average larger neurons, with decreasing neuronal densities (Figure 7B), although Iguania is the only clade that shows on its own a clear decrease in cerebellar neuronal density as the cerebellum gains neurons across species (Table 7).

687 A power function with an exponent of 1.257±0.048, statistically indistinguishable from
688 the reptilian exponent, applies to the cerebellum of early derived birds: Accipitriformes,
689 Anseriformes, Columbiformes, Galliformes and Palaeognathae, and also to Strigiformes (Figure
690 13A, grey line), although this curve is shifted to the right with respect to reptiles, just as seen in
691 the case of the telencephalon/pallium between Testudine and crocodilian reptiles and early-
692 derived birds (Figure 12E). Remarkably, a similar power function to the one that applies to these
693 six bird clades describes the scaling of the non-primate, non-eulipotyphlan mammalian
694 cerebellum (Herculano-Houzel et al., 2007, 2014; Sarko et al., 2009; Jardim-Messeder et al.,
695 2017), with a matching exponent of 1.223±0.024 (Figure 13A, red line; Figure 14A,B). Indeed, the
696 scaling relationship that applies to the combination of these two groups of birds and mammals
697 has an undistinguishable exponent of 1.234±0.021 (Figure 14A,B; Table 6). Additionally, the
698 scaling exponent that applies to early-derived birds, plus Strigiformes, is virtually identical to the
699 scaling exponent that applies to reptiles as a whole (1.160±0.047 and 1.159±0.046, respectively),
700 with a distribution that is simply shifted to the right, with more neurons in a same structure mass
701 (Figure 14C; Table 6). Across the other three bird clades (Falconiformes, Passeriformes including
702 corvids, and Psittaciformes), yet another seemingly parallel power function relates cerebellar
703 mass to number of neurons, with exponent 1.223±0.053 (Table 6), not significantly different from
704 the others (Figure 13A, Figure 14). Strikingly, the neuronal scaling rules that apply to the
705 cerebellum can be further distinguished across Falconiformes and Psittaciformes on the one
706 hand, and Passeriformes on the other, with even higher neuronal densities in the cerebellum of
707 the latter (Figure 14F).
708 The similar exponents that describe the scaling of cerebellar mass as it gains neurons
709 across reptiles, birds, and most mammalian species stems from the similar slope of the decrease
710 in cerebellar neuronal densities with increasing numbers of neurons across the three groups
711 described above (Figure 13B, compare green, grey/red, and black lines), with exponents of
712 around -0.25, with parallel power functions that apply to each clade (Figure 14F, Table 7). As
713 described previously (Herculano-Houzel, 2014a), primates and eulipotyphlans are the only
714 groups amongst mammals that clearly depart from these allometric relationships, with no
715 significant change in neuronal density in the cerebellum as it gains neurons (Figure 13B), which

716 translates into cerebellar mass that scales linearly with numbers of neurons (Figure 13A, 14B;
717 Tables 6, 7).
718 Mapping these scaling relationships onto the phylogenetic tree of all species of amniotes
719 in the dataset indicates that while there has been a major step increase in numbers of cerebellar
720 neurons in the two groups of endotherms compared to reptiles, and apparently two further step
721 increases at the origin of more recently derived birds, the allometric exponent that applies to the
722 scaling of neuronal density with numbers of neurons in the cerebellum only diverged at the origin
723 of primates and eulipotyphlans, amongst mammals; and at the origins of Serpentes, and Iguania
724 amongst reptiles (Figure 7C). The significance of such step increases in the context of the
725 evolution of endothermy is addressed separately (Herculano-Houzel, 2025).
726


A
Cerebellar mass (g)
100
10
1
0.1
0.01
0.001
0.0001
reptiles
birds
mammals
birds
100e+3
1e+6
10e+6
100e+6
1e+9
10e+9
Cerebellar neurons
B
Neurons/mg
2,000,000
1,000,000
800,000
700,000
600,000
500,000
400,000
300,000
200,000
100,000
80,000
70,000
60,000
50,000
40,000
birds
primates
birds
mammals
Serpentes
reptiles
100e+3
10e+6
1e+9
100e+9
Cerebellar neurons
C
1.223* more neurons for same mass
Marsupials
Afrotherians
Primates 0.976
Glires
Eulipotyph. 1.028
Chiropterans
Artiodactyls
Carnivorans
Gekkos
Skinks
Worm lizards
Snakes 1.086
Monitor lizards
Iguanas 1.536
1.271
Turtles
Crocodiles
1.257* more neurons for same mass
Palaeognaths
Ducks
Landfowl
Pigeons
Birds of prey
Owls
Cerebellum, mass x neurons
1.223** more neurons for same mass
Falcons
Parrots
Corvids
Other songbirds

727

728

Figure 13. Reptiles, birds and non-primate, non-eulipotyphlans mammals share allometric exponents for the neuronal composition of the cerebellum, although relationships are shifted to the right in the two endotherm clades. A, scaling of cerebellar mass with numbers of neurons across non-primate, non-eulipotyphlan mammals (in red, exponent 1.223±0.024), all reptiles minus serpents and iguanas (in green, with 95% prediction interval; exponent, 1.271±0.051), early-derived birds (Galliformes, Palaeognathae, Anseriformes, plus Columbiformes, Accipitriformes and Strigiformes, in gray, with near-perfect overlap with mammals; exponent, 1.257±0.048), and late-derived birds (Falconiformes, Passeriformes, Psittaciformes, in black; exponent, 1.223±0.053). For the sake of clarity, the 95% prediction interval is only plotted for reptilian species. All power functions are listed in Table 6. **B**, Neuronal density in the cerebellum (number of neurons per milligram of cerebellar mass) decreases steeply with increasing numbers of cerebellar neurons in parallel scaling functions across reptilian, non-primate, non-eulipotyphlan mammalian, and early-derived bird species alike, while late-derived birds have higher neuronal densities. Power functions plotted have exponents -0.287±0.046 (reptiles minus serpents, in green), -0.223±0.024 (non-primate, non-eulipotyphlan mammals, in red), -0.257±0.048 (early-derived birds, in gray) and -0.223±0.053 (late-derived birds, in black). For the sake of clarity, the 95% prediction interval is only plotted for reptilian species. All power functions are listed in Table 7. **C**, Putative cladogram for the evolution of the exponent that describes the scaling relationship between cerebellar mass and number of neurons, with a shared exponent across most extant reptilian, basal bird, and mammalian species, with a grade shift towards more neurons in a similar cerebellar mass in the newly endothermic species, then again in primates, eulipotyphlans, and late-derived birds. The scaling relationship shared by most reptilian species can thus be inferred to have applied to ancestral ectothermic amniotic species. Each data point corresponds to one species. The key used to depict each clade is shown to the right.

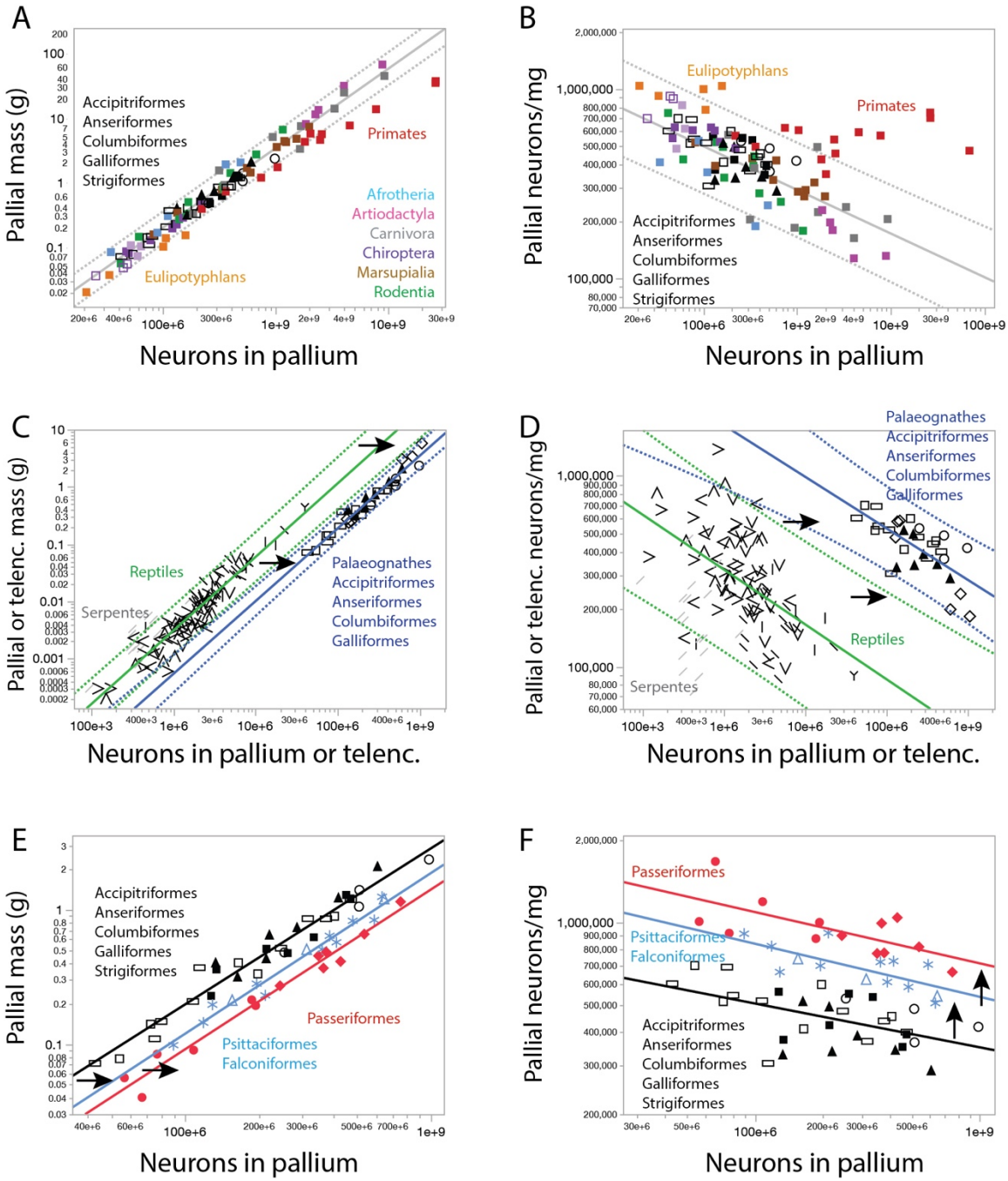

A
Pallial mass (g)
Accipitriformes
Anseriformes
Columbiformes
Galliformes
Strigiformes
Primates
Afrotheria
Artiodactyla
Carnivora
Chiroptera
Marsupialia
Rodentia
Eulipotyphlans
Neurons in pallium
B
Pallial neurons/mg
Eulipotyphlans
Primates
Accipitriformes
Anseriformes
Columbiformes
Galliformes
Strigiformes
Neurons in pallium
C
Pallial or telenc. mass (g)
Reptiles
Serpentes
Palaeognathes
Accipitriformes
Anseriformes
Columbiformes
Galliformes
Neurons in pallium or telenc.
D
Pallial or telenc. neurons/mg
Palaeognathes
Accipitriformes
Anseriformes
Columbiformes
Galliformes
Reptiles
Serpentes
Neurons in pallium or telenc.
E
Pallial mass (g)
Accipitriformes
Anseriformes
Columbiformes
Galliformes
Strigiformes
Passeriformes
Psittaciformes
Falconiformes
Neurons in pallium
F
Pallial neurons/mg
Passeriformes
Psittaciformes
Falconiformes
Accipitriformes
Anseriformes
Columbiformes
Galliformes
Strigiformes
Neurons in pallium

Figure 14. Neuronal scaling rules for the cerebellum of mammals, reptiles and birds. A, C, E, scaling of cerebellar mass with numbers of cerebellar neurons. **B, D, F,** scaling of neuronal density in the cerebellum with numbers of cerebellar neurons. **A, B,** Early-derived birds and mammals other than primates and eulipotyphlans share neuronal scaling rules for the cerebellum. Power function plotted applies to non-primate, non-eulipotyphlan mammalian species plus the bird clades indicated. **C, D,** neuronal scaling rules for the cerebellum of reptiles (minus Serpentes) and of early-derived bird clades have similar exponents, indicative of a grade shift. **E, F,** neuronal scaling rules for the cerebellum of three different groups of birds, indicated in black, blue and red, have similar exponents, indicative of two grade shifts in bird evolution. All power functions are listed in Tables 6 and 7.

Table 6. Neuronal scaling rules for the cerebellum of reptiles, birds and mammals. Values correspond to the equation $M_{cb} = e^{a\pm SE} N_{cb}^{b\pm SE}$, the p-values for a and b, and the r^2 for the power fit, where M_{cb} is cerebellar mass and N_{cb} is the number of neurons in the cerebellum.

M_{cb} x N_{cb}	n	a in e^a	b in N_{cb}^b	p, a	p, b	r^2
Reptiles						
All	108	-21.597±0.658	**1.159**±0.046	<0.0001	<0.0001	0.856
Anguimorpha	7	-20.551±1.135	**1.099**±0.077	<0.0001	<0.0001	0.976
Crocodilia	1					
Gekkota	14	-22.341±2.108	**1.179**±0.153	<0.0001	<0.0001	0.833
Iguania	20	-27.286±1.536	**1.536**±0.148	<0.0001	<0.0001	0.857
Lacertoidea	15	-21.123±2.516	**1.111**±0.179	<0.0001	<0.0001	0.747
Scincoidea	14	-22.206±2.128	**1.179**±0.155	<0.0001	<0.0001	0.828
Serpentes	18	-20.114±2.679	**1.086**±0.206	<0.0001	<0.0001	0.635
Testudines	19	-19.549±1.908	**1.043**±0.125	<0.0001	<0.0001	0.803
Testudines and Crocodilia	20	-22.828±1.500	**1.128**±0.098	<0.0001	<0.0001	0.881
All minus Serpentes	90	-23.527±0.673	**1.285**±0.047	<0.0001	<0.0001	0.897
All minus Serpentes, Iguania	70	-23.313±0.729	**1.271**±0.051	<0.0001	<0.0001	0.903
Birds						
All	65	-24.549±1.213	**1.229**±0.063	<0.0001	<0.0001	0.859
Accipitriformes	4	-23.486±3.313	**1.178**±0.165	0.0193	0.0191	0.962
Anseriformes	7	-23.887±3.008	**1.214**±0.155	0.0005	0.0005	0.924
Columbiformes	5	-22.998±2.267	**1.156**±0.121	0.0020	0.0024	0.968
Falconiformes	3	-24.558±0.304	**1.220**±0.016	0.0079	0.0081	0.999
Galliformes	9	-23.365±1.703	**1.180**±0.090	<0.0001	<0.0001	0.961
Palaeognathae	6	-30.001±1.405	**1.529**±0.072	<0.0001	<0.0001	0.991
Passeriformes	13	-24.284±1.171	**1.188**±0.061	<0.0001	<0.0001	0.972
Psittaciformes	11	-23.931±1.264	**1.183**±0.065	<0.0001	<0.0001	0.974
Strigiformes	7	-22.131±3.078	**1.114**±0.159	0.0008	0.0009	0.908

Galliformes, Anseriformes, Accipitriformes, Columbiformes, Strigiformes	32	-23.000±0.896	**1.160**±0.047	<0.0001	<0.0001	0.954
Galliformes, Anseriformes, Accipitriformes, Columbiformes, Strigiformes, Palaeognathae	38	-24.822±0.928	**1.257**±0.048	<0.0001	<0.0001	0.950
Falconiformes, Passeriformes, Psittaciformes	27	-24.822±1.025	**1.223**±0.053	<0.0001	<0.0001	0.955
Falconiformes, Psittaciformes	14	-24.142±1.039	**1.195**±0.053	<0.0001	<0.0001	0.977
Mammals						
All	71	-22.539±0.553	**1.135**±0.028	<0.0001	<0.0001	0.961
All non-primates	58	-24.586±0.495	**1.245**±0.025	<0.0001	<0.0001	0.977
All non-primates, non-eulipotyphlans	53	-24.111±0.478	**1.223**±0.024	<0.0001	<0.0001	0.981
Afrotheria	6	-21.115±1.027	**1.079**±0.051	<0.0001	<0.0001	0.991
Artiodactyla	5	-26.632±2.588	**1.351**±0.118	0.0020	0.0014	0.978
Carnivora	8	-21.332±2.667	**1.095**±0.126	0.0002	0.0001	0.927
Chiroptera	13	-23.582±1.610	**1.183**±0.089	<0.0001	<0.0001	0.941
Eulipotyphla	5	-21.165±1.520	**1.028**±0.084	0.0008	0.0012	0.980
Marsupialia	10	-23.421±0.746	**1.186**±0.037	<0.0001	<0.0001	0.992
Primata	13	-19.572±0.794	**0.976**±0.036	<0.0001	<0.0001	0.985
Glires	10	-26.462±1.406	**1.349**±0.073	<0.0001	<0.0001	0.977
Scandentia	1					
All non-primates, non-eulipotyphlans, Accipitriformes, Anseriformes, Columbiformes, Galliformes, Palaeognathae, Strigiformes	84	-24.283±0.403	**1.234**±0.021	<0.0001	<0.0001	0.978

765
766 **Table 7.** Scaling of neuronal density with varying numbers of neurons in the cerebellum of reptiles, birds and
767 mammals. Values correspond to the equation $D_{Ncb} = e^{a \pm SE} N_{cb}^{b \pm SE}$, the p-values for a and b, and the r^2 for the power
768 fit, where D_{Ncb} is neuronal density in the cerebellum and N_{cb} is the number of neurons in the cerebellum.
769

D_{Ncb} x N_{cb}	n	a in e^a	b in N_{cb}^b	p, a	p, b	r^2
Reptiles						
All	108	14.685±0.659	**-0.159**±0.046	<0.0001	0.0009	0.100
Anguimorpha	7	13.531±1.117	**-0.092**±0.076	<0.0001	0.2762	0.230
Crocodilia	1					
Gekkota	14	15.756±2.081	**-0.202**±0.151	<0.0001	0.2041	0.131
Iguania	20	20.425±2.176	**-0.539**±0.147	<0.0001	0.0018	0.426
Lacertoidea	15	14.226±2.515	**-0.111**±0.179	<0.0001	0.5448	0.029
Scincoidea	14	15.458±2.127	**-0.190**±0.155	<0.0001	0.2431	0.116
Serpentes	18	12.875±2.662	**-0.061**±0.204	0.0002	0.7687	0.006
Testudines	19	12.631±1.908	**-0.042**±0.125	<0.0001	0.7423	0.007
Testudines and Crocodilia	20	13.914±1.500	**-0.127**±0.098	<0.0001	0.2097	0.086
All minus Serpentes	90	16.651±0.673	**-0.287**±0.046	<0.0001	<0.0001	0.303
Birds						
All	65	17.632±1.214	**-0.228**±0.063	<0.0001	0.0006	0.173
Accipitriformes	4	16.587±3.319	**-0.179**±0.166	0.0378	0.3933	0.368
Anseriformes	7	16.983±3.018	**-0.214**±0.156	0.0025	0.2282	0.274
Columbiformes	5	16.100±2.272	**-0.156**±0.121	0.0058	0.2877	0.357
Falconiformes	3	17.663±0.295	**-0.220**±0.015	0.0106	0.0434	0.995
Galliformes	9	16.451±1.729	**-0.180**±0.092	<0.0001	0.0903	0.355
Palaeognathae	6	23.080±1.405	**-0.528**±0.072	<0.0001	0.0018	0.932
Passeriformes	13	17.363±1.171	**-0.188**±0.061	<0.0001	0.0105	0.463
Psittaciformes	11	17.000±1.256	**-0.182**±0.065	<0.0001	0.0202	0.468
Strigiformes	7	15.248±3.071	**-0.116**±0.159	0.0042	0.4990	0.096
Galliformes, Anseriformes, Accipitriformes, Columbiformes, Strigiformes	32	16.091±0.901	**-0.160**±0.047	<0.0001	0.0018	0.251
Galliformes, Anseriformes, Accipitriformes, Columbiformes,	38	17.909±0.930	**-0.257**±0.048	<0.0001	0.0018	0.440

Strigiformes, Palaeognathae						
Falconiformes, Passeriformes, Psittaciformes	27	17.900±1.024	**-0.223**±0.053	<0.0001	0.0003	0.414
Falconiformes, Psittaciformes	14	17.218±1.035	**-0.194**±0.053	<0.0001	0.0033	0.526
Mammals						
All	71	15.626±0.554	**-0.134**±0.028	<0.0001	<0.0001	0.256
All non-primates	58	17.688±0.495	**-0.245**±0.025	<0.0001	<0.0001	0.630
All non-primates, non-eulipotyphlans	53	17.210±0.477	**-0.223**±0.024	<0.0001	<0.0001	0.628
Afrotheria	6	14.205±1.017	**-0.079**±0.050	0.0002	0.1904	0.383
Artiodactyla	5	19.724±2.588	**-0.351**±0.118	0.0047	0.0509	0.747
Carnivora	8	14.424±2.667	**-0.095**±0.126	0.0017	0.4771	0.087
Chiroptera	13	16.579±1.625	**-0.178**±0.090	<0.0001	0.0732	0.263
Eulipotyphla	5	14.241±1.452	**-0.027**±0.081	0.0023	0.7633	0.035
Marsupialia	10	16.513±0.746	**-0.186**±0.037	<0.0001	0.0010	0.761
Primata	13	12.578±0.776	**0.028**±0.035	<0.0001	0.4401	0.055
Glires	10	19.447±1.376	**-0.343**±0.071	<0.0001	0.0014	0.743
Scandentia	1					
All non-primates, non-eulipotyphlans, Accipitriformes, Anseriformes, Columbiformes, Galliformes, Palaeognathae, Strigiformes	84	17.376±0.403	**-0.231**±0.021	<0.0001	<0.0001	0.608

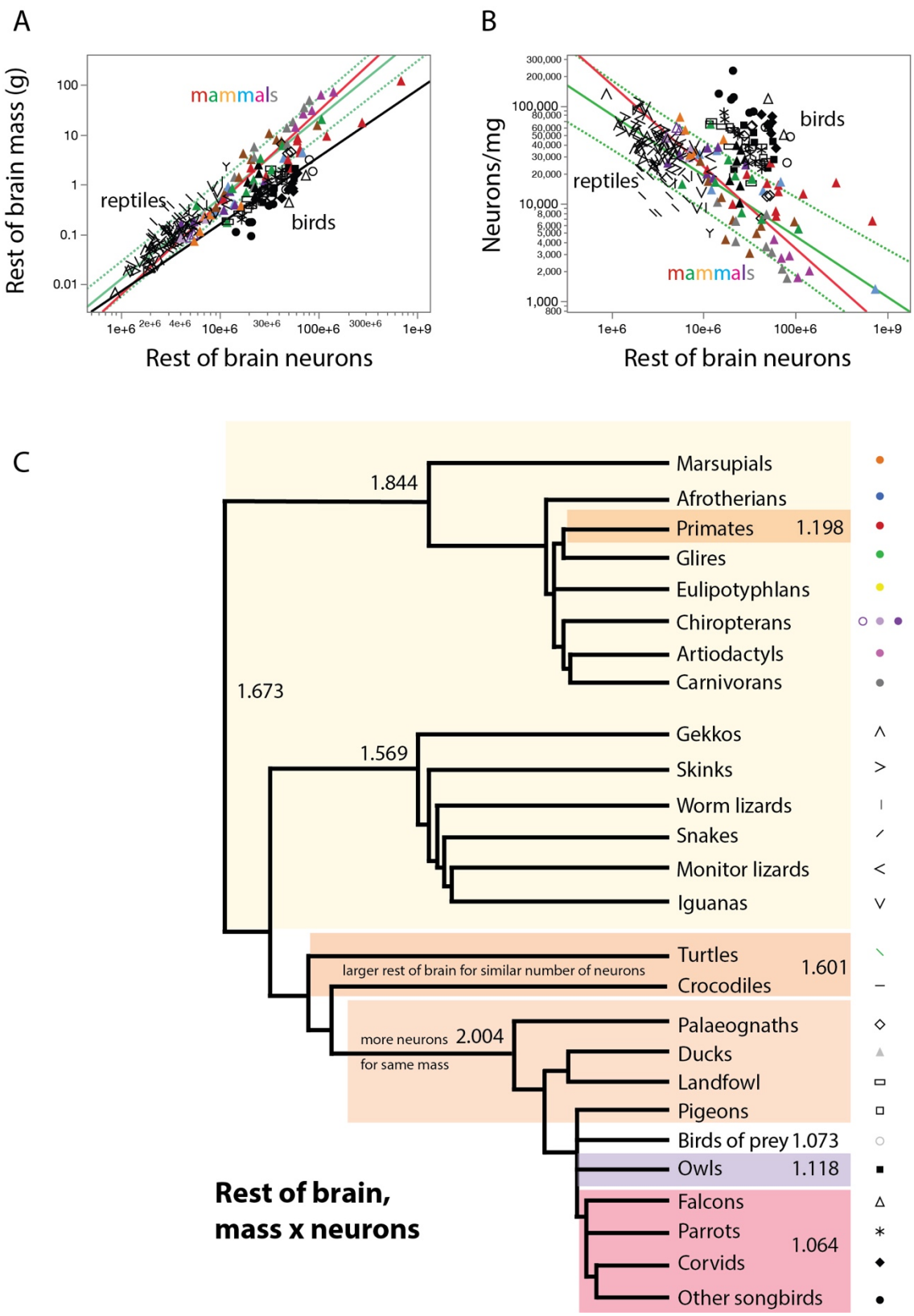
Neuronal scaling rules for the rest of brain are shared between reptiles and non-primate mammals

Similarly to the telencephalon, the neuronal scaling rules that apply to the rest of brain (brainstem, diencephalon and subpallium in mammals, or brainstem plus diencephalon in reptiles and birds; Kverkova et al., 2022) overlap across most reptiles and mammals (Figure 15A, Table 8), with the exception of primates, which diverge from other mammals as reported previously (Herculano-Houzel et al., 2014a). As shown in Figures 15A and 16A, the 95% prediction interval of the scaling relationship for reptiles between the mass of the rest of brain and its number of neurons includes the majority of non-primate mammals, including large artiodactyls and carnivorans, with scaling exponents that are not significantly different (non-primate mammals, 1.844±0.076; reptiles, 1.569±0.067, excluding Testudines and crocodile; combined sample, 1.673±0.035; Table 6). Increases in numbers of neurons in the rest of brain are thus accompanied by decreasing neuronal densities with a scaling relationship across reptiles (excluding Testudines and crocodile) that includes most mammalian species (Figure 16B, Table 8). In contrast, and as found for the telencephalon, the rest of brain of Testudines and the Nile crocodile is larger in mass than in other reptilian species with similar numbers of neurons in the structure (Figure 16, Table 8).

The conformity of most reptilian and mammalian species to the same scaling relationship between numbers of neurons in the rest of brain and average neuronal density in these structures, with continuity across these species in scaling (Figure 15), indicates that the neuronal scaling rule that they share also applied to their common ancestral amniote species (Figure 15C). Thus, as for the telencephalon, what differentiates the rest of brain of mammals from the majority of reptiles seems to be simply the vastly larger numbers of neurons in the former, but apparently added in conformity to the same scaling rules.

Birds, in contrast, have more neurons in the rest of brain than both reptiles and mammals with similar mass in these structures (Figure 15B, Figure 16C). The scaling relationship that applies to the rest of brain of the early-derived birds might also be simply shifted to the right compared to reptiles (as found for the cerebellum), with an exponent of 2.004±0.183 across Galliformes, Anseriformes, Columbiformes and Palaeognathae that is statistically indistinguishable from the exponent of 1.601±0.205 that applies to Testudines and crocodile (Figure 16C). Amongst birds, however, different relationships between numbers of neurons and neuronal density apply to the

806 early-derived Palaeognathae, Galliformes, Anseriformes and Collumbiformes versus the later-
807 derived Falconiformes, Passeriformes and Psittaciformes (Tables 8 and 9; Figure 16D).
808


A
Rest of brain mass (g)
mammals
reptiles
birds
Rest of brain neurons
B
Neurons/mg
birds
reptiles
mammals
Rest of brain neurons
C
1.844
1.673
1.569
Marsupials
Afrotherians
Primates 1.198
Glires
Eulipotyphlans
Chiropterans
Artiodactyls
Carnivorans
Gekkos
Skinks
Worm lizards
Snakes
Monitor lizards
Iguanas
Turtles
Crocodiles
1.601
larger rest of brain for similar number of neurons
more neurons 2.004
for same mass
Palaeognaths
Ducks
Landfowl
Pigeons
Birds of prey 1.073
Owls 1.118
Falcons
Parrots
Corvids
1.064
Other songbirds
Rest of brain,
mass x neurons

809

Figure 15. Reptiles and non-primate mammals share allometric exponents for the neuronal composition of the rest of brain, while the scaling relationship for birds is shifted to the right. A, scaling of rest of brain mass with numbers of neurons plotted for non-primate mammals (in red, exponent 1.844±0.076), all reptiles minus Testudines and crocodile (in green, exponent 1.569±0.067), and all birds (in black, exponent, 1.346±0.173). For the sake of clarity, the 95% prediction interval is only plotted for reptilian species. All power functions are listed in Table 8. **B**, Neuronal density in the rest of brain decreases steeply with increasing numbers of rest of brain neurons across reptilian and non-primate mammalian species, while birds have higher neuronal densities. Power functions plotted have exponents -0.573±0.067 (reptiles minus Testudines and crocodile, in green) and -0.845±0.076 (non-primate mammals, in red). Power functions for birds, listed in Table 9, are clade-specific and are not plotted for the sake of clarity. **C**, Putative cladogram for the evolution of the exponent that describes the scaling relationship between rest of brain mass and number of neurons, showing a shared exponent across most extant reptilian and mammalian species that can be inferred to have applied to ancestral amniotic species. Colored areas indicate clade-specific changes. Each data point corresponds to one species. The key used to depict each clade is shown to the right.

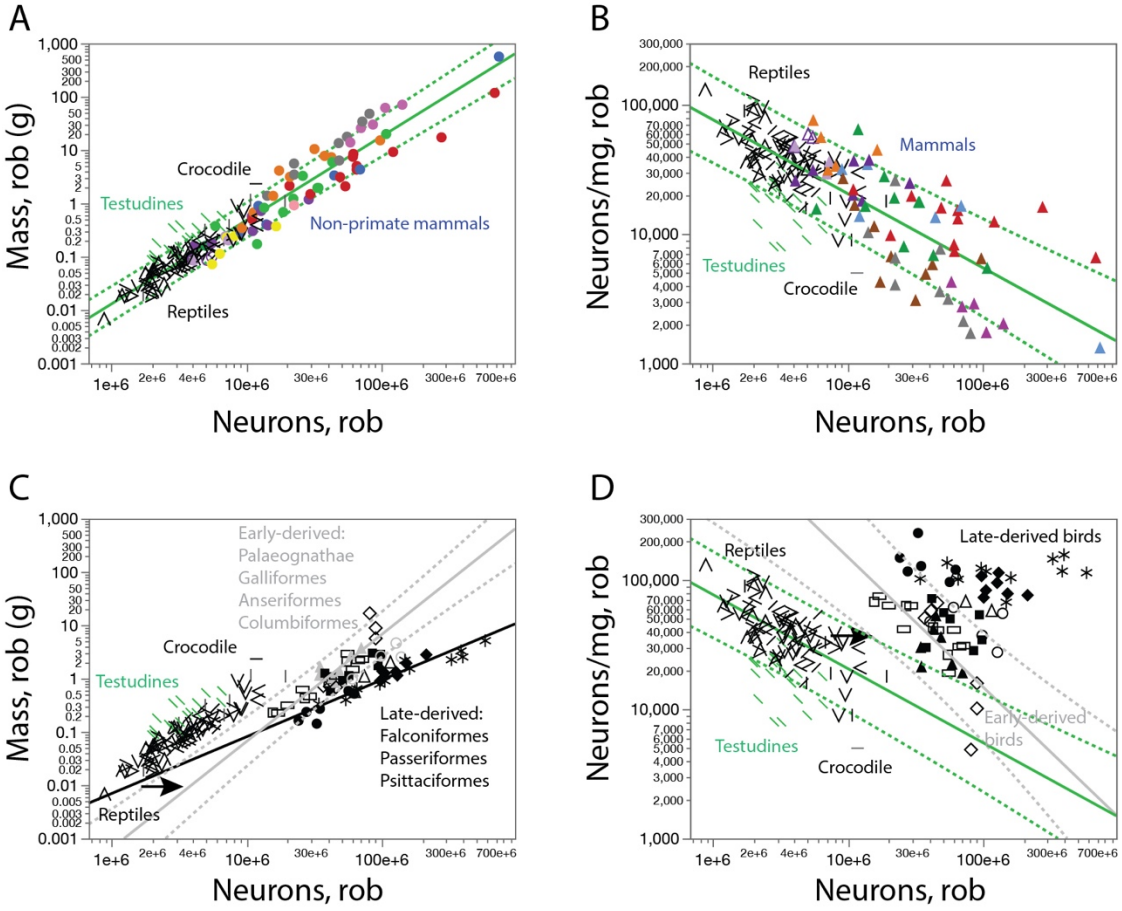


Figure 16. Neuronal scaling rules for the rest of brain of reptiles, mammals and birds. A, C, scaling of rest of brain mass with numbers of rest of brain neurons. **B, D,** scaling of neuronal density in the rest of brain with numbers of rest of brain neurons. **A, B,** The scaling rule that applies to Reptiles (minus Testudines and crocodile; plotted in green) includes most mammalian species in the dataset, in a continuum. **C, D,** parallel neuronal scaling rules with similar exponents apply to the rest of brain of reptiles and the early-derived bird clades. All power functions are listed in Tables 8 and 9.

Table 8. Neuronal scaling rules for the rest of brain of reptiles, birds and mammals. Values correspond to the equation $M_{rob} = e^{a \pm SE} N_{rob}^{b \pm SE}$, the p-values for a and b, and the r^2 for the power fit, where M_{rob} is mass of the rest of brain and N_{rob} is the number of neurons in the rest of brain. In reptiles and birds, rest of brain consists of the brainstem and diencephalon; in mammals, it additionally contains the striatum.

M_{rob} x N_{rob}	n	a in e^a	b in N_{rob}^b	p, a	p, b	r^2
Reptiles						
All	108	-25.833±1.299	**1.568**±0.086	<0.0001	<0.0001	0.757
Anguimorpha	7	-26.920±4.430	**1.640**±0.284	0.0017	0.0022	0.870
Crocodilia	1					
Gekkota	14	-26.507±3.878	**1.603**±0.265	<0.0001	<0.0001	0.753
Iguania	20	-26.795±2.325	**1.619**±0.152	<0.0001	<0.0001	0.863
Lacertoidea	15	-25.422±1.832	**1.519**±0.121	<0.0001	<0.0001	0.924
Scincoidea	14	-24.170±2.686	**1.442**±0.180	<0.0001	<0.0001	0.842
Serpentes	18	-23.542±3.538	**1.411**±0.235	<0.0001	<0.0001	0.692
Testudines	19	-22.191±3.894	**1.371**±0.260	<0.0001	<0.0001	0.621
Testudines and Crocodilia	20	-25.628±3.083	**1.601**±0.205	<0.0001	<0.0001	0.773
All minus Testudines, Crocodilia	88	-26.022±1.012	**1.569**±0.067	<0.0001	<0.0001	0.864
Birds						
All	65	-23.554±2.997	**1.346**±0.173	<0.0001	<0.0001	0.490
Accipitriformes	4	-18.846±6.594	**1.073**±0.362	0.0289	0.0252	0.594
Anseriformes	7	-12.654±5.552	**0.745**±0.320	0.0417	0.0384	0.311
Columbiformes	5	-28.177±2.120	**1.621**±0.125	0.0009	0.0010	0.983
Falconiformes	3	-43.646±25.189	**2.430**±1.409	0.3332	0.3345	0.748
Galliformes	9	-29.695±4.118	**1.717**±0.241	0.0002	0.0002	0.879
Palaeognathae	6	-73.806±19.991	**4.252**±1.144	0.0210	0.0205	0.776
Passeriformes	13	-32.429±2.616	**1.815**±0.150	<0.0001	<0.0001	0.930
Psittaciformes	11	-38.150±2.968	**2.203**±0.173	<0.0001	<0.0001	0.947
Strigiformes	7	-19.472±8.383	**1.118**±0.480	0.0678	0.0673	0.520
Galliformes, Anseriformes, Columbiformes, Palaeognathae	27	-35.008±3.219	**2.004**±0.183	<0.0001	<0.0001	0.827
Falconiformes, Passeriformes, Psittaciformes	27	-19.663±1.305	**1.064**±0.071	<0.0001	<0.0001	0.900

Mammals						
All	69	-27.111±1.270	**1.630**±0.074	<0.0001	<0.0001	0.878
All non-primates	57	-30.607±1.290	**1.844**±0.076	<0.0001	<0.0001	0.914
Afrotheria	6	-27.952±2.498	**1.663**±0.142	0.0004	0.0003	0.972
Artiodactyla	5	-30.323±5.553	**1.850**±0.303	0.0121	0.0089	0.925
Carnivora	8	-29.260±4.244	**1.803**±0.243	0.0005	0.0003	0.902
Chiroptera	13	-22.765±2.573	**1.343**±0.162	<0.0001	<0.0001	0.862
Eulipotyphla	5	-22.360±7.566	**1.297**±0.476	0.0598	0.0722	0.712
Marsupialia	9	-26.017±4.666	**1.598**±0.274	0.0008	0.0006	0.829
Primata	12	-19.962±2.087	**1.198**±0.116	<0.0001	<0.0001	0.915
Glires	10	-26.202±4.283	**1.568**±0.252	0.0003	0.0003	0.829
Scandentia	1					
All non-primate mammals, all reptiles minus Testudines, crocodile	145	-27.633±0.548	**1.673**±0.035	<0.0001	<0.0001	0.942

Table 9. Scaling of neuronal density with varying numbers of neurons in the rest of brain of reptiles, birds and mammals. Values correspond to the equation $D_{Nrob} = e^{a\pm SE} N_{rob}^{b\pm SE}$, the p-values for a and b, and the r^2 for the power fit, where D_{Nrob} is neuronal density in the rest of brain and N_{rob} is the number of neurons in the rest of brain. In reptiles and birds, rest of brain consists of the brainstem and diencephalon; in mammals, it additionally contains the striatum.

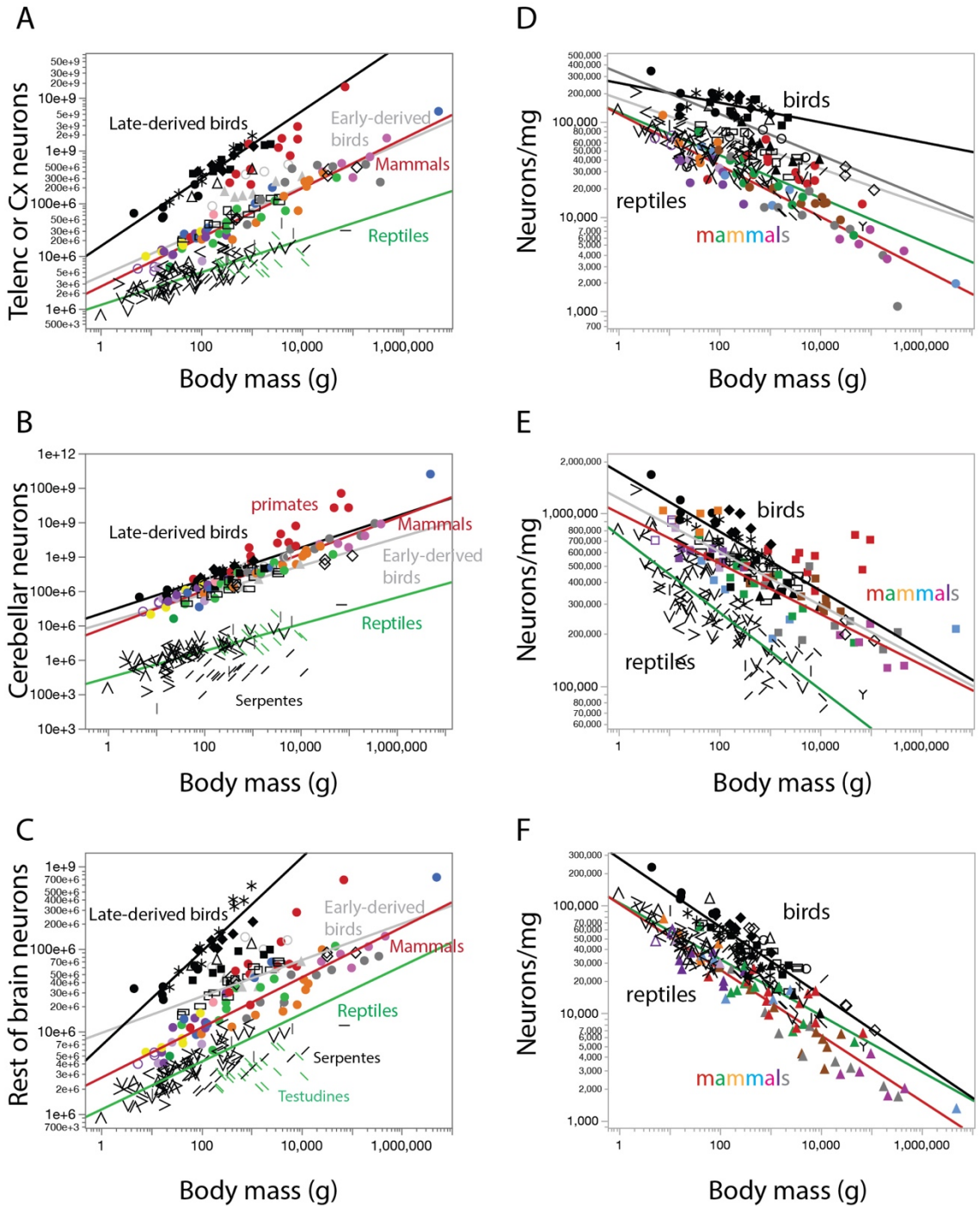
D_{Nrob} x N_{rob}	n	a in e^a	b in N_{rob}^b	p, a	p, b	r^2
Reptiles						
All	108	18.988±1.306	**-0.572**±0.087	<0.0001	<0.0001	0.291
Anguimorpha	7	20.0455±4.455	**-0.641**±0.285	0.0064	0.0744	0.503
Crocodilia	1					
Gekkota	14	19.654±3.864	**-0.605**±0.264	0.0003	0.0409	0.304
Iguania	20	19.971±2.353	**-0.625**±0.154	<0.0001	0.0007	0.479
Lacertoidea	15	18.613±1.844	**-0.526**±0.122	<0.0001	0.0008	0.589
Scincoidea	14	17.280±2.684	**-0.443**±0.180	<0.0001	0.0299	0.336
Serpentes	18	16.789±3.585	**-0.421**±0.238	0.0002	0.0962	0.163
Testudines	19	15.473±3.996	**-0.384**±0.267	0.0012	0.1683	0.109
Testudines and Crocodilia	20	18.854±3.151	**-0.610**±0.209	<0.0001	0.0092	0.321
All minus Testudines, Crocodilia	90	19.168±1.017	**-0.573**±0.067	<0.0001	<0.0001	0.456

Birds						
All	65	16.611±2.991	**-0.344**±0.173	<0.0001	0.0505	0.059
Accipitriformes	4	11.919±6.627	**-0.072**±0.364	0.1222	0.8489	0.007
Anseriformes	7	5.491±5.602	**0.269**±0.323	0.3463	0.4210	0.055
Columbiformes	5	21.172±2.138	**-0.615**±0.126	0.0022	0.0163	0.889
Falconiformes	3	36.340±25.388	**-1.407**±1.420	0.3882	0.5027	0.496
Galliformes	9	22.759±4.091	**-0.715**±0.239	0.0008	0.0202	0.561
Palaeognathae	6	66.530±19.270	**-3.230**±1.102	0.0260	0.0428	0.682
Passeriformes	13	25.522±2.616	**-0.815**±0.150	<0.0001	0.0002	0.728
Psittaciformes	11	31.242±2.968	**-1.203**±0.173	<0.0001	<0.0001	0.843
Strigiformes	7	12.655±8.411	**-0.123**±0.481	0.1928	0.8084	0.013
Galliformes, Columbiformes, Palaeognathae	32	27.464±4.190	**-0.990**±0.244	<0.0001	0.0007	0.479
Accipitriformes, Falconiformes, Passeriformes	20	25.948±2.948	**-0.842**±0.168	<0.0001	<0.0001	0.583
Mammals						
All	69	20.163±1.272	**-0.627**±0.074	<0.0001	<0.0001	0.515
All non-primates	57	23.707±1.290	**-0.845**±0.076	<0.0001	<0.0001	0.690
Afrotheria	6	21.029±2.519	**-0.662**±0.144	0.0011	0.0099	0.842
Artiodactyla	5	23.412±5.552	**-0.850**±0.303	0.0244	0.0677	0.724
Carnivora	8	22.353±4.245	**-0.803**±0.243	0.0019	0.0163	0.646
Chiroptera	13	15.823±2.532	**-0.340**±0.160	<0.0001	0.0564	0.292
Eulipotyphla	5	15.344±7.440	**-0.290**±0.468	0.1312	0.5789	0.114
Marsupialia	9	19.109±4.666	**-0.598**±0.274	0.0046	0.0654	0.405
Primata	12	12.734±2.035	**-0.180**±0.113	<0.0001	0.1413	0.203
Glires	10	19.215±4.232	**-0.563**±0.249	0.0019	0.0535	0.390
Scandentia	1					
All non-primate mammals, all reptiles minus Testudines, crocodile	145	20.717±0.549	**-0.672**±0.035	<0.0001	<0.0001	0.724

Relationships of numbers of neurons to body mass

849 In contrast to the marked continuity in the relationship between structure mass and
850 numbers of neurons across amniote clades pointed out above, the numbers of neurons that
851 compose the telencephalon/pallium (Figure 17A), cerebellum (Figure 17B) and rest of brain
852 (Figure 17C) are not universally related to body mass across all amniotes. Across reptiles, while
853 the telencephalon of all species conforms to the same scaling relationship between numbers of
854 neurons and body mass (Figure 17A), Serpentes deviate markedly from all other reptilian clades
855 in their much shallower scaling of numbers of neurons in the cerebellum with body mass (Figure
856 17B), and Serpentes, Testudines and Crocodilians together differ from other reptilian clades in
857 how numbers of neurons in the rest of brain scales with body mass (Figure 17C; Table 10).
858 Most importantly, it is not the case that there was a simple, one-time grade shift in both
859 mammals and birds with the advent of endothermy towards more brain neurons for a given body
860 mass, as suggested recently (Kverkova et al., 2022). Instead, different clades of endothermic
861 amniotes have different relationships between body mass and numbers of neurons in each brain
862 structure (Figure 17, Table 10). The pallium of non-primate mammals and the early-derived bird
863 clades does scale similarly in numbers of neurons together with increasing body mass (Figure
864 17A), but Accipitriformes and Falconiformes, then the late-derived Passeriformes, Psittaciformes
865 and Strigiformes show a shift towards more pallial neurons in a similar body mass (Figures 17A,
866 18D), as do primates compared to other mammals (Herculano-Houzel et al., 2014a). At the same
867 time, neuronal densities in the pallium/telencephalon remained similar across reptiles, early-
868 derived birds and mammalian species of a similar body mass (Figure 17D). Likewise, the
869 cerebellum of birds and mammals scales similarly in number of neurons with increasing body
870 mass, but with a pronounced shift to more than 10 times as many cerebellar neurons for a given
871 body mass (Figure 17B), with similarly increased neuronal densities in both groups (Figure 17E).
872 Importantly, the scaling of numbers of neurons in the "rest of brain" differs markedly
873 between early-derived birds and mammals (Figure 11C). As a result, numbers of neurons in this
874 collection of structures, which are directly involved in operating the body, vary by about 50-fold
875 across reptiles, birds, and mammals of similar body mass. This discrepancy is consistent with
876 recent reports that body mass and brain mass are quite free to vary independently of each other
877 in mammalian and avian evolution (Ksepka et al., 2020; Bertrand et al., 2022) and that body mass

is not a determinant of numbers of brain neurons (Herculano-Houzel et al., 2015b). Nevertheless, the striking finding remains that the parallel, independent shifts to endothermy in birds and mammals occurred with increased numbers of neurons in all brain structures compared to ancestral species of a similar body mass.



884 **Figure 17. Clade-specific scaling of numbers of neurons and neuronal density in the different brain structures with**
885 **body mass across mammals, reptiles and birds.** A-C, scaling of numbers of neurons in the telencephalon or pallium
886 (A), cerebellum (B) and rest of brain (C) with body mass. D-F, scaling of neuronal density in the telencephalon or
887 pallium (D), cerebellum (E) and rest of brain (F) with body mass. Power functions plotted apply to reptiles (green,
888 minus Testudines and crocodile in **A**, minus Serpentes in **B**, and minus Serpentes, Testudines and crocodile in **C**),
889 non-primate mammals (red), early-derived birds (light gray: Palaeognathae, Galliformes and Columbiformes in **A**;
890 Anseriformes, Palaeognathae, Galliformes and Columbiformes in **B** and **C**), and late-derived birds (black:
891 Passeriformes, Psittaciformes and Strigiformes in **A**, Accipitriformes, Falconiformes, Passeriformes and
892 Psittaciformes in **B**, and Passeriformes and Psittaciformes in **C**). Power functions are listed in Table 10.
893

894 **Table 10.** Scaling of numbers of neurons in the different brain structures of reptiles, birds and mammals with varying
895 body mass. Values correspond to the equation $N_{str} = e^{a \pm SE} M_{bd}^{b \pm SE}$, the p-values for a and b, and the r^2 for the power
896 fit, where N_{str} is the number of neurons in a given brain structure and M_{bd} is the average body mass for the species.
897

N_{str} x M_{bd}	n	a in e^a	b in M_{bd}^b	p, a	p, b	r^2
Cortex/pallium/telencephalon						
Reptiles						
All	108	14.063±0.107	**0.278**±0.020	<0.0001	<0.0001	0.649
Anguimorpha	7	13.561±0.406	**0.444**±0.062	<0.0001	0.0008	0.912
Crocodilia	1					
Gekkota	14	13.803±0.276	**0.414**±0.093	<0.0001	0.0008	0.623
Iguania	20	13.531±0.148	**0.339**±0.030	<0.0001	<0.0001	0.880
Lacertoidea	15	13.866±0.219	**0.412**±0.055	<0.0001	<0.0001	0.811
Scincoidea	14	13.942±0.252	**0.390**±0.066	<0.0001	<0.0001	0.743
Serpentes	18	13.780±0.328	**0.345**±0.054	<0.0001	<0.0001	0.719
Testudines	19	14.752±0.551	**0.154**±0.078	<0.0001	0.0639	0.188
Testudines and Crocodilia	20	14.298±0.460	**0.222**±0.063	<0.0001	0.0023	0.412
All minus Testudines, Crocodilia	88	13.956±0.116	**0.311**±0.024	<0.0001	<0.0001	0.658
All minus Serpentes	90	14.083±0.110	**0.286**±0.021	<0.0001	<0.0001	0.676
Birds						
All	65	17.803±0.452	**0.225**±0.073	<0.0001	0.0029	0.133
Accipitriformes	4	15.879±0.947	**0.518**±0.134	0.0035	0.0611	0.882
Anseriformes	7	17.231±0.673	**0.243**±0.094	<0.0001	0.0487	0.573
Columbiformes	5	14.937±0.480	**0.503**±0.085	<0.0001	0.0095	0.922
Falconiformes	3	16.913±0.183	**0.437**±0.033	0.0069	0.0478	0.994
Galliformes	9	15.097±0.210	**0.432**±0.032	<0.0001	<0.0001	0.963
Palaeognathae	6	15.194±0.304	**0.427**±0.035	<0.0001	0.0002	0.975
Passeriformes	13	16.398±0.331	**0.657**±0.071	<0.0001	<0.0001	0.885

Psittaciformes	11	16.139±0.200	**0.748**±0.038	<0.0001	<0.0001	0.978
Strigiformes	7	17.920±0.566	**0.405**±0.092	<0.0001	0.0070	0.795
Passeriformes, Psittaciformes, Strigiformes	31	16.534±0.217	**0.645**±0.041	<0.0001	<0.0001	0.893
Galliformes, Columbiformes, Palaeognathae	20	15.217±0.147	**0.425**±0.021	<0.0001	<0.0001	0.959
Accipitriformes, Falconiformes	7	16.941±0.611	**0.390**±0.095	<0.0001	0.0092	0.773
Mammals						
All	70	14.772±0.283	**0.519**±0.038	<0.0001	<0.0001	0.737
All non-primates	58	14.728±0.141	**0.472**±0.019	<0.0001	<0.0001	0.917
Afrotheria	6	15.046±0.187	**0.484**±0.023	<0.0001	<0.0001	0.991
Artiodactyla	5	14.815±2.420	**0.468**±0.208	0.0088	0.1097	0.628
Carnivora	8	16.617±1.258	**0.287**±0.129	<0.0001	0.0673	0.453
Chiroptera	13	14.787±0.344	**0.417**±0.093	<0.0001	0.0009	0.647
Eulipotyphla	5	15.175±0.221	**0.410**±0.063	<0.0001	0.0075	0.933
Marsupialia	9	13.797±0.671	**0.565**±0.080	<0.0001	0.0002	0.876
Primata	12	14.195±0.755	**0.825**±0.097	<0.0001	<0.0001	0.878
Glires	11	14.556±0.344	**0.469**±0.052	<0.0001	<0.0001	0.902
Scandentia	1					
Cerebellum						
Reptiles						
All	108	12.701±0.228	**0.305**±0.042	<0.0001	<0.0001	0.328
Anguimorpha	7	8.846±1.324	**0.925**±0.201	0.0011	0.0059	0.808
Crocodilia	1					
Gekkota	14	12.240±0.298	**0.567**±0.100	<0.0001	0.0001	0.728
Iguania	20	13.494±0.189	**0.273**±0.038	<0.0001	<0.0001	0.744
Lacertoidea	15	12.673±0.354	**0.370**±0.089	<0.0001	0.0012	0.568
Scincoidea	14	12.259±0.556	**0.402**±0.146	<0.0001	0.0174	0.387
Serpentes	18	12.156±0.573	**0.144**±0.094	<0.0001	0.1457	0.128
Testudines	19	13.501±0.815	**0.245**±0.115	<0.0001	0.0479	0.211
Testudines and Crocodilia	20	12.728±0.691	**0.361**±0.063	<0.0001	0.0012	0.451
All minus Testudines, Crocodilia, Serpentes	70	12.534±0.197	**0.413**±0.044	<0.0001	<0.0001	0.559

All minus Serpentes	90	12.607±0.168	**0.389**±0.032	<0.0001	<0.0001	0.625
Birds						
All	65	17.441±0.212	**0.312**±0.034	<0.0001	<0.0001	0.571
Accipitriformes	4	17.497±0.455	**0.367**±0.065	0.0007	0.0296	0.942
Anseriformes	7	16.545±0.610	**0.398**±0.085	<0.0001	0.0054	0.814
Columbiformes	5	15.502±0.539	**0.585**±0.095	<0.0001	0.0086	0.927
Falconiformes	3	16.766±0.226	**0.513**±0.041	0.0086	0.0502	0.994
Galliformes	9	15.698±0.384	**0.494**±0.059	<0.0001	<0.0001	0.910
Palaeognathae	6	16.455±0.182	**0.374**±0.021	<0.0001	<0.0001	0.988
Passeriformes	13	16.882±0.209	**0.524**±0.045	<0.0001	<0.0001	0.925
Psittaciformes	11	16.620±0.306	**0.540**±0.058	<0.0001	<0.0001	0.907
Strigiformes	7	16.942±0.380	**0.399**±0.062	<0.0001	0.0013	0.893
Accipitriformes, Falconiformes, Passeriformes, Psittaciformes	21	15.933±0.276	**0.477**±0.042	<0.0001	<0.0001	0.872
Anseriformes, Galliformes, Columbiformes, Palaeognathae	27	16.343±0.203	**0.406**±0.028	<0.0001	<0.0001	0.891
Mammals						
All	72	15.871±0.223	**0.585**±0.029	<0.0001	<0.0001	0.854
All non-primates	59	15.953±0.145	**0.535**±0.019	<0.0001	<0.0001	0.931
Afrotheria	6	14.729±0.485	**0.733**±0.059	<0.0001	0.0002	0.975
Artiodactyla	5	16.527±2.072	**0.463**±0.178	0.0041	0.0801	0.693
Carnivora	8	16.179±0.551	**0.522**±0.056	<0.0001	<0.0001	0.935
Chiroptera	13	16.496±0.252	**0.448**±0.068	<0.0001	<0.0001	0.797
Eulipotyphla	5	15.049±0.306	**0.873**±0.088	<0.0001	0.0022	0.970
Marsupialia	9	15.422±0.317	**0.577**±0.037	<0.0001	<0.0001	0.967
Primata	12	15.656±0.622	**0.754**±0.073	<0.0001	<0.0001	0.906
Glires	11	15.583±0.459	**0.540**±0.069	<0.0001	<0.0001	0.872
Scandentia	1					
Rest of brain						
Reptiles						
All	108	14.242±0.101	**0.168**±0.019	<0.0001	<0.0001	0.429
Anguimorpha	7	13.564±0.555	**0.325**±0.084	<0.0001	0.0120	0.748
Crocodilia	1					
Gekkota	14	13.806±0.177	**0.292**±0.060	<0.0001	0.0004	0.667

Iguania	20	14.086±0.165	**0.262**±0.033	<0.0001	<0.0001	0.781
Lacertoidea	15	14.003±0.165	**0.317**±0.042	<0.0001	<0.0001	0.816
Scincoidea	14	13.791±0.252	**0.313**±0.066	<0.0001	0.0005	0.651
Serpentes	18	14.192±0.306	**0.142**±0.050	<0.0001	0.0120	0.334
Testudines	19	13.927±0.430	**0.152**±0.061	<0.0001	0.0223	0.271
Testudines and Crocodilia	20	13.529±0.363	**0.212**±0.049	<0.0001	0.0004	0.506
Testudines, Crocodilia, Serpentes	38	14.035±0.226	**0.153**±0.033	<0.0001	<0.0001	0.370
All minus Testudines, Crocodilia, Serpentes	70	13.924±0.085	**0.290**±0.019	<0.0001	<0.0001	0.770
Birds						
All	65	17.185±0.290	**0.140**±0.047	<0.0001	0.0038	0.125
Accipitriformes	4	17.123±0.869	**0.189**±0.123	0.0026	0.2646	0.541
Anseriformes	7	16.543±0.481	**0.157**±0.067	<0.0001	0.0668	0.522
Columbiformes	5	15.296±0.222	**0.353**±0.039	<0.0001	0.0026	0.967
Falconiformes	3	16.994±0.215	**0.224**±0.038	0.0080	0.1083	0.971
Galliformes	9	15.374±0.202	**0.329**±0.031	<0.0001	<0.0001	0.942
Palaeognathae	6	16.599±0.176	**0.154**±0.020	<0.0001	0.0015	0.937
Passeriformes	13	16.180±0.224	**0.434**±0.048	<0.0001	<0.0001	0.881
Psittaciformes	11	14.941±0.298	**0.749**±0.056	<0.0001	<0.0001	0.952
Strigiformes	7	16.449±0.521	**0.247**±0.085	<0.0001	0.0328	0.631
Passeriformes, Psittaciformes	24	15.707±0.251	**0.571**±0.051	<0.0001	<0.0001	0.853
Anseriformes, Galliformes, Columbiformes, Palaeognathae	27	16.065±0.145	**0.221**±0.020	<0.0001	<0.0001	0.826
Accipitriformes, Falconiformes	7	17.158±0.356	**0.188**±0.055	<0.0001	0.0191	0.699
Mammals						
All	70	14.785±0.162	**0.330**±0.022	<0.0001	<0.0001	0.775
All non-primates	58	14.793±0.119	**0.307**±0.016	<0.0001	<0.0001	0.869
Afrotheria	6	14.771±0.294	**0.375**±0.036	<0.0001	0.0005	0.965
Artiodactyla	5	15.569±1.320	**0.235**±0.113	0.0013	0.1294	0.590
Carnivora	8	14.909±0.412	**0.269**±0.042	<0.0001	0.0007	0.872
Chiroptera	13	14.343±0.271	**0.431**±0.073	<0.0001	0.0001	0.759

Eulipotyphla	5	14.610±0.435	**0.383**±0.125	<0.0001	0.0548	0.758
Marsupialia	9	14.159±0.589	**0.349**±0.071	<0.0001	0.0017	0.778
Primata	12	14.037±0.691	**0.525**±0.089	<0.0001	0.0002	0.777
Glires	11	14.538±0.408	**0.363**±0.061	<0.0001	0.0002	0.796
Scandentia	1					

Scaling relationships of mass ratios across structures distinguish reptiles from birds and mammals

The non-telencephalic, non-cerebellar rest of brain comprises the brain structures that operate the body. These "rest of brain" structures, which are readily comparable in organization and function across clades of amniotes, provide the anatomical and circuit-related scaffolding on top of which the pallium and the cerebellum function. It is also composed of structures derived from the near entirety of the cranial neural tube, minus the first two neuromeres (Puelles et al., 2013). Thus, I use the rest of brain as an anchor to which I compare the scaling of the other brain structures across clades of amniotes. This procedure allows for a measurement of relative allocation of neurons across brain structures that is completely irrespective of body mass or brain mass.

Despite the 100,000-fold range of variation in the mass of the rest of brain across the 242 species in the dataset, the pallium (or whole telencephalon, in reptiles) scales in mass faster than the rest of brain in a uniform, shared manner across all amniotes, with the notable exceptions of primates and owls (Strigiformes), with a shared exponent of 1.189±0.013, significantly above unity (Figure 18A; Table 11). As a consequence, the mass ratio between pallium (or telencephalon) and rest of brain increases together with the absolute mass of the rest of the brain in a continuous manner across reptiles, mammals, and birds (exponent, 0.189±0.013; Figure 18B; Table 12) minus primates and owls, which show a step increase away from the shared pattern, with a larger pallium than expected for an amniote of similar mass of the rest of brain (Figure 18B).

In contrast, the cerebellum of mammals and birds, the endothermic amniotes, shows a marked difference from the scaling relationship in mass with the rest of brain that applies to the

924 non-avian reptiles in the dataset, with ca. 10-fold larger cerebellar mass in the warm-blooded
925 amniotes compared to reptiles of similar rest of brain mass (Figure 18C). As a result, while the
926 cerebellum is on average only about 1/20th the mass of the rest of brain in reptiles, it jumps to a
927 mass equivalent to ca. 1/3 to ½ the mass of the rest of brain in birds and mammals (Figure 18D,
928 Table 12). Strikingly, the mass scaling relationship between cerebellum and rest of brain is shared
929 across most avian and mammalian species (Figure 18C-D), although the cerebellum appears
930 relatively smaller in parrots than in mammals of similar rest of brain mass (30% of the mass of
931 the rest of brain or less in parrots vs. 50% in non-primate mammals; Table 12). As a consequence,
932 the ratio between the mass of the pallium (or telencephalon) and of the cerebellum is very large
933 in reptiles, whose telencephalons may be from 6 to over 100 times larger than the cerebellum,
934 but this ratio is 4-10 in birds, and only 3-5 in most mammals (Figure 18E-F, Table 12). Thus,
935 examination of the scaling relationships that apply to structure mass across the three main
936 divisions of amniote brains suggests that a distinctive signature of endothermic amniotes is
937 increased relative mass of the cerebellum, in a mass proportionality to the rest of brain that is
938 shared by the vast majority of the evolutionarily unrelated mammals and birds. Remarkably, the
939 shift to endothermy per se does not appear to have changed the proportionality with which
940 telencephalic mass (whether cortical, pallial, or telencephalic as a whole) is added on top of the
941 rest of brain, which remains shared across most amniotes. In terms of scaling of brain structure
942 mass, the main difference in how bird and mammalian brains are built is that there is slightly
943 more pallial mass relative to the cerebellum in songbirds, parrots and owls than in other birds
944 and in non-primate mammals (Figure 18F) – but otherwise, bird and non-primate mammalian
945 brains are built to fairly similar proportions across their main structures. These proportions are
946 illustrated in Figure 19.
947

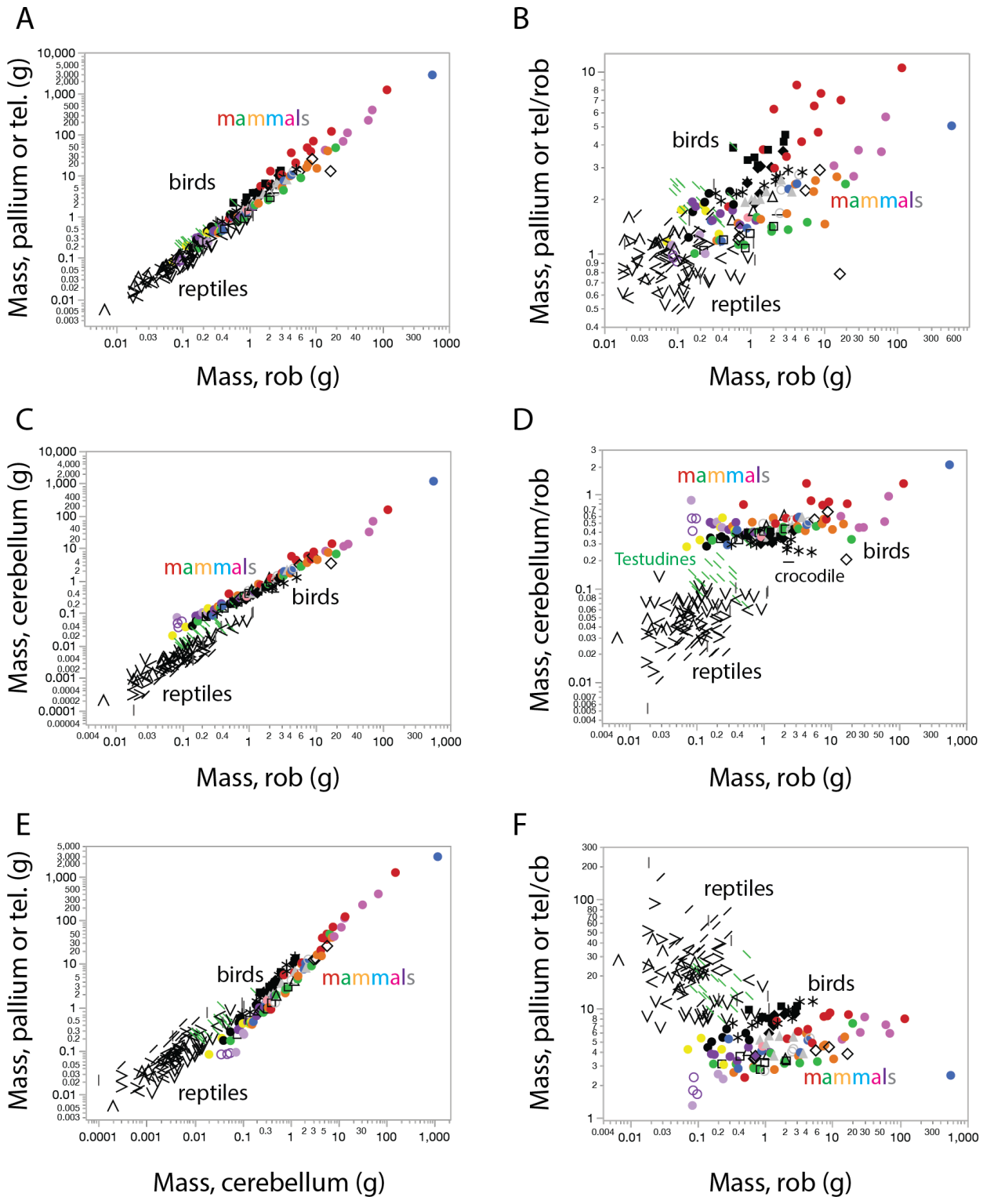

A
Mass, pallium or tel. (g)
mammals
birds
reptiles
Mass, rob (g)
B
Mass, pallium or tel/rob
birds
mammals
reptiles
Mass, rob (g)
C
Mass, cerebellum (g)
mammals
birds
reptiles
Mass, rob (g)
D
Mass, cerebellum/rob
mammals
Testudines
birds
crocodile
reptiles
Mass, rob (g)
E
Mass, pallium or tel. (g)
birds
mammals
reptiles
Mass, cerebellum (g)
F
Mass, pallium or tel/cb
reptiles
birds
mammals
Mass, rob (g)

Figure 18. Mass scaling relationships across brain structures in mammals, reptiles and birds. A, C, E, scaling of structure mass across the structures indicated. **B, D, F,** scaling of the mass ratio across the brain structures indicated, as a function of the mass of the rest of brain. Each data point represents one species, using the same symbols as in all other figures. All applicable power functions, not plotted for clarity, are listed in Tables 11 and 12.

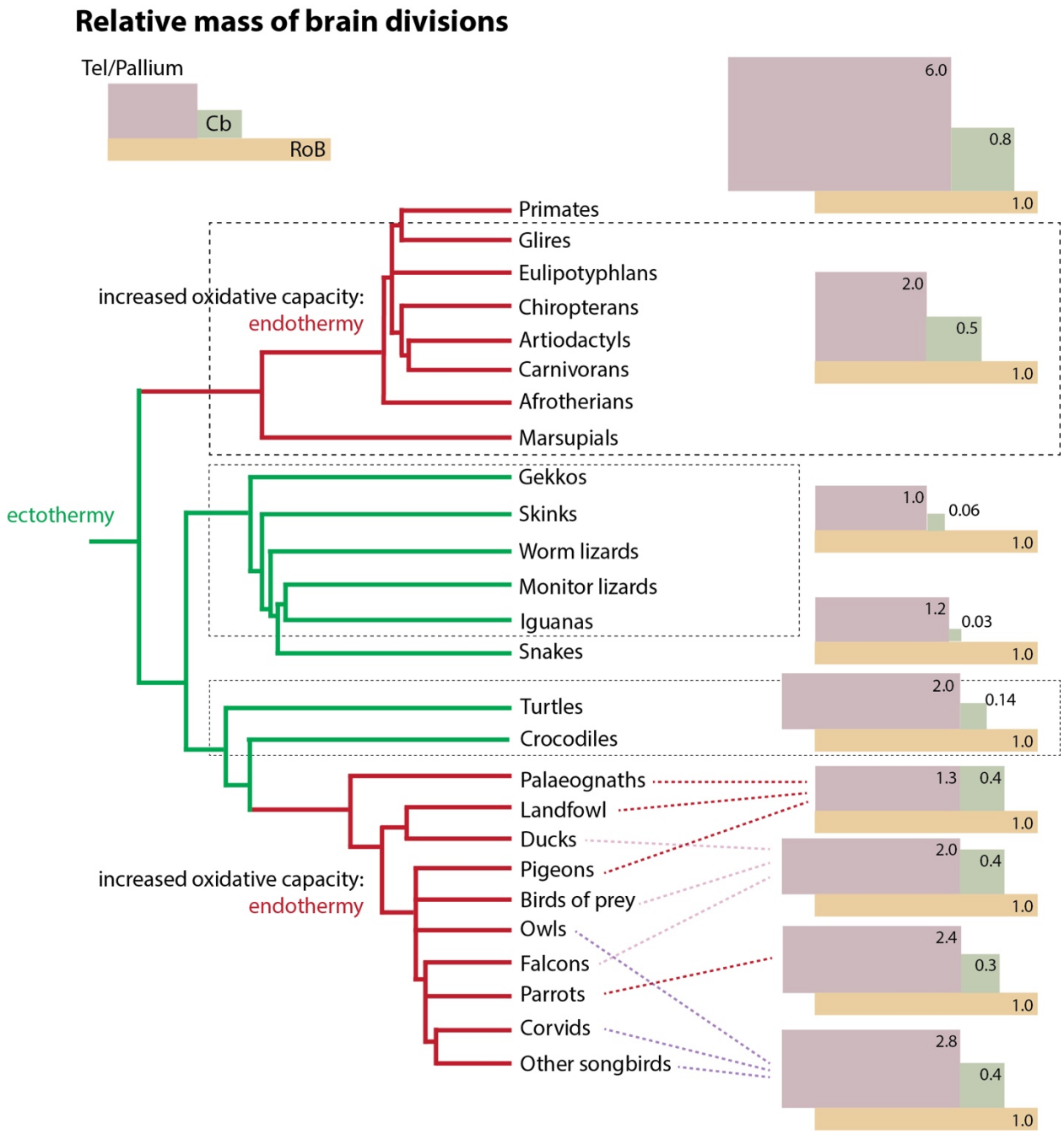


Figure 19. A relatively enlarged cerebellum is a signature of the brain of endothermic amniotes. The non-overlapping rectangles of varying sizes represent the relative mass of the telencephalon or pallium (red) and cerebellum (green) in proportion to the rest of brain (tan rectangle). The surface area of each rectangle is proportional to the mass of that brain structure relative to the rest of brain. The schematics illustrates the finding that while relative enlargement of the telencephalon over the rest of brain does not distinguish endothermic from ectothermic clades, the two independently evolved endothermic clades (mammals and avians) are characterized by a marked increase in mass of the cerebellum over the rest of brain compared to reptiles. Note that the distribution of relative brain structure mass can be shared across unrelated groups among birds.

Table 11 – Scaling of the mass of the telencephalon or pallium (M_{tel}; reptilian telencephalon or bird or mammalian pallium), mass of the cerebellum (M_{cb}), and mass of the rest of brain (M_{rob}; reptilian or bird brainstem and diencephalon, or mammalian brainstem, diencephalon plus striatum) as a function of one another in the different groups. Values correspond to the equation $M_{structure1} = e^{a\pm SE}\ M_{structure2}^{b\pm SE}$, the p-values for a and b, and the r^2 for the power fit.

M_{tel} x M_{rob}	**n**	**a in e^a**	**b in N_{rob}^b**	**p, a**	**p, b**	**r^2**
Reptiles						
All	108	0.341±0.092	**1.112**±0.038	0.0003	<0.0001	0.891
Testudines and crocodile	20	0.614±0.115	**0.952**±0.067	<0.0001	<0.0001	0.918
All minus Testudines and crocodile	88	0.041±0.087	**1.035**±0.034	0.6410	<0.0001	0.917
Mammals						
All	69	0.640±0.051	**1.231**±0.024	<0.0001	<0.0001	0.975
Primates	12	1.137±0.144	**1.294**±0.069	<0.0001	<0.0001	0.972
All minus primates	57	0.533±0.037	**1.193**±0.017	<0.0001	<0.0001	0.988
All reptiles and mammals minus Testudines and crocodiles, and primates	145	0.457±0.032	**1.189**±0.013	<0.0001	<0.0001	0.983
Birds						
Anseriformes, Accipitriformes, Falconiformes	14	0.571±0.049	**1.227**±0.065	<0.0001	<0.0001	0.968
Palaeognathae, Galliformes, Columbiformes	20	0.236±0.059	**1.107**±0.051	0.0009	<0.0001	0.963
Passeriformes, Strigiformes	20	1.020±0.048	**1.301**±0.053	<0.0001	<0.0001	0.971

Psittaciformes	11	0.848±0.016	**1.132**±0.018	<0.0001	<0.0001	0.998
M_{cb} x M_{rob}	**n**	**a in e^a**	**b in N_{rob}^b**	**p, a**	**p, b**	**r^2**
Reptiles						
All	108	-2.225±0.139	**1.318**±0.057	<0.0001	<0.0001	0.835
Testudines and crocodile	20	-1.856±0.172	**1.111**±0.100	<0.0001	<0.0001	0.872
All minus Testudines and crocodile	88	-2.623±0.143	**1.215**±0.056	<0.0001	<0.0001	0.848
Mammals						
All (minus elephant)	67	-0.712±0.038	**1.080**±0.019	<0.0001	<0.0001	0.981
Primates	11	-0.481±0.145	**1.123**±0.067	0.0091	<0.0001	0.969
All minus primates, elephant	56	-0.762±0.035	**1.055**±0.018	<0.0001	<0.0001	0.985
Birds						
All	65	-1.004±0.027	**1.054**±0.028	<0.0001	<0.0001	0.958
All minus Psittaciformes	54	-0.961±0.026	**1.084**±0.027	<0.0001	<0.0001	0.970
Psittaciformes	11	-1.198±0.032	**0.913**±0.036	<0.0001	<0.0001	0.986
M_{tel} x M_{cb}	**n**	**a in e^a**	**b in N_{rob}^b**	**p, a**	**p, b**	**r^2**
Reptiles						
All	108	1.634±0.190	**0.730**±0.036	<0.0001	<0.0001	0.799
Testudines and crocodile	20	1.905±0.275	**0.772**±0.075	<0.0001	<0.0001	0.855
All minus Testudines and crocodile	88	1.407±0.265	**0.694**±0.047	<0.0001	<0.0001	0.719
Mammals						
All (minus elephant)	67	1.444±0.039	**1.143**±0.018	<0.0001	<0.0001	0.983
Primates	11	1.651±0.139	**1.149**±0.066	<0.0001	<0.0001	0.971
All minus primates, elephant	56	1.395±0.040	**1.124**±0.019	<0.0001	<0.0001	0.984
Birds						

Anseriformes, Accipitriformes, Falconiformes	14	1.460±0.066	**1.007**±0.087	<0.0001	<0.0001	0.917
Palaeognathae, Galliformes, Columbiformes	20	1.304±0.023	**1.060**±0.016	<0.0001	<0.0001	0.996
Passeriformes, Psittaciformes, Strigiformes	31	2.280±0.041	**1.226**±0.029	<0.0001	<0.0001	0.984

Table 12 – Scaling of the mass ratios between structures as a function of the mass of the rest of the brain in the different groups. Average ratios across species within each group ± SD are provided in parentheses. M_{tel}, mass of the reptilian telencephalon or bird or mammalian pallium; M_{cb}, mass of the cerebellum; M_{rob}, mass of the rest of brain, which is the reptilian or bird brainstem and diencephalon, or the mammalian brainstem, diencephalon plus striatum. Values correspond to the equation $M_{structure1} = e^{a\pm SE}\ M_{structure2}^{b\pm SE}$, the p-values for a and b, and the r^2 for the power fit.

M_{tel} /M_{rob} x M_{rob}	**n**	**a in e^a**	**b in N_{rob}^b**	**p, a**	**p, b**	**r^2**
Reptiles						
All (1.20±0.56)	108	0.341±0.092	**1.112**±0.038	0.0003	0.0037	0.077
Serpentes (1.16±0.43)	18	0.508±0.375	**0.184**±0.155	0.1945	0.2547	0.080
Testudines and crocodile (2.05±0.56)	20	0.614±0.115	**-0.048**±0.067	<0.0001	0.4818	0.028
All minus Testudines and crocodile (1.08±0.33)	88	0.041±0.087	**0.035**±0.034	0.6410	0.3022	0.012
All minus Serpentes, Testudines and crocodile (0.97±0.30)	70	-0.022±0.083	**0.021**±0.032	0.7868	0.4996	0.007
Mammals						
All (2.73±1.98)	69	0.640±0.051	**0.231**±0.024	<0.0001	<0.0001	0.580
Primates (5.57±2.55)	12	1.137±0.144	**0.294**±0.069	<0.0001	0.0017	0.642

All minus primates (2.13±1.18)	57	0.533±0.037	**0.193**±0.017	<0.0001	<0.0001	0.691
All reptiles and mammals minus Testudines and crocodiles, and primates (1.45±0.96)	145	0.457±0.032	**0.189**±0.013	<0.0001	<0.0001	0.592
Birds						
Anseriformes, Accipitriformes, Falconiformes (2.01±0.38)	14	0.571±0.049	**0.227**±0.065	<0.0001	0.0044	0.505
Palaeognathae, Galliformes, Columbiformes (1.34±0.47)	20	0.236±0.059	**0.107**±0.051	0.0009	0.0514	0.195
Passeriformes, Strigiformes (2.81±0.90)	20	1.020±0.048	**0.301**±0.053	<0.0001	<0.0001	0.643
Psittaciformes (2.44±0.30)	11	0.848±0.016	**0.132**±0.018	<0.0001	<0.0001	0.860
M_{cb}/M_{rob} x M_{rob}	**n**	**a in e^a**	**b in N_{rob}^b**	**p, a**	**p, b**	**r^2**
Reptiles						
All (0.07±0.05)	108	-2.225±0.139	**0.318**±0.057	<0.0001	<0.0001	0.228
Serpentes (0.03±0.01)	18	-3.199±0.336	**0.193**±0.139	<0.0001	0.1842	0.107
Testudines and crocodile (0.14±0.05)	20	-1.856±0.172	**0.111**±0.100	<0.0001	0.2818	0.064
All minus Testudines and crocodile (0.05±0.03)	88	-2.623±0.143	**0.215**±0.056	<0.0001	0.0002	0.149
All minus Serpentes, Testudines and	70	-2.471±0.137	**0.223**±0.052	<0.0001	<0.0001	0.211

crocodile (0.06±0.02)						
Mammals						
All (minus elephant) (0.55±0.21)	67	-0.712±0.038	**0.080**±0.019	<0.0001	<0.0001	0.217
Primates (0.80±0.28)	11	-0.481±0.145	**0.123**±0.067	0.0091	0.1006	0.271
All minus primates, elephant (0.50±0.15)	56	-0.762±0.035	**0.055**±0.018	<0.0001	0.0026	0.156
Birds						
All (0.38±0.09)	65	-1.004±0.027	**0.054**±0.028	<0.0001	0.0552	0.057
All minus Psittaciformes (0.39±0.08)	54	-0.961±0.026	**0.084**±0.027	<0.0001	0.0026	0.162
Psittaciformes (0.30±0.04)	11	-1.197±0.032	**-0.087**±0.036	<0.0001	0.0377	0.397
M_{tel} /M_{cb} x M_{rob}	**n**	**a in e^a**	**b in N_{rob}^b**	**p, a**	**p, b**	**r^2**
Reptiles						
All (26.87±27.66)	108	2.566±0.148	**-0.206**±0.060	<0.0001	0.0009	0.099
Testudines and crocodile (16.15±6.31)	20	2.4470±0.177	**-0.160**±0.103	<0.0001	0.1389	0.118
All minus Testudines and crocodile (29.30±30.00)	88	2.664±0.188	**-0.180**±0.073	<0.0001	0.0155	0.066
Mammals						
All (minus elephant) (4.60±1.95)	67	1.338±0.040	**0.162**±0.019	<0.0001	<0.0001	0.515
Primates (6.85±2.09)	11	1.536±0.149	**0.194**±0.069	<0.0001	0.0206	0.466
All minus primates,	56	1.296±0.038	**0.141**±0.019	<0.0001	<0.0001	0.499

elephant (4.16±1.61)						
Birds						
Anseriformes, Accipitriformes, Falconiformes (4.39±0.91)	14	1.429±0.077	**0.062**±0.102	<0.0001	0.5571	0.029
Palaeognathae, Galliformes, Columbiformes (3.52±0.40)	20	1.243±0.020	**0.062**±0.017	<0.0001	0.0019	0.422
Passeriformes, Psittaciformes, Strigiformes (7.88±1.90)	31	2.033±0.025	**0.231**±0.028	<0.0001	<0.0001	0.702

Mass relationships across structures differ from scaling of numbers of neurons

Despite the enormous diversity in absolute numbers of neurons composing the brains of the different amniotes, striking patterns emerge in how they vary across structures within each group of amniotes. While the scaling of structure mass does not distinguish between bird and mammalian brains, the scaling of numbers of neurons across structures does, and indeed characterizes each of the three groups of amniotes, as I show next.

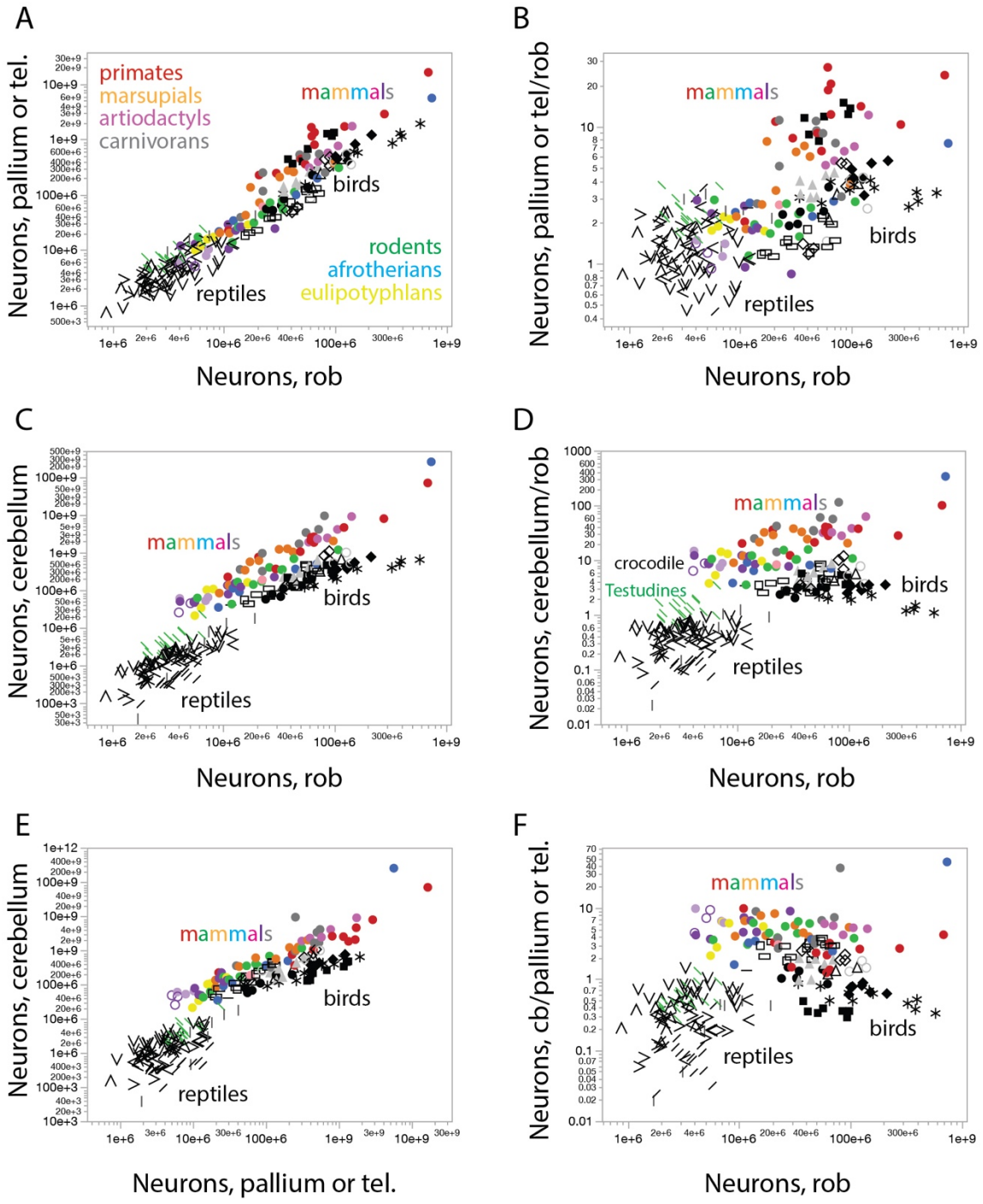
The mass relationships across brain structures do not inform about the scaling of numbers of neurons across brain structures in amniotes. The shared scaling of pallial (or telencephalic) mass as a function of the mass of the rest of brain across most amniotes in the dataset (Figure 18A,B), with the exception of owls and primates, conceals the fact that artiodactyls, carnivorans and large marsupials, besides owls and primates, have increased numbers of pallial neurons compared to the prediction for a generic amniote of their numbers of neurons in the rest of brain (Figure 20A; Table 13). As a result, these clades have markedly larger ratios of numbers of neurons in the pallium over the rest of brain that set them apart from all other amniotes (Figure 20B).

Table 13 – Scaling of neurons in the reptilian telencephalon or bird/mammalian pallium (N_{tel}) as a function of numbers of neurons in the rest of brain (N_{rob}; reptilian or bird brainstem and diencephalon, or mammalian brainstem, diencephalon plus striatum). Values correspond to the equation $N_{Tel} = e^{a \pm SE} N_{rob}^{b \pm SE}$, the p-values for a and b, and the r^2 for the power fit.

N_{Tel} x N_{rob}	n	a in e^a	b in N_{rob}^b	p, a	p, b	r^2
Reptiles						
All	108	-0.168±1.252	**1.035**±0.083	0.8935	<0.0001	0.594
Anguimorpha	7	-1.508±3.300	**1.145**±0.211	0.6668	0.0029	0.854
Crocodilia	1					
Gekkota	14	-3.634±3.081	**1.271**±0.211	0.2612	<0.0001	0.752
Iguania	20	-1.524±1.977	**1.087**±0.129	0.4508	<0.0001	0.797
Lacertoidea	15	-2.045±2.602	**1.149**±0.172	0.4461	<0.0001	0.775
Scincoidea	14	0.078±2.390	**1.023**±0.160	0.9744	<0.0001	0.772
Serpentes	18	0.846±5.039	**0.970**±0.335	0.8688	0.0106	0.344
Testudines and Crocodilia	20	0.473±1.937	**1.025**±0.129	0.8099	<0.0001	0.779
All minus Serpentes, Testudines, Crocodilia	70	-0.542±1.275	**1.050**±0.084	0.6722	<0.0001	0.694
Birds						
All	65	-5.027±1.826	**1.341**±0.101	0.0077	<0.0001	0.736
Accipitriformes	4	-15.931±12.473	**1.921**±0.677	0.3298	0.1049	0.801
Anseriformes	7	-5.344±4.309	**1.376**±0.244	0.2699	0.0024	0.864
Columbiformes	5	-5.907±3.841	**1.365**±0.222	0.2216	0.0086	0.927
Falconiformes	3	-14.767±8.525	**1.870**±0.468	0.3333	0.1561	0.941
Galliformes	9	-4.157±2.056	**1.259**±0.118	0.0830	<0.0001	0.942
Palaeognathae	6	-28.708±5.017	**2.654**±0.280	0.0046	0.0007	0.957
Passeriformes	13	-7.678±1.235	**1.491**±0.068	<0.0001	<0.0001	0.977
Psittaciformes	11	1.707±0.991	**0.973**±0.053	0.1192	<0.0001	0.974
Strigiformes	7	-4.614±3.495	**1.392**±0.195	0.2440	0.0008	0.911
All minus Strigiformes	58	-5.559±1.220	**1.362**±0.068	<0.0001	<0.0001	0.879
Mammals						
All	70	11.563±0.103	**-0.304**±0.014	<0.0001	<0.0001	0.881
All non-primates	58	11.592±0.099	**-0.315**±0.013	<0.0001	<0.0001	0.913
Afrotheria	6	11.372±0.306	**-0.265**±0.306	<0.0001	0.0020	0.927

Artiodactyla	5	9.726±1.751	**-0.161**±0.150	0.0115	0.3630	0.276
Carnivora	8	10.916±0.385	**-0.271**±0.039	<0.0001	0.0005	0.888
Chiroptera	13	11.256±0.228	**-0.235**±0.062	<0.0001	0.0029	0.570
Eulipotyphla	5	11.689±0.502	**-0.285**±0.144	0.0002	0.1425	0.566
Marsupialia	9	11.628±0.540	**-0.330**±0.065	<0.0001	0.0014	0.788
Primata	12	10.780±0.407	**-0.171**±0.052	<0.0001	0.0085	0.516
Glires	10	11.735±0.410	**-0.314**±0.059	<0.0001	0.0007	0.778
Scandentia	1					
All mammals, all reptiles	177	11.725±0.060	**-0.301**±0.010	<0.0001	<0.0001	0.850

Likewise, the shared scaling in mass of the cerebellum with the rest of brain across birds and mammals (Figure 18C), the endothermic amniotes, contrasts with the very diverse relationships between numbers of neurons in the cerebellum and the rest of brain across birds, small mammals, and large mammals (Figure 20C; Table 14). As a consequence, mammals and birds of similar mass ratios between cerebellum and rest of brain (Figure 18D) have ratios of neurons between the two structures that differ by up to a factor of ten, with much larger and variable ratios in mammals than in birds (Figure 20D). Finally, the much larger mass of the telencephalon relative to the cerebellum in reptiles compared to birds and mammals (Figure 18E,F) is no indication of the fact that the proportion of neurons between the cerebellum and the telencephalon (or pallium) is similar between many reptiles and birds (Figure 20E,F; Table 15).


A
Neurons, pallium or tel.
Neurons, rob
primates
marsupials
artiodactyls
carnivorans
mammals
birds
rodents
afrotherians
eulipotyphlans
reptiles
B
Neurons, pallium or tel/rob
Neurons, rob
mammals
birds
reptiles
C
Neurons, cerebellum
Neurons, rob
mammals
birds
reptiles
D
Neurons, cerebellum/rob
Neurons, rob
mammals
crocodile
Testudines
birds
reptiles
E
Neurons, cerebellum
Neurons, pallium or tel.
mammals
birds
reptiles
F
Neurons, cb/pallium or tel.
Neurons, rob
mammals
birds
reptiles

1020

Figure 20. Scaling of numbers of neurons across structures defines clades of amniotes. A, B, the pallium or telencephalon gains neurons coordinately with the rest of brain across reptiles, birds, and all small mammals, while some large mammals, with larger numbers of neurons in the rest of brain, have significantly increased numbers of pallial neurons over the rest of brain (primates, red; artiodactyls, lavender; carnivorans, gray; marsupials, orange). Power functions and clade averages are listed in Tables 13 and 16. **C**, **D,** the cerebellum gains neurons in clade-specific relationships with the rest of brain across reptiles, birds, and mammals, while some large mammals, with larger numbers of neurons in the rest of brain, have significantly increased numbers of cerebellar neurons. Power functions and clade averages are listed in Tables 14 and 17. **E**, **F:** as a result of the parallels between the distributions shown in (**A, B**) and (**C, D**), the ratio between cerebellar and pallial (or telencephalic) neurons does not scale significantly with numbers of neurons in the rest of brain across reptiles and birds, and is fairly constant at a higher value across mammalian species. Interestingly, this ratio is higher in early-derived birds than in later-derived birds. Power functions and clade averages are listed in Tables 15 and 18.

Table 14 – Scaling of neurons in the cerebellum (N_{cb}) as a function of numbers of neurons in the rest of brain (N_{rob}; reptilian or bird brainstem and diencephalon, or mammalian brainstem, diencephalon plus striatum). Values correspond to the equation $N_{cb} = e^{a \pm SE} N_{rob}^{b \pm SE}$, the p-values for a and b, and the r^2 for the power fit.

N_{Cb} x N_{rob}	n	a in e^a	b in N_{rob}^b	p, a	p, b	r^2
Reptiles						
All	108	-7.329±2.201	**1.429**±0.146	0.0012	<0.0001	0.475
Anguimorpha	7	-25.867±6.062	**2.597**±0.388	0.0080	0.0011	0.900
Crocodilia	1					
Gekkota	14	-9.390±4.080	**1.587**±0.279	0.0401	0.0001	0.729
Iguania	20	-0.185±1.526	**0.977**±0.100	0.9049	<0.0001	0.842
Lacertoidea	15	-3.750±3.205	**1.172**±0.211	0.2631	<0.0001	0.703
Scincoidea	14	-8.557±3.160	**1.492**±0.212	0.0190	<0.0001	0.805
Serpentes	18	-5.528±4.058	**1.233**±0.270	0.1920	0.0003	0.566
Testudines and Crocodilia	20	-8.934±2.882	**1.612**±0.191	0.0062	<0.0001	0.798
All minus Serpentes, Testudines, Crocodilia	70	-7.008±1.653	**1.405**±0.110	<0.0001	<0.0001	0.708
Birds						
All	65	4.487±1.462	**0.822**±0.081	0.0032	<0.0001	0.620
Accipitriformes	4	-2.245±10.904	**1.209**±0.591	0.8559	0.1776	0.676
Anseriformes	7	-13.063±6.875	**1.837**±0.389	0.1159	0.0053	0.817
Columbiformes	5	-8.072±5.515	**1.549**±0.318	0.2395	0.0166	0.888
Falconiformes	3	-20.443±10.178	**2.196**±0.559	0.2941	0.1586	0.939
Galliformes	9	-5.606±4.027	**1.399**±0.230	0.2065	0.0005	0.841
Palaeognathae	6	-21.326±5.267	**2.287**±0.294	0.0155	0.0015	0.938
Passeriformes	13	-1.796±1.077	**1.160**±0.060	0.1237	<0.0001	0.972
Psittaciformes	11	6.063±1.284	**0.709**±0.068	0.0011	<0.0001	0.923

Strigiformes	7	-1.128±5.866	**1.141**±0.327	0.8551	0.0174	0.709
All minus Psittaciformes	54	-2.085±1.627	**1.196**±0.091	0.2056	<0.0001	0.768
Mammals						
All	70	11.563±0.103	**-0.304**±0.014	<0.0001	<0.0001	0.881
All non-primates	58	11.592±0.099	**-0.315**±0.013	<0.0001	<0.0001	0.913
Afrotheria	6	11.372±0.306	**-0.265**±0.306	<0.0001	0.0020	0.927
Artiodactyla	5	9.726±1.751	**-0.161**±0.150	0.0115	0.3630	0.276
Carnivora	8	10.916±0.385	**-0.271**±0.039	<0.0001	0.0005	0.888
Chiroptera	13	11.256±0.228	**-0.235**±0.062	<0.0001	0.0029	0.570
Eulipotyphla	5	11.689±0.502	**-0.285**±0.144	0.0002	0.1425	0.566
Marsupialia	9	11.628±0.540	**-0.330**±0.065	<0.0001	0.0014	0.788
Primata	12	10.780±0.407	**-0.171**±0.052	<0.0001	0.0085	0.516
Glires	10	11.735±0.410	**-0.314**±0.059	<0.0001	0.0007	0.778
Scandentia	1					
All mammals, all reptiles	177	11.725±0.060	**-0.301**±0.010	<0.0001	<0.0001	0.850

Table 15 – Scaling of neurons in the cerebellum (N_{cb}) as a function of numbers of neurons in the telencephalon or pallium (N_{tel}; reptilian telencephalon or bird or mammalian pallium). Values correspond to the equation $N_{cb} = e^{a \pm SE} N_{tel}^{b \pm SE}$, the p-values for a and b, and the r^2 for the power fit.

N_{Cb} x N_{tel}	**n**	**a in e^a**	**b in N_{rob}^b**	**p, a**	**p, b**	**r^2**
Reptiles						
All	108	-1.222±1.767	**1.000**±0.114	0.4904	<0.0001	0.419
Anguimorpha	7	-19.526±5.283	**2.091**±0.323	0.0141	0.0013	0.894
Crocodilia	1					
Gekkota	14	-1.849±3.082	**1.047**±0.206	0.5597	0.0003	0.683
Iguania	20	2.548±1.187	**0.809**±0.079	0.0457	<0.0001	0.855
Lacertoidea	15	0.378±2.560	**0.888**±0.167	0.8848	0.0001	0.686
Scincoidea	14	-3.054±4.078	**1.092**±0.266	0.4684	0.0015	0.584
Serpentes	18	7.087±3.523	**0.384**±0.228	0.0614	0.1120	0.150

Testudines and Crocodilia	20	-6.533±2.718	**1.375**±0.171	0.0272	<0.0001	0.782
All minus Serpentes, Testudines, Crocodilia	70	-0.005±1.759	**0.928**±0.115	0.9977	<0.0001	0.490
Birds						
All	65	9.310±1.006	**0.522**±0.052	<0.0001	<0.0001	0.611
Accipitriformes	4	7.638±3.477	**0.637**±0.178	0.1592	0.0703	0.864
Anseriformes	7	-1.860±6.735	**1.120**±0.355	0.7934	0.0253	0.665
Columbiformes	5	-0.881±3.526	**1.107**±0.199	0.8189	0.0114	0.912
Falconiformes	3	-3.120±0.088	**1.176**±0.005	0.0179	0.0025	0.999
Galliformes	9	-1.401±2.108	**1.134**±0.118	0.5277	<0.0001	0.930
Palaeognathae	6	3.352±0.923	**0.865**±0.049	0.0221	<0.0001	0.987
Passeriformes	13	4.395±0.840	**0.767**±0.043	0.0003	<0.0001	0.966
Psittaciformes	11	4.876±1.224	**0.727**±0.061	0.0032	<0.0001	0.940
Strigiformes	7	1.172±2.350	**0.893**±0.115	0.6390	0.0006	0.923
Anseriformes, Accipitriformes, Galliformes, Columbiformes, Palaeognathae	31	3.991±1.100	**0.826**±0.059	0.0011	<0.0001	0.869
Passeriformes, Psittaciformes	24	5.600±0.874	**0.698**±0.044	<0.0001	<0.0001	0.918
Mammals						
All	70	11.563±0.103	**-0.304**±0.014	<0.0001	<0.0001	0.881
All non-primates	58	11.592±0.099	**-0.315**±0.013	<0.0001	<0.0001	0.913
Afrotheria	6	11.372±0.306	**-0.265**±0.306	<0.0001	0.0020	0.927
Artiodactyla	5	9.726±1.751	**-0.161**±0.150	0.0115	0.3630	0.276
Carnivora	8	10.916±0.385	**-0.271**±0.039	<0.0001	0.0005	0.888
Chiroptera	13	11.256±0.228	**-0.235**±0.062	<0.0001	0.0029	0.570
Eulipotyphla	5	11.689±0.502	**-0.285**±0.144	0.0002	0.1425	0.566
Marsupialia	9	11.628±0.540	**-0.330**±0.065	<0.0001	0.0014	0.788
Primata	12	10.780±0.407	**-0.171**±0.052	<0.0001	0.0085	0.516
Glires	10	11.735±0.410	**-0.314**±0.059	<0.0001	0.0007	0.778
Scandentia	1					
All mammals, all reptiles	177	11.725±0.060	**-0.301**±0.010	<0.0001	<0.0001	0.850

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1047
1048 ## Mammals are not defined by expansion of pallial neurons over the rest of brain
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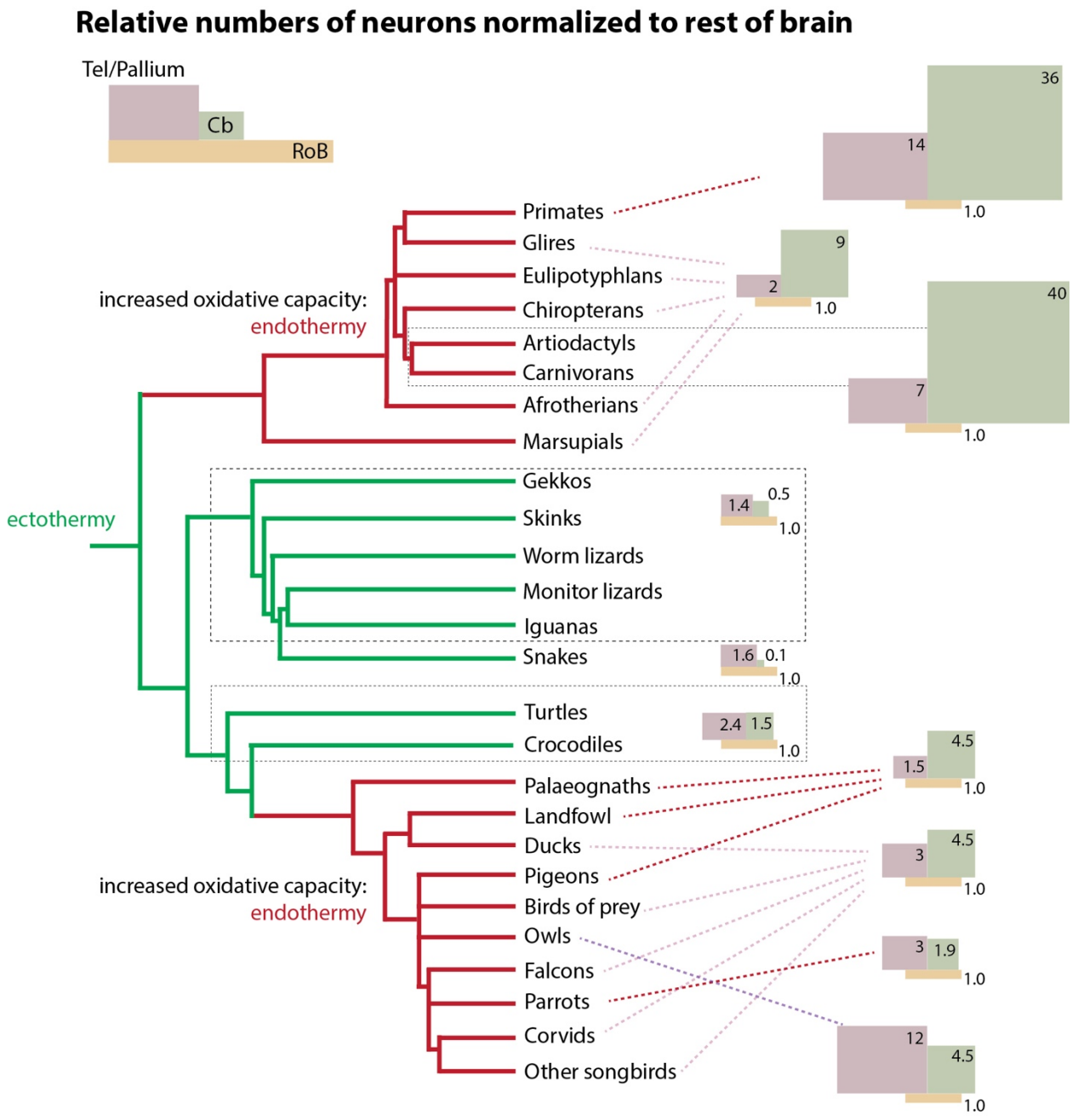
1050 All reptiles in the dataset gain neurons coordinately between the telencephalon and the
1051 rest of brain (Figure 20A), with ratios of numbers of neurons between the structures that vary
1052 from just below 1.0 in Iguania to 2.4 neurons in the telencephalon to every neuron in the rest of
1053 brain of Testudines and the Nile crocodile (Figure 20B; Table 16). On average, reptiles other than
1054 Testudines and the Nile crocodile have 1.4±0.6 neurons in the telencephalon to every neuron in
1055 the rest of brain; Testudines and the Nile crocodile stand out amongst reptiles with 2.4±0.6
1056 neurons in the telencephalon to every neuron in the rest of brain (Figure 21, Table 16).

1057 Strikingly, and despite the common narratives of cortical expansion in mammalian
1058 evolution (Rowe et al., 2011; Bertrand et al., 2022), mammals do not have the expected matching
1059 increase in the ratio of neurons between the cortex and rest of brain that would set them apart
1060 from reptiles. Small mammals (eulipotyphlans, chiropterans, rodents, small afrotherians, and
1061 South American marsupials) have ca. 2 neurons in the cerebral cortex for every neuron in the rest
1062 of brain, as described before (Herculano-Houzel et al., 2014a), which is only slightly more than
1063 most reptiles, and fewer than found in turtles and the Nile crocodile (Figure 20B; Figure 21). It is
1064 only the large mammals – carnivorans, Australian marsupials, primates, and artiodactyls – that
1065 have greatly increased ratios of neurons in the cerebral cortex over the rest of brain, which
1066 average just over 7 in artiodactyls and carnivorans, and can exceed 20 in primates (Figure 20B,
1067 Figure 21; Table 16). These data show that compared to the ancestor shared with modern
1068 reptiles, and to small mammals, there has been a marked expansion of cortical neurons over the
1069 rest of the neural tube in the evolution of *large* mammalian species – but not at the origin of
1070 mammals.

1071 Interestingly, the early-derived Galliformes and Columbiformes, along with the smallest
1072 Palaeognathes, share with reptiles a low ratio of 1.5 neurons in the pallium to every neuron in
1073 the rest of brain (Figure 20B, Table 16). In contrast, most bird species in the dataset have a
1074 significantly larger ratio of ca. 3 neurons in the pallium to every neuron in the rest of brain (Table
1075 16, Figure 21). The striking outliers are the Strigiformes (owls), with on average 12 neurons in the

1076 pallium for every neuron in the rest of brain, on par with primate species in the dataset, and well
1077 above passerines and parrots (Figure 21, Table 16), with which owls share a similar range of
1078 absolute numbers of pallial neurons (Figure 20A).

1079 The similarities across reptiles, small mammals and the early-derived birds in the ratios in
1080 numbers of neurons between the pallium and rest of brain indicate that while the advent of
1081 endothermy was associated with vastly increased absolute numbers of neurons in the brain, it
1082 did not lead on its own to any relative expansion of "cortical processing power" over the rest of
1083 brain (see Herculano-Houzel, 2025). That increase happened later, and separately, in primates,
1084 artiodactyls, and carnivorans.


Relative numbers of neurons normalized to rest of brain
Tel/Pallium
Cb
RoB
Primates
Glires
Eulipotyphlans
Chiropterans
Artiodactyls
Carnivorans
Afrotherians
Marsupials
increased oxidative capacity:
endothermy
ectothermy
Gekkos
Skinks
Worm lizards
Monitor lizards
Iguanas
Snakes
Turtles
Crocodiles
Palaeognaths
Landfowl
Ducks
Pigeons
Birds of prey
Owls
Falcons
Parrots
Corvids
Other songbirds
increased oxidative capacity:
endothermy
36
14
1.0
9
2
1.0
40
7
1.0
1.4
0.5
1.0
1.6
0.1
1.0
2.4
1.5
1.0
4.5
1.5
1.0
4.5
3
1.0
3
1.9
1.0
12
4.5
1.0

1085

Figure 21. Signature ratios of numbers of neurons between the telencephalon/pallium and rest of brain describe the brains of different amniote clades. The schematics in varying sizes represent the rest of brain (tan rectangle), telencephalon (red) and cerebellum (green). All schematics are thus scaled to a similar number of neurons in the rest of brain; in this way, the surface area of each brain part represents the relative number of neurons in that structure compared to the rest of brain (which has a value of 1.0). The schematics illustrate that reptilian brains are characterized by modestly larger numbers of neurons in the telencephalon compared to the rest of brain, and fewer neurons in the cerebellum (green lines). Birds (pink lines), with increased oxidative capacity, diverged away from reptiles with a step increase to a larger ratio of 4.5 neurons in the cerebellum for every neuron in the rest of brain, followed in most bird clades (other than the early derived Galliformes, as well as Columbiformes) by an increase to on average 3 neurons in the pallium to every neuron in the rest of brain, and reaching a peak in Strigiformes. Independently increased oxidative capacity occurred in mammals with a different brain signature of an increased average of 4 cerebellar neurons for every pallial neuron in all extant mammals, while the ratio of pallial/rest of brain neurons remained low at ca. 2 in small species, but increased in carnivorans, artiodactyls, large marsupials, and reached peak values in primates.

Table 16 – Scaling of the ratio N_{tel}/N_{rob} between neurons in the telencephalon or pallium (N_{tel}; reptilian telencephalon or bird or mammalian pallium) and in the rest of brain (N_{rob}; reptilian or bird brainstem and diencephalon, or mammalian brainstem, diencephalon plus striatum) as a function of numbers of neurons in the rest of brain (N_{rob}). Values correspond to the equation $N_{tel}/N_{rob} = e^{a\pm SE}\ N_{rob}^{b\pm SE}$, the p-values for a and b, and the r^2 for the power fit. Values in parentheses are the average ratio N_{tel}/N_{rob} for the clade ± standard deviation.

N_{tel}/N_{rob} x N_{rob}	**n**	**a in e^a**	**b in N_{rob}^b**	**p, a**	**p, b**	**r^2**
Reptiles						
All (1.602±0.754)	108	-0.168±1.252	**0.035**±0.083	0.8935	0.6748	0.002
Anguimorpha (2.242±0.775)	7	-1.508±3.300	**0.145**±0.211	0.6668	0.5243	0.086
Crocodilia (2.550)	1					
Gekkota (1.466±0.493)	14	-3.634±3.081	**0.271**±0.211	0.2612	0.2222	0.121
Iguania (0.864±0.306)	20	-1.524±1.977	**0.087**±0.129	0.4508	0.5112	0.024
Lacertoidea (1.317±0.525)	15	-2.045±2.602	**0.149**±0.172	0.4461	0.4024	0.054
Scincoidea (1.593±0.471)	14	0.078±2.390	**0.023**±0.160	0.9744	0.8884	0.002
Serpentes (1.644±0.784)	18	0.846±5.039	**-0.030**±0.335	0.8688	0.9287	0.001
Testudines and Crocodilia (2.393±0.617)	20	0.473±1.937	**0.025**±0.129	0.8099	0.8505	0.002
All minus Serpentes,	70	-0.542±1.275	**0.050**±0.084	0.6722	0.5559	0.005

Testudines, Crocodilia (1.365±0.621)						
Birds						
All	65	-5.027±1.826	**0.341**±0.101	0.0077	0.0013	0.153
Accipitriformes (3.073±1.326)	4	-15.931±12.473	**0.921**±0.677	0.3298	0.3067	0.481
Anseriformes (3.721±0.644)	7	-5.344±4.309	**0.376**±0.244	0.2699	0.1836	0.322
Columbiformes (1.561±0.417)	5	-5.907±3.841	**0.365**±0.222	0.2216	0.1980	0.475
Falconiformes (3.040±0.879)	3	-14.767±8.525	**0.870**±0.468	0.3333	0.3142	0.776
Galliformes (1.490±0.363)	9	-4.157±2.056	**0.259**±0.118	0.0830	0.0633	0.410
Palaeognathae (3.045±2.024)	6	-28.708±5.017	**1.654**±0.280	0.0046	0.0041	0.897
Passeriformes (3.546±1.303)	13	-7.678±1.235	**0.491**±0.068	<0.0001	<0.0001	0.825
Psittaciformes (3.329±0.486)	11	1.707±0.991	**-0.028**±0.053	0.1192	0.6162	0.029
Strigiformes (11.536±2.503)	7	-4.614±3.495	**0.392**±0.195	0.2440	0.1002	0.448
Galliformes, Columbiformes (1.515±0.369)	14	-4.436±1.729	**0.277**±0.099	0.0247	0.0163	0.394
Mammals						
All (5.425±5.464)	69	-7.601±1.115	**0.521**±0.065	<0.0001	<0.0001	0.489
All non-primates (3.710±2.873)	57	-5.932±1.118	**0.414**±0.066	<0.0001	<0.0001	0.416
Afrotheria (minus elephant) (2.412±0.415)	5	-0.124±1.869	**0.059**±0.110	0.9514	0.6319	0.086
Artiodactyla (7.349±2.778)	5	-14.592±3.155	**0.904**±0.172	0.0190	0.0135	0.902
Carnivora (7.360±3.339)	8	-1.611±6.173	**0.200**±0.353	0.8028	0.5923	0.051
Chiroptera	13	3.190±3.095	**-0.176**±0.195	0.3248	0.3852	0.069

(1.598±0.665)						
Eulipotyphla (1.934±0.213)	5	1.733±2.264	**-0.068**±0.142	0.4998	0.6664	0.070
Marsupialia (4.610±2.294)	9	-5.267±4.025	**0.392**±0.236	0.2320	0.1411	0.282
Primata (13.571±7.411)	12	-4.617±2.854	**0.391**±0.158	0.13681	0.0329	0.380
Glires (2.164±0.602)	10	-1.015±2.208	**0.103**±0.130	0.65791	0.4509	0.073
Scandentia (2.686)	1					
Small mammals: Afrotheria (minus elephant), Chiroptera, Eulipotyphla, Glires, Scandentia (1.965±0.630)	34	-1.405±1.162	**0.124**±0.071	0.2355	0.0908	0.087

Expansion of cerebellar neurons over the rest of brain defines endothermic amniotes

The analysis of the scaling of numbers of neurons across structures reveals that the ratio at which neurons are added to the cerebellum over the rest of brain is particularly well conserved across reptilian species, with on average 0.5 neurons in the cerebellum to every neuron in the rest of brain in other reptiles (Figure 20C,D, Table 17). The exceptions are snakes, which have only about 1 neuron in the cerebellum for every 10 neurons in the rest of brain, and, in the opposite direction, Testudines and the Nile crocodile, with 1.5 cerebellar neurons for every neuron in the rest of brain (Table 17; Figure 21).

Compared to other reptiles, birds seem to have experienced a step increase to an average of 4.5±2.0 neurons in the cerebellum to every neuron in the rest of brain (Figure 20D, Figure 21; Table 17). The only exception is Psittaciformes, with lower ratios of 1 to 3 cerebellar neurons to

1122 every neuron in the rest of brain, which decrease with increasing numbers of neurons in the latter
1123 structure (Table 17).

1124 Mammals as a whole, the other endothermic amniotes, also exhibit an expansion of
1125 numbers of cerebellar neurons over the rest of brain, which in this case is even more pronounced
1126 than in birds (Figure 20D). Across small mammals, there are on average 9 neurons in the
1127 cerebellum for every neuron in the rest of brain; larger mammals have increasing ratios of
1128 neurons in the cerebellum for every neuron in the rest of brain, reaching 30 to 40 neurons in the
1129 cerebellum to every neuron in the rest of brain in primates, artiodactyls and carnivorans (Figure
1130 21; Table 17).

1131

1132 **Table 17** – Scaling of the ratio N_{cb}/N_{rob} between neurons in the cerebellum (N_{cb}) and in the rest of brain (N_{rob}; reptilian
1133 or bird brainstem and diencephalon, or mammalian brainstem, diencephalon plus striatum) as a function of numbers
1134 of neurons in the rest of brain (N_{rob}). Values correspond to the equation $N_{cb}/N_{rob} = e^{a\pm SE}\ N_{rob}^{b\pm SE}$, the p-values for a
1135 and b, and the r^2 for the power fit. Values in parentheses are the average ratio N_{cb}/N_{rob} for the clade ± standard
1136 deviation.
1137

N_{Cb}/N_{rob} x N_{rob}	n	a in e^a	b in N_{rob}^b	p, a	p, b	r^2
Reptiles						
All (0.602±0.572)	108	-7.329±2.201	**0.429**±0.146	0.0012	0.0041	0.075
Anguimorpha (0.646±0.447)	7	-25.867±3.062	**1.597**±0.388	0.0080	0.0092	0.772
Crocodilia	1					
Gekkota 0.487±0.188	14	-9.390±4.080	**0.587**±0.279	0.0401	0.0572	0.269
Iguania (0.598±0.155)	20	-0.185±1.526	**-0.023**±0.100	0.9049	0.8164	0.003
Lacertoidea (0.352±0.157)	15	-3.750±3.205	**0.172**±0.211	0.2631	0.4298	0.049
Scincoidea (0.326±0.130)	14	-8.557±3.160	**0.492**±0.212	0.0190	0.0385	0.310
Serpentes (0.143±0.061)	18	-5.528±4.058	**0.233**±0.270	0.1920	0.4008	0.044
Testudines and Crocodilia (1.463±0.775)	20	-8.934±2.882	**0.616**±0.191	0.0062	0.0050	0.362
All minus Serpentes,	70	-7.008±1.653	**0.405**±0.110	<0.0001	0.0004	0.167

Testudines, Crocodilia (0.474±0.232)						
Birds						
All	65	4.487±1.462	**-0.178**±0.081	0.0032	0.0316	0.071
Accipitriformes (5.196±1.794)	4	-2.245±10.904	**0.209**±0.591	0.8559	0.7576	0.059
Anseriformes (5.779±1.785)	7	-13.063±6.875	**0.837**±0.389	0.1159	0.0843	0.480
Columbiformes (4.469±1.825)	5	-8.072±5.515	**0.549**±0.318	0.2395	0.1831	0.498
Falconiformes (4.083±1.561)	3	-20.443±10.178	**1.196**±0.559	0.2941	0.2781	0.821
Galliformes (4.249±1.886)	9	-5.606±4.027	**0.399**±0.230	0.2065	0.1266	0.300
Palaeognathae (6.439±3.749)	6	-21.326±5.267	**1.287**±0.294	0.0155	0.0119	0.827
Passeriformes (3.037±0.511)	13	12.633±0.096	**0.160**±0.060	0.1237	0.0212	0.396
Psittaciformes (1.898±0.583)	11	6.063±1.284	**-0.291**±0.068	0.0011	0.0021	0.669
Strigiformes (4.235±1.162)	7	-1.128±5.866	**0.141**±0.327	0.8551	0.6834	0.036
All minus Psittaciformes (4.478±2.048)	54	-2.085±1.627	**0.196**±0.091	0.2056	0.0360	0.082
Mammals						
All (26.985±43.398)	68	-6.389±1.078	**0.540**±0.063	<0.0001	<0.0001	0.527
All non-primates (minus elephant) (19.677±19.195)	56	-5.637±1.413	**0.493**±0.084	0.0002	<0.0001	0.390
Afrotheria (minus elephant) (6.869±1.993)	5	-0.990±3.292	**0.170**±0.195	0.7832	0.4461	0.203
Artiodactyla (38.321±13.840)	5	-9.891±5.574	**0.737**±0.305	0.1741	0.0941	0.661

Carnivora (47.426±30.782)	8	-9.555±4.646	**0.758**±0.266	0.0854	0.0291	0.576
Chiroptera (9.397±2.471)	13	3.374±1.962	**-0.073**±0.124	0.1135	0.5649	0.031
Eulipotyphla (9.143±4.579)	5	-7.648±11.087	**0.612**±0.697	0.5399	0.4442	0.205
Marsupialia (24.157±9.613)	9	-2.588±3.609	**0.334**±0.212	0.4965	0.1591	0.262
Primata (35.913±23.055)	11	-2.233±2.014	**0.315**±0.112	0.2961	0.0199	0.470
Glires (10.301±3.601)	10	-0.892±3.024	**0.186**±0.178	0.7755	0.3271	0.120
Scandentia	1					
Small mammals: Afrotheria (minus elephant), Chiroptera, Eulipotyphla, Glires, Scandentia (9.220±3.164)	34	1.171±1.279	**0.060**±0.078	0.3667	0.4459	0.018

Ratios of cerebellar to pallial neurons define clades of amniotes

The cerebellum and pallium develop from entirely different progenitor cell populations in the brain. It is thus not surprising that while numbers of neurons in these two structures tend to vary together across species of reptiles (Figure 20E, Table 18), they occur at no particular ratio: that is, the cerebellum/telencephalon ratio of numbers of neurons is neither shared across reptilian species, nor scales systematically as reptilian brains vary in size (Figure 20F, Table 18). Rather, while almost all reptilian clades have more neurons in the telencephalon than in the cerebellum, different clades have different characteristic ratios of numbers of neurons between the cerebellum and telencephalon, with Serpentes on the low end (with a ratio of 0.1, amounting to almost ten neurons in the telencephalon to every neuron in the cerebellum), Iguania (0.7) and Testudines and Crocodilia (0.6) on the high end (slightly more than one neuron in the

telencephalon for every neuron in the cerebellum), and most other reptilian clades in between (Table 18). These ratios are illustrated by the size of the circles in Figure 22.

While all birds have in common their increased absolute numbers of neurons in the cerebellum compared to reptiles (Figure 20C), even when matched for cerebellar mass (Figure 14C), different bird clades have characteristic ratios of numbers of neurons between the cerebellum and the pallium. As summarized in Figure 22, early-derived birds have a predominance of neurons in the cerebellum over the pallium, akin to mammals, which is maintained in Falconiformes; Passeriformes have similar numbers of neurons in the cerebellum and pallium; Psittaciformes have a prevalence of pallial over cerebellar neurons; and Strigiformes, like reptiles, have several times more neurons in the telencephalon than in the cerebellum (Table 18). Importantly, the predominance of pallial over cerebellar neurons in Psittaciformes and Strigiformes is due not to a “reversal” to the reptilian pattern, but rather to a relative decrease in numbers of cerebellar neurons in parrots compared to the avian norm given the number of neurons in the rest of brain, and to the separate and striking increase in absolute and relative numbers of neurons in the pallium of owls over the rest of brain (Figure 20).

Mammals, on the other hand, are characterized by a fairly constant average of 3-6 neurons in the cerebellum for every neuron in the cerebral cortex (Figure 22). This is the consequence of the striking similarity between the scaling of numbers of neurons in the mammalian pallium against the rest of brain, and the scaling of numbers of neurons in the cerebellum against the rest of brain (Figure 20F; Table 18).

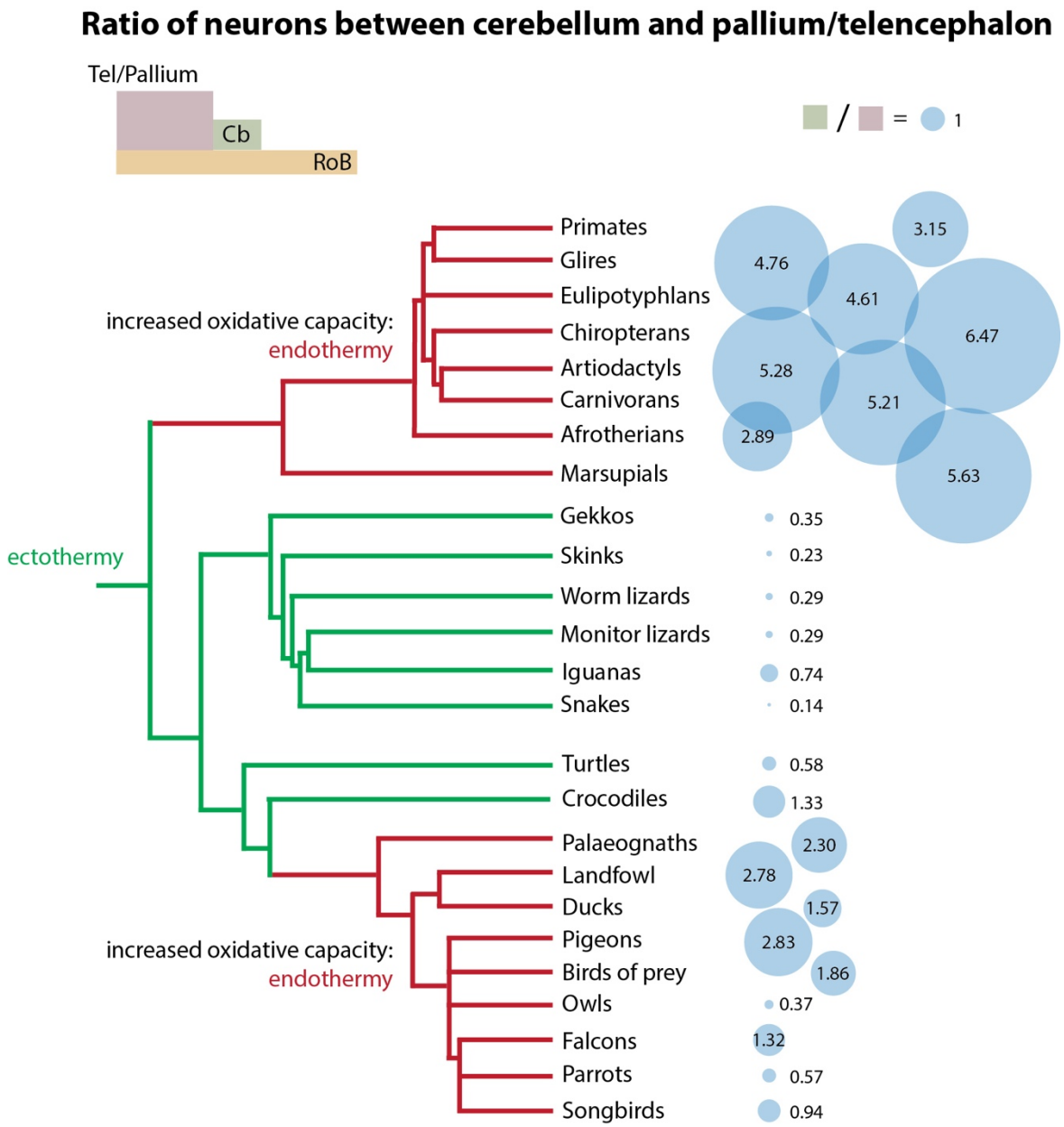


Figure 22. Signature ratios of numbers of neurons between the cerebellum and the telencephalon/pallium describe the brains of different amniote clades. The diameter of the circles in varying sizes represents the ratio of numbers of neurons between the pallium or telencephalon and the cerebellum. The schematics illustrate that reptilian brains, with the exception of Crocodilians, are characterized by ratios smaller than 1, that is, by having more neurons in the telencephalon than in the cerebellum. The endothermic, early-derived birds have around 2 neurons in the cerebellum for every neuron in the pallium, whereas the more recent groups of birds show decreased ratios again, due to the independent expansion of numbers of pallial neurons, which is most extreme in Strigiformes (owls). In contrast, the independently endothermic mammals have a characteristic signature of an increased average of 4 cerebellar neurons for every pallial neuron in all extant mammals, ranging from 3 to 6 (Table 18).

Table 18 – Scaling of the ratio N_{cb}/N_{tel} between neurons in the cerebellum (N_{cb}) and telencephalon (N_{tel}; reptilian telencephalon or bird or mammalian pallium) as a function of numbers of neurons in the rest of brain (N_{rob}; reptilian or bird brainstem and diencephalon, or mammalian brainstem, diencephalon plus striatum). Values correspond to the equation $N_{cb}/N_{tel} = e^{a\pm SE}\ N_{rob}^{b\pm SE}$, the p-values for a and b, and the r^2 for the power fit. Values in parentheses are the average ratio N_{cb}/N_{tel} for the clade ± standard deviation.

N_{Cb}/N_{tel} x N_{rob}	**n**	**a±SE in e^a**	**b±SE in N_{rob}^b**	**p, a**	**p, b**	**r^2**
Reptiles						
All (0.403±0.293)	108	-7.161±2.242	**0.394**±0.149	0.0018	0.0093	0.062
Anguimorpha (0.291±0.201)	7	-24.359±4.994	**1.452**±0.320	0.0046	0.0061	0.805
Crocodilia (1.331)	1					
Gekkota (0.348±0.142)	14	-5.756±4.222	**0.316**±0.289	0.1978	0.2957	0.091
Iguania (0.737±0.226)	20	1.340±1.640	**-0.110**±0.107	0.4247	0.3179	0.055
Lacertoidea (0.286±0.120)	15	-1.705±3.350	**0.024**±0.221	0.6193	0.9162	0.001
Scincoidea (0.228±0.123)	14	-8.635±4.175	**0.470**±0.280	0.0609	0.1195	0.190
Serpentes (0.112±0.092)	18	-6.373±6.778	**0.263**±0.451	0.3611	0.5671	0.021
Testudines (0.583±0.256)	19	-8.233±3.491	**0.508**±0.233	0.0306	0.0434	0.219
Testudines and Crocodilia (0.621±0.300)	20	-9.407±2.641	**0.587**±0.175	0.0022	0.0036	0.384
All minus Iguania, Serpentes, Testudines, Crocodilia (0.288±0.143)	50	-5.903±2.198	**0.299**±0.146	0.0099	0.0467	0.080
Birds						
All	65	9.514±1.920	**-0.520**±0.106	<0.0001	<0.0001	0.274
Accipitriformes (1.859±0.721)	4	13.687±8.180	**-0.712**±0.444	0.2362	0.2499	0.563
Anseriformes (1.567±0.428)	7	-7.719±8.659	**0.461**±0.490	0.4136	0.3909	0.150
Columbiformes	5	-2.165±4.771	**0.184**±0.276	0.6809	0.5523	0.129

(2.834±0.626)						
Falconiformes (1.316±0.140)	3	-5.676±1.653	**0.326**±0.091	0.1804	0.1725	0.928
Galliformes (2.777±0.641)	9	-1.449±2.764	**0.140**±0.158	0.6163	0.4055	0.101
Palaeognathae (2.295±0.445)	6	7.382±2.368	**-0.367**±0.132	0.0356	0.0501	0.658
Passeriformes (0.940±0.287)	13	5.882±1.353	**-0.331**±0.075	0.0012	0.0010	0.641
Psittaciformes (0.572±0.168)	11	4.356±1.191	**-0.263**±0.063	0.0053	0.0024	0.658
Strigiformes (0.366±0.062)	7	3.486±2.578	**-0.251**±0.144	0.2342	0.1411	0.379
Accipitriformes, Anseriformes, Galliformes, Columbiformes, Palaeognathae (2.301±0.742)	31	3.393±2.085	**-0.148**±0.118	0.1145	0.2195	0.052
Passeriformes, Psittaciformes (0.771±0.301)	24	6.313±0.974	-0.360±0.053	<0.0001	<0.0001	0.679
Mammals						
All minus bear, elephant (4.856±2.153)	66	3.304±0.910	**-0.108**±0.053	0.0006	0.0480	0.060
All non-primates (minus bear, elephant) (5.197±1.944)	55	1.756±0.932	**-0.011**±0.055	0.0651	0.8479	0.001
Afrotheria (minus elephant) (2.886±0.846)	5	-0.867±3.581	**0.112**±0.212	0.8244	0.6348	0.085
Artiodactyla (5.276±0.695)	5	4.701±3.804	**-0.166**±0.208	0.3044	0.4818	0.176
Carnivora (minus bear) (5.212±2.469)	7	1.264±6.114	**0.017**±0.352	0.8444	0.9638	0.000
Chiroptera (6.473±2.098)	13	0.184±2.601	**0.103**±0.164	0.9448	0.5425	0.035

Eulipotyphla (4.610±1.986)	5	-9.381±8.832	**0.680**±0.555	0.3661	0.3080	0.333
Marsupialia (5.631±1.676)	9	2.679±2.482	**-0.058**±0.146	0.3163	0.7021	0.022
Primata (3.148±2.424)	11	2.203±3.057	**-0.069**±0.169	0.4893	0.6942	0.018
Glires (4.759±1.238)	10	0.123±1.918	**0.083**±0.113	0.9504	0.4839	0.063
Scandentia	1					

Evolution of signature ratios of numbers of neurons in birds and mammals

Taking it all together, each of the three groups of amniotes, and many of their main clades, can be defined by the 3D space they occupy in the relationship between the absolute number of neurons in the rest of brain; the proportion of neurons in the pallium (or telencephalon) over the rest of brain; and the proportion of neurons in the cerebellum over the rest of brain. Strikingly, while the equivalent mass relationships separate reptiles from the endothermic amniotes, they fail to distinguish among birds and mammals (Figure 23). Thus, what clearly distinguishes the two clades of endothermic amniotes from each other and from the ectothermic amniotes is the distribution of numbers of neurons across brain structures. Combined with the increased numbers of neurons that accompanied the evolution of endothermy, the three groups of amniotes can be separated using the diagnostic features illustrated in Figure 23A.

Reptiles are the amniotes with few neurons in the rest of brain as well as proportionately few neurons in the cerebellum and the telencephalon, normalized to the rest of brain. Modern reptiles have brains with fewer than 10 million neurons in the rest of brain, typically half as many in the cerebellum, and a slight (1.4-fold) predominance of neurons in the telencephalon over the rest of brain.

Birds deviate from reptiles with a shift to a higher, non-overlapping range of numbers of neurons in the rest of brain together with a jump to an also higher, non-overlapping range of

numbers of neurons in the cerebellum. Compared to the closest living non-avian reptilian relatives, turtles and crocodiles, birds appeared with a 3-fold step increase in numbers of neurons in the cerebellum for every neuron in the rest of brain, shifting to a new ratio of 4.5 neurons in the cerebellum to every neuron in the rest of brain that remains a stable signature of the bird brain. The sole known exception so far is Psittaciformes, in which this ratio drops progressively with increasing numbers of neurons, resulting in an average 1.9 neurons in the cerebellum to every neuron in the rest of brain (Figure 21). Developmentally, the cerebellum is part of the hindbrain (Puelles et al., 2013), which is a key component of the "rest of brain" here. Thus, I propose that birds arose with a modification(s) in the developmental program of the hindbrain that resulted in the generation of 3-fold larger numbers of neurons in the cerebellum. Mechanistically, that could be implemented through two doublings of the numbers of early progenitor cells that give rise to the cerebellum in quantal developmental units, followed by apoptosis (Herrup, 1986).

While the higher cerebellum/rest of brain neuronal ratio remains steady, more recent bird clades are defined by an increased ratio of pallial neurons over the rest of brain, ranging from a reptile-like 1.5 in early-derived birds to 12 in owls, but averaging 3 pallial neurons per neuron in the rest of brain in most bird clades, including Passeriformes and Psittaciformes. As a result, the ratio of neurons between the cerebellum and the pallium is characteristic of each clade of birds (Figure 22). Mechanistically, this means that the pallium, which originates from the dorsal cap of the second neuromere (Puelles et al., 2013), gains neurons fairly independently from both the cerebellum and the rest of brain in birds. This freedom in the addition of numbers of neurons between pallium and cerebellum in bird species is consistent with the lack of major projections linking the two structures in birds, as the bird cerebellum is predominantly connected to brainstem structures instead of the pallium (Gutiérrez-Ibáñez et al., 2018). The lack of major connection pathways between the cerebellum and the pallium in birds together with the shared developmental hindbrain identity of the cerebellum and most of the rest of brain is presumably sufficient to account for the concerted addition of numbers of neurons to the cerebellum and rest of brain across most bird species. It remains to be determined whether the strong link between numbers of neurons formed in the rest of brain and cerebellum of birds is associated

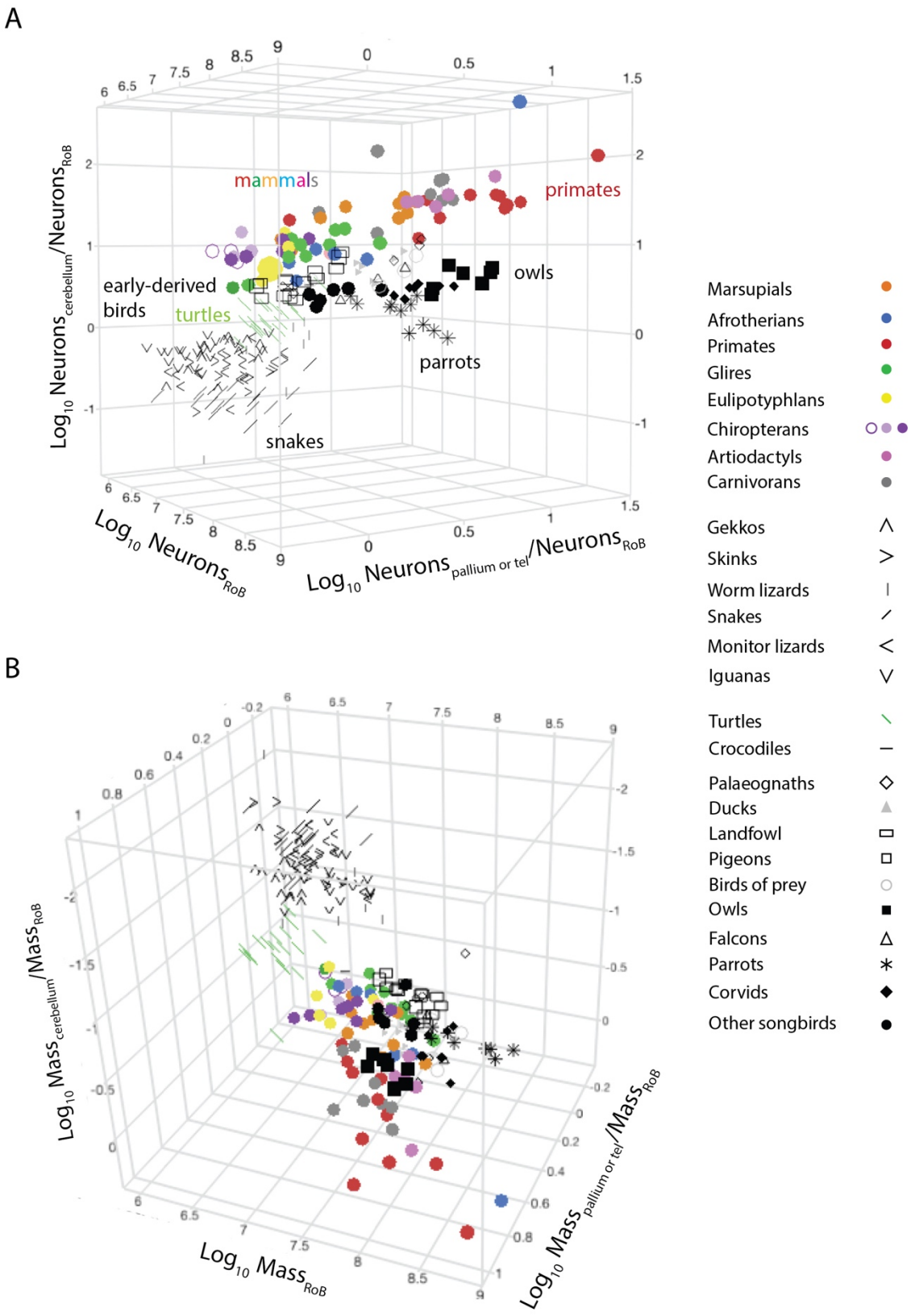
with the advent of any major bird-specific neuronal pathways between the two parts of the brain, compared to reptiles, or simply constitutes a quantitative variation, made possible by increased oxidative and cardiovascular capacity in birds, of a qualitatively similar organization to the rest of brain and cerebellum of reptiles.

Birds can thus be defined as the group of amniotes with more than 10 million neurons in the rest of brain and in the cerebellum, with ratios between the two that favor the cerebellum by nearly 2 to 4.5 times. In contrast, the smallest mammalian species still share with reptiles numbers of neurons in the rest of brain below 10 million; what defines mammals is an enormously increased ratio of numbers of neurons in the cerebellum over the rest of brain (Figure 23A), which occurs in coordination with increased numbers of neurons in the cerebral cortex, such that a fairly steady average ratio of 4 neurons in the cerebellum to every neuron in the pallium applies to most species, as described previously.

While the mammalian cerebellum is a hindbrain structure derived from neuromeres r0-r1 exactly like in birds (Puelles et al., 2013), mammals differ from birds in that the former exhibit massive connectivity between the cerebral cortex and cerebellum, mediated by the pontine nuclei of the hindbrain, and back to the cortex through the ventral thalamus (Ramnani, 2006). I thus propose that a key defining innovation at the evolutionary origin of mammals was the formation of the dominant cortico-pontine-cerebellar pathway, reciprocated by cerebello-thalamo-cortical projections, which, combined with the increased oxidative and cardiovascular capacities that allowed for increased numbers of neurons to be supported (as well as for the evolution of endothermy; see the following chapter, Herculano-Houzel 2025), led to the concerted scaling of numbers of neurons in the cerebral cortex and cerebellum that I postulate to define mammals. This hypothesis cannot at present differentiate between the possibilities that increased numbers of neurons in the cortex drove increased numbers of neurons in the cerebellum, or that conversely, increased numbers of neurons in the cerebellum drove increased numbers of neurons in the cerebral cortex. However, since numbers of cerebellar neurons are only established after birth, once adult numbers of neurons in the cerebral cortex have already been attained (Goldowitz and Hamre, 1998), it seems more likely that, if numbers of neurons in one structure drive the formation of proportional numbers of neurons in the others, the driver is

the cerebral cortex – which only occurs in mammals, not in birds, for the latter lack strong connectivity between cerebral cortex and cerebellum.

The proposition that the advent of a strong anatomical and functional connection between cerebral cortex and cerebellum lies at the origin of mammalian brains is compatible with the finding that while the expansion of the olfactory bulb is a very obvious and diagnostic development in the evolution of modern mammals (Rowe et al., 2011), it is accompanied by expansion of the lateral hemispheres of the cerebellum (Kielan-Jaworowska et al., 2004). Because the predicted increased in numbers of cerebellar neurons in coordination with increased cerebral cortical neurons at the origin of mammals (Figure 21) is accompanied by an increase in cerebellar mass compared to both the mass of the rest of brain and the mass of the cerebral cortex (Figure 19), relative cerebellar mass defined in this manner can be used as a diagnostic feature of endothermic, mammalian brains. The development of segmentation methods that will make it possible to estimate the volume of the cerebellum in endocasts of fossil species should allow for this new line of investigation to be explored.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Marsupials
Afrotherians
Primates
Glires
Eulipotyphlans
Chiropterans
Artiodactyls
Carnivorans
Gekkos
Skinks
Worm lizards
Snakes
Monitor lizards
Iguanas
Turtles
Crocodiles
Palaeognaths
Ducks
Landfowl
Pigeons
Birds of prey
Owls
Falcons
Parrots
Corvids
Other songbirds

1288

Figure 23. Each group of amniotes, and several clades within them, can be defined by the 3D space they occupy in the relationships between absolute numbers of neurons in the rest of brain and the normalized numbers of neurons in the pallium (or telencephalon) and cerebellum (A). In contrast, the corresponding mass relationships across the structures single out reptiles, but fail to separate birds and mammals (**B**). Each data point corresponds to one species. The key used to depict each clade is shown to the right.

Clade-specific extremes: snakes and owls

While similarities and shared differences across clades reveal patterns that are informative and even diagnostic of what constitutes a reptilian, bird, or mammalian brain, clade-specific features are also enlightening of the mechanisms of biology and evolution. In the present dataset, Serpentes are the most obvious outlier group amongst reptiles, with fewer cerebellar neurons than expected for both their body mass and for their numbers of neurons in the rest of brain. The obvious explanation for the fewer cerebellar neurons than expected for body mass is that Serpentes are characterized by their extremely elongated body, in which case the more biologically correct statement would be that Serpentes have evolved a larger body mass than expected for both the size of their brain structures (Figures 1-4) and their numbers of neurons in the cerebellum and rest of brain (Figure 17). However, the finding that Serpentes do have fewer cerebellar neurons than expected for a generic reptile with their numbers of rest of brain and pallial neurons (Figure 20C-F) calls for a clade-specific feature that would have either driven a reduction of numbers of cerebellar neurons, or allowed it to suffice. One possibility is the loss of limbs, which should lift the imposition on cerebellar processing that otherwise mediates the stabilization of the sensory surfaces of the limbs through fine motor control. This possibility is consistent with the other extreme in neuronal composition that is the cerebellum of the African elephant, which harbors 12 times the predicted number of neurons for a generic mammal, which we have speculated that might be associated to fine sensorimotor processing of the uniquely large appendage, the trunk (Herculano-Houzel et al., 2014b), mediated by a massively enlarged trigeminal ganglion (Pukart et al., 2022). Comparison with other animals of similarly elongated bodies and reduced limbs, such as the caecilian amphibians, should shed light on this possibility.

Owls (Strigiformes) are another interesting outlier group, with the largest ratios of pallial neurons per neuron in the rest of brain amongst birds, averaging 12, on par with some primates

(Figure 21), which seems to be due to an expansion of the pallium that while remaining in conformity to the neuronal scaling rules that apply to other late-derived bird clades (Figure 11). As a consequence, the exceptionally large ratio of pallial/rest of brain neurons in Strigiformes is reflected in a similarly exceptionally large ratio of pallial/rest of brain mass (Figure 18B). Importantly, whatever the number of neurons in the rest of brain, the large numbers of pallial neurons mean owls have a presumably enlarged signal processing capacity that should be on par with that of crows (Kabadayi et al., 2016), which we have recently showed to be associated with large numbers of associative pallial neurons rather than pallial mass (Ströckens et al., 2022). Indeed, a comparative studies of behavioral flexibility in the form of innovative behavior across the present bird clades confirms that increased numbers of pallial neurons correlate with increased cognitive capacity (Sol et al., 2022).

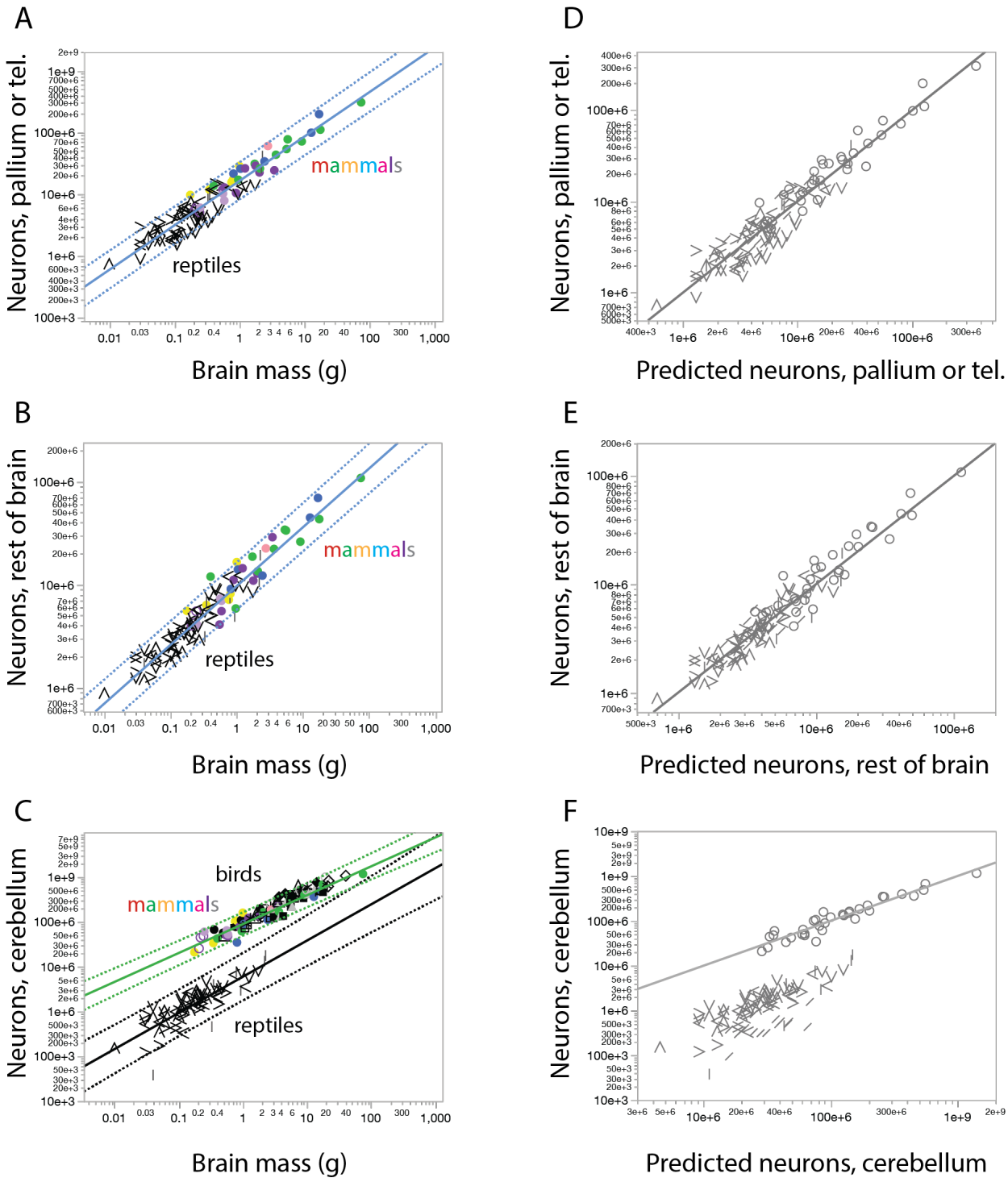
Predictions for early reptiles and mammaliaformes

Under the principle of parsimony, the similarities and continuities in the neuronal scaling rules observed between most reptilian and mammalian species must reflect shared scaling rules that also applied to stem amniote species ancestral to synapsids and diapsids (sauropsids) (Figures 11, 15). The data above show that extant reptiles and mammals share not only the neuronal scaling relationships for the telencephalon (Figure 11) and rest of brain (Figure 15), but, importantly for predictive purposes, also the scaling relationship between the mass (Figure 18A) and numbers of neurons (Figure 20A) in these two structures. Additionally, assuming that ancestral amniotes were ectothermic like modern reptiles (Nespolo et al., 2011), it is also reasonable to assume that the scaling rules that apply to the cerebellum of the latter also applied to ancestral amniotes. Thus, using the present findings, one can predict that the neuronal scaling rules that apply similarly to the telencephalon, and to the rest of brain, of modern mammals and reptiles (Figures 11C and 15C), and separately to the cerebellum of modern reptiles (Figure 13C), can be extended to their shared ancestors.

The neuronal scaling rules that putatively applied to ancestral amniotes can be expressed further as a function of brain mass, which allows the estimation of the numbers of neurons that composed those early brains since the advent of high-resolution 3D computerized tomography

has allowed for the size of the brain in fossil species to be estimated from their endocasts (Macrini, 2006). Figure 24 shows the neuronal scaling relationships that apply jointly to the cerebral cortex of small extant mammalian species (with brain mass below 100g, excluding primates) and to the telencephalon of extant reptiles excluding turtles and crocodiles. Across these 122 species in the dataset, the number of cortical (or telencephalic) neurons can be predicted from brain mass according to the equation $N_{tel} = e^{16.609\pm0.040} M_{br}^{0.719\pm0.021}$ ($p<0.0001$) with an r^2 value of 0.906 (Figure 24A). That is, over 90% of the variation in the number of cortical (in mammals) or telencephalic (in reptiles) neurons in extant species as distinct as ectothermic reptiles and endothermic mammals can be predicted from brain mass. Similarly, across the same 122 species, the number of neurons in the rest of brain can be predicted from brain mass according to the equation $N_{rob} = e^{16.087\pm0.030} M_{br}^{0.570\pm0.016}$ ($p<0.0001$) with an r^2 value of 0.913 (Figure 24B).

In contrast, the relationship between numbers of cerebellar neurons and brain mass differs strikingly between ectothermic reptiles and endothermic mammals (as well as birds). Here, two markedly different scaling relationships apply across 70 ectothermic reptiles (minus Serpentes, Testudine and Nile crocodile) and the mammalian clades comprised of 34 small species in the dataset: $N_{cb} = e^{15.593\pm0.133} M_{br}^{0.807\pm0.064}$ ($p<0.0001$, $r^2 = 0.699$) and $N_{cb} = e^{18.294\pm0.052} M_{br}^{0.644\pm0.035}$ ($p<0.0001$, $r^2 = 0.913$), respectively (Figure 20C). The relationship between predicted and measured numbers of neurons across the same species is depicted in Figure 20D-F, which shows that brain mass can be used to make accurate predictions of numbers of neurons in the main divisions of the brain of living reptiles and small mammals.


A
Neurons, pallium or tel.
mammals
reptiles
Brain mass (g)
D
Neurons, pallium or tel.
Predicted neurons, pallium or tel.
B
Neurons, rest of brain
mammals
reptiles
Brain mass (g)
E
Neurons, rest of brain
Predicted neurons, rest of brain
C
Neurons, cerebellum
birds
mammals
reptiles
Brain mass (g)
F
Neurons, cerebellum
Predicted neurons, cerebellum

1373

1374

Figure 24. Predictive scaling relationships for numbers of neurons in the different brain structures of ancestral amniotes. A-C, power functions describing numbers of neurons in the telencephalon or pallium (A), rest of brain (B) and cerebellum (C) as a function of whole brain mass (minus the olfactory bulbs). Predictive power functions are $N_{tel} = e^{16.609\pm0.040} M_{br}^{0.719\pm0.021}$ (r^2=0.906, p<0.0001), $N_{rob} = e^{16.087\pm0.030} M_{br}^{0.570\pm0.016}$ (r^2=0.913, p<0.0001) and $N_{cb} = e^{15.593\pm0.133} M_{br}^{0.807\pm0.064}$ (across 70 ectothermic reptilian species, excluding Serpentes, Testudine and the Nile crocodile; p<0.0001, r^2 = 0.699) or $N_{cb} = e^{18.294\pm0.052} M_{br}^{0.644\pm0.035}$ (across the 34 small mammalian species in the dataset; p<0.0001, r^2 = 0.913). D-F, comparison between measured and predicted numbers of neurons in the telencephalon (D), rest of brain (E) and cerebellum (F, using the scaling rule for small mammalian species). All graphs are fit with linear functions with slope = 1 and intercept = 0.

It follows from the excellent fit between actual numbers of brain neurons and estimates predicted from brain mass (Figure 24D-F) using the scaling functions above that the numbers of neurons that composed the telencephalon and rest of brain of early amniotes can be predicted directly from their brain mass estimated from reconstructed endocasts of fossil skulls. As to the cerebellum, however, the clear shift in the neuronal scaling rules that apply between mammals and reptiles means that inferring the neuronal scaling rules that applied to early mammaliaformes, which may or may not have already been endothermic, requires further evidence to infer which neuronal scaling rules applied: whether the allometry that describes ectotherms like the modern reptiles, or endotherms like modern mammals. Importantly, which allometric rules applied to the cerebellum of fossil early amniote species can be inferred from the relationship between body mass and cerebellar mass (Figure 3) and/or by the different scaling relationship between the mass of the cerebellum and that of the whole brain (Figure 6) across extant reptiles and mammals. For the sake of the current estimates, I will use the assumption that early mammaliaformes, with their relatively enlarged cerebella (Kielan-Jaworowska et al., 2004), already had numbers of neurons that conform to the scaling rules that apply to modern, endotherm mammalian species.

The equations above, depicted in Figure 24, can be used to predict the numbers of neurons that composed the brain of early amniote species by applying them to data on estimated brain volume (assumed to equal brain mass, using a specific density of brain tissue of 1 g/cm^3) from endocast reconstructions that excluded the olfactory bulbs in mammaliaformes, or that had barely distinguishable olfactory bulbs in cynodonts and other early Therapsid taxa. Brain mass and body mass values in fossil mammaliaformes and stem amniote species were compiled from the literature (Benoit et al., 2017a,b; Boonstra, 1968; Laas, 2015; Castanhinha et al., 2013; Laass

and Kaestner, 2017; Jerison, 1973; Hopson, 1979; Rowe et al., 2011; Sigurdsen et al., 2012; Rodrigues et al., 2014; Quiroga, 1980; Luo et al., 2001; Macrini, 2006; Macrini et al., 2007; Bertrand et al., 2019, 2020, 2022; Cameron et al., 2018; Maugoust and Orliac, 2021), and are listed in Table 18. The results are shown in Figure 25A-C, plotted against estimated body mass for each species solely for illustration purposes. Analysis of the estimated numbers of neurons that composed the brains of early amniotes indicates, for a given body mass, a clear shift from modern reptile-like absolute numbers of neurons in the telencephalon (Figure 25A), cerebellum (Figure 25B) and rest of brain (Figure 25C) of early therapsid species in the Permian and Triassic to modern mammal-like numbers of neurons in the Eocene, with intermediate numbers in species living during the Cretaceous and Paleocene. Of note, *Hadrocodium wui*, considered the earliest mammaliaform (Luo et al., 2001), from the Jurassic period, had an estimated 14.03 million neurons in the brain, 1.6 million neurons of which located in the telencephalon, fewer than in living mammals and on par with the similarly small Sumatran flying dragon (*Draco sumatranus*, which however has far fewer neurons in the cerebellum and thus in the brain as a whole, barely exceeding 5 million; Kverkova et al., 2022). *Morganucodon*, a larger mammaliaform that also lived during the Jurassic, had an estimated 52.32 million brain neurons, 6.9 million of which in the telencephalon, comparable to extant microbats in the dataset – although *Morganucodon* had a body mass estimated at ca. 5 times the body mass of small extant bats with similarly small numbers of cortical neurons (Herculano-Houzel et al., 2020). The largest Jurassic mammaliaform in the dataset, *Triconodon mordax*, had the body mass of a hamster but the predicted number of cortical neurons, 13 million, found in a laboratory mouse of ¼ the body mass (Herculano-Houzel et al., 2006).

In Cretaceous therapsids of known brain volume, the range of numbers of cortical neurons is expanded compared to Jurassic species: while the lower values remain at 6-7 million cortical neurons (in the multituberculate *Kryptobaatar* and the mammal *Kennalestes*), the upper values extend to 118 million cortical neurons in the allotherian *Vintana sertichi*, comparable to the 111 million cortical neurons found in the modern agouti *Dasyprocta primnolopha*, although the Cretaceous animal weighed 6.8 kg and the modern agouti, only 2.8 kg (Herculano-Houzel et al., 2006; Table 18). In the Paleocene, the upper end of the range expanded further to reach 316.5

million cortical neurons in the pantodontan *Leptolambda schmiditi*, of 256 kg body mass (Table 17) – similar to the 306 million cortical neurons found in the much smaller modern capybara, at ca. 47 kg (Herculano-Houzel et al., 2006).

Eocene mammals attained even larger numbers of cortical neurons in bodies that were closer in size, but still larger, than modern mammals of similar numbers of cortical neurons. The largest estimated number of cortical neurons in the dataset belongs to *Tetheopsis ingens*, of the stem mammalian taxon Dinocerata, with 1.1 billion cortical neurons – about 1/5 the number of cortical neurons of the African elephant (Herculano-Houzel et al., 2014) - in a body of 6 tons (Table 19), even larger than the 4-5 tons of the modern African elephant. In contrast, the Eocene mammals with the fewest cortical neurons, the chiropterans *Palaeophyllophora quercyi* and *P. oltina*, had an estimated 8-10 million cortical neurons in bodies of 24-36 g, on par with the modern microchiropteran *Cardioderma cor*, with 11 million cortical neurons in a body of 26 g (Herculano-Houzel et al., 2020). All estimates are listed in Table 19.

Taken together, the numbers obtained here indicate that the earliest mammals of the Jurassic had fewer telencephalic neurons than the smallest modern species, but over time, both the lower and the upper ends of the range progressively increased, reaching modern numbers of neurons for body mass in the Eocene. In comparison, the modern range of mammalian body masses is already found in fossils of the Paleocene, showing that mammalian evolution was characterized by “brawn before brains”, and not by a concerted increase in body and brain masses (Bertrand et al., 2022). However, while that study suggested that larger brains evolved later under positive selective pressure because of the cognitive advantage that they posed, I favor an alternate interpretation, focused on possibilities and opportunities. The analysis of numbers of telencephalic neurons estimated by brain mass untainted by body mass, shown in Figure 25D, indicates that large brains with moderately large numbers of telencephalic neurons similar to those found in modern cats and dogs already occurred in Permian therapsids such as *Moschops* (231 million neurons) and *Struthiocephalus* (329 million neurons; Table 19). The ensuing decrease in brain mass and range of estimated numbers of telencephalic neurons towards an apparent minimum in the Jurassic period (driven by the diminutive Jurassic fossil *Hadrocodium*; Rowe et al., 2011) coincides with the rise of large dinosaurs that came to dominate land habitats in the

Mesozoic (Brusatte, 2018), although the small range and low values could be an artifact of the small sample size. Still, it seems more parsimonious that the factors behind what range of numbers of brain neurons and brain mass were found at any period were first and foremost biological possibility (for instance, depending on rate of energy intake, which increases together with body mass; Fonseca-Azevedo and Herculano-Houzel, 2012) and opportunity (which depends on environmental conditions and competition with other species), before any considerations of "need" or "advantages". Thus, I favor a data-based account of mammalian evolution in which moderately large, modern mammal-like numbers of brain neurons, and thus brain mass, were already viable very early, in large Permian endothermic species that could ingest proportionately large amounts of food; possibly decreased in early therapsids as these species faced the rise of dinosaurs, and as smaller mammals, which could only afford small numbers of brain neurons, had a survival advantage over larger mammals; then increased back once larger-bodied mammals became once again *viable* (not more advantageous) after the K-Pg mass extinction that obliterated dinosaurs (Alvarez et al.,1980; Brusatte, 2018). In this scenario, brains with more neurons evolved not because they were advantageous (for species with fewer neurons, that is, reptiles and small mammals, were never replaced out of existence), but simply because they were finally possible, thanks to the combination of physiological changes that also allowed endothermy, and to the energetic and ecological possibilities opened up by the demise of the dinosaurs. The association between physiological changes that allowed endothermy and the advent of increased numbers of neurons in the brains of mammals and birds are explored in the following chapter (Herculano-Houzel, 2025).

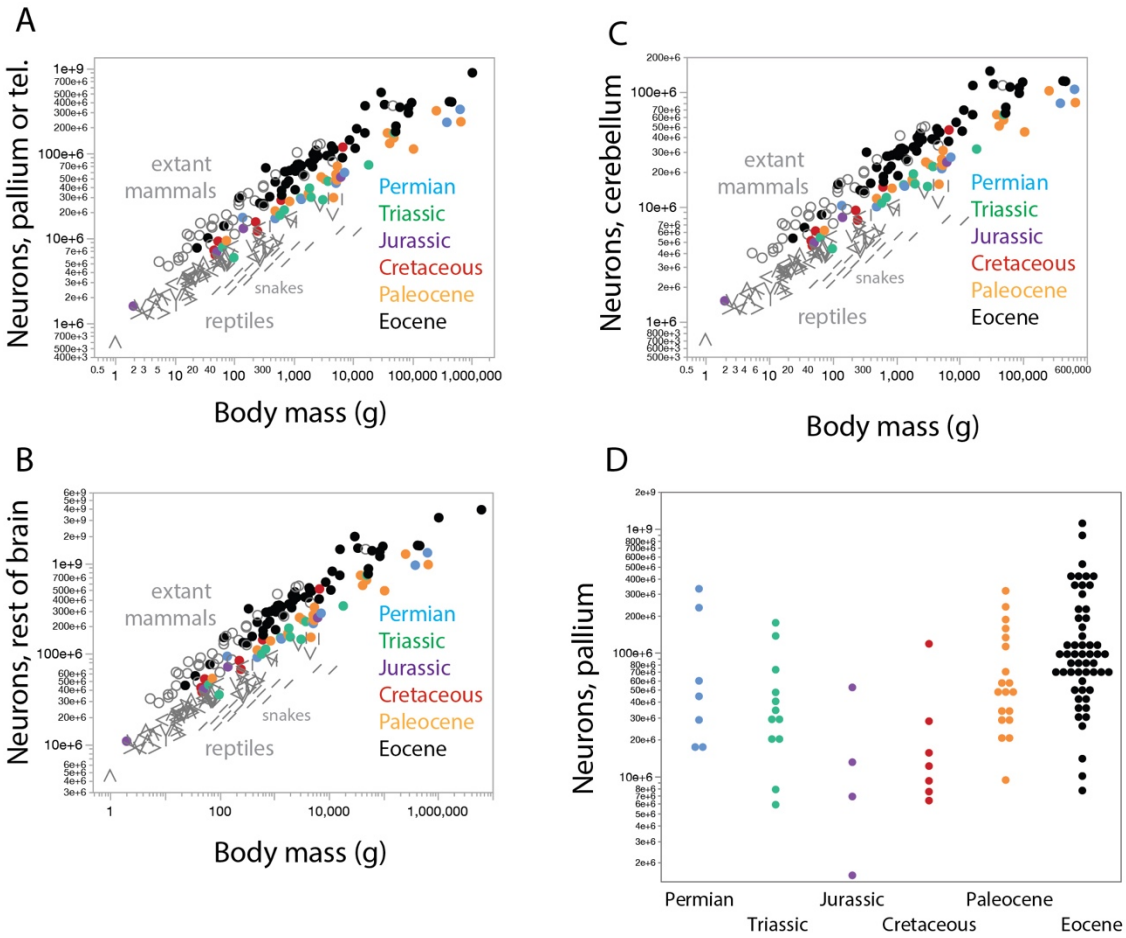


Figure 25. Predicted neuronal composition of the brains of fossil mammaliaform species. Note that for a given body mass, numbers of neurons in all parts of the brain (telencephalon or pallium, **A**; cerebellum, **B;** rest of brain, **C**) increase from the earliest species in the Permian/Triassic to the later species in the Eocene. **D,** In contrast, when body mass is not a confounding variable, the range of the distribution of inferred numbers of pallial neurons in fossil therapsid species appears to decrease from Permian to Jurassic periods, then increase progressively until the Eocene. Data listed in Table 19.

Table 19 – Numbers of neurons in the three parts of the brain of fossil Therapsids: telencephalon (N_{tel}), cerebellum (N_{cb}), and rest of brain (N_{rob}), estimated from reported brain mass (M_{br}, minus olfactory bulbs; in grams) inferred from cranial endocasts according to the equations $N_{tel} = e^{16.609\pm0.040}\ M_{br}^{0.719\pm0.021}$ ($p<0.0001$, $r^2=0.906$), $N_{cb} = e^{18.294\pm0.052}\ M_{br}^{0.644\pm0.035}$ ($p<0.0001$, $r^2 = 0.913$, calculated for extant mammals) and $N_{rob} = e^{16.087\pm0.030}\ M_{br}^{0.570\pm0.016}$ ($p<0.0001$, $r^2=0.913$). Brain mass in grams was calculated from endocranial volume (ECV) in cm^3 assuming 1 cm^3 = 1 g. M, million neurons; B, billion neurons. N_{br}, estimated total number of brain neurons, calculated as the sum $N_{tel} + N_{cb} + N_{rob}$.

Permian									
Clade	**Species**	**Body mass**	**ECV, cm^3**	**ECV minus OB, cm3**	**References**	**Estimated N_{tel}**	**Estimated N_{cb}**	**Estimated N_{rob}**	**Estimated N_{br}**

Therapsida, Biarmosuchia	*Lemurosaurus*	5.219 kg	4.02 cm3	4.02 cm3	Benoit et al. (2017a)	44.43 M	215.83 M	18.18 M	281.68 M
Therapsida: Dinocephalia	*Struthiocephalus*	644.088 kg	65 cm3	65 cm3	Boonstra (1968)	328.61 M	1.30 B	104.68 M	1.73 B
Therapsida, Gorgonopsia	*Aelurosaurus*	7.255 kg	6.0 cm3	6.0 cm3	Benoit et al. (2017a)	59.25 M	279.33 M	26.92 M	365.49 M
Therapsida, Dicynodontia	*Pristerodon*	491 g	1.06 cm3	1.06 cm3	Laas (2015)	17.04 M	91.47 M	10.02 M	118.53 M
Therapsida, Dicynodontia	*Niassodon*	139 g	1.10 cm3	1.10 cm3	Castanhinha et al. (2013)	17.50 M	93.68 M	10.24 M	121.41 M
Therapsida, Dicynodontia	*Kawingasaurus*	1.358 kg	2.18 cm3	2.18 cm3	Laass and Kaestner (2017)	28.61 M	145.53 M	15.12 M	189.26 M
Therapsida, Dinocephalia	*Moschops*	385.341 kg	39.85 cm3	39.85 cm3	Benoit et al. (2017b)	231.16 M	945.49 M	79.20 M	1.26 B
Therapsida, Dicynodontia	*Lystrosaurus*	18.511 kg	8.00 cm3	8.00 cm3	Jerison (1973)	72.86 M	336.18 M	31.71 M	440.76 M
Triassic									
Clade	**Species**	**Body mass**	**ECV, cm³**	**ECV minus OB, cm3**	**References**				
Therapsida, Cynodontia	*Thrinaxodon*	700 g	1.46 cm3	1.46 cm3	Rowe et al. (2011)	21.45 M	112.42 M	12.03 M	145.89 M
Therapsida, Cynodontia	*Trirachodon*	3.125 kg	2.15 cm3	2.15 cm3	Hopson (1979)	28.33 M	144.24 M	15.00 M	187.56 M
Therapsida, Therocephalia	*Tetracynodon darti*	1.317 kg	2.28 cm3	2.28 cm3	Sigurdsen et al. (2012)	29.55 M	149.79 M	15.51 M	194.85 M
Therapsida, Cynodontia	*Diademodon sp.*	50 kg	26.9871 cm3	26.9871 cm3	Rowe et al. (2011)	174.66 M	735.61 M	63.42 M	973.70 M
Therapsida, Therocephalia	*Microgomphodon*	1.797 kg	2.36 g	2.36 g	Benoit et al. (2017a)	30.29 M	153.16 M	15.81 M	199.26 M
Therapsida, Cynodontia	*Brasilitherium riograndensis*	98.57 g	0.378 cm3	0.243 cm3	Rodrigues et al. (2014)	5.91 M	35.43 M	4.33 M	45.66 M
Therapsida, Cynodontia	*Exaeretodon*	46.877 kg	19.19 cm3	19.19 cm3	Quiroga (1980)	136.69 M	590.59 M	52.22 M	779.50 M

Therapsida, Cynodontia	*Massetognathus*	1.865 kg	3.33 cm3	3.33 cm3	Quiroga (1980)	38.80 M	191.18 M	19.24 M	249.22 M
Therapsida, Cynodontia	*Therioherpeton*	64 g	0.36 cm3	0.36 cm3	Quiroga (1984)	7.84 M	45.63 M	5.41 M	58.88 M
Therapsida, Cynodontia	*Probainognathus*	590 g	1.20 cm3	1.20 cm3	Quiroga (1980)	18.63 M	99.08 M	10.76 M	128.46 M
Therapsida, Cynodontia	*Probelesodon*	3.807 kg	4.33 cm3	4.33 cm3	Quiroga (1980)	46.86 M	226.40 M	22.35 M	295.62 M
Jurassic									
Clade	**Species**	**Body mass**	**ECV, cm³**	**ECV minus OB, cm3**	**References**				
Mammaliaformes	*Hadrocodium wui*	0.002 kg (2 g)	0.045 cm³	0.039 cm3	Luo et al. (2001), Macrini (2006)	1.59 M	10.91 M	1.53 M	14.02 M
Mammaliaformes, Morganucodonta	*Morganucodon*	51 g	0.33 cm3	0.30 cm3 (assuming 10% OB)	Rowe et al. (2011)	6.87 M	40.57 M	4.88 M	52.33 M
Therapsida, Cynodontia	*Tritylodon*	6.278 kg	5.06 cm3	5.06 cm3	Benoit et al. (2017a)	52.42 M	250.30 M	24.43 M	327.14 M
Mammalia	*Triconodon mordax*	0.143 kg	0.82 cm3	0.73 cm3	Bertrand et al. (2022)	13.03 M	71.94 M	8.10 M	93.07 M
Cretaceous									
Clade	**Species**	**Body mass**	**ECV, cm³**	**ECV minus OB, cm3**	**References**				
Theriiformes (stem therian); Cladotheria	*Vincelestes neuquenianus*	0.619 kg	2.37 cm3	2.11 cm3	Macrini et al. (2007)	27.95 M	142.50 M	14.84 M	185.29 M
Multituberculate	*Kryptobaatar dashzevegi*	45.82 g	0.34 cm3	0.32 cm3	Bertrand et al. (2022)	7.20 M	42.30 M	5.06 M	54.56 M

Multituberculate	*Litovoitholocephalos*	0.248 kg	0.77 cm3 ECV	0.66 cm3	Bertrand et al. (2022)	12.12 M	67.42 M	7.65 M	87.19 M
Mammalia, Asioryctitheria	*Kennalestes gobiensis*	47.89 g	0.30 cm3 ECV	0.27 cm3	Bertrand et al. (2022)	6.37 M	37.91 M	4.60 M	48.88 M
Mammalia, Asioryctitheria	*Asioryctes nemegetensis*	53.76 g	0.50 cm3 ECV	0.45 cm3	Bertrand et al. (2022)	9.20 M	52.68 M	6.15 M	68.03 M
Mammalia, Zalambdalestidae	*Zalambdalestes lechei*	230.73 g	1.02 cm3 ECV	0.93 cm3	Bertrand et al. (2022)	15.51 M	84.08 M	9.30 M	108.89 M
Mammalia, Allotheria	*Vintana sertichi*	6.793 kg	18.30 cm3 ECV	15.64 cm3	Bertrand et al. (2022)	117.99 M	517.69 M	46.47 M	682.16 M
Paleocene									
Clade	**Species**	**Body mass**	**ECV, cm³**	**ECV minus OB, cm3**	**References**				
Multituberculate	*Ptilodus montanus*	0.216 kg	1.48 cm3 ECV	1.32 cm3	Bertrand et al. (2022)	19.95 M	105.35 M	11.36 M	136.65 M
Mammalia, Arctocyonidae	*Loxolophus priscus*	4.734 kg	2.44 cm3 ECV	2.33 cm3	Bertrand et al., 2022	30.01 M	151.90 M	15.70 M	197.61 M
Mammalia, Arctocyonidae	*Claenodon ferox*	38.41 kg	29.17 cm3 ECV	26.71 cm3	Bertrand et al., 2022	173.37 M	730.74 M	63.05 M	967.16 M
Mammalia, Condylarth, Arctocyonidae	*Chriacus baldwini*	1.833 kg	2.7 cm3	2.513 cm3	Bertrand et al. (2020)	31.69 M	159.48 M	16.39 M	207.56 M
Mammalia, Pantodonta	*Pantolambda_bathmodon*	41.919 kg	19.0 cm3 ECV	18.0 cm3	Bertrand et al. (2022)	130.54 M	566.73 M	50.35 M	747.62 M
Mammalia, Pantodonta	*Alcidedorbignya_inopinata*	0.861 kg	2.20 cm3 ECV	2.02 cm3	Bertrand et al. (2022)	27.09 M	138.56 M	14.47 M	180.12 M

Mammalia, Periptychidae	*Ectoconus ditrigonus*	105.644 kg	16.24 cm3 ECV	14.58 cm3	Bertrand et al. (2022)	112.19 M	494.82 M	44.65 M	651.65 M
Mammalia, Periptychidae	*Anisonchus sectorius*	1.789 kg	3.30 cm3 ECV	2.74 cm3	Bertrand et al. (2022)	33.72 M	168.61 M	17.22 M	219.56 M
Mammalia, Taeniodonta	*Onychodectes tisonensis*	5.033 kg	4.83 cm3 ECV	4.37 cm3	Bertrand et al. (2022)	47.17 M	227.75 M	22.47 M	297.39 M
Mammalia, Cimolestidae	*Acmeodon secans*	0.492 kg	1.64 cm3 ECV	1.41 cm3	Bertrand et al. (2022)	20.92 M	109.92 M	11.79 M	142.63 M
Mammalia, Phenacodontidae	*Tetraclaenodon pliciferus*	5.433 kg	5.22 cm3 ECV	4.51 cm3	Bertrand et al. (2022)	48.26 M	232.42 M	22.88 M	303.55 M
Mammalia, Arctocyonidae	*Arctocyon primaevus*	49.28 kg	23.81 cm3 ECV	22.21 cm3	Bertrand et al., 2022	151.83 M	648.87 M	56.76 M	857.47 M
Mammalia, Arctocyonidae	*Arctocyonides arenae*	5.477 kg	8.3 cm3 ECV	7.60 cm3	Bertrand et al., 2022	70.23 M	325.26 M	30.80 M	426.28 M
Mammalia, Pantodonta	*Titanoides primaevus*	664.06 kg	43.65 cm3 ECV	40.79 cm3	Bertrand et al. (2022)	235.06 M	959.80 M	80.26 M	1.28 B
Mammalia, Pantodonta	*Leptolambda schmidti*	256.33 kg	69.00 cm3 ECV	61.70 cm3	Bertrand et al. (2022)	316.53 M	1.25 B	101.62 M	1.67 B
Mammalia, Condylarthra, Perissodactyla	*Pleuraspidotherium aumonieri*	5.208 kg	6.00 cm3 ECV	5.60 cm3	Bertrand et al. (2022)	56.38 M	267.19 M	25.88 M	349.45 M
Mammalia, Apatemyidae	*Labidolemur kayi*	74 g	0.52 cm3 ECV	0.46 cm3	Bertrand et al. (2022)	9.35 M	53.43 M	6.23 M	69.01 M
Mammalia, Plesiadapiforms	*Plesiadapis cookei*	3.387 kg	5.00 cm3 ECV	4.61 cm3	Bertrand et al. (2022)	49.02 M	235.73 M	23.16 M	307.91 M

Mammalia, Plesiadapiforms	*Plesiadapis tricuspidens*	2.925 kg	5.21 cm3 ECV	5.07 cm3	Bertrand et al. (2022)	52.49 M	250.62 M	24.45 M	327.56 M
Eocene									
Clade	**Species**	**Body mass**	**ECV, cm³**	**ECV minus OB, cm3**	**References**				
Mammalia, Pantodonta (stem taxa)	*Coryphodon hamatus*	425.837 kg	93.0 cm3 ECV	87.0 cm3	Bertrand et al. (2022)	405.24 M	1.56 B	123.60 M	2.09 B
Mammalia, Pantodonta (stem taxa)	*Coryphodon elephantopus*	463.837 kg	90.0 cm3	86.0 cm3	Bertrand et al. (2022)	401.88 M	1.55 B	122.79 M	2.08 B
Mammalia, Taeniodonta (stem taxa)	*Ectoganus copei*	53.395 kg	38.95 cm3	34.62 cm3	Bertrand et al. (2022)	208.92 M	863.59 M	73.10 M	1.15 B
Mammalia, Euungulata (stem taxa)	*Hyopsodus miticulus*	0.630 kg	3.20 cm3	3.06 cm3	Bertrand et al. (2022)	36.51 M	181.05 M	18.34 M	235.90 M
Mammalia, Perissodactyla	*Xenicohippus sp.*	16.00 kg	29.40 cm3 ECV	26.71 cm3	Bertrand et al. (2022)	173.37 M	730.74 M	63.05 M	967.16 M
Mammalia, Phenacodontidae (stem taxa)	*Meniscotherium chamense*	6.69 kg	11.03 cm3 ECV	10.50 cm3	Bertrand et al. (2022)	88.60 M	400.52 M	37.03 M	526.16 M
Mammalia, Phenacodontidae (stem taxa)	*Phenacodus wortmani*	10.971 kg	16.19 cm3 ECV	14.99 cm3	Bertrand et al. (2022)	114.45 M	503.73 M	45.36 M	663.54 M
Mammalia, Phenacodontidae (stem taxa)	*Phenacodus primaevus*	52.8 kg	35 cm3	28.20 cm3	Cameron et al. (2018)	180.27 M	756.73 M	65.03 M	1.00 B
Mammalia, Afrotheria	*Prorastomus sirenoides*	98.156 kg	86.87 cm3 ECV	83.79 cm3	Bertrand et al. (2022)	394.43 M	1.53 B	120.98 M	2.04 B
Mammalia, Artiodactyla	*Diacodexis ilicis*	0.830 kg	4.7 cm3	4.38 cm3	Bertrand et al. (2020, 2022)	47.25 M	228.08 M	22.50 M	297.83 M
Mammalia, Palaeoryctidae (stem taxa)	*Eoryctes melanus*	66.98 g	0.96 cm3 ECV	0.80 cm3	Bertrand et al. (2022)	13.92 M	76.31 M	8.54 M	98.76 M

Mammalia, Glires	*Paramys copei*	1.030 kg	7.53 cm3 ECV	7.07 cm3	Bertrand et al. (2022)	66.67 M	310.46 M	29.56 M	406.69 M
Mammalia, Plesiadapiforms (stem taxa)	*Ignacius graybullianus*	270.56 g	2.00 cm3 ECV	1.89 cm3	Bertrand et al. (2022)	25.82 M	132.75 M	13.93 M	172.50 M
Mammalia, Euungulata (stem taxa)	*Hyopsodus paulus*	1.068 kg	3.42 cm3 ECV	3.14 cm3	Bertrand et al. (2022)	37.20 M	184.08 M	18.61 M	239.89 M
Mammalia, Euungulata (stem taxa)	*Hyopsodus lepidus*	0.633 kg	2.79 cm3	2.55 cm3	Cameron et al. (2018), Bertrand et al. (2019)	32.03 M	160.99 M	16.53 M	209.54 M
Mammalia, Perissodactyla	*Hyrachyus modestus*	62.220 kg	76.52 cm3 ECV	70.48 cm3	Bertrand et al. (2022)	348.30 M	1.37 B	109.62 M	1.82 B
Mammalia, Artiodactyla	*Agriochoerus sp.*	11.634 kg	33.00 cm3 ECV	31.36 cm3	Bertrand et al. (2022)	194.58 M	810.31 M	69.09 M	1.07 B
Mammalia, Artiodactyla	*Leptotragulus sp.*	8.818 kg	21.42 cm3 ECV	20.46 cm3	Bertrand et al. (2022)	143.13 M	615.47 M	54.16 M	812.77 M
Mammalia, Tillodontia (stem taxa)	*Trogosus hillsii*	86.686 kg	61.02 cm3 ECV	56.59 cm3	Bertrand et al. (2022)	297.45 M	1.19 B	96.73 M	1.58 B
Mammalia, Tillodontia (stem taxa)	*Trogosus grangeri*	86.605 kg	78.60 cm3 ECV	68.82 cm3	Bertrand et al. (2022)	342.38 M	1.34 B	108.14 M	1.79 B
Mammalia, Lepticticida (stem taxa)	*Leptictis sp.*	742.95 g	4.31 cm3 ECV	3.90 cm3	Bertrand et al. (2022)	43.47 M	211.66 M	21.06 M	276.18 M
Mammalia, Palaeanodonta (stem taxa)	*Metacheiromys marshi*	713.36 g	6.64 cm3	6.22 cm3	Bertrand et al. (2022)	60.80 M	285.88 M	27.48 M	374.16 M
Mammalia, Dinocerata (stem taxa)	*Uintatherium anceps*	1,037.06 kg	300.00 cm3 ECV	259.00 cm3	Bertrand et al. (2022)	887.89 M	3.16 B	230.18 M	4.27 B

Mammalia, Dinocerata (stem taxa)	*Tetheopsis ingens*	6,270.20 kg	365.00 cm3 ECV	354.00 cm3	Bertrand et al. (2022)	1.11 B	3.86 B	275.06 M	5.25 B
Mammalia, Hyaenodonta (stem taxa)	*Cynohyaenodon cayluxi*	1.359 kg	8.30 cm3 ECV	7.80 cm3	Bertrand et al. (2022)	71.55 M	330.74 M	31.26 M	433.55 M
Mammalia, Hyaenodonta (stem taxa)	*Sinopa lania*	4.189 kg	11.60 cm3 ECV	11.10 cm3	Bertrand et al. (2022)	92.21 M	415.12 M	38.22 M	545.55 M
Mammalia, Carnivoramorpha	*Miacis sylvestris*	1.157 kg	8.45 cm3 ECV	8.12 cm3	Bertrand et al. (2022)	73.65 M	339.42 M	31.98 M	445.05 M
Mammalia, Carnivoramorpha	*Oodectes herpestoides*	1.172 kg	7.64 cm3 ECV	7.27 cm3	Bertrand et al. (2022)	68.02 M	316.09 M	30.03 M	414.14 M
Mammalia, Carnivoramorpha	*Viverravus minutus*	313.20 g	2.03 cm3 ECV	1.86 cm3	Bertrand et al. (2022)	35.53 M	131.39 M	13.81 M	170.72 M
Mammalia, Carnivoramorpha	*Vulpavus profectus*	2.573 kg	12.07 cm3 ECV	11.16 cm3	Bertrand et al. (2022)	92.57 M	416.56 M	38.34 M	547.47 M
Mammalia, Carnivoramorpha	*Vulpavus ovatus*	3.788 kg	12.36 cm3 ECV	11.30 cm3	Bertrand et al. (2022)	93.40 M	419.92 M	38.61 M	551.94 M
Mammalia, Plesiadapiforms (stem taxa)	*Microsyops annectens*	1.432 kg	5.90 cm3 ECV	5.60 cm3	Bertrand et al. (2022)	56.38 M	267.19 M	25.88 M	349.45 M
Mammalia, Glires	*Paramys delicatus*	2.154 kg	12.57 cm3 ECV	11.97 cm3	Bertrand et al. (2022)	97.35 M	435.79 M	39.90 M	573.04 M
Mammalia, Glires	*Pseudotomus horribilis*	4.850 kg	15.19 cm3 ECV	14.38 cm3	Bertrand et al. (2022)	111.08 M	490.43 M	44.30 M	645.81 M
Mammalia, Glires	*Pseudotomus oweni*	3.666 kg	12.06 cm3 ECV	11.35 cm3	Bertrand et al. (2022)	93.70 M	421.11 M	38.71 M	553.53 M

Mammalia. Glires	*Pseudotomus petersoni*	4.386 kg	17.01 cm3 ECV	16.31 cm3	Bertrand et al. (2022)	121.61 M	531.87 M	47.660 M	701.07 M
Mammalia, Glires	*Pseudotomus hians*	2.306 kg	13.68 cm3 ECV	12.94 cm3	Bertrand et al. (2022)	102.96 M	458.21 M	41.72 M	602.89 M
Mammalia, Glires	*Reithroparamys delicatissimus*	0.749 kg	6.43 cm3 ECV	6.23 cm3	Bertrand et al. (2022)	60.87 M	286.18 M	27.50 M	374.55 M
Mammalia, Glires	*Rapamys atramontis*	1.080 kg	6.56 cm3 ECV	6.33 cm3	Bertrand et al. (2022)	61.58 M	289.13 M	27.75 M	378.45 M
Mammalia, Primata	*Rooneyia viejaensis*	341.3 g	7.23 cm3 ECV	7.16 cm3	Bertrand et al. (2022)	67.28 M	313.00 M	29.77 M	410.05 M
Mammalia, Primata	*Notharctus tenebrosus*	2.100 kg	7.62 cm3 ECV	7.47 cm3	Bertrand et al. (2022)	69.36 M	321.66 M	30.50 M	421.52 M
Mammalia, Primata	*Smilodectes gracilis*	1.239 kg	8.37 cm3 ECV	8.23 cm3	Bertrand et al. (2022)	74.37 M	342.37 M	32.23 M	448.97 M
Mammalia, Primata	*Necrolemur antiquus*	0.121 kg	2.36 cm3 ECV	2.31 cm3	Bertrand et al. (2022)	29.83 M	151.06 M	15.62 M	196.51 M
Mammalia, Artiodactyla	*Bathygenys reevesi*	2.390 kg	14.36 cm3 ECV	13.91 cm3	Bertrand et al. (2022)	108.45 M	480.05 M	43.47 M	631.97 M
Mammalia, Artiodactyla	*Robiacina lavergnensis*	0.397 kg	2.50 cm3 ECV	2.41 cm3	Bertrand et al. (2022)	30.75 M	155.24 M	16.00 M	202.00 M
Mammalia, Artiodactyla	*Dichobune leporina*	4.556 kg	15.84 cm3 ECV	14.63 cm3	Bertrand et al. (2022)	112.46 M	495.91 M	44.74 M	653.11 M
Mammalia, Artiodactyla	*Mouillacitherium elegans*	0.864 kg	6.96 cm3 ECV	6.46 cm3	Bertrand et al. (2022)	62.48 M	292.94 M	28.08 M	383.49 M

Mammalia, Artiodactyla	*Tapirulus hyracinus*	2.25 kg	10.71 cm3 ECV	9.91 cm3	Bertrand et al. (2022)	84.99 M	385.88 M	35.83 M	506.70 M
Mammalia, Hyaenodonta (stem taxa)	*Hyaenodon horridus*	34.35 7 kg	85.00 cm3 ECV	78.00 cm3	Bertrand et al. (2022)	374.64 M	1.46 B	116.14 M	1.95 B
Mammalia, Carnivoramorpha	*Prohesperocyon wilsoni*	30.04 3 kg	127.6 3 cm3 ECV	123.1 2 cm3	Bertrand et al. (2022)	520.17 M	1.96 B	150.65 M	2.63 B
Mammalia, Carnivoramorpha	*Dinictis felina*	16.14 0 kg	77.10 cm3 ECV	74.41 cm3	Bertrand et al. (2022)	362.16 M	1.41 B	113.06 M	1.89 B
Mammalia, Primata	*Adapis parisiensis*	1.870 kg	8.81 cm3 ECV	8.60 cm3	Bertrand et al. (2022)	76.75 M	352.21 M	33.05 M	462.01 M
Mammalia, Primata	*Microchoerus erinaceus*	0.493 kg	4.26 cm3 ECV	4.22 cm3	Bertrand et al. (2022)	46.00 M	222.68 M	5.33 M	290.71 M
Mammalia, Chiroptera	*Palaeophyllophora quercyi*	23.64 g	0.378 g with OB	0.35 cm3	Maugoust and Orliac (2021)	7.68 M	44.81 M	5.33 M	57.82 M
Mammalia, Chiroptera	*Palaeophyllophora oltina*	36.1 g	0.545 g with OB	0.51 cm3	Maugoust and Orliac (2021)	10.07 M	57.10 M	6.60 M	73.77 M

On disregarding body mass

I have made a point in this study to ignore body mass, even though it is obviously a relevant variable in terms of ecology, energy consumption and physiology. Part of the reason is that the original analysis of the same dataset already focused on relationships between brain mass and numbers of neurons to body mass (Kverkova et al., 2022), and established that birds and mammals evolved with increased numbers of brain neurons for their body mass compared to reptiles and ancestral species. Most importantly to this author, however, is the reiterated demonstration that there is no obligatory scaling relationship between body mass and number

of neurons in any brain structure, specially the rest of brain, which directly operates the body (Burish et al., 2010; Herculano-Houzel et al., 2015a,c; Ngwenya et al., 2016). In this case, then body mass cannot be used as a universal predictor of brain scaling, and its use as a normalizer is unwarranted and should be discontinued, for there is much more information to be gained in the direct analysis of variables pertaining to brain size and composition without contamination by the confounding factor that is body mass. Naturally, the finding that brain mass increases independently in birds and mammals for a same body size with the advent of endothermy is fundamental to the understanding of how endothermy is transformative; but increased body mass should only be treated as a cause or driver of diversity where mechanistically warranted, such as through the ingestion of more energy per unit time allowed by increased body mass (Fonseca-Azevedo and Herculano-Houzel, 2012; Herculano-Houzel, 2015). Importantly, I have recently showed that body mass is not a direct predictor of life history variables such as age at sexual maturity and maximal longevity across warm-blooded amniotes; numbers of pallial neurons are, and with a much higher r^2 of 0.74, compared to 0.44 for body mass (Herculano-Houzel, 2019). The finding that the pace of life slows down with increasing numbers of pallial neurons offers a new fundamental insight into the evolution of warm-blooded amniotes: namely, that larger numbers of pallial neurons in birds and mammals compensate for the shortening of lifespan that comes with endothermy (de Magalhães and Costa, 2009), however that happens. In this scenario, what lifespan the increased metabolic capacity of endotherms takes away, it provides back through the now affordable larger numbers of pallial neurons. It will be interesting to work out the mathematical (im)balance of this trade-off.

The end of the “reptilian brain”

The unequivocal continuity shown here between the cousin clades of mammals and reptiles in the relationship between numbers of neurons and structure mass of the telencephalon or cerebral cortex should put to rest any lingering remnants of the incorrect, unwarranted, yet still popular notion of a “triune brain” with a “mammalian neocortex” expanding over a “reptilian brain” in evolution (MacLean, 1990; Herculano-Houzel, 2016). The pallium, whether organized in visible or in cryptic layers (Stacho et al., 2020), and regardless of how much it proliferates and

expands over the rest of the brain, has the same developmental origin from the dorsal cap of the second neuromere in the neural tube across different amniotes (Puelles et al., 2013). Thus, reptiles do have a pallium, which forms as a major part of a telencephalon that I show to be composed according to the same neuronal scaling rules that are shared with mammals. Conversely, the neuronal composition of the supposed "reptilian" rest of brain is also shared between reptiles and mammals. In both cases, the main difference between mammals and reptiles seems to lie in how many neurons the developing body can afford in each brain structure. Whether the body has the increased oxidative capacity that also allows for endothermy seems to be a key factor in determining whether a modern amniote has fewer or more than 10 million neurons in its telencephalon, with all its consequences for cognitive capabilities, energetic economy, and pace of life, as I explore in the following chapter.

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