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Breakdown of brain-body allometry and the encephalization of birds and mammals

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Supplementary Information

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Supplementary Figure 1-3
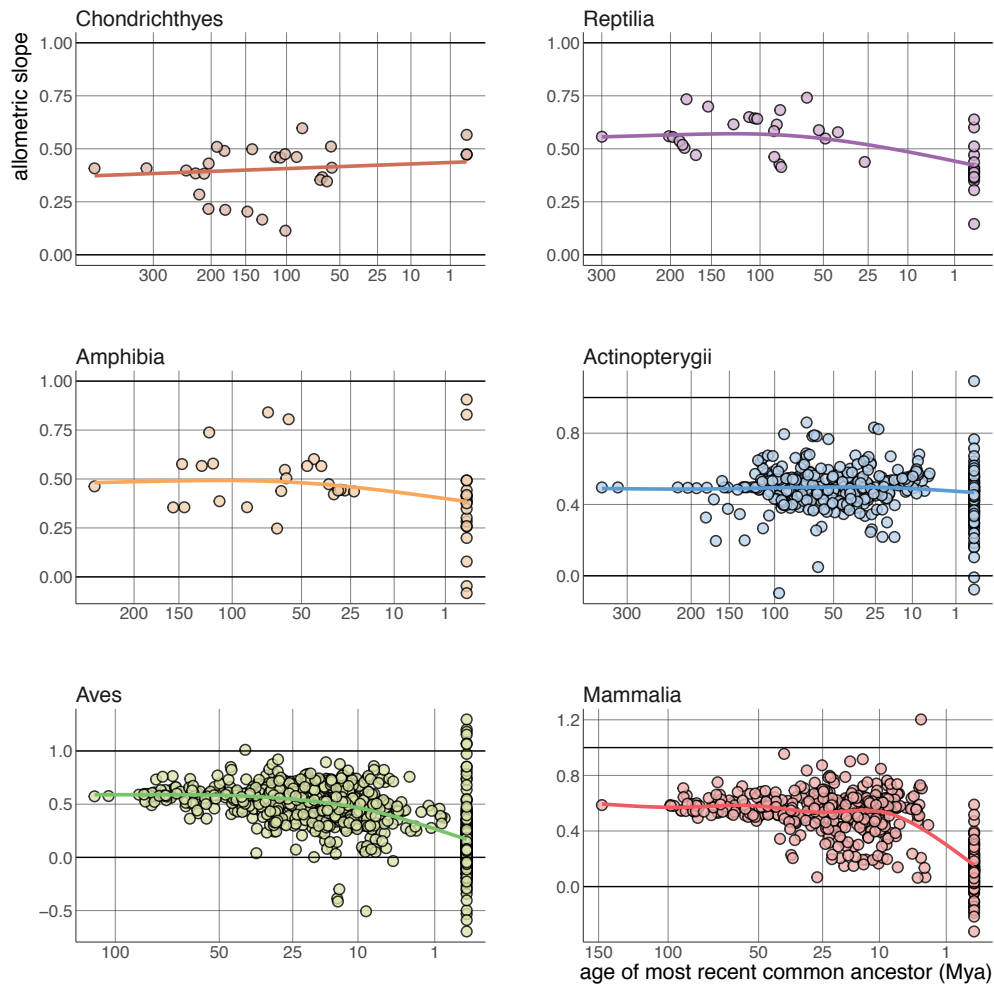
Supplementary Figure 1 I Brain-body allometry through time. Plots show evolutionary allometric slope estimated from phylogenetic generalized least squares at all nodes with ≥ 6 descendants plotted against the node age (Mya) for Chondrichthyes (brown), 'Reptilia' (e.g. non-avian reptiles, purple), Amphibia (orange), Actinopterygii (blue), Aves (green) and Mammalia (red). At present (right end of each panel), the plot shows within-species (static) allometric slopes estimated for species with ≥ 10 individual observations controlling for sex and method of brain size measurement (i.e. volume or mass). Trends for each class are represented by penalized thin-plate regression splines.
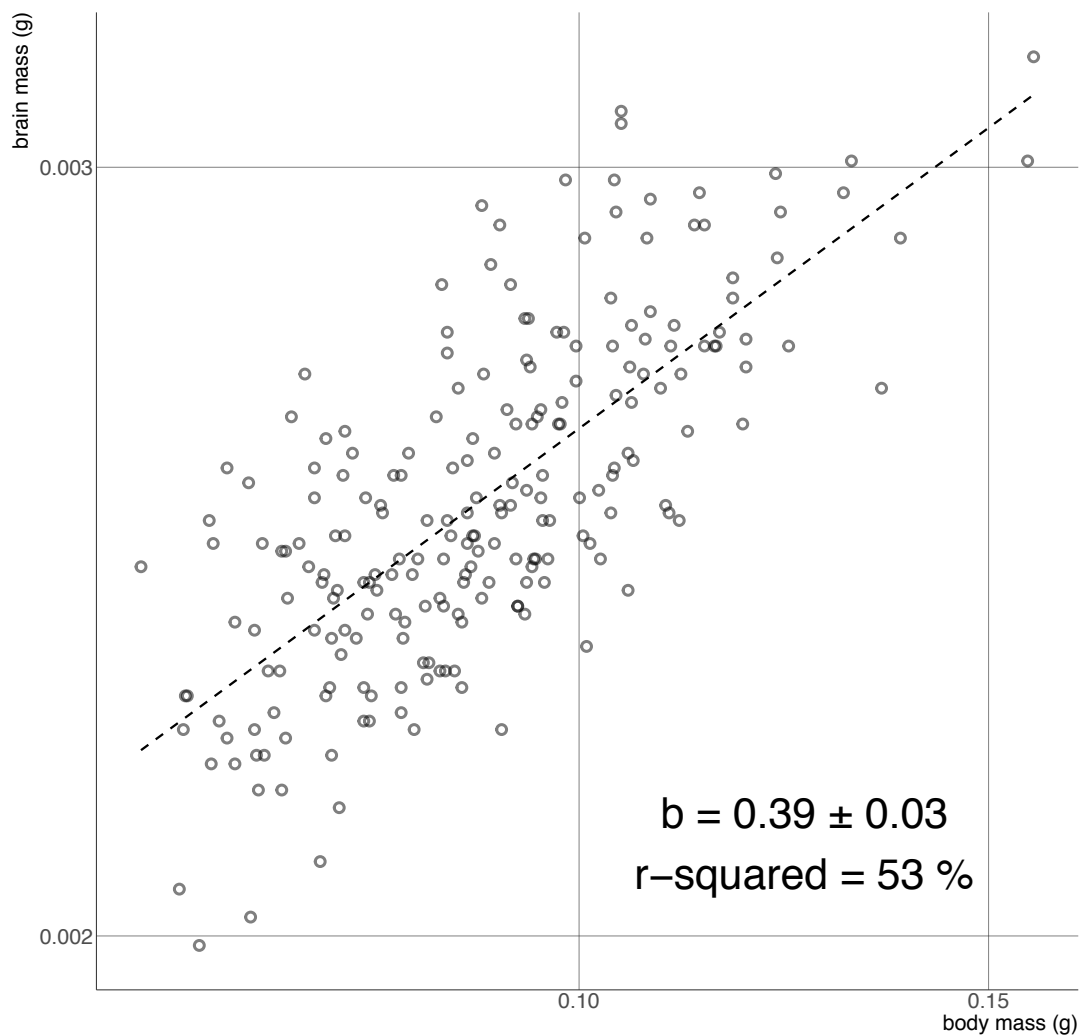
Supplementary Figure 2 | The strict-sense static allometry of male guppy *Poecilia reticulata*. Plot shows a relationship between $\log_{10}$ brain mass (g) against $\log_{10}$ body mass (g) of 218 adult male individuals. Animals were reared in the lab as described in (Kotrschal *et al.* 2013). This dataset only includes individuals of between 111 and 119 days old, thus representing the static allometry in a strict sense. The slope 0.39 ± 0.03 (slope ± standard error) is substantially steeper than the averages of the static slopes in mammals and birds (Supplementary Table 1). It indicates that the differences in static slopes among classes are not an artifact of the extended age and size range of species with indeterminate growth compared to determinate growth.
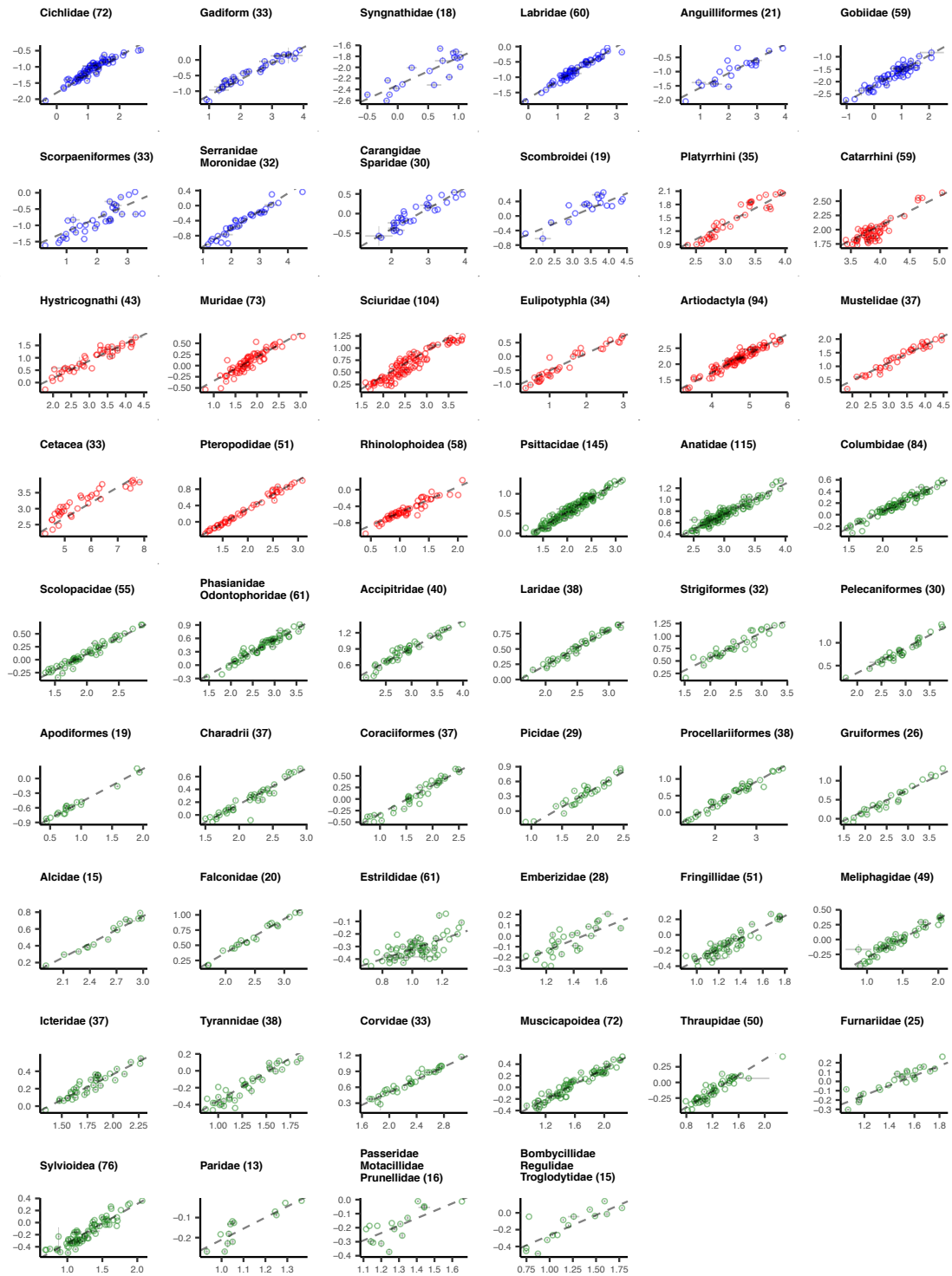
Supplementary Figure 3 I Brain-body allometry of 52 selected vertebrate clades. Plots show the relationship between $\log_{10}$ brain mass (g) and $\log_{10}$ body mass (g) of 52 vertebrate taxa. Numbers next to taxa names indicate sample size (number of species). Three classes are shown in different colors; Teleost: blue, Mammalia: red, Aves: green. Dashed lines are evolutionary allometry estimated by *SLOUCH* analyses (Supplementary Table 3). Error bars are standard errors of mean $\log_{10}$ body mass and $\log_{10}$ brain mass. Groups represented by multiple family names indicate that these families were treated as one group to allow estimating the evolutionary parameters while maximizing the number of included taxa in which within-species variance is available.

Supplementary Table 1-7

Supplementary Table 1 I Brain-body allometry at each taxonomic rank.

	Evolutionary allometry (slope ± s.e.)				Static allometry (slope ± s.e.)
	Class	Order	Family	Genus	Species
Mammalia	0.59 ± 0.01	0.58 ± 0.03 (13)	0.55 ± 0.03 (48)	0.51 ± 0.03 (34)	0.13 ± 0.01 (110)
Aves	0.57 ± 0.01	0.57 ± 0.02 (22)	0.56 ± 0.01 (67)	0.42 ± 0.04 (40)	0.14 ± 0.02 (213)
Actinopterygii	0.50 ± 0.01	0.51 ± 0.03 (13)	0.49 ± 0.02 (29)	0.50 ± 0.03 (18)	0.44 ± 0.02 (90)
Amphibia	0.46 ± 0.03	0.49 ± 0.09 (2)	0.52 ± 0.11 (4)	0.51 (1)	0.36 ± 0.05 (20)
Non-avian Reptilia	0.56 ± 0.02	0.56 (1)	0.62 ± 0.03 (4)	0.57 (1)	0.41 ± 0.03 (16)
Chondrichthyes	0.41 ± 0.02	0.31 ± 0.04 (4)	0.45 ± 0.15 (2)	0.43 (1)	0.50 ± 0.03 (3)

Table shows average allometric slopes at each taxonomic level (i.e. Class, Order, Family, Genus, Species) for six vertebrate clades. The across-species (evolutionary) allometric slopes were estimated with generalized least squares with residual variance modeled as Brownian motion with phylogenetic heritability (λ, Lynch 1991). Numbers in parenthesis represent the number of clade at each taxonomic scale with ≥ 6 species. The within-species (static) allometric slopes were estimated with ordinary least squares controlling for sex and methods for brain size measurement (i.e. either volume or mass), and numbers in parenthesis represent the number of species with ≥ 10 individuals. Note that standard error of allometric slope represents the estimated standard errors (s.e.) from the generalized least squares at the Class level, whereas the rest indicates the s.e. across all slopes estimated at the respective taxonomic level.

Supplementary Table 2 | Summary of bias in allometric slope due to measurement error

	Reliability ratio (k ± s.e.)				Error variance (CV ± s.e.)
	Class	Order	Family	Genus	Species
Mammalia	0.998	0.994 ± 0.001 (5)	0.958 ± 0.019 (15)	0.827 ± 0.049 (9)	46.5 ± 4.6 (70)
Aves	0.997	0.992 ± 0.001 (17)	0.981 ± 0.003 (44)	0.938 ± 0.012 (25)	37.2 ± 3.3 (143)
Actinopterygii	0.973	0.967 ± 0.008 (6)	0.940 ± 0.013 (14)	0.852 ± 0.053 (4)	28.1 ± 2.8 (62)
Amphibia	0.991	0.989 ± 0.004 (2)	0.986 ± 0.004 (4)	0.984 (1)	20.9 ± 5.7 (13)
Non-avian Reptilia	0.998	0.997 (1)	0.994 (1)	-	17.6 ± 4.6 (4)
Chondrichthyes	0.941	0.945 (1)	-	-	-

Table shows the reliability ratio (Hansen and Bartoszek 2012), k, averaged over all taxonomic units at each taxonomic rank for evolutionary allometries and the amount of error variance in body size that is necessary to generate observed static allometric slope when true slope equals the evolutionary allometric slope at the selected group level (Supplementary Table 3) for static allometries. Error variance is expressed as the coefficient of variation (CV, %). Numbers in parenthesis represent the number of clades or species examined at each taxonomic scale.

Supplementary Table 3 | Summary of OU model parameters estimated by *SLOUCH* analyses

Group (*N*)	Root age (mya)	Phylogenetic half-life (support region)	Stationary variance (support region)	Evolutionary allometry (slope ± s.e.)	r^2 (%)
Teleostei					
Cichlidae (72)	71.4	1.598 (0.245 - ∞)	0.037 (0.008 - 0.069)	0.564 ± 0.022	90.3
Gadiformes (33)	70.0	∞ (0.408 - ∞)	0.073 (0.008 - 0.167)	0.512 ± 0.027	93.7
Syngnathidae (18)	96.9	0.025 (0.000 - 0.384)	0.024 (0.012 - 0.051)	0.502 ± 0.075	70.7
Labridae (60)	82.8	0.008 (0.000 - 0.050)	0.005 (0.003 - 0.009)	0.563 ± 0.018	94.7
Anguilliformes (21)	101.8	0.000 (0.000 - 0.051)	0.048 (0.024 - 0.102)	0.512 ± 0.060	75.0
Gobiidae (59)	75.6	0.270 (0.000 - ∞)	0.018 (0.011 - 0.039)	0.617 ± 0.032	85.4
Scorpaeniformes (33)	120.0	0.917 (0.204 - ∞)	0.064 (0.031 - 0.918)	0.411 ± 0.040	76.0
Serranidae & Moronidae (32)	106.5	0.094 (0.000 - ∞)	0.009 (0.004 - 0.032)	0.471 ± 0.026	91.0
Carangidae & Sparidae (30)	115.2	9.796 (0.204 - ∞)	0.043 (0.004 - 0.193)	0.524 ± 0.036	87.6
Scombroidei (19)	116.4	0.400 (0.204 - ∞)	0.024 (0.020 - 0.653)	0.415 ± 0.054	74.6
Mammalia					
Platyrrhini (35)	23.2	10.00 (0.612 - ∞)	0.102 (0.012 - 0.180)	0.701 ± 0.068	74.4
Catarrhini (59)	34.4	0.748 (0.408 - ∞)	0.010 (0.006 - 0.153)	0.516 ± 0.044	69.4
Hystricognathi (43)	45.8	0.000 (0.000 - ∞)	0.025 (0.016 - 0.043)	0.703 ± 0.039	89.2
Muridae (73)	48.1	0.94 (0.408 - ∞)	0.014 (0.008 - 0.155)	0.537 ± 0.030	80.2
Sciuridae (104)	41.5	0.197 (0.122 - 0.384)	0.008 (0.006 - 0.013)	0.523 ± 0.025	80.9
Cricetidae (58)	48.1	0.727 (0.200 - ∞)	0.010 (0.005 - 0.019)	0.524 ± 0.028	85.4
Eulipotyphla (34)	82.5	9.592 (0.612 - ∞)	0.147 (0.016 - 0.294)	0.623 ± 0.040	87.2
Artiodactyla (94)	70.7	0.621 (0.253 - ∞)	0.015 (0.008 - 0.243)	0.607 ± 0.020	90.6
Mustelidae (37)	24.1	0.722 (0.204 - ∞)	0.015 (0.010 - 0.214)	0.650 ± 0.036	89.7
Cetacea (33)	52.2	∞ (0.894 - ∞)	0.180 (0.024 - 0.310)	0.480 ± 0.027	90.7
Pteropodidae (51)	25.1	0.053 (0.000 - 0.226)	0.002 (0.001 - 0.003)	0.702 ± 0.013	98.4
Rhinolophoidea (58)	61.8	10.00 (0.816 - ∞)	0.045 (0.006 - 0.076)	0.618 ± 0.028	90.5
Aves					
Psittacidae (145)	45.7	0.021 (0.000 - 0.163)	0.005 (0.004 - 0.007)	0.728 ± 0.016	93.6
Anatidae (115)	32.1	0.014 (0.010 - 0.051)	0.003 (0.002 - 0.004)	0.530 ± 0.016	89.8
Columbidae (84)	36.3	0.172 (0.000 - 0.531)	0.002 (0.002 - 0.004)	0.566 ± 0.020	90.8
Estrildidae (61)	14.1	0.124 (0.000 - 0.633)	0.004 (0.003 - 0.007)	0.394 ± 0.057	40.6
Emberizidae (28)	15.2	∞ (0.612 - ∞)	0.041 (0.006 - 0.073)	0.514 ± 0.075	61.1
Scolopacidae (55)	38.1	2.309 (0.324 - ∞)	0.009 (0.003 - 0.054)	0.622 ± 0.028	89.8
Phasianidae & Odontophoridae (61)	30.7	0.171 (0.000 - 1.071)	0.004 (0.002 - 0.008)	0.516 ± 0.019	91.2
Fringillidae (51)	27.4	0.087 (0.000 - 0.265)	0.004 (0.002 - 0.006)	0.708 ± 0.045	82.4
Meliphagidae (49)	30.5	0.000 (0.000 - 0.337)	0.003 (0.002 - 0.005)	0.658 ± 0.028	91.6
Laridae (38)	17.3	0.063 (0.000 - 0.269)	0.001 (0.001 - 0.003)	0.575 ± 0.023	94.1
Icteridae (37)	14.3	0.431 (0.000 - ∞)	0.003 (0.002 - 0.008)	0.587 ± 0.039	85.7
Accipitridae (40)	56.0	0.135 (0.036 - 0.343)	0.004 (0.002 - 0.007)	0.514 ± 0.025	91.4
Tyrannidae (38)	33.2	0.571 (0.000 - ∞)	0.006 (0.003 - 0.014)	0.670 ± 0.054	79.7
Corvidae (33)	26.4	2.245 (0.204 - ∞)	0.008 (0.002 - 0.030)	0.600 ± 0.041	86.9
Muscicapoidea (72)	29.0	0.000 (0.000 - 0.008)	0.004 (0.003 - 0.006)	0.662 ± 0.023	91.9
Strigiformes (32)	77.6	0.041 (0.000 - 0.220)	0.008 (0.005 - 0.014)	0.505 ± 0.034	87.2
Pelecaniformes (30)	70.8	0.596 (0.082 - ∞)	0.004 (0.002 - 0.011)	0.551 ± 0.031	91.4
Apodiformes (19)	62.2	0.313 (0.000 - ∞)	0.002 (0.001 - 0.008)	0.677 ± 0.029	96.5
Charadrii (37)	44.0	0.232 (0.061 - ∞)	0.002 (0.001 - 0.006)	0.561 ± 0.026	92.7
Coraciiformes (37)	82.8	0.213 (0.082 - 0.980)	0.006 (0.004 - 0.018)	0.614 ± 0.030	91.9
Picidae (29)	28.0	∞ (0.498 - ∞)	0.069 (0.008 - 0.127)	0.715 ± 0.048	88.7
Thraupidae (50)	15.0	0.126 (0.000 - 1.071)	0.004 (0.003 - 0.009)	0.637 ± 0.033	83.9
Furnariidae (25)	20.7	9.796 (0.000 - ∞)	0.024 (0.002 - 0.048)	0.527 ± 0.042	87.0
Procellariiformes (38)	62.7	0.000 (0.000 - 0.224)	0.007 (0.005 - 0.012)	0.681 ± 0.022	96.0
Gruiformes (26)	51.4	1.071 (0.127 - ∞)	0.011 (0.005 - 0.149)	0.536 ± 0.033	90.9
Alcidae (15)	14.8	∞ (0.204 - ∞)	0.008 (0.001 - 0.021)	0.545 ± 0.027	96.5
Falconidae (20)	43.3	0.115 (0 - 2.939)	0.001 (0.001 - 0.010)	0.557 ± 0.022	97.0
Sylvioidea (76)	54.1	0.411 (0.200 - ∞)	0.006 (0.004 - 0.015)	0.647 ± 0.036	82.7
Paridae (13)	18.9	1.192 (0.200 - ∞)	0.002 (0.001 - 0.030)	0.553 ± 0.080	78.7
Passeridae & Motacillidae & Prunellidae(16)	35.7	0.289 (0.200 - ∞)	0.004 (0.002 - 0.017)	0.527 ± 0.089	67.4
Bombycillidae & Regulidae & Troglodytidae (15)	43.4	0.254 (0.200 - ∞)	0.012 (0.006 - 0.046)	0.479 ± 0.093	64.1

Table shows the phylogenetic half-life (ln2/α) in units of tree length scaled to the total height of one, the stationary variance (σ²/2α) in units of (log$_{10}$ brain mass (g))^2, evolutionary allometric slope and r^2 of each group estimated by *SLOUCH* analyses where OU model was fitted to the residual variance of a linear model: log$_{10}$ brain mass (g) ~ log$_{10}$ body mass (g). Support regions shown in parenthesis represents the range of parameter within 2 maximum-likelihood (ML) units from the ML estimates. All parameters are accounted for by measurement errors in both brain and body mass. Root age (mya) of each groups are also shown. Groups represented by multiple family names indicate that these families were treated as one group to allow for the estimation of the evolutionary parameters, while maximizing the number of included taxa in which within-species variance is available.

Supplementary Table 4 | Results of *SLOUCH* analyses relating within- and among-species variance in relative brain size

Predictor variables	N	Intercept±s.e.	Slope±s.e. Root age	C_{brain}	r^2 (%)	AICc
(Mammalia)			Root age	C_{brain}		
Root age	9	0.100±0.027	0.0006±0.0005	-	17.7	-19.2
C_{brain}	**9**	**0.082±0.023**		**7.23±3.43**	**42.9**	**-21.2**
C_{brain} + Root age	9	0.013±0.021	0.0009±0.0003	11.08±2.03	86.8	-16.3
			Root age	Δ_{slope}		
Root age	**12**	**0.073±0.031**	**0.0008±0.0006**	**-**	**15.7**	**-31.0**
Δ_{slope}	12	0.083±0.047		0.059±0.096	4.0	-29.8
Δ_{slope} + Root age	12	0.039±0.005	0.0008±0.0006	0.069±0.082	20.4	-25.2
(Aves)			Root age	C_{brain}		
Root age	31	0.050±0.006	0.0003±0.0001	-	15.3	-160.5
C_{brain}	31	0.045±0.004		2.97±0.49	20.8	-162.6
***C_{brain}* + Root age**	**31**	**0.029±0.006**	**0.0004±0.0001**	**3.23±0.43**	**39.4**	**-168.3**
			Root age	Δ_{slope}		
Δ_{slope}	31	0.079±0.005	-	-0.033±0.005	0.3	-155.2
Δ_{slope} + Root age	31	0.080±0.006	0.0003±0.0001	-0.061±0.007	16.4	-158.3
(Teleostei)			Root age	C_{brain}		
Root age	**10**	**0.131±0.081**	**-0.0001±0.0009**	**-**	**0.2**	**-12.6**
C_{brain}	10	0.113±0.042		0.68±4.25	0.3	-12.6
C_{brain} + Root age	10	0.120±0.107	-0.0001±0.001	0.79±3.10	0.3	-3.6
			Root age	Δ_{slope}		
Δ_{slope}	**10**	**0.065±0.013**	**-**	**0.430±0.104**	**66.4**	**-23.1**
Δ_{slope} + Root age	10	0.041±0.048	0.00003±0.0005	0.719±0.068	67.6	-14.5

Table shows the complete results testing the relationship between $\sqrt{V_{st}}$ and predictor variables (C_{brain}, Δ_{slope}, and root age). Sample size (number of groups included in each model), intercept, r^2, sample size-corrected Akaike Information Criterion (AICc) and estimated slopes are presented. Estimated evolutionary parameters are accounted for by standard errors in C_{brain} and Δ_{slope}, and by the approximate 95% confidence intervals in $\sqrt{V_{st}}$ (see Methods for detail). The best models within each nested models, based on AICc, are shown in bold font. Phylogenetic half-lives were set to zero in these analyses, meaning that these results shown here are without controlling for phylogenetic relatedness among compared clades. See Supplementary Table 7 for results where phylogenetic relatedness was accounted for.

Supplementary Table 5 | Phylogenetic mean and variance of conditional variance and Δslope

Trait	Class (N)	Root (mya)	Phylogenetic half-life (support region)	Stationary variance (support region)	Mean ± s.e.	Tip variance (100 myr^{-1})
Conditional variance	Mammalia (66)	96.1	0.000 (0.000 - 0.025)	0.111 (0.080 - 0.161)	0.595 ± 0.041	0.115
	Aves (214)	103.8	0.170 (0.112 - 0.261)	0.424 (0.349 - 0.545)	0.563 ± 0.075	0.408
	Teleostei (84)	219.3	0.014 (0.000 - 0.033)	0.501 (0.372 - 0.687)	0.924 ± 0.083	0.229
Static slope	Mammalia (78)	96.1	0.353 (0.061 - ∞)	0.0073 (0.0039 - ∞)	0.145 ± 0.021	0.0076
	Aves (214)	103.8	0.002 (0.000 - 0.018)	0.0218 (0.0154 - 0.0311)	0.117 ± 0.013	0.0211
	Teleostei (84)	219.3	0.033 (0.000 - 0.173)	0.0079 (0.0048 - 0.0139)	0.449 ± 0.014	0.0036
ΔSlope	Mammalia (78)	96.1	1.212 (0.303 - ∞)	0.0191 (0.007 - ∞)	0.440 ± 0.035	0.0199
	Aves (207)	103.8	0.001 (0.000 - 0.018)	0.0231 (0.0162 - 0.0327)	0.464 ± 0.014	0.0222
	Teleostei (74)	204.9	0.073 (0.021 - 0.273)	0.0107 (0.0064 - 0.0190)	0.061 ± 0.018	0.0052

Table shows the result of *SLOUCH* analyses fitted to three components of within-species variances in brain size shown in the first column. The phylogenetic half-life ($\ln 2/\alpha$) in units of tree length scaled to the total height of one, the stationary variance ($\sigma^2/2\alpha$) in units of (trait unit)^2, and the phylogenetic mean (i.e. adaptive peak θ in single-optimum OU model) are presented. Support regions shown in parenthesis represents the range of each parameter within 2 maximum-likelihood (ML) units from the ML estimates. Estimated evolutionary parameters for static slopes and Δslope are accounted for by standard errors in estimated allometric slopes. Tip variances are calculated as: [stationary variance × (1 - e$^{-\alpha 2t}$)] and scaled to 100 millions of years according to the root age (mya) of each group.

Supplementary Table 6 | Summary of ontogenetic allometric trajectories

Taxa	Common name	Slope at RGP ± s.e.	Slope at SGP ± s.e.	Body mass at breakpoint ± s.e.
Teleostei				
Cyprinus carpio	Common carp	0.831 ± 0.023	0.448 ± 0.001	0.473 ± 0.063
Pagrus major	Red seabream	1.018 ± 0.081	0.553 ± 0.012	-1.409 ± 0.130
Mammalia				
Bos taurus	Cow	0.706 ± 0.012	0.255 ± 0.014	4.303 ± 0.055
Homo sapiens	Human	0.937 ± 0.004	0.104 ± 0.017	3.959 ± 0.015
Macropus giganteus	Eastern grey kangaroo	0.869 ± 0.014	0.234 ± 0.013	2.980 ± 0.033
Oryctolagus cuniculus	European rabbit	0.708 ± 0.024	0.265 ± 0.032	2.545 ± 0.083
Stenella coeruleoalba	Striped dolphin	1.150 ± 0.024	0.198 ± 0.035	4.088 ± 0.039
Aves				
Gallus gallus	Chicken	0.888 ± 0.031	0.378 ± 0.013	1.145 ± 0.052

Table shows the ontogenetic allometric exponent of the relationship between $\log_{10}$ brain mass against $\log_{10}$ body mass at the rapid growth phase (RGP), slow growth phase (SGP) and body mass in $\log_{10}$ at the breakpoint between RGP and SGP.

Supplementary Table 7 | Results of *SLOUCH* analyses relating within- and among-species variance in relative brain size accounting for phylogeny

Predictor variables	Phylogenetic half-life (Support Region)	Intercept±s.e.	Slope±s.e.		r^2 (%)	AICc
(Mammalia)			Root age	C_{brain}		
Root age	0 (0 - ∞)	0.100±0.026	0.0006±0.0005	-	18.7	-18.7
C_{brain}	**17.55 (0 - ∞)**	**0.082±0.023**	**-**	**7.52±3.44**	**45.1**	**-20.7**
C_{brain} + Root age	∞ (0 - ∞)	0.015±0.023	0.0009±0.0003	11.00±2.02	83.2	-15.0
			Root age	Δ_{slope}		
Root age	**4.38 (0.82 - ∞)**	**0.074±0.032**	**0.0009±0.0006**	**-**	**18.6**	**-25.3**
Δ_{slope}	0.30 (0 - ∞)	0.082±0.059	-	0.061±0.116	3.3	-24.1
Δ_{slope} + Root age	4.80 (0.92 - ∞)	0.039±0.057	0.0009±0.0006	0.066±0.094	22.1	-18.3
(Aves)			Root age	C_{brain}		
Root age	0.97 (0 - ∞)	0.047±0.008	0.0004±0.0002	-	13.8	-161.4
C_{brain}	9.79 (0.2 - ∞)	0.045±0.006	-	3.43±0.43	27.4	-166.9
C_{brain} + Root age	**9.18 (0 - ∞)**	**0.034±0.008**	**0.0003±0.0001**	**3.12±0.40**	**35.8**	**-168.2**
			Root age	Δ_{slope}		
Δ_{slope}	2.34 (0 - ∞)	0.083±0.007	-	-0.050±0.005	0.5	-156.6
Δ_{slope} + Root age	2.14 (0 - ∞)	0.085±0.009	0.0004±0.0002	-0.080±0.004	15.2	-159.2
(Teleostei)			Root age	C_{brain}		
Root age	**0.15 (0 - ∞)**	**0.155±0.088**	**-0.0003±0.001**	**-**	**1.3**	**-11.6**
C_{brain}	0.16 (0 - ∞)	0.125±0.050	-	-0.0003±4.67	0.0	-11.4
C_{brain} + Root age	0.16 (0 - ∞)	0.170±0.125	-0.0004±0.001	-1.30±3.36	1.65	-2.6
			Root age	Δ_{slope}		
Δ_{slope}	**0.021 (0 - ∞)**	**0.067±0.016**	**-**	**0.464±0.123**	**62.8**	**-20.6**
Δ_{slope} + Root age	0.020 (0 - ∞)	0.056±0.060	-0.0001±0.0006	0.756±0.084	63.5	-11.7

Table shows the complete results testing the relationship between $\sqrt{V_{st}}$ and predictor variables (C_{brain}, Δ_{slope}, and root age). The phylogenetic half-life (ln2/α) in units of tree length scaled to the total height of one, intercept, r^2, sample size-corrected Akaike Information Criterion (AICc) and estimated slopes are presented. Support regions shown in parenthesis represents the range of half-life within 2 maximum-likelihood (ML) units from the ML estimates. Estimated evolutionary parameters are accounted for by standard errors in C_{brain} and Δ_{slope}, and by the approximate 95% confidence intervals in $\sqrt{V_{st}}$ (see Methods for detail). The best models within each nested models, based on AICc, are shown in bold font. Phylogenetic half-lives were estimated in these analyses (i.e. phylogenetic relatedness among clades are accounted for).