Encephalization is not a universal macroevolutionary phenomenon in mammals but is associated with sociality

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Evolutionary encephalization, or increasing brain size relative to body size, is assumed to be a general phenomenon in mammals. However, despite extensive evidence for variation in both absolute and relative brain size in extant species, there have been no explicit tests of patterns of brain size change over evolutionary time. Instead, allometric relationships between brain size and body size have been used as a proxy for evolutionary change, despite the validity of this approach being widely questioned. Here we relate brain size to appearance time for 511 fossil and extant mammalian species to test for temporal changes in relative brain size over time. We show that there is wide variation across groups in encephalization slopes across groups and that encephalization is not universal in mammals. We also find that temporal changes in brain size are not associated with allometric relationships between brain and body size. Furthermore, encephalization trends are associated with sociality in extant species. These findings test a major underlying assumption about the pattern and process of mammalian brain evolution and highlight the role sociality may play in driving the evolution of large brains.

carnivores | cetaceans | primates | social brain

A primary motivation for understanding evolutionary changes in brain size, or encephalization, is to understand what evolutionary pressures have led to the large brain and complex cognition of humans. Across vertebrates, variation in total and relative brain size across mammals is marked (1), and is assumed to have a functional basis, because brains are metabolically costly (2, 3). As species should be expected to maximize the cost-benefit ratio of supporting costly tissues, encephalization should be associated with significant advantages. A large and expanding literature has identified associations between relative brain size among extant species and ecological and behavioral correlates, including social characteristics (4, 5), ecological flexibility (6), resilience (7, 8), innovation (9, 10), and social learning (11).

Although there have been extensive efforts to document associations between brain size and ecology or behavior in extant taxa, the important issue of how and why taxonomic groups vary in the extent to which they have become encephalized over time has been overlooked. This arises in part because evaluating cross-taxonomic signals for encephalization is notoriously contentious. Across vertebrates, brain and body size are tightly coupled allometrically. The conventional method of estimating brain size relative to body size is to use deviations from a predicted allometry using residuals or an encephalization quotient (1). However, the practice of comparing scaling across distantly related species using encephalization quotients or residuals is, as Deacon (12) pointed out, unlikely to illuminate functional cognitive differences. This is because it can be difficult to disentangle selection for brain size from ecological pressures impacting on body morphology, which are subject to constraints imposed by locomotor adaptations, feeding ecology, and habitat use.

An alternative way of evaluating evolutionary signals in brain size increase is to consider the slope of the allometric relationship between brain size and body size within a taxon (13, 14).

Finarelli and Flynn (15) use this approach to evaluate encephalization in carnivores and demonstrate that there are taxonomic differences in allometric slopes. However, there are several caveats to interpreting these slopes as evidence for evolutionary processes. First, it has long been known that estimating the slope from simple bivariate plots is problematic because it is influenced both by species composition and the method of analysis (16, 17). Second, Finarelli and Flynn assume that grade shifts (where either the slope or the intercept changes between taxonomic groups) represent ontogenetic changes in brain/ body allometries, which in turn reflect changes in selective pressure on brain size. However, differences in slope may also be statistical artifacts: at low taxonomic levels, slopes tend to be low, but at higher levels the slope increases (18). In other words, Finarelli and Flynn's model is not specifically evolutionary; rather, it describes variation in allometric relationships that may or may not indicate evolutionary transitions. Additionally, as with residuals, comparing allometric slopes across divergent groups may tell us little about either evolutionary patterns or relative cognitive abilities.

A more appropriate way to address patterns and processes in brain evolution across groups may be to examine macroevolutionary trends in brain size within related groups. Jerison (1) argued that encephalization over macroevolutionary time is a general pattern among amniotes. Although this paradigm is widely accepted (15), his original descriptive analyses do not so much indicate directional selection as increasing variance in brain size over time. With the increase in variance, it is difficult to separate evolutionary models of directional selection from one of drift or random walk. Additionally, Jerison compared a standardized measure of encephalization across groups, which is necessarily vulnerable to the body size issues noted above.

Here we propose a quantitative macroevolutionary approach by explicitly evaluating encephalization trends within taxa over evolutionary time. Instead of relying on allometric relationships, we specifically evaluate temporal changes in relative brain size within groups. We then address several crucial questions: (*i*) Is encephalization a general trend across mammals? (*ii*) Do some taxa show stronger signals of encephalization than others? and (*iii*) Can we identify traits in extant species associated with strong encephalization signals in their taxon? We collated data on estimated and measured brain size and body size for 511 extant and fossil species of mammals, representing six orders (including the polyphyletic Insectivores; Table S1). We limited our analyses to taxa where both fossil and extant species were available. We then evaluated temporal signatures in relative brain size changes based

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on date of first appearance estimated from fossil evidence and molecular genetic estimates of genus time of first appearance.

Results

To estimate the temporal trend in brain size changes, we used phylogenetic least squares analyses (PGLS), with log brain size as the dependent variable and log body size and first appearance time (million years before present, Mya) as independent variables. The slope, or coefficient associated with first appearance time, is used as the encephalization slope for the taxon (Table 1). For example, a negative slope indicates a reduction in relative brain size over time, a positive slope indicates an increase in brain size, and a slope not significantly different from zero indicates no temporal trend.

We also calculated encephalization slopes using nonphylogentically controlled general linear models (GLMs). Our GLM and PGLS slopes were highly correlated at the order ($R = 0.83$, $P = 0.04$) and suborder level ($R = 0.89$, $P = 0.001$; Table S1). Finally, we calculated relative brain size using PGLS and regressed the resulting residuals against first appearance time as another estimate the encephalization slope (Table S1). Encephalization slopes calculated using total brain size corrected for body size (PGLS) also were highly correlated with the encephalization slopes calculated with residual brain size (order: $R = 0.94$, $P = 0.02$; suborder $R = 0.82$, $P = 0.004$).

Over all taxa, there was a significant trend toward increasing brain size over time ($F_{1, 508} = 71.62$, $P < 0.001$). However, at the order level, there is more variation in the encephalization trend (Table 1): Primates, Cetaceans, Perissodactyls, and Carnivores all had significant encephalization slopes, whereas Insectivores and Artiodactyls did not. As we move to down the taxonomic scale to suborders, the variation in encephalization slope becomes even more pronounced. Anthropoids, Strepsirrhines, Odontoceti, Hippomorpha, Tylopoda, and Caniformes all have significant encephalization slopes, whereas Feliformes, Ceratomorpha, and Ruminanta do not. At the order level, Cetaceans, Primates, and Perissodactyls had higher encephalization slopes than Carnivores and Insectivores (Fig. 1A and Table S2). Primates also had a higher slope than Artiodactyla. At the suborder level, Anthropoids, Tylopoda, Strepshirines, and Hippomorpha had higher slopes than Feliformes (Fig. 1B and Table S3).

To assess whether temporal trends track changes in allometric relationships (sensu 15), we then calculated taxon brain:body allometries using both ordinary least squares (OLS) and type II
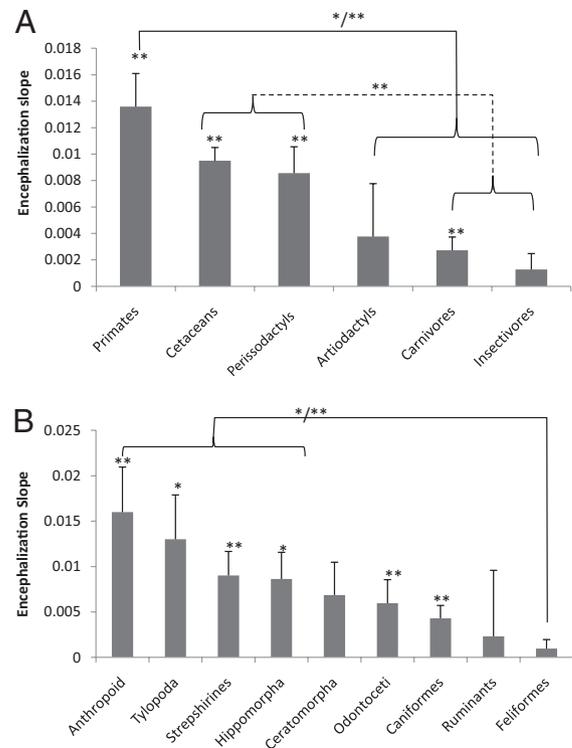
Fig. 1. Encephalization slopes calculated with optimized lambda PGLS analyses across mammalian (A) orders and (B) suborders. **$P < 0.01$, *$P < 0.05$. Overlain brackets and lines indicate significant pairwise differences in the slope coefficients.

major axis (MA) (19) regressions. We compared the allometries with our estimated encephalization slopes. Neither of the temporal slope estimates were correlated with either the MA or OLS allometric relationships (Table 2). This indicates that the within-taxon allometric relationships do not measure macroevolutionary trends in brain size.

Finally, we examine the influence of the composition of fossil vs. extant species on the estimated encephalization slope. If poor fossil representation leads to either an over- or underestimation of slope, then we would expect a relationship between the percentage

Table 1. Encephalization slopes over time within suborders

Order	Suborder	No. fossils (%)	df	PGLS slope (SE)	Lambda	F	P	Species-stable groups, %	Species social, %
Insectivores		4 (12.1)	1, 32			0.84	**0.37**	0.18	0.25
Primates		20 (32.3)	1, 59	0.0136 (0.0025)	0.07	77.59	**0.001**	0.74	0.81
	Anthropoid	6 (19.4)	1, 28	0.0160 (0.0049)	0.99	59.94	**<0.001**	1.0	1.0
	Strepsirrhine	9 (34.6)	1, 23	0.0090 (0.0026)	0	10.326	**0.004**	0.35	0.53
Perissodactyla		14 (58.3)	1, 21	0.0086 (0.0020)	0	16.83	**<0.001**	0.50	0.70
	Hippomorpha	7 (58.3)	1, 9	0.0086 (0.0029)	0	6.407	**0.032**	0.80	1.0
	Ceratomorpha	7 (58.3)	1, 8	0.0069 (0.0036)	0	2.628	0.144	0.20	0.40
Cetaceans		25 (43.9)	1, 55	0.0095 (0.0010)	0.48	14.97	**<0.001**	0.69	0.87
	Odontoceti	20 (38.5)	1, 24	0.0060 (0.0026)	0.32	4.98	**<0.03**	0.69	0.87
Artiodactyla		20 (44.4)	1, 42	0.0038 (0.0040)	0.84	1.06	0.31	0.32	0.72
	Ruminanta	8 (33.3)	1, 21	0.0023 (0.0073)	0.91	0.088	0.769	0.06	0.63
	Tylopoda	11 (78.6)	1, 11	0.0130 (0.0048)	0	5.586	**0.038**	1.0	1.0
Carnivores		129 (44.5)	1, 287	0.0027 (0.0010)	0.76	7.03	**0.008**	0.25	0.42
	Caniformes	87 (48.7)	1, 178	0.0043 (0.0014)	0.69	9.088	**0.003**	0.35	0.54
	Feliformes	42 (38.5)	1, 106	0.0010 (0.0010)	0.10	0.785	0.378	0.11	0.24

F values are associated with the PGLS.lam analyses, except for insectivores, where *t* values associated with nonphylogenetic GLM analyses are presented. Boldface indicates significant encephalization slopes.

Table 2. Pearson's correlations between encephalization slopes (PGLS and GLM) and within taxon brain-body allometries

	PGLS slope	MA allometry	OLS allometry
Order (n = 6)			
PGLS slope		−0.32 (0.54)	−0.49 (0.32)
GLM	0.83 (0.04)	−0.67 (0.14)	−0.79 (0.06)
Suborder (n = 10)			
PGLS slope		0.34 (0.33)	0.38 (0.28)
GLM	0.89 (0.001)	0.49 (0.15)	0.49 (0.16)

P values are in parentheses.

of the sample composed of fossils and the estimated slope. There was no relationship between the percentage of fossil species in the samples (Table 1) and the calculated encephalization slopes (order, $R = 0.29$, $P = 0.56$; suborder $R = 0.09$, $P = 0.82$). Another possible confound is that poor fossil representation may result in poor confidence in the slope (high variance). However, there was no relationship between the SE of the slope and the percent of fossil species (order $R = 0.20$, $P = 0.70$; suborder $R = −0.04$, $P = 0.90$). As a second independent check of the influence fossil species have on the estimated slopes, we evaluated the encephalization slope based only on first appearance times for extant genera with the encephalization slope for the entire dataset (i.e., excluding all fossil specimens). At the order level, the slopes were highly correlated ($R = 0.92$, $P = 0.02$, $n = 6$). Thus, we argue that although fossil species provide extra anchors to the dataset, the estimated slopes are not dependent upon them.

We then tested support for the social brain hypothesis by evaluating the relationship between encephalization slopes and the proportion of social taxa at both the order and suborder level. Encephalization slopes were correlated with both the proportion of species with stable groups (order $R = 0.92$, $P = 0.005$, $n = 6$; suborder $R = 0.767$, $P = 0.008$, $n = 9$; Fig. 2 A and B) and the proportion in either facultative or stable social groups (order $R = 0.804$, $P = 0.027$, $n = 6$; suborder $R = 0.63$, $P = 0.04$, $n = 9$). However, there was no relationship between allometric slopes and proportion of species with stable groups (MA: order $R = −0.46$, $P = 0.35$, $n = 6$; suborder $R = 0.25$, $P = 0.52$, $n = 9$) or the proportion in with either facultative or stable social groups (MA: order $R = 0.70$, $P = 0.12$, $n = 6$; suborder $R = 0.48$, $P = 0.19$, $n = 9$).

Discussion

Encephalization trends vary across mammalian taxa, with some showing strong evidence for macroevolutionary increase in brain size and others not. These findings challenge the conventional assumption that encephalization is a general trend across mammalian taxa.

Encephalization was not associated with taxon-specific allometric relationships between brain and body. Thus, not only is using allometric slopes to infer encephalization methodologically problematic (18), it also does not appear to describe evolutionary trends or identify patterns of directional selection. In fact, the variation in allometric relationships between brain and body size across taxonomic scales has been suggested to result from processes other than selection for brain size itself. Shallow allometric relationships at low taxonomic levels indicate selection acting on body size rather than relative brain size (14), or may result from sampling error (18). Therefore, inferring macroevolutionary patterns from brain-body allometry, especially at lower taxonomic levels, is fraught with issues. We suggest that our analyses, which specifically evaluate temporal changes in relative brain size, should be less prone to methodological error.

Conventional attempts to classify relative encephalization across species evaluate deviations from expected brain size rel-

ative to a given body size. Deacon (12) argues that such a "progressive" view of brain evolution is unhelpful because of underlying variation in basic allometric relationships between brain and body size between groups. A common analogy is drawn with computer technology; over time, size does not directly relate to functional efficacy (20), even though within comparable technologies it is more likely for a size/function relationship to hold (e.g., when comparing hard drive or RAM size, or dual vs. single Pentium processor speed). Additionally, an evaluation of variability in total or relative brain size within taxa cannot address general patterns of variation in patterns of brain evolution across groups.

Those taxa that did show a strong encephalization trend also had a high proportion of extant species found in stable social groups. This provides an independent test and further evidence for the social brain hypothesis (4, 5). Consistent with previous efforts (15), we find no relationship between brain-body allometry and sociality. However, given that both the temporal signature and the model intercepts were associated with sociality and not with allometry, we are unconvinced that allometries tell us about evolutionary patterns.

These analyses represent a first attempt to quantitatively investigate temporal trends in brain size evolution across a divergent group of mammals. We suggest that explicitly evaluating the temporal change in relative brain size across taxonomic groups is the most appropriate way to identify macroevolutionary patterns in brain size change. Despite the large number of species included in the database, we do accept that these analyses have a number of limitations. For example, the representation of fossil species varies across groups; some taxa have relatively few fossil specimens. The primate fossil record is notoriously patchy; early catarrhines and specifically apes are underrepresented. Although our dataset includes brain size estimates of fossil species from across the primate order, the number of fossil species is patchy and is likely to introduce some error to our estimates. The insectivores are also problematic, as there are few fossil species across the order. For example, the entire suborders Afrosoricida, Erinaceomorpha, Macroscelidea, and Scandentia have no fossil representatives. As the Insectivores are one of two orders that show no indication of encephalization, sampling issues are a concern. However, the mean genera appearance times for the included extant taxa are older for the Insectivores than for other taxa (Insectivore 26.08 Mya ± 1.42 SE; Primates 15.25 ± 1.18; Artiodactyla 13.07 ± 1.53; Perissodactyla 12.69 ± 2.42; Carnivora 11.10 ± 0.60; Cetacea 6.72 ± 1.35). This not only indicates that we have captured a large window of evolutionary time, but that there appears to be more stasis in Insectivores than in other orders. This said, we do accept that for Insectivores, as well as other groups, future sampling of fossil species would increase the reliability of our encephalization estimates. There was no relationship between encephalization slopes and the percent of fossils in the dataset, nor was there a relationship between the variance of the encephalization estimate and the fossil composition (see above). In addition, the slopes estimated only from extant taxa were highly correlated with the slopes estimated over the whole dataset (extant taxa plus fossils). Therefore, although we recognize that the fossil coverage could be improved by further sampling, we do not believe that our analyses are consistently biased by the fossil representation.

Despite these caveats, these analyses show variation across taxonomic groups in the degree of encephalization through time. Some taxa exhibit significant encephalization and others very little or none at all. More importantly, we show that high encephalization is associated specifically with sociality (and particularly stable groups). This suggests that the pressure for increased encephalization is associated with some aspect of bonded sociality. There are still unresolved questions regarding the cognitive demands of bonded sociality and what aspects of a taxon's ecology that made bonded sociality evolutionarily so advantageous.

Fig. 2. Proportion of taxa in social groups is positively correlated with encephalization slope at the (*A*) order and (*B*) suborder level.

Methods

We collated brain size data from the published literature (Table S1). Extant and fossil brain size and body size estimates came from the following sources: Primates (1, 21–27), Carnivores (15, 28), Ungulates (1, 28–31), Cetaceans (32, 33), and Insectivores (34–36). All data used in the analyses were estimated brain volume rather than endocranial volume or wet weight. Body and brain estimates, especially from fossils, are subject to measurement error. We rely on the published data for these estimates; however, we used bootstrapping to evaluate the error associated with estimated means

(see description of analyses). We argue that this measurement error should impact on groups equally, such that the measurement error is not biasing the encephalization slopes in one taxon more than others.

To establish first appearance dates for genera, we used two approaches. For fossil species, we used the maximum (or earliest) estimated first appearance date for the genus from the Paleobiology Database (http://paleodb. org/cgi-bin/bridge.pl). These estimates are the best approximation available for first appearance times, but we do accept that there are potential biases such that common species and those in habitats more likely to facilitate

deposition are likely to be better represented and thus have more precise estimates. For extant species, we used molecular divergence times as an approximation of first appearance dates for the genus given in the following sources: lemurs (37); New World monkeys (38); Old World monkeys and apes (39, 40); Cetaceans (41); Ruminants (42); Carnivores (43). First appearance dates are also given in the *SI Text* (Table S1).

We characterized each extant species according to three social categories: solitary, facultatively social (temporally variable or unstable aggregations), and stable social groups. Species typical behavior was taken from Nowak (44), the Animal Diversity Web (http://animaldiversity.ummz.umich.edu/site/index.html), and the Committee for Migratory Species (http://www.cms.int/) for Cetaceans. For each taxon, the proportion of taxa that demonstrated any social aggregations (facultative plus stable groups) or only stable social groups was calculated.

We downloaded publically available phylogenetic trees from Treebase (http://www.treebase.org/). Carnivore phylogeny follows ref. 45; Primates, ref. 46; Ruminants and Cetaceans, ref. 47; and Perissodactyla, ref. 48. We did not construct a tree for Insectivores because the phylogeny is poorly resolved and it is almost certainly a polyphyletic group. However, we included Insectivores in the analyses as an example of basal mammalian morphology.

We conducted multiple regressions using GLM and Phylogenetic GLM analysis (pglmEstLambda in R package CAIC), with log brain size as the dependent variable and log body and time before present (Mya) as the independent predictors. This function optimizes Pagel's lambda (49) through an iterative process. The slope estimate for time before present (Mya) is used as the signal for temporal trend in brain size. We estimated within-taxon allometric slopes using MA and OLS regression using the lmodel2 function within the R package. We also calculated brain size residuals (using the PGLM function) and regressed these against time as a confirmation of our findings using total brain size corrected for body size (Table S2). We used pairwise *t* tests to compare slopes between taxa (Table S3 *A and B*, and Fig. 1). To evaluate the impact of sampling on the estimated mean, we used resampled bootstrapping (*n* = 999) to obtain a distribution of means (Fig. S1).

We also ensured that the analyses were robust by evaluating whether there were systematic biases in the encephalization parameter. There was no correlation between encephalization slope and sample size for each taxonomic group ($R = -0.0173$, $P = 0.41$) or between slope and time span of specimens ($R = 0.92$, $P = 0.66$). We also used paired *t* tests to determine whether there were systematic changes in slope between higher and lower taxonomic grades: there were not (order/suborder, $t = -0.41$, $P = 0.69$). This indicates that, unlike allometries, our approach is not necessarily sensitive to taxonomic level. Finally, we compared temporal changes in body size with temporal changes in absolute brain size to identify taxa with disproportionate changes in brain size (Fig. S3).

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