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Commentary

Comment on relative brain size in early primates and the use of encephalization quotients in primate evolution

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1. Introduction

In their recent article, Harrington et al. (2016) describe new and important adapoid endocasts and provide insightful comparative data detailing neuroanatomical similarities and differences within euprimates, as well as between euprimates and plesiadapiforms. Their analysis utilizes high-resolution CT scan data, as well as the latest technology and methodology in 3D visualization, resulting in beautiful figures and the illumination of informative morphological features. Given their analyses, Harrington et al. (2016) broadly conclude that 1) adapoids had smaller frontal lobes (and smaller relative brain sizes) compared to extant primates, 2) adapoids had smaller olfactory bulbs (relative to brain volume), but more expanded temporal and occipital lobes compared to plesiadapiforms, suggesting an increasing reliance on vision over olfaction, and 3) these differences in shape and sensory system input preceded any substantial increase in brain size during early primate evolution. While the comparative anatomy and the first two broad evolutionary conclusions of the study are sound and welcome additions to the literature, it is this third inference that requires further scrutiny.

In support of Conclusion 3, the authors provide a number of comparisons between encephalization quotients (EQs) derived for plesiadapiforms and euprimates preserving enough of the neurocranium to make such analyses possible. On the basis of overlapping EQ values between some plesiadapiforms and euprimates (their Fig. 11), they suggest that brain size did not significantly increase during early primate evolution (see also Silcox et al., 2009b, 2010). As the analyses below will demonstrate, we believe the authors were led astray by an over-reliance on EQs that poorly model brain scaling relationships within fossil euprimates, plesiadapiforms, and mammals more generally. When the estimated EQs used by Harrington et al. (2016) are analyzed in relation to estimated size (= mass), it becomes clear that they are negatively allometric with respect to the interspecific regression they chose to use as a criterion of subtraction. The evidence at hand indicates that there is probably no overlap in EQ values between euprimates and plesiadapiforms at any given size. Furthermore, when a more straightforward comparison of brain size relative to body size is performed using a narrow allometric approach (sensu Smith, 1980, 1984; Jungers, 1987), it becomes apparent that fossil euprimates have larger brains than any plesiadapiform of similar estimated body size. These data have important implications for early primate evolution and illustrate the well known pitfalls of EQs as a comparative measure of relative brain size across primates and other mammals.

2. EQs and relative brain size comparisons

The EQ is a relative measure of brain size attempting to take body size into account. Jerison (1973) introduced the ratio in an attempt to control for the fact that brain size scales allometrically across vertebrates, thereby complicating simple comparisons of brain volume between animals of greatly differing size. The equation he derived is based on a regression of brain mass to body mass across living mammals, with the regression line representing the “expected value” of brain mass for any given mammal. An EQ for any mammal is essentially the ratio of the observed brain mass value divided by the expected brain mass value at a given body

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mass: $EQ = E/(0.12^{*}W^{0.67})$, where EQ is the encephalization quotient, E is brain mass or volume, and W is body mass. In log–log plots, the logEQ is a residual above or below the line.

As Harrington et al. (2016) point out (see also Martin, 1990), Jerison's equation tends to yield quite disparate results for very small and very large mammals, so they also used Eisenberg's (1981) modified equation: $EQ = E/(0.055^{*}W^{0.74})$. The problem with these mouse-to-elephant equations, as hinted at both by Martin (1990) and Harrington et al. (2016) themselves, is that they are based on averages across all mammals and cannot effectively model changes in brain mass that might be expected within more restricted clades, such as the Order Primates. In other words, the scaling across mammals may be quite different from the scaling within Primates, just as scaling trends for major clades within Primates differ from the overall trend line when all primate taxa are pooled (e.g., Napier and Napier, 1967; Isler et al., 2008; Fleagle et al., 2012). In addition, these older equations are not phylogenetically informed and they do not focus specifically on the clades(s) of primary interest—the Order Primates. However, our observations below still apply even if we use the new primate-specific regression and attendant EQs developed by Grabowski et al. (2016) within an explicitly phylogenetic context.

As any EQ is dependent on a reliable estimate of body mass, we first evaluated the body mass estimates provided by Harrington et al. (2016) for their likely accuracy. Some workers believe that weight-bearing elements of the postcranium are the best predictors of body mass (e.g., Hylander, 1985; Grabowski et al., 2015), but "best" is ultimately an empirical determination (Smith, 2002). Regardless, associated crania and postcrania are rare in the early primate fossil record. The only measurements that are available across relevant fossil euprimates and pleasiadapiforms are craniodental ones, making body mass predictions from these measurements the only consistent way to place all species on a common scale. Harrington et al. (2016) provided multiple craniodental estimates of mass for their euprimate and plesiadapiform sample, and we first evaluated the accuracy of these equations before reanalyzing them here. We excluded the Dagosto and Terranova (1992) dental equations because they are strepsirrhine-specific, were not used to calculate an estimated body mass for plesiadapiform taxa, and should probably not be used to estimate body mass for primitive/stem haplorhine taxa such as omomyoids. In fact, there are four equations presented that can be used to estimate body mass across all fossil euprimate and plesiadapiform taxa: the skull (= cranial) length equation from Martin (1990), the vertical phylogenetic generalized least squares (VPGLS) and horizontal phylogenetic generalized least squares (HPGLS) cranial length equations from Silcox et al. (2009a), and the M^1 dental equation from Gingerich et al. (1982). To test their accuracy, we calculated the body mass of known living prosimian primates using these equations and compared these estimates to the known average body mass of each species (Supplementary Online Material [SOM] Table 1).

Our results demonstrate that the Gingerich et al. (1982) M^1 equation and the Silcox et al. (2009a) VPGLS cranial length equation are particularly poor at estimating body mass among living prosimian primates, and there is no reason to expect that they would perform better for fossil euprimates and plesiadapiforms. VPGLS has an average error of 42% and typically underestimates the body mass of prosimian taxa by ~338 g. The Gingerich et al. (1982)

Table 1
Estimates of euprimate and plesiadapiform body mass and Eisenberg's Encephalization Quotient (EEQ).[a]

Taxon	Euprimate/ Plesiadapiform	Average cranial length	Estimated body mass (g)	Estimated ECV (cm^3)	EEQ	Source of body mass estimate
Notharctus tenebrosus	Euprimate	–	2500	10.4	0.58	Comparative Skeletal (Harrington et al., 2016)
Notharctus tenebrosus ($n = 3$)	Euprimate	73.8	1500	7.6	0.62	Cranial Equation (Martin, 1990)
Notharctus tenebrosus ($n = 3$)	Euprimate	73.8	1320	7.6	0.68	Cranial Equation (HPGLS Silcox et al., 2009a)
Smilodectes gracilis	Euprimate	–	2450	9.5	0.54	Comparative Skeletal (Harrington et al., 2016)
Smilodectes gracilis ($n = 2$)	Euprimate	71.4	1321	8.0	0.72	Cranial Equation (Martin, 1990)
Smilodectes gracilis ($n = 2$)	Euprimate	71.4	1162	8.0	0.79	Cranial Equation (HPGLS Silcox et al., 2009a)
Adapis parisiensis	Euprimate	–	2500	8.3	0.46	Comparative Skeletal (Harrington et al., 2016)
Adapis parisiensis ($n = 2$)	Euprimate	84.5	2544	8.8	0.48	Cranial Equation (Martin, 1990)
Adapis parisiensis ($n = 2$)	Euprimate	84.5	2252	8.8	0.53	Cranial Equation (HPGLS Silcox et al., 2009a)
Leptadapis magnus ($n = 4$)*	Euprimate	109.0	6855	21.7	0.57	Cranial Equation (Martin, 1990)
Leptadapis magnus ($n = 4$)*	Euprimate	109.0	6130	21.7	0.62	Cranial Equation (HPGLS Silcox et al., 2009a)
Pronycticebus gaudryi	Euprimate	63.0	812	4.8	0.61	Cranial Equation (Martin, 1990)
Pronycticebus gaudryi	Euprimate	63.0	710	4.8	0.68	Cranial Equation (HPGLS Silcox et al., 2009a)
Rooneyia viejaensis	Euprimate	51.6	373	7.2	1.64	Cranial Equation (Martin, 1990)
Rooneyia viejaensis	Euprimate	51.6	324	7.2	1.82	Cranial Equation (HPGLS Silcox et al., 2009a)
Microchoerus erinaceus	Euprimate	(46.1)	241	4.3	1.34	Cranial Equation (Martin, 1990)
Microchoerus erinaceus	Euprimate	(46.1)	208	4.3	1.49	Cranial Equation (HPGLS Silcox et al., 2009a)
Necrolemur antiquus ($n = 4$)	Euprimate	40.4	144	3.8	1.75	Cranial Equation (Martin, 1990)
Necrolemur antiquus ($n = 4$)	Euprimate	40.4	124	3.8	1.95	Cranial Equation (HPGLS Silcox et al., 2009a)
Tetonius homunculus	Euprimate	31.0	51	1.5	1.48	Cranial Equation (Martin, 1990)
Tetonius homunculus	Euprimate	31.0	44	1.5	1.66	Cranial Equation (HPGLS Silcox et al., 2009a)
Ignacius graybullianus ($n = 2$)	Plesiadapiform	(47.0)	260	2.0	0.59	Cranial Equation (Martin, 1990)
Ignacius graybullianus ($n = 2$)	Plesiadapiform	(47.0)	225	2.0	0.66	Cranial Equation (HPGLS Silcox et al., 2009a)
Microsyops annectens	Plesiadapiform	(78.0)	1863	5.9	0.41	Cranial Equation (Martin, 1990)
Microsyops annectens	Plesiadapiform	(78.0)	1710	5.9	0.43	Cranial Equation (HPGLS Silcox et al., 2009a)
Plesiadapis tricuspidens	Plesiadapiform	(107.0)	6372	5.2	0.14	Cranial Equation (Martin, 1990)
Plesiadapis tricuspidens	Plesiadapiform	(107.0)	5854	5.2	0.15	Cranial Equation (HPGLS Silcox et al., 2009a)
Plesiadapis cookei	Plesiadapiform	–	2176	5.0	0.31	Postcranial Estimate (Gingerich and Gunnell, 2005)
Plesiadapis cookei	Plesiadapiform	90.0	3251	5.0	0.23	Cranial Equation (Martin, 1990)
Plesiadapis cookei	Plesiadapiform	90.0	2885	5.0	0.25	Cranial Equation (HPGLS Silcox et al., 2009a)

[a] See Figures 1–4 for plots derived from the above table. Note that species averages were calculated only from specimens preserving both cranial length and ECV. Average cranial length for each taxon taken from Gingerich and Martin (1981), Kay and Kirk (2000), Gingerich and Gunnell (2005), and Harrington et al. (2016); numbers in parentheses represent estimates taken by calculating back from body mass estimation equations. ECV values taken from Martin (1990), Silcox et al. (2009a), Long et al. (2015), and Harrington et al. (2016). *Note that *Leptadapis magnus* has been recently divided into a number of genera and that the sample here included *L. magnus*, *Magnadapis quercyi*, and possibly other genera (specimens QU 10870, 10872, 10875, and 11002).