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THE RELATIVITY OF RELATIVE BRAIN MEASURES AND HOMINID MOSAIC EVOLUTION

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Several developments in recent years have renewed interest in finding measures or parameters to characterize brain and body size relationships both quantitatively and objectively. Among three developments the most outstanding are 1) a deepening appreciation and understanding of all metric relationships in evolutionary change and of formal comparisons among extant species (Bauchot and Stephan, 1969; Gould, 1975; Holloway, 1976; 1979; Jerison, 1973; Passingham, 1973; Passingham and Ettlinger, 1975; Sacher, 1975; Stephan et al., 1970; Hemmer, 1971; Leutenegger, 1973); 2) the publication of Jerison's (1973) volume on brain size and intelligence in evolutionary perspective; 3) the attempts to quantify body size parameters of certain early hominid specimens by physical anthropologists, McHenry (1974,1975) and Holloway (1975); and 4) the recent designation (Johansen and White, 1979) of the Hadar and Laetoli (Ethiopia and Tanzania, respectively) hominids to a new taxon, *Australopithecus afarensis*, a taxon clearly having a small ape-sized brain, yet with other morphological attributes indicative of true hominid status (e.g., bipedality, dentition).

Frequently a variety of neural values, foremost among them encephalization quotient scores (E.Q.) and "extra neurons," are determined for particular fossil hominids (e.g., Tobias, 1971), and reports of such determinations are accompanied by discussions of the role of neural or brain evolution in the overall dynamics of human evolution (see above references, plus White, 1980). Although some of us who work directly with brain evolution data are aware of the relativistic nature of such measures (e.g., Jerison, 1973; Hemmer, 1971; Leutenegger, 1973; Martin, this volume; Radinsky, this volume), we observe that many scientists do not appear to appreciate that most of these measures are *relative to the data base chosen,*

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and that little progress has been made in establishing criteria to determine which data base should be selected for particular purposes.

During the past several years, one of us (RH) has had the opportunity to prepare brain endocasts from original hominid fossils and to reconstruct those brains, both to find the most accurate volume estimates possible and to learn what the actual fossil evidence suggests about the evolution of the brain. In the course of these researches, encephalization quotients were seen to be a useful preliminary heuristic device to compare stages of brain size development in hominids, once some relatively accurate estimation of body size (weight) had been made; however, E.Q. scores were also observed not to be an invariant, inherent property of a given fossil specimen (or extant species) and therefore, functional or taxonomic judgments based on these scores have to be made with caution. Our intent here is twofold: (a) to demonstrate the often unappreciated dependence of E.Q. scores on the specific form of the reference equation and data bases used for their computation and (b) to spark some necessary discussion and debate regarding the best criteria for selecting particular data bases.

ENCEPHALIZATION

Allometric techniques have played a major role in the analysis of brain evolution, starting with the pioneering studies of Snell (1892) and of Eugene Dubois (1897). As "the study of size and its consequence" (Gould, 1966), allometry has unarguable relevance for our attempts to interpret the diversity of brain size both among extant organisms of different body weights and within phyletic lineages. We will not review the insight this approach has provided, nor comment on many of the more controversial aspects of this method (e.g., which regression model is most approprate for curve-fitting purposes, the interpretation of y-intercepts,the treatment of outliers--see Smith, 1980; Martin, this volume; Radinsky, this volume). We will focus instead on the use of empiricially-determined regression lines as "criteria of subtraction" (Gould, 1975) wherein deviations from the line are interpreted as size-independent, functional adaptations.

Encephalization coefficients exemplify the "criteria of subtraction" approach. An encephalization coefficient or quotient is simply a measure of the vertical residual or deviation of the observed brain size of an individual or species from a bivariate regression line constructed using brain and body size values for a group of organisms (e.g., all mammals, insectivores, primates). That is, on the assumption that brain-body relationships can be described by a power equation of the form:

$$V = k\,W^{\alpha}$$

where V = brain size, W = body weight, and α = power to which body weight is raised.

k = empirically determined parameters

a linear equation of the following form is fit, generally by the least-squares or major-axis techniques, to these data points:

$$\log V = \log k + \alpha \log W$$

The E.Q. for any specimen i (EQ_i) is then computed as the ratio of observed-to-expected brain weight, or

$$EQ_i = \frac{V_i}{k\, W_i^{\alpha}}$$

where V_i and W_i are the brain and body weights, respectively, for specimen i.

Obviously, each set of data points chosen will provide a somewhat different reference equation, with different values for the parameter k and α, and the E.Q. score of any particular specimen will change accordingly; the consequences of this fact will be examined below. Regardless of the data base selected, two salient facts are apparent when looking at primate and fossil hominid E.Q.'s: (1) modern *Homo sapiens* has the highest E.Q., and (2) fossil hominids are always intermediate between extant pongids and modern *Homo, but the degree of intermediacy depends on the data base selected.*

EMPIRICAL CONSIDERATIONS

Table 1 gives a sample of reference equations for the computations of E.Q.'s. The formulas are derived from least-squares regressions of Bauchot and Stephan (1969) in which the data base (89 primate species including modern *Homo*) is a combination of empirical determinations and results of their review of the literature. The equations for the various taxa or combinations thereof were determined from the SPSS scattergram and regression packages (Nie et al., 1975). In addition, #10, the "Homocentric" equation, was derived simply by using Bauchot and Stephan's values for *Homo sapiens*, and completing the regression line through "origin," i.e., zero-body weight and zero-brain weight. The "Homocentric" equation is derived from the premise that *Homo sapiens* is the highest encephalized animal known and has the advantage that an E.Q. score derived from it is *directly* expressed as a percentage of the modern *Homo* value. Table 2 is a listing of hypothetical brain and body weights for a sample of 20 early fossil hominids, in which the brain weights (volumes) are accurate and the body weights were chosen to cover a reasonable range from light to heavy.

TABLE 1. Ten Empirically Derived Equations Resulting From Plotting Log_{10} Brain Weight Against Log_{10} Body Weight For Different Combinations of Primate Taxa

Equation No.	Equation	Exponent Values	Correlation Coefficient R	Data Base	Data Source
1	Brain y = .12 x Body	.66	N.A.[a]	All mammals, N=198	Jerison 1973
2	= .0429 Body	.63	.98	Insectivores, N=22	Bauchot & Stephan 1969
3	= .0407 "	.64818	.99329	Basal insectivores, N=11	"
4	= .0893 "	.77698	.96937	All primates, including *Homo*, N = 89	"
5	= .0991 "	.76237	.97062	All Primates, No *Homo*, N = 88	"
6	= .1482 "	.65683	.94980	Prosimians, N = 24	"
7	= .0963 "	.79855	.98931	New World monkeys, N = 21	"
8	= .5477 "	.57750	.91439	Old World monkeys, N = 36	"
9	= .6216 "	.58152	.98135	Pongids, N = 7	"
10	= 1.0 "	.64906[b]		*Homo sapiens*, N=1	Holloway

[a] N.A. = Not available (fitted by convex polygon method, Jerison 1973).

[b] This exponent is the result of choosing a brain weight of 1330 grams, and a body weight of 65,000 grams. The line passes through origin.

TABLE 2. Hypothetical Brain and Body Weights for a Sample of 20 Early Fossil Hominids and Known Weights for 4 Extant Hominoids

	Hominid No.	Brain Volume (ml)	Body Weight (grams)[a]
	1	400	20000
	2	400	18144
	3	442	28020
	4	442	23900
	5	442	21700
	6	585	20412
	7	485	22680
	8	485	24947
	9	485	27215
	10	485	29483
	11	485	34019
	12	485	54359
	13	530	36500
	14	530	31500
	15	530	34019
	16	530	29483
	17	530	27215
	18	508	22680
	19	508	34019
	20	508	45359
(Gorilla)	21	465	165000
(Chimpanzee)	22	420	46000
(Orangutan)	23	370	55000
(Homo)	24	1,330	65000

[a] The occasional appearance of *gram* figures in the body weights reflects conversion from ranges initially rounded in *pound* units.

Hominids #1-5, for example, could represent small-brained australopithecines, because the value of 400 to 442 g more or less represents the Taung specimen. The 485 g values of hominids #6-12 represent the volume for the STS5 australopithecine, and the 530 g value of #13-16 represents the OH5 and SK1585 robust australopithecines. The 508 g value is that for KNM-ER-1813, a small East African hominid.

Table 3 provides the E.Q. scores for chimpanzee, gorilla, orangutan, *Homo sapiens*, and the 20 hominids, and their raw percentages of the modern human value based on the equations in Table 2.

Table 4 shows the difference between the *highest and lowest* percent of *Homo sapiens* values for the 10 equations listed in Table 1, which is always between equations #7 and #8, that is, between the equations for New

TABLE 3. Encephalization Quotient (E.Q.) Scores and Their Raw Percentages of the Modern Human Value[a,b]

HOMINOID #	EQUATION NUMBER 1	2	3	4	5	6	7	8	9	10
1	4.55	18.19	16.02	2.04	2.12	4.04	1.53	2.40	2.03	.65
	65.90	63.20	64.60	75.10	74.00	65.20	77.20	59.40	59.40	65.00
2	4.86	19.35	17.06	2.20	2.29	4.30	1.65	2.53	2.15	.69
	70.30	67.20	68.80	81.10	79.70	69.50	83.30	62.80	63.20	69.00
3	4.02	16.26	14.22	1.73	1.81	3.57	1.29	2.18	1.84	.57
	58.20	56.50	57.30	63.90	63.20	57.70	65.10	54.00	54.20	57.40
4	4.47	17.97	15.77	1.96	2.05	3.97	1.46	2.39	2.02	.64
	64.70	62.40	63.50	72.30	71.40	64.10	73.70	59.20	59.50	63.60
5	4.77	19.10	16.79	2.11	2.20	4.29	1.58	2.53	2.14	.68
	69.00	66.30	67.70	77.90	76.80	68.30	79.80	62.60	62.90	67.70
6	5.45	21.78	19.17	2.43	2.53	4.83	1.82	2.87	2.43	.77
	78.90	75.60	77.30	89.70	88.30	78.00	91.90	71.20	71.50	77.30
7	5.08	20.38	17.90	2.24	2.34	4.51	1.67	2.70	2.29	.72
	73.50	70.80	72.10	82.60	81.50	72.80	84.30	67.00	67.30	72.20
8	4.76	19.19	16.83	2.08	2.17	4.23	1.55	2.56	2.16	.68
	69.00	66.70	67.80	76.70	75.80	68.40	78.30	63.40	63.60	68.00
9	4.50	18.17	15.91	1.95	2.03	4.00	1.45	2.43	2.06	.64
	65.10	63.10	64.10	71.70	70.90	64.60	73.20	60.30	60.50	64.20
10	4.26	17.28	15.10	1.83	1.91	3.79	1.36	2.32	1.96	.61
	61.70	60.00	60.90	67.40	66.70	61.30	68.70	57.60	57.80	60.90
11	3.88	15.79	13.76	1.64	1.72	3.45	1.21	2.14	1.81	.55
	56.10	54.80	55.50	60.30	59.80	55.80	61.10	53.00	53.10	55.50
12	2.84	11.75	10.16	1.14	1.20	2.54	.83	1.63	1.37	.41
	41.10	40.80	40.90	41.90	41.70	41.00	41.90	40.40	40.50	40.90
13	4.04	16.50	14.37	1.69	1.78	3.60	1.25	2.24	1.89	.58
	58.50	57.30	57.90	62.40	62.00	58.20	63.10	55.60	55.70	57.90
14	4.46	18.11	15.81	1.90	1.99	3.97	1.41	2.44	2.04	.64
	64.60	62.90	63.70	70.00	69.30	64.10	71.20	60.50	60.70	63.80
15	4.24	17.25	15.04	1.79	1.88	3.77	1.32	2.34	1.97	.61
	61.30	59.90	60.60	65.90	65.40	61.00	66.70	57.90	58.10	60.70
16	4.66	18.88	16.50	2.00	2.09	4.15	1.48	2.54	2.15	.66
	67.50	65.60	66.50	73.70	72.90	67.00	74.70	62.90	63.10	66.60
17	4.91	19.85	17.38	2.13	2.22	4.37	1.58	2.66	2.25	.70
	71.20	69.00	70.00	78.40	77.50	70.60	79.80	66.00	66.10	70.10
18	5.32	21.35	18.75	2.35	2.45	4.72	1.75	2.83	2.39	.76
	77.00	74.10	75.60	86.60	85.40	76.30	88.40	70.20	70.50	75.60
19	3.35	13.80	12.00	1.37	1.44	2.99	1.01	1.90	1.60	.48
	48.50	47.90	48.40	50.50	50.30	48.40	51.00	47.00	47.10	88.20
20	3.35	13.79	11.96	1.37	1.44	2.99	1.01	1.90	1.60	.48
	48.50	47.90	48.20	50.50	50.30	48.40	51.00	47.00	47.10	48.20
21 (Gorilla)	1.56	6.67	5.68	.57	.61	1.41	.41	.97	.81	.23
	22.60	23.20	22.90	21.00	21.30	22.70	20.70	24.00	23.90	22.90
22 (Chimp)	.74	11.30	9.80	1.12	1.18	2.45	.82	1.55	1.31	.39
	39.70	39.30	39.50	41.30	41.20	39.60	41.40	38.60	38.60	39.50
23 (Orang)	2.15	8.90	7.69	.86	.91	1.92	.63	1.24	1.04	.31
	31.10	30.90	31.00	31.70	31.60	31.00	31.80	30.60	30.70	31.00
24 (*Homo*)	6.91	28.80	24.81	2.71	2.87	6.19	1.98	4.03	3.40	1.00
	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

[a]Based on the equations in Table 1 and hominoids in Table 2.
[b]The top number is the actual E.Q. value, and the bottom value is the percentage of modern Homo's E.Q. (e.g., Hominid #7, E.Q. of 5.08 represents 73.5% of 6.91, the modern *Homo sapiens'* 6.91 E.Q.)

TABLE 4. Sample Percentage Differences Between Extremes in Sets of Equations[a]

	Hominoid number	Differences between equations: #4 and #8 (all primates, N.W. monkeys)	Differences between equations: #7 and #8 (N.W. and O.W. monkeys)
	1	15.7	17.8
	2	18.1	20.5
	3	9.9	11.1
	4	13.1	14.5
	5	15.3	17.2
	6	18.5	20.7
	7	15.7	17.3
	8	13.3	14.9
	9	11.4	12.9
	10	9.8	11.1
	11	7.3	8.1
	12	1.5	1.5
	13	6.8	7.5
	14	9.4	10.7
	15	8.0	8.8
	16	10.7	11.8
	17	12.5	13.8
	18	12.4	18.2
	19	7.6	4.0
	20	3.5	4.0
Gorilla	21	-2.9	-3.3
Chimpanzee	22	2.7	2.8
Orangutan	23	1.0	1.2
Homo sapiens	24	0.0	0.0

[a]Based on the percentage of modern *Homo* E.Q. values in Table 3.

World and Old World monkeys, a consequence of the fact that these equations have the highest and lowest exponents, respectively (see below). We have included the differences between equations #4 and #8 to show that the difference between the "usual" E.Q.'s, i.e., those used by Jerison (1973) and Stephan, et al., (1970) or the "Homocentric" one, are minimal.

Table 5 gives rank-order correlations for the E.Q. scores of 89 species when different reference equations are used. Although the correlations are generally extremely high (and all are significantly different from zero), their nonunity implies that the rank order of these species is not necessarily invariant under a change of reference equation (see below).

TABLE 5. Rank-Order Correlations for the E.Q. Scores of 89 Species When Different Reference Equations from Table 1 are Used[a,b]

	1	2	3	4	5	6	7	8	9	10
1	---	.98	.99	.76	.82	1.00	.68	.95	.95	.99
2	.90	---	.99	.66	.73	.99	.57	.99	.99	.99
3	.95	.95	---	.71	.77	1.00	.62	.97	.97	1.00
4	.60	.50	.55	---	.99	.74	.99	.57	.57	.71
5	.66	.56	.61	.94	---	.80	.97	.64	.65	.78
6	.97	.93	.97	.57	.63	---	.65	.96	.96	1.00
7	.52	.42	.47	.92	.86	.49	---	.47	.48	.63
8	.82	.92	.87	.42	.48	.85	.34	---	1.00	.97
9	.82	.92	.88	.43	.49	.85	.35	.99	---	.97
10	.95	.95	1.00	.55	.61	.98	.47	.87	.87	---

[a]The figures in the top right-hand portion of the table are Spearman's rho's, those in the bottom left portion are Kendall's taus. For example, equation 5 shows the highest correlation with equation 4 in both Kendall's tau (.94) and Spearman's rho (.99).

[b]Although the E.Q.'s of primates are in close agreement for all 89 species, they are not perfect, indicating changes in rank order depending on the equations used.

THEORETICAL CONSIDERATIONS

The "reversibility" of the E.Q. rank orders of different taxa when different reference equations are used, documented on the above empirical data base, presents a serious problem in the interpretation of E.Q. scores, particularly because there seems to be little informed agreement (or, indeed, little debate) concerning which reference equation is most appropriate for examining brain-body relationships within any particular group of related organisms. We will now briefly examine the general behavior of E.Q. scores as a function of a small number of parameters; in particular, we will show that the *relative* magnitude of the E.Q.'s change and thus can be, in many cases, arbitrarily manipulated to provide almost any rank order the researcher prefers.

Let

V_i = brain volume (or weight) of species i
V_j = brain volume (or weight) of species j
W_i = body weight of species i
W_j = body weight of species j

Using an equation of the form

$$y = kW^{\alpha}$$

we can compute the E.Q.'s of species i and j (=EQ_i and EQ_j respectively) as:

(1a) $EQ_i = V_i / kW_i^{\alpha}$ and

(1b) $EQ_j = V_j / kW_j^{\alpha}$

Thus, $EQ_i = EQ_j$ if and only if

$$V_i / kW_i^{\alpha} = V_j / kW_j^{\alpha} \text{ or}$$

(2) $V_i / V_j = (W_i/W_j)^{\alpha}$

By taking logarithms of equation 2, we get the following expression for the conditions under which $EQ_i = EQ_j$:

$$\log (V_i/V_j) = \alpha \log (W_i/W_j)$$

Changing the latter equation to an inequality, we find that:

(3a) if $\alpha < \log (V_i/V_j)/\log (W_i/W_j)$

$EQ_i > EQ_j$ <u>if</u> $W_i/W_j > 1$ and $EQ_i < EQJ_j$ if $W_i/W_j < 1$

(3b) if $\alpha > \log V_i/V_j \log (W_iW_j)$

$EQ_i > EQ_j$ <u>if</u> $W_i/W_j < 1$ and $EQ_1 < EQ_j$ if $W_iW_j > 1$

(Note that the above expressions are undefined if $W_i = W_j$, in which case $EQ_i/EQ_j = V_i/V_j$ for all values of α).

The parameter k, which determines the y-intercept of the logarithmically transformed version of the brain-body equation, has no effect whatsoever on the *relative* magnitudes of the two species' E.Q.'s (although it will, of course, influence the absolute magnitude of those scores).

Thus, using equations 3a and 3b and brain and body weights, we can define for any pair of taxa a value for the exponent of the reference equation (α^*) above which one species has the higher E.Q. and below which the other is judged more "highly cephalized." The values of α^* for each pair of hypothetical hominids in Table 2 are given in Table 6. Although most values of α^* lie outside the range of exponent values normally encountered in a "reasonable" set of potential reference equations approximately ($.4 < \alpha < .8$), a substantial number do not (these have been <u>*underlined*</u> in Table 6). In these cases the choice of a reference equation from among a "reasonable" set of potential reference equations will be critical in forming our

TABLE 6. Values of α* For Each Pair of Hypothetical Hominids[a]

	12	20	13	11	19	15	14	10	16	3	9	17	8	4	7	18	5	6	1	2
12	--	-.26	-.22	0	-.10	-.19	-.16	0	-.15	.14	0	-.13	0	.11	0	-.05	.10	0	.19	.18
20		--	-.20	.16	0	-.15	-.12	.11	-.10	.29	.09	-.08	.08	.22	.07	0	.19	.06	.29	.26
13			--	1.26	.60[b]	0	0	.42	0	.69	.30	0	.23	.43	.19	.09	.35	.15	.47	.40
11				--	x[c]	x	-1.15	0	-.62	.48	0	-.40	0	.26	0	-.11	.21	0	.36	.31
19					--	x	-.55	.32	-.30	.72	.21	-.19	.15	.39	.11	0	.31	.09	.45	.38
15						--	0	.62	0	.94	.40	0	.29	.51	.22	.10	.40	.17	.53	.45
14							--	1.34	0	1.55	.61	0	.38	.66	.27	.13	.49	.20	.62	.51
10								--	x	1.82	0	-1.11	0	.44	0	-.18	.30	0	.50	.40
16									--	3.57	1.11	0	.53	.86	.34	.16	.59	.24	.73	.58
3										--	-3.18	-6.23	-.80	0	-.44	-.66	0	-.29	.30	.23
9											--	x	0	.71	0	-.25	.41	0	.63	.48
17												--	1.02	1.40	.49	.23	.80	.31	.91	.69
8													--	2.17	0	-.49	.67	0	.87	.61
4														--	-1.77	-2.66	0	-.59	.56	.36
7															--	x	2.10	0	1.53	.86
18																--	3.15	.44	1.90	1.07
5																	--	-1.52	1.22	.56
6																		--	9.45	1.64
1																			--	0
2																				

[a]Entries are values of α (α*) below which the row hominid will have a higher encephalization coefficient than the column hominid.

[b]Values of α* between 0.4 and 0.8 are underlined. See text for details.

[c]Entries of "x" indicate hominid pairs with the same body weight.

judgments concerning the relative encephalization of that particular pair. Without some explicit *a priori* criterion for choosing the "best" equation, those judgments are, to a large extent, a matter of taste. Thus, we take issue with Gould's claim that the use of E.Q.'s "avoids a reliance upon very precise (and probably incorrect) values for allometric exponents" (1975). The above suggests that the "choice" of exponent is ultimately dependent on the data base chosen, and affects the relative E.Q. scores of different taxa and hence our interpretations of evolutionary relationships among them. This will present a serious problem *unless* one of the two following conditions hold:

(a) An allometric exponent could be chosen on the basis of some well-established *a priori* functional hypothesis. That is, if some exponent were known, from structural or "engineering" principles, to represent functional equivalence within the interspecific brain/body weight allometric relationship, that exponent could be used with confidence for the calculation of the E.Q.'s of various taxa, functioning as a "criterion of subtraction." The scaling exponent of 0.66 comes immediately to mind, for it appears frequently in empirical studies and, more important, it implies a functional determination of brain weight by body surfaces rather than volumes. As Gould (1975) argued, however, the underlying causes of this surface-dependence have never been adequately explained, and "we cannot ever be sure that the presumed surface-dependency is more than coincidental." Furthermore, the scaling could vary in different taxa for different reasons (see also Martin, this volume).

(b) In the absence of an understanding of the functional requirements for size increase, and if, regardless of the data base chosen, all exponents varied within narrow limits, perhaps some average could be taken for the reference equation. As can be seen in Table 1, the exponents for the various combinations of primate taxa vary from .577 in Old World monkeys (N=36) to .798 in New World monkeys (N=21). Although an "average" value of around .66 is suggested, the observed variability in the scaling exponents is not simply a function of small-sample fluctuations, as can be seen in Figure 1 where 95% confidence limits for the exponents have been plotted. We are aware that any attempt at a functional or adaptive interpretation of this variability in scaling parameters, which is in any case beyond the more limited scope of this report, must come to grips with several serious methodological problems. For example, within the New World monkeys, the slopes for the Callithricidae and Cebidae are both close to .66, yet given the relative placement of these two groups with respect to brain and body weight, the combination of the two families within one higher-order taxon yields a slope of .798. At which taxonomic level are comparisons of slope meaningful?

In this paper, we have concentrated on equations based on intergeneric or higher-order taxonomic groupings, because these have been used most often. Hemmer (1971) and Leutenegger (1973) used intrageneric data, which yield slopes of roughly .2 to .3 in most cases. For the same reasons

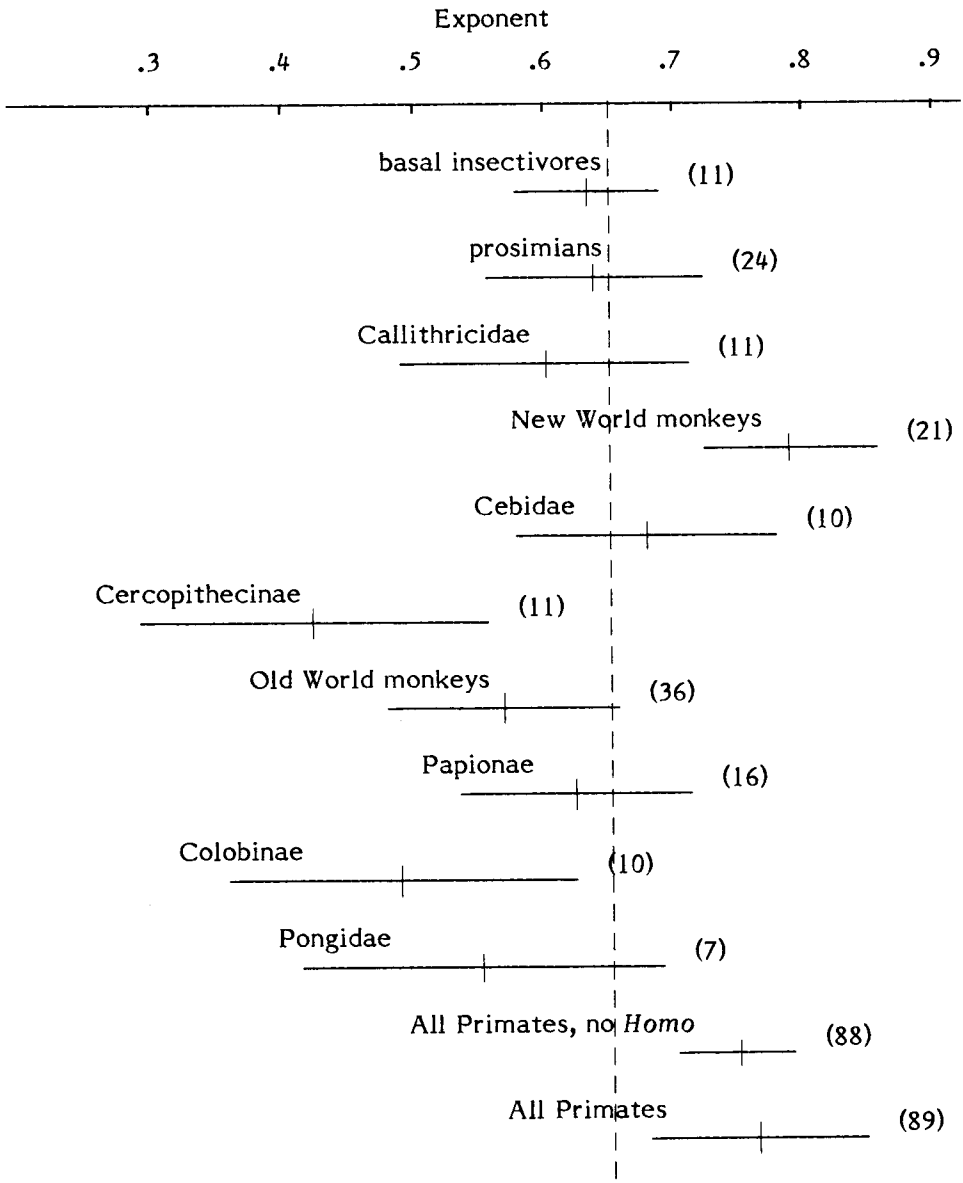

Fig. 1. The mean and 95% confidence intervals for different Primate taxa. The values in parentheses are the number of species in each group. The dashed line gives the exponential value of 0.66.

indicated here, we are not convinced that any one particular intrageneric allometric curve is any less selective or meaningful than for higher-order taxa combinations. Nor are we certain that the data bases for such intrageneric groups are any more accurate or adequate than the others. Slopes of values lower than .6 do have the effect of lowering E.Q. scores for smaller-brained species. Using a slope of .23, for example, gives *Homo sapiens* an E.Q. of 103.96, and *Pan troglodytes* a value of 35.55. *Gorilla* has a value of 29.34.

The australopithecine E.Q.'s are relatively lower than those given in Table 3, varying from about 41 to 45. The Hadar specimen provides an E.Q. of about 40.5. These values are still significantly higher than any pongid value, but respectively lower than those based on an exponent of roughly .6. This illustrates, again, two major points: (1) the australopithecine E.Q.'s remain advanced over pongid values, and (2) the values as a percentage of modern *Homo* are sensitive to the slopes chosen. We frankly do not see any empirically derived reasons or physiological ones to convince us that intrageneric slopes are more appropriate.

Variability of slopes exists and no one reference equation has such a high frequency that it appears regardless of the data points on which the equation is based.

HUMAN MOSAIC EVOLUTION

As the above data should make clear, one's interpretation of where any particular hominid (or choice of brain and body weight combinations) fits in relationship to modern *Homo* will depend not only on the choice of weights, but on the data base used for calculating E.Q.'s. If "brain evolution" is equated with brain size increase and thereby encephalization, one could conclude that brain evolution was the terminal phase of hominid evolution (McHenry, 1974, 1975; White, 1980), following dental, locomotory, and other musculoskeletal changes. Alternatively, one could regard high encephalization scores indicative of early brain evolutionary changes, at least with respect to size. Thus, as some have argued, the australopithecines had apelike brains, or as others of us have argued (Holloway, 1976, 1979; Leutenegger, 1973), they show truly hominid characteristics, *including their E.Q.'s*. Of course, hypotheses about early human evolution are speculative, and vary according to the weight placed on functional systems evolving through time, e.g., bipedalism, the brain, tool-use and tool-making, manual dexterity, hunting and gathering, and sexual division of labor.

The question of weighting and interpretation takes on even greater significance the further back into prehistory we go, and the most recent discoveries of the Hadar and Laetolil specimens require, we believe, careful consideration of which data bases are most appropriate for the eventual judging of whether or not the brain had an important role in the earliest phases of human evolution.

WHICH DATA BASES FOR WHAT?

The question really revolves about the extrapolation from extant living forms to fossil species. Is it logical to compute E.Q.'s for hominids from an equation based on extant living species ranging from mouse to whale in size, and including order upon order of mammals only distantly related to hominids? Or is it more logical to compute E.Q's from some data base more closely related to actual phylogenetic relationships, e.g., hominids from pongids, Old World primates, or just modern *Homo*, as in equation 10? Or, should intrageneric or specific exponents of .2 to .3 be used? Obviously, the only secure data bases available are from living species, as we can never be certain about the body weights for fossil specimens. If we desire a purely comparative, phyletically uniform paradigm, then either the Jerison (1973) or Bauchot and Stephan (1969) and Stephan et al. (1970) equations (#1 and #2) make sense. We prefer the latter, because it represents a group of animals that seems overall most similar to the original ancestors of many of the mammalian groups, and to the primates in particular. Because equation #10, the "Homocentric" equation, allows the E.Q. to be immediately expressed in a percentage of the modern human value, and because we *are* the most highly cephalized creature, this equation serves the same descriptive purpose of equation #1, except that we ourselves become the standard for comparison.

But what of phylogenetic realtionships? Why not compute E.Q.'s for the Prosimii from a "basal insectivore" line? Why not compute E.Q.'s of New World monkeys from a prosimian line, or those of Old World monkeys from prosimians, or indeed, given the small-sized and primitive Oligocene "pongids" (Simons, 1972), compute E.Q.'s for extant pongids from the Prosimian or Old World (or New World) forms? Should the hominids' E.Q.'s be computed from the extant pongid equation, from "basal" insectivores, from a composite of mice, whales, giraffes, lions, walruses, bovids, and dogs, or from a general intrageneric equation that will also vary depending on genera and species chosen?

Two assumptions are inherent in the above discussion: (1) E.Q.'s are useful measures, and we should continue to grind them out; and (2) we really do know something about the ancestral lines from which various taxa (at whatever level) are derived. Both assumptions require challenging and much more thought than they have received previously. E.Q.'s are useful as a composite indicator of brain-body size relationships, and if accurate brain and body weights and absolute dates are available, they could provide a more refined indication of evolutionary dynamics through time. And yes, we do believe we know something about ancestral relationships of extant and even fossil species, however brightly or dimly in particular groups.

Figure 2 shows graphically the results of calculating E.Q.'s for each major primate taxon on the basis of the popular conception of what approximates *the next* lowest taxonomic grade. In other words, prosimian E.Q.'s have been calculated from a "basal insectivore" line, and so forth.

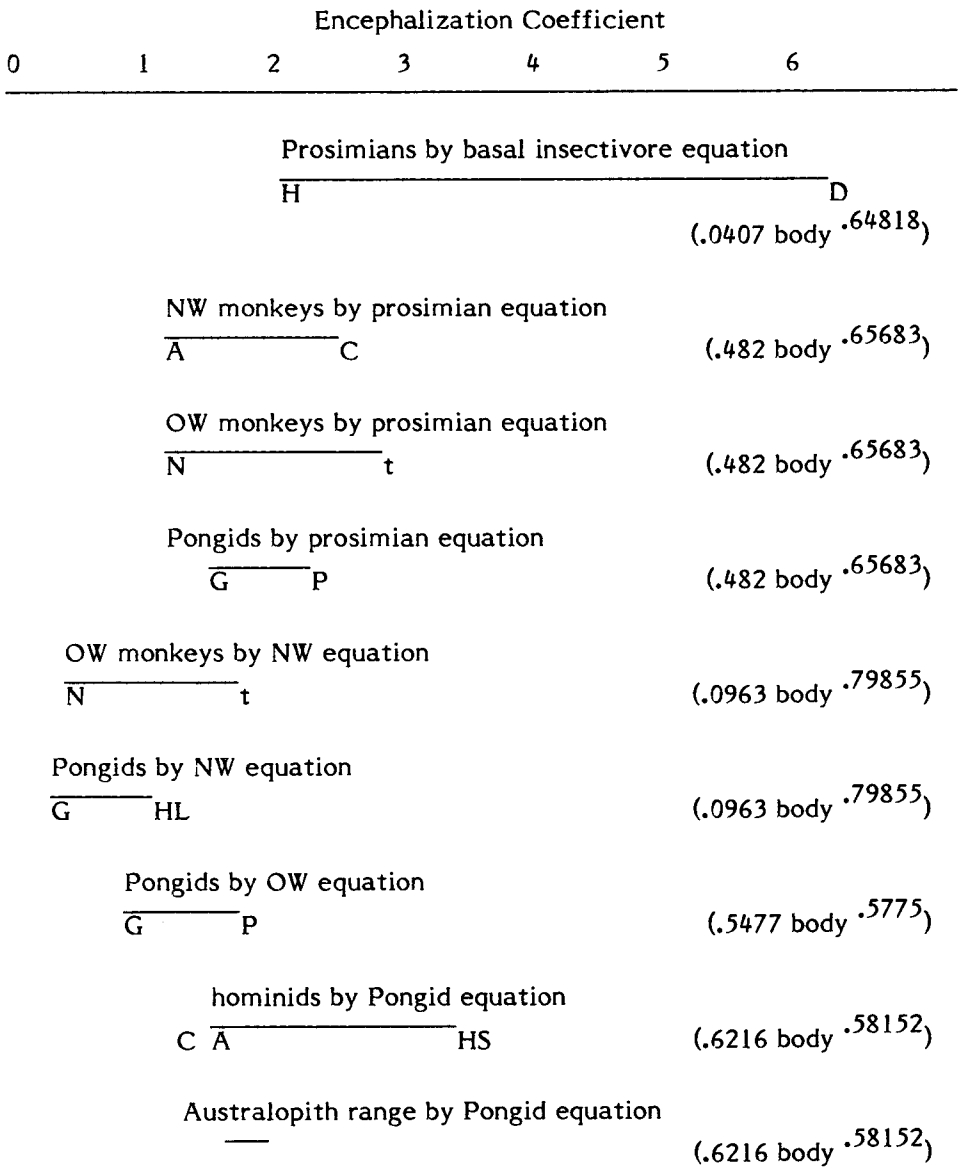

Fig. 2. E.Q.'s computed for different primate taxa based on next-lower grouping. Figures in parentheses are the power equations used to obtain E.Q. values. H = *Hapalemur*; D = *Daubentenoia* (aye-aye); A = *Aotus*; C = *Cebus* (capuchin); N = *Nasalis*; t = talapoin monkey; G = *Gorilla*; P = *Pan troglodytes*; HL = *Hylobates lar*; HS = *Homo sapiens*.

The authors are *not* claiming that these taxa necessarily evolve from their "lower" groups. The figure is purely for descriptive purposes. Indeed, one could justifiably derive the pongids from either a prosimian--or New World monkey--like ancestral base, for example, and both New World and Old World monkeys from a prosimian-like base. The most striking aspect of the figure is that almost all groups are considerably overlapping in their E.Q. ranges when approached in this manner. The exceptions are the Old World monkeys and pongids from their respective base lines and the Prosimian range based on an insectivore line. One *could* conclude that the Prosimians show the highest relative E.Q. scores of all primates, including modern *Homo.*

We are not claiming this approach to be more logical than using equations based on distantly related species, as in equations 1 or 2, or 10. Indeed, the lie is given away when one places some of the newest, and one supposes more accurate, estimations of Gurche's (1978, this volume) brain and body weights for certain fossil prosimians along the prosimian-from-basal insectivore regression equation. Only *Rooneyia* falls within the extant prosimian range, suggesting that ancestral groups differed in brain-body scaling relationships. The derivation of hominid E.Q. scores from the extant pongid line is interesting in that even the heaviest of the hypothetical STS 5 *Australopithecus africanus*, with a body weight of 54 kg (119 pounds), does not overlap the highest encephalized pongid, the chimpanzee.

Perhaps a more specific and recent example would help in this question. The newly discovered Hadar 133-45 adult cranium (Johansen and White, 1979) has a reconstructed endocast whose volume is about 500 ml (RH, unpublished). If the brain/body weights ratio were the same as the chimpanzee average, body weight would be 55,555.5 grams, or 122.5 pounds, a value considerably above published estimates. With a figure of 75 pounds for body weight and 500 ml for brain volume, the E.Q. scores for the Hadar adult range from 54.7 to 63.1% of the E.Q. for modern *Homo sapiens.* The two extreme values are for equations #8 and #7 respectively, or Old World and New World monkeys. In Table 3 the chimpanzee E.Q. percent of the modern *Homo sapiens* values are 38.6 and 41.4% respectively.

Three points should be emphasized here. First, assuming a body weight of 75 pounds for the Hadar adult, the E.Q.'s are well advanced over the pongid range. Second, the differences between values (based on different equations) increase as the brain/body weights ratios increase (Table 3). Third, if the body weight for the Hadar 133-45 adult were lighter, the percentage of modern human E.Q. score would increase. White's (1980) discussion of hominid mosaic evolution overlooks the clear possibility that relative brain size had undergone evolutionary change by 3.5 million years ago. *For all we know at the present time, relative brain size could have preceded full bipedal locomotion in hominid evolution, and such an interpretation could be dependent on the data base chosen to calculate the E.Q. scores.*

This point is not an attack on the *mosaic* nature of human evolution (McHenry, 1975; White, 1980). If evidence suggested that brain/body ratios were higher than those of pongids during the earlier phases of hominid evolution, we would suggest that selection pressure on growth and development had altered in the past, with concomitant effects on such factors as postnatal dependency time and brain maturation, all of which occurred within a social-environmental matrix. One of us (Holloway, 1975, 1976, 1979) has consistently explored these ideas. The point we are making is that a strict adherence to any one "just-so" mosaic theory of human evolution could dim our perceptions regarding the importance of the brain throughout our evolutionary history.

These statistical exercises show that relative brain size parameters, such as E.Q.'s, are relative to the data bases chosen, and that although the rank-order correlations between E.Q.'s for some 89 primate species are high regardless of the chosen base lines, rank-orders do shift, and placements of hominids with regard to modern *Homo*, or chimpanzee, can vary by almost 20%. These kinds of shifts can effect interpretations of time-related shifts in the nature of hominid mosaic evolution, leading to a polarization of conceptual viewpoints regarding the role of the brain in human evolution. The tendency to reify these primitive heuristic devices (E.Q.'s) needs examination and correction, so that E.Q.'s remain a useful "first-step" tool in analyzing evolutionary trends, rather than being enshrouded with an unrelativistic and objective "mystique." E.Q.'s are residuals from a log-log regression line between two variables, brain and body weights, and although surely some biologically relevant connection exists between the two, perhaps in terms of "minimal brain mass," or body surface area to volume, relationships to behavioral evolution or other biologically relevant factors are neither known nor explained. Furthermore, one should not assume (except for purposes of testing hypotheses) that the same set of biological relationships is homogeneous throughout all taxa of animals. That is, different taxa could scale differently for different reasons.

Finally, there is a critical need for evaluating the data bases to be chosen when using these E.Q. scores, as well as articulating their purposes, whether purely descriptive or phylogenetic. Until this is done, these heuristic devices really tell us nothing about brain-behavioral evolution.

SPECULATIVE COMMENTS

This paper has been purposefully lacking in speculation about brain evolution in the Hominidae. Our queries regarding appropriate data bases for calculation of E.Q. scores, and the various tables presented in this paper should not be construed as a blanket acceptance of allometry being a sufficient explanatory base for hominid brain evolution. Indeed, as indicated elsewhere (Holloway, 1979, 1976, 1975), brain-size changes through time are viewed as but one phenotypic facet that requires synthesis with other levels of neurobiological structuring, such as reorganization and heirarchy (or

timing differentiation, development, and growth of the brain and its parts). Here we show that, insofar as gross brain and body size units are to be manipulated to measure neural evolutionary change, i.e., E.Q.'s or other measurements of cortical cephalization (e.g., Jerison's N_C's or "extra cortical neurons," 1973), the relational position of any given hominid (or primate) will vary according to the data base. Viewpoints on the nature of mosaic human evolution, meaning the interpretation of major evolutionary "events" (e.g., bipedalism, canine reduction, tool-making and manual dexterity, brain evolution) will covary with the weighting of E.Q. values. Whatever the "true" australopithecine or habiline configurations of brain and body weights, those figures and the resulting E.Q.'s do not address such important issues as reorganization and/or hierarchy during the evolution of the brain. E.Q.'s are not currently related to hemispheric asymmetry and specialization in modes of cognitive functioning. Yet comparative studies are showing very distinct asymmetrical (petalial) patterns between pongid and hominid endocasts (Holloway and de Lacoste, in preparation; LeMay et al., this volume). Nor are E.Q.'s correlated with endocast stereoplotting studies (Holloway, 1981), which suggests that once allometric changes are taken into consideration, hominid and pongid taxa significantly differ in endocast surface shape, particularly in the inferior parietal region. Nor have E.Q.'s yet been used to investigate the extremely thorny issues of the position of the lunate sulcus (Falk, this volume) and its significance for differentiating between pongid and hominids, both structurally and functionally.

The relativism in relative brain size should be kept in perspective, as *one* element in brain evolutionary change. Allometric explanations are interesting initial attempts to provide a window on complex changes that occurred through time. Ultimately, the alterations will be linked to changes in regulatory DNA, that part of the genome that initiates, terminates, and sustains complex molecular events at the level of structural DNA, and that controls the unfolding of sequences in interaction within a bodily and social environment.

A preoccupation with what is *presently* quantifiable can blind us in seeking more holistic syntheses between comparative and paleoneurological evidence or mask the probable complexity of evolutionary change in primate brains.

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