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JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN
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Irving T. Diamond, *Evolution of the Primate Neocortex*; March 23, 1981

*Robert D. Martin, *Human Brain Evolution in an Ecological Context*; April 27, 1982

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*Published versions of these lectures can be obtained from The American Museum of Natural History, Central Park West at 79th St., New York, N.Y. 10024.

†Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.

HUMAN BRAIN EVOLUTION IN AN ECOLOGICAL CONTEXT

INTRODUCTION

Several previous James Arthur Lectures have dealt with the question of overall brain size and morphology in human evolution (Harman, 1956; Tobias, 1971; Holloway, 1973a; Radinsky, 1979), considering the question from a variety of different angles. It is by now well established (see Gould, 1966, 1975; Jerison, 1973) that any discussion of brain size in evolution must be accompanied by appropriate reference to body size, taking into account any effects of *allometric scaling*. In overall evolutionary terms, reference to the absolute size of the brain alone is of little value, and if scaling of the brain to body size is found to be non-linear (i.e., *allometric*, as opposed to *isometric*), use of simple ratios is equally uninformative. Many studies have now revealed that various biological parameters of vertebrate groups (e.g., brain size in mammals) scale allometrically with body size and there is widespread use of the *empirical allometric formula*:

$$Y = k \cdot X^{\alpha}$$

to describe the overall relationship between any given parameter (Y) and body size (X). In its logarithmic form, this equation becomes linear:

$$\log Y = \alpha \cdot \log X + \log k$$

and it is a relatively simple matter to determine a best-fit straight line for any set of logarithmically transformed data. This permits inference of values for the allometric exponent (α) and for the allometric coefficient (k). There is still some controversy over which line-fitting technique to use for determining allometric relationships and varying use has been made of the three best known techniques: regression, reduced major axis and major axis. For reasons discussed elsewhere (Pilbeam and Gould, 1974; Harvey and Mace, 1982; Martin, 1982) the major axis is used throughout the present paper. In some cases, it is found that logarithmically transformed data for

paired values of a given parameter (e.g., brain size and body size) fit a single straight line fairly closely, and where the correlation coefficient (r) is high it makes little difference which line-fitting technique is employed. In other cases, however, it is found that the data show wide scatter and the choice of best-fit line then affects the conclusions drawn. Finally, it is commonly found that the data fit two or more separate lines (characteristically with closely similar slopes) of differing elevation, as shown in figure 1. In such cases, one can recognize the existence of different *grades* in the allometric relationship between the selected parameter and body size (Martin, 1980). When the data are derived exclusively from living species, the recognition of distinct grades is relatively unproblematic, though a certain degree of subjectivity in interpretation may be involved. However, caution must be exercised when relationships are determined for fossil forms. As pointed out previously (Martin, 1980), description of an allometric relationship for a time series of fossil forms approximating an evolutionary sequence ("phylogenetic allometry"—see Gould, 1966) may be of little value, since this combines the two phenomena of a grade-shift through time and phylogenetic change in body size. For instance, in hominid evolution it happens to be the case that there has been an overall trend toward increase in body size as well as a trend in increased brain size, and the high slope value obtained by fitting a best-fit line to brain and body size data for a time sequence of hominid fossils (e.g., Pilbeam and Gould, 1974) results from the combination of these two trends (see fig. 1). If in human evolution the trend toward increased brain size had been combined instead with a gradual *decrease* in body size over time (phyletic dwarfing), a *negative* slope value would have been obtained despite the enhancement of relative brain size. Failure to separate the effects of phyletic size change from allometric scaling effects has been a major source of confusion in discussions of size-related characters in human evolution.

Proper application of allometric analysis to quantifiable characters such as brain size permits effective comparison of large numbers of species of widely differing body sizes. This greatly increases the generality of any conclusions which may be drawn and avoids the common problem encountered in studies of human evolution where

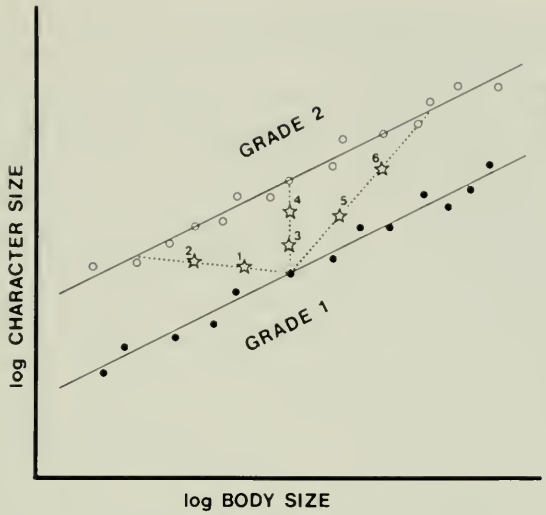

FIG. 1. The concept of allometric "grades." Species belonging to two separate grades (black circles = grade 1; open circles = grade 2) obey the same scaling principle, reflected in the common slope of the parallel straight lines. Grade shifts in the course of evolution involve vertical readjustment on the graph, relative to the scaling trend. When fossil forms (stars 1–6) are available to document such a grade-shift, fitting of best-fit lines confuses change in body size with vertical readjustment on the graph. Decrease in body size combined with an upward grade shift (stars 1 and 2) results in a negative slope value, while increase in body size (stars 5 and 6) produces a positive value and maintenance of constant body size (stars 3 and 4) would produce a value of infinity! [Diagram modified from Martin, 1980.]

far-reaching conclusions are drawn from a very restricted data base. There are now numerous examples, notably with respect to brain size : body size relationships, demonstrating the value of allometric analysis in the following areas:

1. Recognition of general scaling principles, as reflected by the empirically determined value of the slope (exponent α) for logarithmically transformed data plots.
2. Recognition of differential adaptations, where individual species (outliers) or entire groups of species (distinctive grades—fig. 1) separate out on the logarithmic data plot. Here, the empirically determined allometric relationship can be used as a basis for calculating indices reflecting the departure of individual species

from an overall trend. Such indices have, for example, been calculated in various ways for mammals to provide a measure of relative brain size which effectively takes account of body size differences (e.g., "encephalization index" of Stephan, 1972; "encephalization quotient" of Jerison, 1973 and of Eisenberg, 1981).

3. Testing of specific hypotheses, by predicting scaling relationships for individual species from consideration of other evidence.
4. Prediction of unknown values (or, simply, "expected" values) for species where the body size is known but the dimension of a particular parameter, such as brain size, may not be known in advance. This application may, of course, fall under the heading of hypothesis-testing as well.
5. Inference of functional relationships from empirically determined patterns of allometric scaling. The manner in which a given parameter varies with body size, following some recognizable scaling principle, may suggest underlying functional processes. However, it must be emphasized that allometric analysis is a purely *empirical* procedure and that any hypotheses generated from the results must be subjected to detailed scrutiny using other evidence before the *correlations* recognized can be confidently linked to underlying *causal relationships* (see later).

APPLICATION OF ALLOMETRIC ANALYSIS TO THE EVOLUTION OF THE HUMAN BRAIN

In the following discussion, the basic concepts of allometric analysis are applied in a number of different ways in order to identify special features of human brain evolution. Wherever possible, the comparisons involved will be as broad as available data permit in order to place *Homo sapiens* in perspective among his closest relatives, the primates, and indeed among the placental mammals generally. In some cases, the allometric relationships concerned involve an analysis of the typical adult condition for a wide range of species (*interspecific allometry*), whereas in others developmental aspects within individual species (*ontogenetic allometry*) are considered. In all instances, however, the common goal will be to identify what is

so special about the size of the human brain (including its ontogenetic development to reach that size) and to extract clues which indicate possible ecological factors that have promoted the emergence of a particularly large brain during human evolution. In doing this the evolution of the human brain will be examined from a somewhat unusual standpoint. Numerous research workers, including a large proportion of previous lecturers in the James Arthur Lecture series, have concerned themselves with determining, at various levels, how the human brain functions, and spectacular advances have of course been made in this domain. Other investigators have sought explanations for the large size of the human brain in terms of specific selection pressures, such as the requirements of increasing complexity of social life (Holloway, 1973a). In other words, they have asked why human beings should have *needed* increasingly large brains in the course of their evolution. But there is a third approach which may be taken, which is specifically relevant in ecological terms. It is well known that the human brain (especially the gray matter—Thews, 1960) requires a great deal of energy both for its development and for its maintenance (e.g., see Armstrong, 1982a). For instance, in the adult human being the brain represents only about 2 percent of body weight, yet it consumes some 18 percent of the body's energy (Lazorthes et al., 1961—cited in Blinkov and Glezer, 1968). One might therefore ask how, in energetic terms, human beings can support such an exceptionally large brain and how, in the course of human evolution, additional energy was made progressively available to meet the needs of an ever-increasing brain size. This is the question that will be asked in the following pages and, as might be expected from a somewhat unusual approach, some rather unexpected answers will be seen to emerge.

SCALING OF BRAIN SIZE IN PRIMATES AND OTHER MAMMALS

There is now a substantial literature dealing with allometric analysis of brain size in mammals generally and in primates in particular (Bauchot and Stephan, 1966, 1969; Stephan, 1972; Jerison, 1973, 1977; Gould, 1975; Martin, 1981; Passingham, 1975, 1981; Szarski,

1980; Armstrong and Falk, 1982). Considerable success has been achieved in identifying separate grades of relative brain size among the mammals and in examining the brain size of individual species (such as man) in relation to some common baseline. Bauchot and Stephan, for instance (see Stephan, 1972) have taken the allometric relationship for relatively primitive members of the order Insectivora (families Soricidae, Tenrecidae, Erinaceidae) as a baseline against which to compare other mammals, following the rationale that relative brain size in these insectivores represents a minimal condition for modern mammals. The relative enlargement of the brain in other mammals can be expressed as an encephalization index ("index of progression"), using the empirical formula determined for the allometric relationship between brain size (E, in mg) and body size (P, in g) in "basal insectivores":

$$\log_{10}E = 0.63 \cdot \log_{10}P + 1.63 \qquad (1)$$

Calculation of the index value for any individual mammal species simply amounts to dividing the actual brain size of that species by the "expected" value predicted from the basal insectivore equation for the body size concerned. This can be illustrated (fig. 2) by plotting best-fit lines for the relationships between cranial capacity and body weight for the following 4 "grades":

1. "basal" insectivores (hedgehogs, shrews, and tenrecs)
2. "advanced" insectivores (moles, desmans, elephant-shrews, tree-shrews, etc.)
3. strepsirhine primates (lemurs and lorises)
4. haplorhine primates (tarsiers, monkeys, and apes).

[N.B. Cranial capacity in cc. is approximately equivalent to actual brain weight in g, at least for insectivores and primates, and the two measures of brain size are therefore used interchangeably in the following text, though actual brain weight is used wherever possible.] As shown by Bauchot and Stephan for actual brain weights (1969; see also Stephan, 1972), the best-fit lines through these four grades all have similar slopes. Major axes fitted to the data in figure 2 have slopes averaging 0.68 (range: 0.62–0.75). Compared with the basal insectivore line, advanced insectivores typically have brains twice

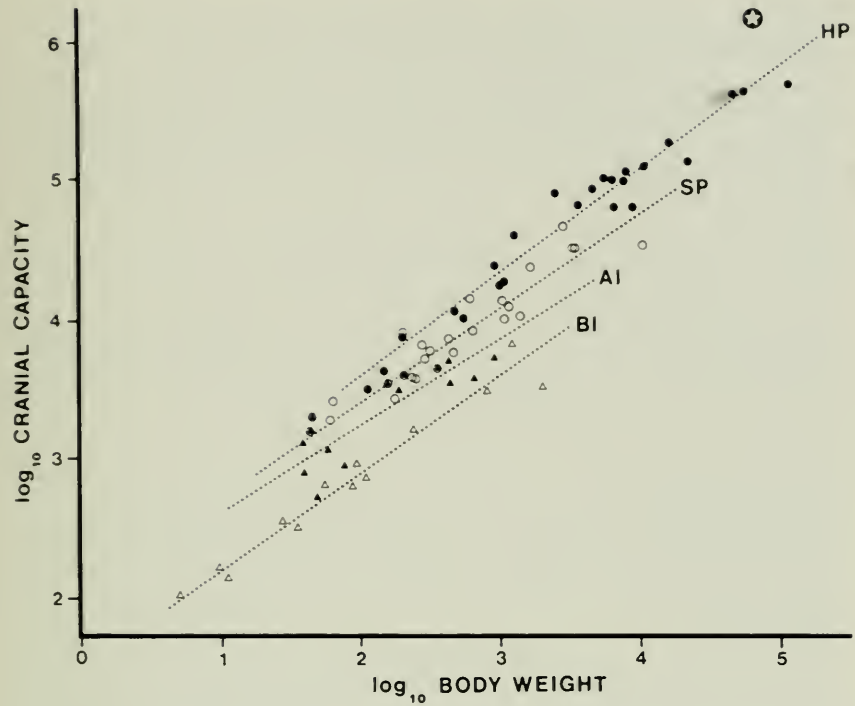

FIG. 2. Logarithmic plot of cranial capacity (C. in mm^3) against body weight (P. in g) for:

(i) "basal" insectivores (BI): open triangles (N = 13)

$$\log_{10}C = 0.68 \cdot \log_{10}P + 1.51 \qquad (r = 0.98)$$

(ii) "advanced" insectivores (AI): black triangles (N = 15)
[N.B. Black triangles for five tree-shrew species surrounded by circles.]

$$\log_{10}C = 0.62 \cdot \log_{10}P + 1.99 \qquad (r = 0.94)$$

(iii) strepsirhine primates (SP): open circles (N = 22)

$$\log_{10}C = 0.68 \cdot \log_{10}P + 2.07 \qquad (r = 0.94)$$

(iv) haplorhine primates (HP): black circles (N = 25)

$$\log_{10}C = 0.75 \cdot \log_{10}P + 2.07 \qquad (r + 0.97)$$

Homo sapiens (not included in haplorhine best-fit line calculation) shown by white star in black circle. Best-fit lines are major axes.

Cranial capacities are based on average measurements for eight skulls (wherever possible) of each species, using sintered glass beads. Body weights are taken from the literature (Stephan, Bauchot, and Andy, 1970; Rudder, 1979; Eisenberg, 1981).

as big, strepsirhines typically have brains almost four times larger, and haplorhines as a group have brains seven times larger. *Homo sapiens* has a brain size about 20 times larger than would be expected for a basal insectivore of the same body size (if such a creature were to exist) and obviously stands out in relation to haplorhine primates, having a brain size about three times larger than typical haplorhines (such as the great apes). Incidentally, figure 2 also shows that the great apes (chimpanzee, gorilla, orang-utan) follow the common haplorhine pattern; although the great apes do have larger brains than monkeys, this can be attributed simply to their larger body size. *Homo sapiens*, by contrast, clearly is more advanced than both monkeys and apes in terms of relative brain size.

An alternative approach to calculating an index of relative brain size has been pioneered by Jerison (1973), who selected as his baseline the *typical* condition for modern mammals, rather than the *minimal* condition. Jerison's "encephalization quotient" is based on an overall best-fit line for mammals, which he expressed by the following formula (converted to the units used throughout this text):

$$\log_{10}E = 0.67 \cdot \log_{10}P + 2.08 \qquad (2)$$

(As before, E = brain weight in mg; P = body weight in g.) On this basis, *Homo sapiens* has an encephalization quotient value of 6.3, indicating that modern man has a brain size just over six times bigger than would be expected for a "typical" mammal lying directly on the best-fit line (Jerison, 1973). In practice, there is little difference between the encephalization index of Bauchot and Stephan (Stephan, 1972) and Jerison's encephalization quotient, since the values taken for the allometric exponent (α) are very similar (0.63 vs. 0.67). Hence, Jerison's quotient values for individual species are approximately one-third of the index values given by Bauchot and Stephan's formula.

Recently, however, a fundamental problem has arisen with respect to the best-fit line for brain : body size relationships in mammals. Jerison (1973) followed a long tradition in accepting the value for the allometric exponent (α) as 0.67 and in fact assumed this value to be correct in determining his allometric equation for calculating encephalization quotient values (see also Pilbeam and Gould, 1974).

Statistical analysis of markedly larger samples of data for mammal species has now shown the exponent value to be closer to 0.75 (Bauchot, 1978; Eisenberg, 1981; Martin, 1981; Hofman, 1982). Eisenberg and Redford (see Eisenberg, 1981) determined the following empirical formula for a sample of 547 mammal species, including marsupials:

$$\log_{10}E = 0.74 \cdot \log_{10}P + 1.74 \qquad (3)$$

[Converted to give units as for equation (1) above.]

Similarly, Martin (1981) determined the following formula for a sample of 309 placental mammals (see fig. 3):

$$\log_{10}E = 0.76 \cdot \log_{10}P + 1.77 \qquad (4)$$

In the latter case, the 95 percent confidence limits on the exponent value obtained from the slope of the major axis (0.73–0.78; r = 0.96) were found to exclude the previously accepted value of 0.67. This obviously has implications both for determination of indices derived from the allometric relationship and for hypotheses regarding the functional significance of relative brain size. In fact, all the potential applications of allometric analysis listed above depend upon the empirical values determined for the relationship between brain size and body size in mammals. It is therefore important to establish a fairly conclusive allometric formula for the mammals.

One justification for accepting the higher value of approximately 0.75 for the allometric exponent in the mammalian brain : body size equation (e.g., fig. 3) is that all analyses involving really large samples of mammal species (N greater than 240) agree in producing exponent values closer to 0.75 than to 0.67. The data set compiled by Crile and Quiring (1940), which has been widely used by previous authors (including Jerison, 1973) and which does actually yield an exponent value close to 0.67 (Martin, 1982), included only 97 mammal species and did not provide a representative selection of mammals (notably at the upper end of the body size range). Nevertheless, it might be argued from an examination of figure 3 that the exponent value determined for the much larger sample of 309 mammal species is biased by the preponderance of relatively small-brained species at

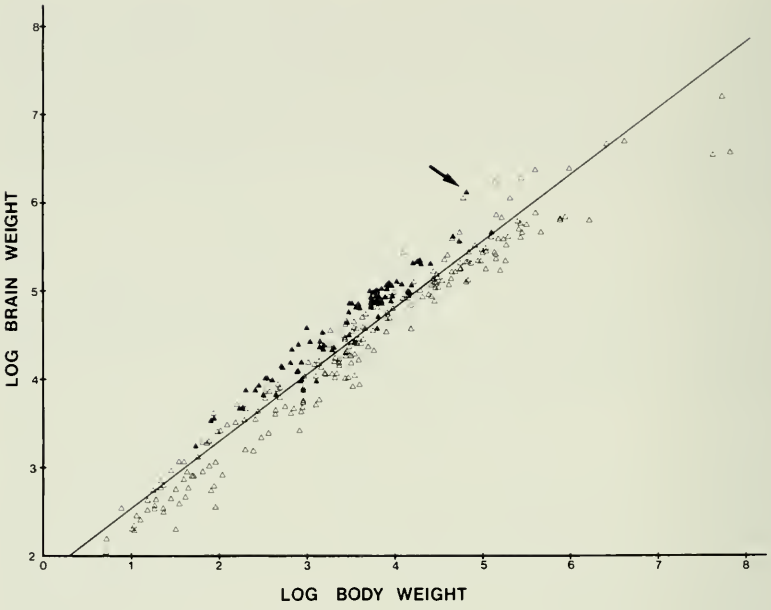

FIG. 3. Logarithmic plot of brain weight (E, in mg) against body weight (P, in g) for a sample of 309 placental mammal species. Open triangles = non-primates; black triangles = primates; arrow indicates *Homo sapiens*. Best-fit line is the major axis. (From Martin, 1981, reprinted by permission from *Nature*, vol. 293, no. 5827, pp. 57–60. Copyright © 1981 Macmillan Journals Ltd.)

the lower end of the graph (though the small-brained whales at the other end would surely counterbalance this, to some extent at least). In order to remove any preponderant influence of one large group of mammals falling into a particular grade of relative brain size, the allometric equation was recalculated for the data in figure 3 by taking the average values for $\log_{10}E$ and $\log_{10}P$ for each of the 10 orders of placental mammals represented. As shown in figure 4, these average values show a very clear straight line relationship, with a very high correlation coefficient ($r = 0.993$) and a slope close to 0.75:

$$\log_{10}E = 0.78 \cdot \log_{10}P + 1.61 \qquad (5)$$

The 95 percent confidence limits of the slope of the major axis (0.72–0.84) once again exclude the value of 0.67 as being too low. It is also interesting to note that this analysis does reveal that the primates

are somewhat distinctive as an order in terms of the overall expression of relative brain size (fig. 4), whereas this is not obvious from a plot of individual species (fig. 3) because of the considerable variability within orders of mammals and overlap between them when values for individual species are plotted. In any event, the evidence suggests that the correct value for the empirically determined allometric exponent governing brain : body size relationships in placental mammals is not 0.67 but significantly higher than that, in the region of 0.75.

There is, however, another major problem involved in identifying exponent values for brain : body size relationships in mammals. It is a well-known fact (e.g., see Pilbeam and Gould, 1974; Gould, 1975; Mace, Harvey, and Clutton-Brock, 1980) that the exponent value tends to decrease with decreasing level of the taxonomic unit examined. Whereas a value close to 0.75 seems to be appropriate for the eutherian mammals overall, individual orders or suborders of mammals tend to yield lower exponent values (e.g., fig. 2) and average exponent values usually decrease further as even lower taxonomic levels (e.g., families; subfamilies; genera) are considered, with the lowest values of all obtained with comparisons of adult individuals of a single species (*intraspecific allometry*). The reasons for this phenomenon remain obscure, though a theoretical explanation may ultimately emerge (e.g., see Martin and Harvey, in press). In practice, this variation in exponent value with taxonomic level means that the conclusions reached may vary with the level at which allometric analysis is conducted, leading to a certain degree of subjectivity and confusion (as was recently aptly pointed out with respect to hominid evolution by Holloway and Post, 1982). Of course, until we understand why exponent values vary in this way, it will remain difficult to decide which is the "correct" value to take in a given situation; but two pragmatic guidelines recommend themselves:

1. The exponent values used should be appropriate to the particular comparisons involved. For instance, in comparing strepsirhine primates with haplorhine primates (fig. 2), we should use allometric equations which are derived from analyses of these two major subgroups of the order primates.

FIG. 4. Average values for logarithms of brain weight (E, in mg) and body weight (P, in g) for 10 orders of placental mammals (circles), with the best-fit line (major axis). Marsupials (M in diamond) actually lie quite close to the best-fit line for placentals. Ungulates (U) are treated as a single order; separate values for artiodactyls do not affect the results of the analysis.

Key:

B = bats (Chiroptera)
I = insectivores (Insectivora), including tree-shrews
R = rodents (Rodentia)
L = rabbits and hares (Lagomorpha)
E = edentates (Edentata)
P = primates (Primates)
C = carnivores (Carnivora)
U = hoofed mammals (Ungulata)
S = seals and sea-lions (Pinnipedia)
D = dolphins and whales (Cetacea)

Note that the average value for primates (arrowed) lies highest relative to the line, indicating a greater emphasis on large brain size in the order Primates overall.

(N.B. an independent regression analysis conducted at the order level by Armstrong, 1982b on 93 mammal species belonging to 16 orders yielded an exponent value of 0.72; r = 0.95).

2. Since at least part of the variation in exponent value with taxonomic level is due to statistical side-effects of decreasing sample size (Martin and Harvey, in press), comparisons should be conducted at the highest possible taxonomic level, wherever there is

a choice, in order to include a maximum number of species and a maximal range of brain and body sizes.

These two guiding principles are used consistently in the following discussion.

FUNCTIONAL INTERPRETATION OF BRAIN SIZE SCALING IN MAMMALS

As long as it was generally accepted that brain size scaled to body size with an exponent value of 0.67 in mammals and in other vertebrates, it was logical to seek some explanation of brain size scaling in terms of surface : volume relationships, which are governed by an exponent of the same value. Indeed, Jerison (1973, p. 49) specifically comments on this possibility: "We should note that an exponent of ⅔ implies a surface : volume relationship and may, therefore, be the basis for theorizing on the significance of brain size." But now that there is good evidence that the exponent value for mammals is considerably higher than 0.67, some alternative explanation of the significance of brain size scaling relationships must be sought. One immediate possibility that presents itself is a link between relative brain size and metabolic turnover. It has been known for some time (Kleiber, 1932, 1947, 1961; Brody, 1945) that basal metabolic rate in mammals and other vertebrates (viz., the quantity of oxygen consumed, or of calories produced, in a standard time at rest) scales to body size with an exponent value of approximately 0.75 ("Kleiber's Law"). More recently (Mace and Harvey, 1982), it has been shown for a sample of mammals and birds that *active* metabolic rate (i.e., total metabolic turnover, including energy spent in activity, over a standard time) also scales in a negatively allometric fashion. The coincidence between the exponent values for basal metabolic scaling and brain size scaling might, therefore, reflect some underlying functional relationship between them. In fact, even in the absence of an adequate sample size for brain and body weights in mammals, Brody (1945, p. 619–622) had already suspected the possibility of such a link:

> for mature mammals of different species, the basal heat production increases with the 0.73 power of body weight; the brain weight increases with the 0.70 power of body weight, virtually the same as for basal heat production. . . . The most conspicuous feature is that the slope of the curve relating brain weight to body weight is virtually the same as the slope relating basal heat production to body weight. . . . Does this close *statistical* correlation imply the presence of a similarly close *causal physiological* interrelation between organ weight and metabolism? It may be so. It is known that the blood supply to the brain—about 13 percent of the cardiac output (Barcroft and others)—is all out of proportion to the relative weight of the brain. Kestner (1935, 1936) estimated that under basal metabolism conditions nearly half of the blood passes through the brain. Hence Kestner's conclusion that under basal metabolism conditions the brain probably conditions the level of basal metabolism. [N.B. Kestner had, in fact, overestimated.]

This prophetic train of thought in fact also underlines one of the major problems involved in proceeding from the results of allometric analysis to inference of functional relationships. It must first of all be established that the similarity of exponent values in metabolic scaling and brain size scaling in mammals is more than a coincidence and reflects some real causal relationship. But it must also be established that this causal relationship operates in a particular direction. Brody's implied suggestion (above) that control of body metabolism depends upon brain size, which was echoed by other authors, has now been largely discredited; but Brody did not mention the alternative interpretation that brain size is instead constrained by the metabolic turnover of the body. This alternative possibility has now been explicitly proposed by Martin (1981) and by Armstrong (1982a, 1982b) and provides an entirely different basis for interpreting brain size evolution in the vertebrates. Even here, there are at least two different hypotheses which can be recognized. The simplest is that an adult mammal requires a particular metabolic turnover to permit operation of its brain tissue, which is (as mentioned above) very expensive in energetic terms. However, this possibility seems unlikely for a number of reasons (Martin, 1981). An alternative hypothesis is that it is the mother's metabolic turnover which, both in direct terms (through the physiology of gestation) and in indirect terms (through the partitioning of resources between maintenance and reproduction), determines the size of the neonate's brain and hence the ultimate size of the adult brain. This latter hypothesis has generated a number of testable predictions, some of which are

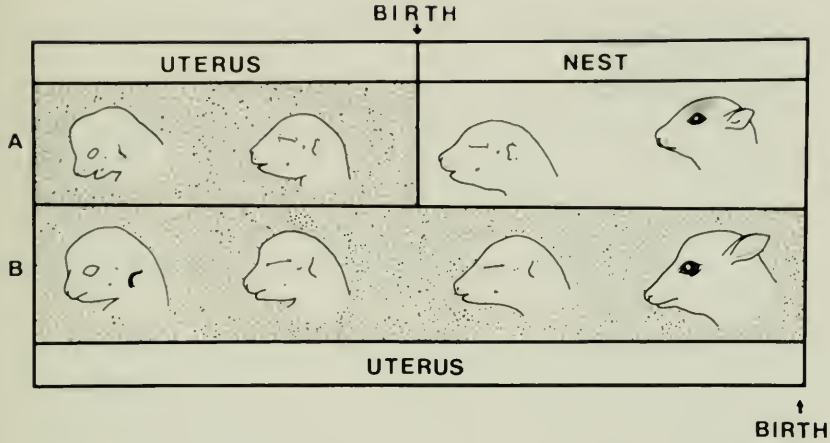

FIG. 5. Contrast between altricial mammals (A) and precocial mammals (B), adapted from Portmann (1962). The gestation period (indicated by stippling) is markedly longer, relative to body size, in precocial mammals compared to altricial species.

considered below, and provides a promising basis for the interpretation of brain size in mammals.

Obviously, if it is the mother's metabolic turnover which exerts a major constraining influence on the developing foetal brain, the size of the neonatal brain will also depend upon the length of the gestation period. For any given maternal body weight with a given metabolic turnover, an increase in gestation period should lead to (or at least permit) an increase in neonatal brain size. This expectation relates directly to a major distinction which can be made among mammals with respect to the state of the offspring at birth (Portmann, 1941, 1962). Once various allometric effects of the mother's body size (e.g., with respect to gestation period and neonate weight) have been taken into account, most mammal neonates can be classified into two major types (fig. 5):

1. *Altricial neonates:* Fairly large litters of small neonates born after a relatively short gestation period. Both brain and body weight are relatively small at birth, associated with a generally poor level of development (eyes and ears closed; no hair through; incomplete development of homeothermy, etc.). They grow into adults with

relatively small brains. [Examples: most insectivores, carnivores, and rodents.]

2. *Precocial neonates:* Small litters of large young (typically only a single neonate) born after a relatively long gestation period. Both brain and body weight are relatively large at birth, associated with a relatively advanced level of development (eyes and ears open; hair through; homeothermy established, etc.). They grow into adults with relatively large brains. [Examples: primates, ungulates, and cetaceans.]

Altricial mammals are usually born in some kind of nest, whereas nests are quite rare among precocial mammals, and postnatal growth in the relatively sheltered conditions of the nest permits altricial mammals to "catch up" to some extent with precocial mammals despite the relatively poor initial state of development of altricial offspring at birth. Nevertheless, there is obviously some limit to this "catching up" process, since precocial mammals typically have larger brains than altricial mammals when they reach adulthood. When clearly precocial mammals (N = 159) and clearly altricial mammals (N = 87) are analyzed separately, fitting of lines of fixed slopes 0.75 to logarithmically transformed brain and body size data yields the following two equations (E_A = adult brain weight):

1. PRECOCIAL MAMMALS: $\log_{10}E_A = 0.75 \cdot \log_{10}P + 1.90$ (6)
2. ALTRICIAL MAMMALS: $\log_{10}E_A = 0.75 \cdot \log_{10}P + 1.74$ (7)

(A fixed slope of 0.75 is used to facilitate direct comparison.) What this means in practical terms is that precocial mammals grow up into adults which typically have brains some 45 percent bigger than adults of altricial species. This difference is, however, far less than the difference in typical neonatal brain weights between precocial and altricial mammals, as is shown by the following allometric formulae for the empirical relationships between neonatal brain weight (E_N) and maternal body weight (P_M):

1. PRECOCIAL MAMMALS (N = 72):
$$\log_{10}E_N = 0.70 \cdot \log_{10}P_M + 1.65 \quad (8)$$
2. ALTRICIAL MAMMALS (N = 24):
$$\log_{10}E_N = 0.74 \cdot \log_{10}P_M + 0.88 \quad (9)$$

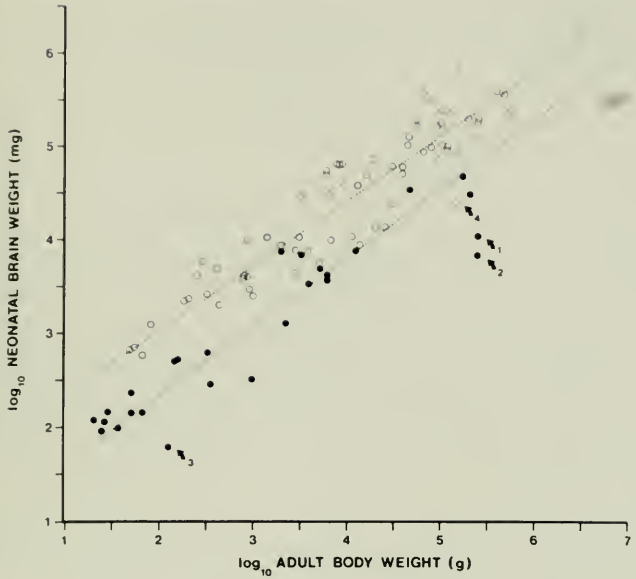

FIG. 6. Logarithmic plot of neonatal brain weight (E_N, in mg) against adult body weight (P, in g) for altricial mammals (black circles; N = 27) and precocial mammals (open circles; N = 72). Best-fit lines are major axes excluding the following aberrant species (outliers arrowed in figure):

1: *Thalarctos maritimus* (lethargic during pregnancy)
2: *Ursus arctos* (hibernating during pregnancy)
3: *Mesocricetus auratus*
4: *Sus scrofa* (unusually large litters)

[Data from Rudder, 1979, and Sacher and Staffeldt, 1974.]

These formulae indicate that precocial mammals have a considerable advantage at birth in terms of neonatal brain weight, which is typically some 4.5 times greater than in altricial mammals (fig. 6).

The distinction between precocial and altricial mammals is important in testing one of the predictions derived from the hypothesis that maternal metabolic turnover (M_M) constrains neonatal brain size (E_N) and hence adult brain size (E_A). For these relationships to lead to a coincidence between the allometric exponents for maternal metabolic turnover and adult brain size (both = 0.75), it must follow that adult brain size scales isometrically ($\alpha = 1$) with respect to neo-

natal brain size. In other words, the relationships should be covered by the following set of formulae (Martin, 1981):

$$\begin{aligned} M_M &= k \cdot P_M^{0.75} \text{ [Kleiber's Law]} \\ E_N &= k' \cdot M_M \\ E_A &= k'' \cdot E_N \\ \text{from which } E_A &= k''' \cdot P_M^{0.75} \text{ [see equation (4)]} \end{aligned} \qquad (10)$$

But equation (10) can only be tested realistically if precocial and altricial mammals are examined separately, since the relationships between E_A and E_N are so radically different between these two groups, primarily because of differences in gestation period not allowed for in the above equations. When adult brain weight is plotted against neonatal brain weight for precocial and altricial mammals separately, the following relationships are found (Martin, 1981):

1. Precocial Mammals (N = 71):

$$\log_{10} E_A = 0.99 \cdot \log_{10} E_N + 0.42 \qquad (11)$$

2. Altricial Mammals (N = 24):

$$\log_{10} E_A = 1.01 \cdot \log_{10} E_N + 0.85 \qquad (12)$$

In both equations, the value determined for the allometric exponent is very close to unity, so the relationships are indeed virtually isometric (viz., $\alpha = 1$) as predicted. In precocial mammals, adult brain size is typically 2.5 times as big as neonatal brain size, whereas in altricial mammals it is typically 7.5 times as big. Unfortunately, neonatal brain weights have only been recorded for relatively few mammals as yet (Sacher and Staffeldt, 1974; Rudder, 1979), so much remains to be done in investigating this key parameter. The best sample as yet available has been obtained for the order Primates (N = 27) and for this particular group of mammals the overall relationship is exactly isometric, with a very high correlation coefficient (r = 0.992):

$$\log_{10} E_A = 1.00 \cdot \log_{10} E_N + 0.37 \qquad (13)$$

This equation indicates that in primates the size of the adult brain is typically 2.3 times as big as the neonatal brain, though there is a limited range of variation among primate species, with the adult brain reaching between 1.5 and 3.5 times its neonatal size (fig. 7).

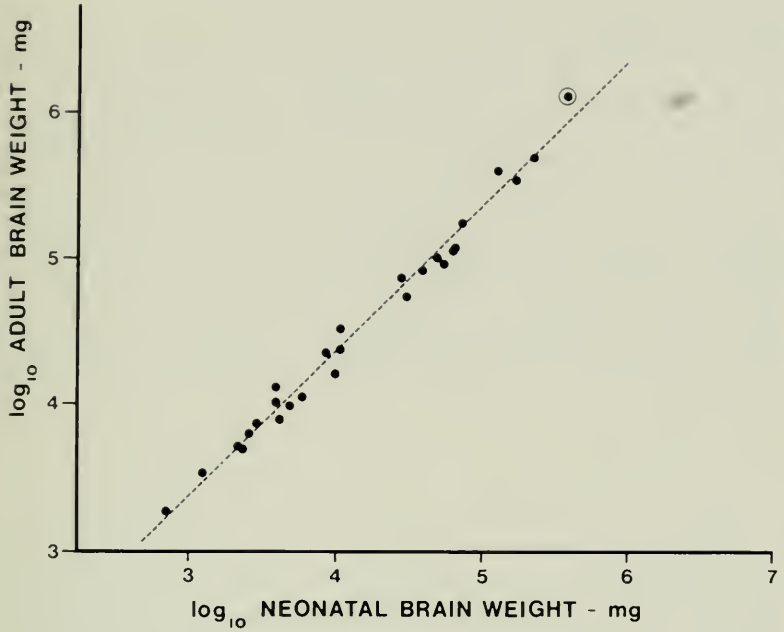

FIG. 7. Logarithmic plot of adult brain weight (E_A, in mg) against neonatal brain weight (E_N, in mg) from primates including man (N = 27 species; outlined circle = *Homo sapiens*); data from Rudder (1979). The slope of the best-fit line (major axis) is exactly unity, indicating isometric scaling (viz., simple proportional size increase) of adult brain relative to neonatal brain. There is a small amount of scatter around the best-fit line, reflecting differential adaptation of individual species (see fig. 15), but the point for *Homo sapiens* shows the greatest upward displacement relative to the line.

In fact, the greatest degree of postnatal brain growth is found in *Homo sapiens* with a value close to 3.5 (see later). This limited amount of variation indicates that, although the relationship between adult brain size and neonatal brain size is isometric in primates overall, there is some permissible individual variation between primate species in the partitioning of brain growth between foetal and postnatal stages. That is to say, individual primate species may follow somewhat different strategies within the general constraint of simple proportional (isometric) increase in size of the brain after birth.

It is fairly obvious that a mammal mother's metabolic capacity

must be related in some way to the growth of her foetus over a given gestation period, and one might therefore expect some relationship to exist between gestation period and the size of the neonate and its component organs. Sacher and Staffeldt have examined this question in a seminal paper published in 1974. They found that a much closer relationship existed between gestation period and neonatal brain size than between gestation period and overall neonatal body size. This provides fairly clear evidence of a particularly intimate connection between gestational processes (including the mother's metabolic capacity) and foetal brain growth, thus singling out the brain as an organ of special significance in the maternal-foetal relationship.

BRAIN GROWTH DURING FOETAL AND POSTNATAL LIFE

There is a particularly interesting relationship between the brain size of mammal species during foetal life, which has been independently recorded by Holt and coworkers (Holt et al., 1975; Holt, Renfrew, and Cheek, 1981) and by Sacher (1982) (see also Gould, 1977). When brain weight is plotted against body weight for mammalian foetal stages of any age, using logarithmic coordinates, it is found that primates are clearly separated from all non-primate mammals (fig. 8). In other words, the growth of the primate foetal brain is found to follow a quite different relationship to total foetal body weight when compared with non-primate mammals generally, though odontocete cetaceans (dolphins, etc.) are a special, intermediate case. Best-fit lines for the available data (fig. 8) yield the following formulae for the relationships between foetal brain weight (E_F) and foetal body weight (P_F):

1. PRIMATES ($r = 0.99$): $\log_{10}E_F = 0.95 \cdot \log_{10}P_F + 2.25$ (14)
2. NON-PRIMATES ($r = 0.98$): $\log_{10}E_F = 0.82 \cdot \log_{10}P_F + 1.87$ (15)
   (excluding cetaceans)

Although the empirically determined values for the slopes are somewhat different (that for primates being almost isometric), thus hindering a direct comparison between the two groups, it can be stated as a crude approximation that a primate foetus of a given weight

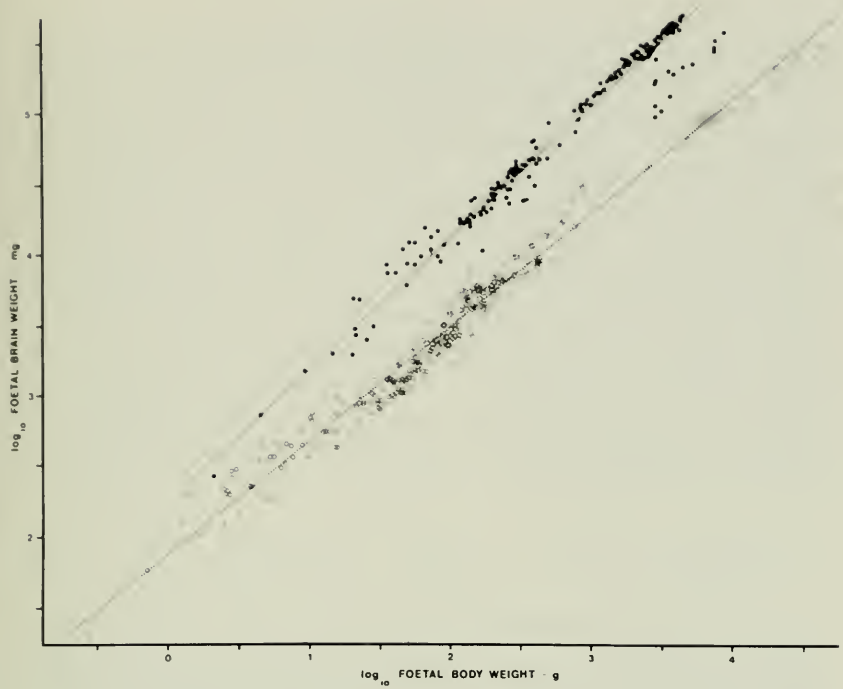

FIG. 8. Logarithmic plot of foetal brain weight (E_F) against foetal body weight (P_F) for primates (black circles), toothed cetaceans (black squares) and other non-primates (open circles). The best-fit lines (major axes) show a major distinction between primates and non-primates. Note that the best-fit line for *Homo sapiens* (uppermost, thin dotted line) coincides very closely with the general best-fit line for primates. Each point represents a single foetus. Data derived from: Latimer (1938), Count (1947), Corder and Latimer (1949), Dickerson and Dobbing (1967), Larroche (1967), Dobbing and Sands (1970), Hendrickx and Houston (1971), Harel et al. (1972), Pirlot and Bernier (1974), Roberts (1975), Holt et al. (1975), Hubert, Stahlheim and Booth (1975), Pirlot and Kamiya (1975), Chambers (1982). These sources yielded 185 points for six primate species (including man) and 305 points for 10 non-primate species.

will typically have a brain weight twice as large as that of a foetus of the same body weight from any other mammal species (see also Sacher, 1982). As yet, data on brain and body weights of foetal stages are only available for a limited number of mammal species and non-primates are particularly poorly represented (fig. 8). For this reason, the distinction between primates and non-primates noted above requires further confirmation. In particular, the data represented in

figure 8 do not include any strepsirhine primate species and numerous non-primate mammal groups are totally unrepresented. But there is some confirmation available for the distinction between primates and non-primates, since the different trajectories shown in figure 8 must logically lead to a difference in the relationship between *neonatal* brain weight and *neonatal* body weight. Sacher (1982) has shown, through an analysis of data from 13 different orders of mammals (see Sacher and Staffeldt, 1974), that there is indeed the expected distinction between all primates (including strepsirhine species) and non-primates in neonatal brain : body weight relationships, with the exception that neonate odontocete cetaceans are again intermediate. The relationships between neonatal brain weight and neonatal body weight for primates and non-primates (fig. 9) are virtually identical with those for foetal development (fig. 8), as predicted:

1. PRIMATES ($r = 0.99$): $\log_{10}E_N = 0.96 \cdot \log_{10}P_N + 2.12$ (16)
2. NON-PRIMATES ($r = 0.99$): $\log_{10}E_N = 0.86 \cdot \log_{10}P_N + 1.85$ (17)

As Sacher (1982, p. 104) points out, the overall pattern suggests that an "extraordinary evolutionary event took place" in the origin of modern primates: "The schedule of primate fetal development was modified by reducing by half the amount of non-neural somatic tissue associated with a given amount of neural tissue throughout the greater part of fetal life."

Apparently, a similar, but less spectacular, change also occurred in the origin of the odontocete cetaceans.

It must be emphasized that figure 8 conveys no information about *rates* of foetal development and that this omission can be a source of confusion. For example, it might be concluded from the difference between primates and non-primates that foetal brain growth has been relatively accelerated in primates. In fact, it is well known that primates have very slow rates of foetal somatic growth compared to other mammals (e.g., see Payne and Wheeler, 1968), so the distinctiveness of primates is doubtless due to a relative deceleration of foetal body growth rather than to acceleration of foetal brain growth (Holt, Renfrew, and Cheek, 1981; Sacher, 1982). Again, this is just what would be expected from the existence of a more intimate connection between maternal metabolic turnover and foetal brain

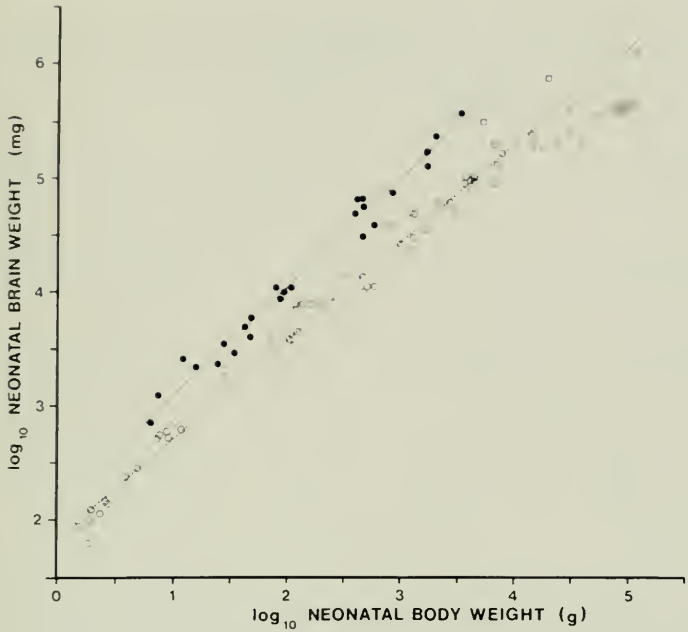

FIG. 9. Logarithmic plot of neonatal brain weight (E_N, in mg) against neonatal body weight (P_N, in g) for primates (black circles; N = 27) and non-primates (open circles; N = 72). Best-fit lines (major axes) are clearly distinct; toothed cetaceans (open squares; N = 3) are again intermediate.

growth than between maternal metabolism and overall foetal body growth. It should also be noted that different primate species may move along the brain growth trajectory shown in figure 8 at different velocities. This is particularly noteworthy in the case of *Homo sapiens*. For instance, the great apes are relatively similar to man in terms of both adult body size (30–100 kg, compared to 57 kg) and gestation period (245–270 days, compared to 270 days; taken from the time of conception in all cases), yet they all produce neonates with brain and body weights approximately half of the neonatal weights found with *Homo sapiens* (table 1). From this it can be concluded that human mothers devote a relatively greater quantity of energy and other resources to foetal brain *and* body development over a standard time than do our closest relatives among the primates, the great apes. But this is achieved by following at a faster

TABLE 1

Neonatal Brain and Body Weights for Man and the Great Apes

Species	Neonatal Body Weight (g)	Neonatal Brain Weight (g)	Source
Homo sapiens	3375[1] (N = 22,413)	384[2] (N = 183)	1. Gibson & McKeown, 1952 2. Jordaan, 1976b
Pan troglodytes	1756[3] (N = 29)	128[4] (N = 2)	3. Keeling & Riddle, 1975 4. Schultz, 1941
Gorilla gorilla	2110[5] (N = 9)	227[6] (N = ?)	5. Joines, 1977; Nadler, 1974; 6. Schultz, 1965
Pongo pygmaeus	1728[7,8] (N = 14)	170[8] (N = 3)	7. Groves, 1971 8. Rudder, 1979

rate the typical primate brain : body growth trajectory shown in figure 8, without significantly departing from it.

Postnatal growth of the brain is also of particular interest with respect to comparison between man and other primates. As has been pointed out by Holt, Renfrew, and Cheek (1981), growth of the brain from conception onward in mammals can be resolved into two relatively distinct phases, an early period of rapid brain growth relative to body size and a subsequent period of slower brain growth. In mammals with precocial young, such as typical primates, the transition from rapid to slow growth of the brain closely coincides with the time of birth, as can be seen from a graph of brain size against age. With altricial mammals, on the other hand, the rapid growth of the brain characteristic of foetal stages in both altricial and precocial mammals is continued for a short period after birth before there is a point of inflection in the growth curve, followed by slower postnatal brain growth (hence the partial "catching up" by altricial mammals noted above).

It is important at this point to recognize that there are two quite different ways of presenting brain growth data. Traditional graphs of brain growth, following the pattern set for body growth, show

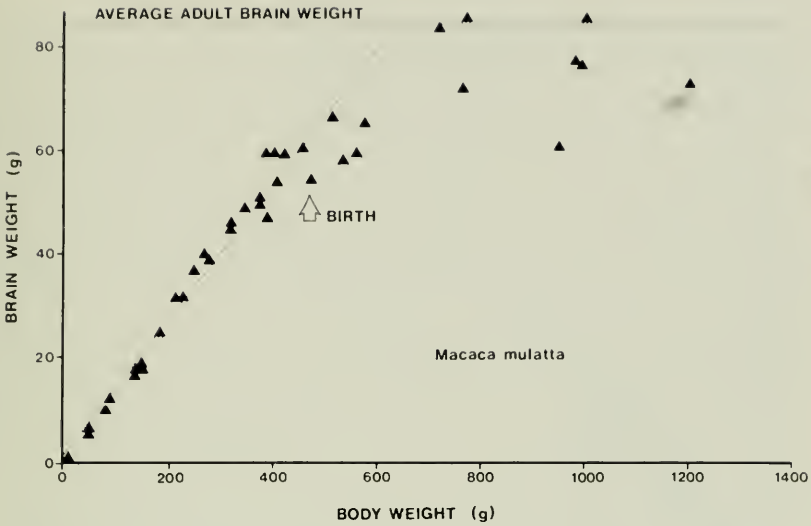

FIG. 10. Plot of brain weight (g) against body weight (g) for developing *Macaca mulatta*. Since the relationship between foetal brain and body weight is virtually isometric [see equation (14)], logarithms have not been used and the major axis (oblique dotted line) has been calculated for the raw data. There is a clear departure from the foetal trajectory at the time of birth in this species, with the brain subsequently developing more slowly with respect to body weight. Data from Holt et al. (1975) and Kerr et al. (1974).

brain size plotted against time and comparisons between species are somewhat complicated. But if brain weight is plotted against body weight on logarithmic coordinates to reflect the trajectory of individual growth, as in figure 8, an approximately straight-line relationship is found for all mammals, though primates and non-primates differ (as shown) in the specific parameters involved. When birth takes place in typical precocial mammals (e.g., primates), further development of the brain follows a flatter trajectory along a line lying beneath the foetal line (as in *Macaca mulatta*—fig. 10). With typical altricial mammals, a similar transition to a flatter trajectory is found, but (as indicated above) this transition is postponed for some time (a period of days or weeks) after birth. *Homo sapiens* is a marked exception to the rule among primates, however, in that the foetal growth relationship between brain and body weight con-

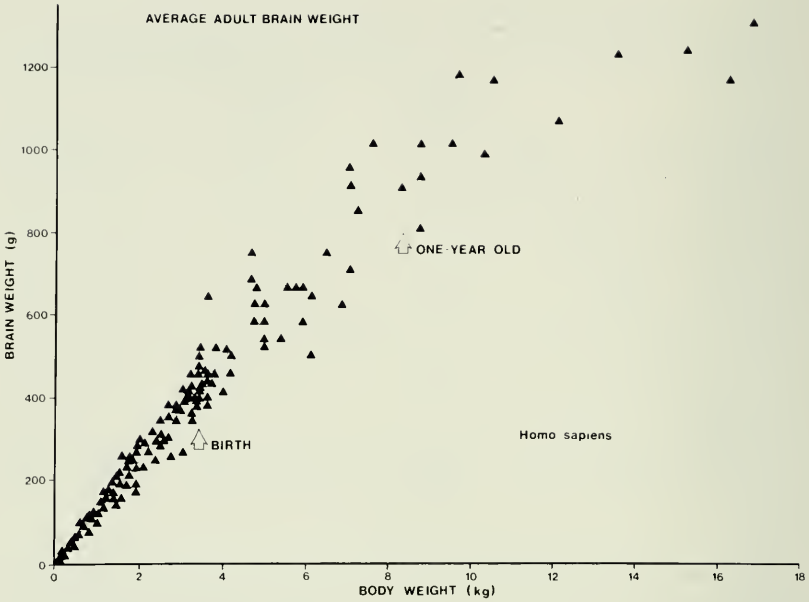

FIG. 11. Plot of brain weight (g) against body weight (kg) for developing *Homo sapiens*. Conventions as for figure 10. Note that there is no clear departure from the foetal trajectory indicated by the major axis (oblique dotted line) until the human infant has reached a postnatal age of approximately 12 months, though scatter about the foetal line increases following birth. Data selected from Larroche (1967), Blinkov and Glezer (1968), Dobbing and Sands (1973), Burn, Birkbeck, and Roberts (1975).

tinues for some time after birth (fig. 11). This peculiarity is connected with the distinctive nature of the human neonate. Although the newborn human infant can correctly be described as precocial in terms of the criteria set out already (see also fig. 5), its degree of helplessness in motor terms is more akin to that found with altricial neonates. It is for this reason that Portmann (1941) referred to the human neonate as "secondarily altricial" and proposed that the one-year-old human infant is closer to the newborn great ape in motor terms (see also Gould, 1977). Portmann cited a number of lines of evidence suggesting that the transition to typical postnatal growth characteristics occurs after the age of one year in humans and concluded that an essentially embryonic growth pattern continues for approximately 12 months after birth. He therefore proposed that

Homo sapiens has the equivalent of a 21-month gestation period, divided into two phases: intrauterine (nine months) and extrauterine (12 months). The plot of brain size against body size for human development (fig. 11) provides dramatic confirmation of Portmann's interpretation, since it clearly shows that a foetal pattern for brain : body relationships is maintained in human ontogeny until at least 12 months after birth. On the one hand, this accounts for the helplessness of young human infants compared with their primate counterparts, since foetal brain growth postponed to the postnatal period may well require relative immobility. On the other hand, the continuation of a foetal pattern of brain growth for such a long period after birth represents a unique feature of *Homo sapiens* in comparison to all other mammals. It is possible, as suggested by Gould (1977), that this special feature of human development can be correctly described as "neotenous" (i.e., involves the retention of characteristics from earlier growth stages), but the situation is complicated since in other respects human development from conception to 12 months after birth is actually accelerated in comparison with, say, the great apes (see also Leutenegger, 1982).

ECOLOGICAL CORRELATES OF RELATIVE BRAIN SIZE

In recent years, a number of attempts have been made to relate relative brain size in primates and other mammals to ecological parameters, notably with respect to feeding ecology (e.g., Eisenberg and Wilson, 1978; Clutton-Brock and Harvey, 1980; Harvey, Clutton-Brock, and Mace, 1980; Mace, Harvey, and Clutton-Brock, 1980, 1981; Mace and Eisenberg, 1982). Among the primates, a particularly good example is provided by analysis of relative brain size in Old World monkeys and apes (Cercopithecoidea + Hominoidea) in relation to differential adaptation for predominant frugivory or predominant folivory. It has been shown by Clutton-Brock and Harvey (1980) that in several primate groups the more frugivorous species tend to have larger brains than related species which can be regarded as specialized folivores. Following the procedure advocated by these authors, one can take generic average values for $\log_{10}$ brain weight

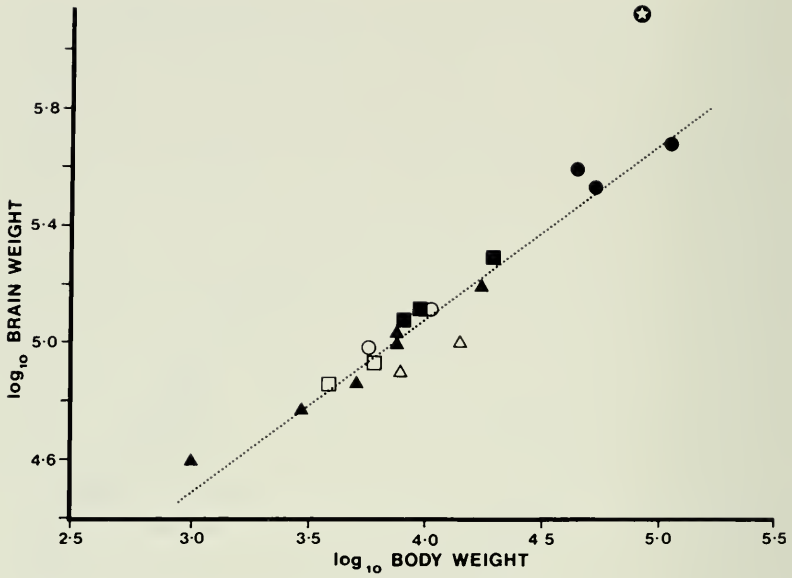

FIG. 12. Plot of average logarithmic values for adult brain weight (E_A, in mg) against adult body weight (P_A, in g) for individual genera of Old World monkeys and apes (Cercopithecoidea + Hominoidea). The best-fit line (major axis) was determined for all genera excluding *Homo*.

Key: Black triangles = forest-living cercopithecines (most *Cercopithecus*; *Miopithecus*; *Allenopithecus*; *Cercocebus*; *Cynopithecus*; *Mandrillus*); open triangles = colobines (*Colobus*; *Presbytis*); open squares = transitional (forest/open-country) cercopithecines (*Cercopithecus aethiops*; *Macaca*); black squares = open-country cercopithecines (*Erythrocebus*; *Papio*; *Theropithecus*); open circles = lesser apes (*Hylobates*; *Symphalangus*); black circles = great apes (*Gorilla*; *Pan*; *Pongo*); white star in black circle = *Homo sapiens*.

[N.B. *Cercopithecus aethiops* has been treated separately from other *Cercopithecus* species because of its distinctive ecological features.]

and $\log_{10}$ body weight (to avoid bias by species-rich genera) and obtain a best-fit line for the data (fig. 12). Following the general rule, this line has a lower slope value than that for the primates as a whole, but it can be taken as the appropriate line for comparison among the Old World monkeys and apes:

$$\log_{10}E = 0.60 \cdot \log_{10}P + 2.68 \qquad [r = 0.97] \qquad (18)$$

It is clear from figure 12 that two genera other than *Homo* lie well

above the best-fit line (*Miopithecus*; *Pan*), whereas the two colobine monkey genera included (*Colobus*; *Presbytis*) lie well below the line. Taking the best-fit line (major axis) as a reference standard, it is possible to calculate special encephalization quotient values (EQ_{OW} = Old World simian encephalization quotient) for the individual species for which data are available. These values are plotted in histogram form in figure 13, which shows that there is no overlap between colobine (leaf-monkey) species and the cercopithecine monkeys + apes. The colobines, which have specialized sacculated stomachs for processing leaf material, all have EQ_{OW} values of less than 0.8. Among the cercopithecine monkeys, it can be seen that there is no obvious distinction between forest-living and savanna-living species (e.g., indicating larger brains in the latter). Indeed, the largest EQ_{OW} value (1.38) is found in the forest-living *Miopithecus talapoin*, so a shift to savanna alone does not correlate with increased brain size. In line with this, the forest-living hylobatids (lesser apes: gibbons and siamang) fall within the cercopithecine monkey range. Finally, the chimpanzee (*Pan*) has a very large EQ_{OW} value of 1.35, whereas the orang (*Pongo*) and the gorilla (*Gorilla*) have only moderate values (1.05 and 0.95, respectively). Among the great apes, the sequence in relative brain size (*Pan* > *Pongo* > *Gorilla*) matches a dietary spectrum ranging from predominant frugivory to predominant folivory, once again confirming the correlation between diet and brain size.

Given these facts, it is possible to frame an explanatory hypothesis in terms of the differential central nervous processing capacity which might be required for feeding on relatively scarce fruiting trees, which tend to be very clumped in both space and time. Feeding upon leaves, which may be regarded as being both more abundantly available and more evenly distributed, might be thought to be less demanding in terms of central nervous processing. This type of explanation has been explicitly proposed by Clutton-Brock and Harvey (1980) and by Mace, Harvey, and Clutton-Brock (1980).

A similar correlation between relative brain size and dietary habits has been found among the bats (Pirlot and Stephan, 1970; Eisenberg and Wilson, 1978; Stephan, Nelson, and Frahm, 1981). Overall, it has now been clearly demonstrated that fruit-eating bats have con-

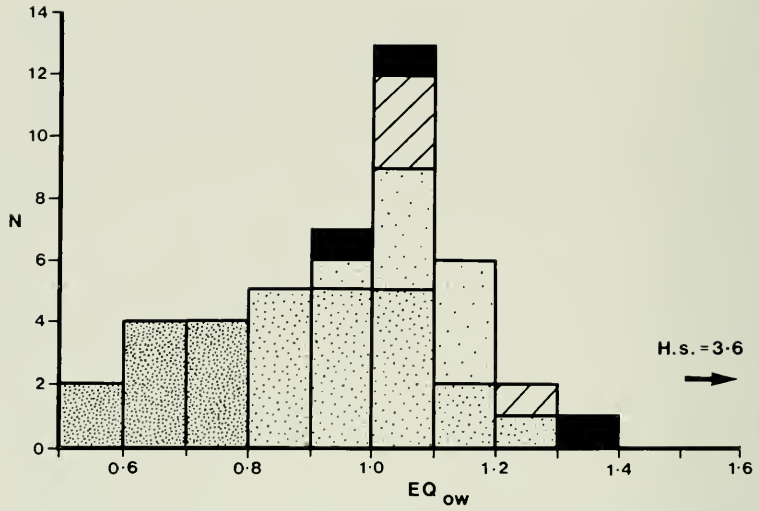

FIG. 13. Histogram of encephalization quotient values (EQ_{ow}) calculated for individual Old World monkey and ape species in relation to the best-fit line shown in figure 12.

Key: Heavy stippling = colobines; medium stippling = forest-living cercopithecines; light stippling = open-country cercopithecines; hatching = lesser apes; black = great apes.

Note that the colobines uniformly have the lowest values (EQ_{ow} less than 0.8) and that there is no overall distinction between forest-living monkeys and lesser apes and open-country monkeys.

siderably larger brains than insect-eating bats, by a factor of approximately two, and that bats with other feeding habits (e.g., nectar-feeding or fish-eating) have intermediate brain sizes. Once again, it has been explicitly proposed that fruit-eating bats require larger brains than other bats, notably the insectivorous forms, because fruits occur as scattered resources which demand an enhanced central nervous processing capacity for their exploitation. Insectivorous bats, it is argued (Eisenberg and Wilson, 1978) do not require such large brains to locate their insect prey.

Now, while it may seem likely that location of scattered food sources, such as fruits, may require more central nervous processing than foraging for relatively abundant food items, such as leaves, it is by no means obvious that hunting for insects (as in the use of

echolocation in microchiropteran bats) is comparatively undemanding in central nervous terms. Further, since it is now widely recognized that the presence of secondary compounds in many leaf species may require considerably greater selectivity in leaf-eating than might be expected at first sight (Freeland and Janzen, 1974; McNab, 1978), it seems likely that folivores may well exhibit quite complex feeding strategies in comparison to frugivores. Once again, we have a situation where a correlation between two variables (relative brain size; foraging behavior) has been interpreted as a *causal relationship* assumed to operate in a given direction. There is, in fact, an alternative explanation which can be advanced in terms of the energy cost of brain development. McNab (1980) has shown that fruit-eating bats have higher metabolic rates than insect-eating bats, once scaling to body size is taken into account. Fruit-eating bats have metabolic rates closely agreeing with the values expected for mammals generally from Kleiber's standard equation (1961), whereas insectivorous bats have values some 50 percent lower than expected. As with relative brain size, bats with other forms of feeding behavior are intermediate in terms of basal metabolic rate. Therefore, it can be suggested that insectivorous bats have smaller relative brain sizes than frugivorous bats because of their lower metabolic turnover. More precisely, it can be proposed that low metabolic rates in gestating female insectivorous bats constrain foetal brain growth such that neonatal brain size is limited in comparison to frugivorous bats. Given general isometric scaling of adult brain size with respect to neonatal brain size, it should automatically follow that adult frugivorous bats would end up with larger brains than adult insectivorous bats. Indeed, since maternal metabolic turnover must obviously constrain foetal development, the difference in basal metabolic rate between frugivorous and insectivorous bats should *inevitably* lead to a difference in adult brain size between these two groups unless there is some systematic difference (e.g., in gestation period) to offset the limitation imposed by low metabolic rate in insectivorous bats.

Unfortunately, data are not yet available for basal metabolic rate in colobine monkeys, so it is not possible to test the prediction that these monkeys, like insectivorous bats, have relatively low metabolic

rates. Nevertheless, McNab (1978, 1980) has shown that in mammalian folivores generally there is a lowering of basal metabolic rate relative to Kleiber's equation for mammals, and this effect increases as the proportion of leaves in the diet increases. It therefore seems highly likely that colobines will be found to have low metabolic rates in comparison with other Old World simians, and this would explain why they have relatively small brains independently of any hypothesis based on the central nervous processing capacity required by their predominantly leaf-eating foraging strategy.

As yet, it is not possible to decide which of the two competing hypotheses (requirements of foraging behavior; limitation imposed by maternal metabolic turnover) best explains differences in relative brain size between mammal groups with different dietary habits. However, there is increasing evidence to show that specialization on leaves or on insect food entails a metabolic cost because of toxic compounds present in the food items which have been developed to discourage predation. It follows from this that specialized mammalian folivores and insectivores will commonly have low metabolic rates as a mechanism for reducing total food intake and hence the burden of ingested toxins (McNab, 1978, 1980). Thus, specialized folivores and insectivores must be expected to have relatively small brains on straightforward metabolic grounds unless they have developed special adaptations (e.g., extension of the gestation period) to offset the limitation imposed by low maternal metabolic turnover during foetal development.

Thus far, gestation period has been taken into account only in a very broad sense through the distinction between precocial mammals (relatively long gestation periods) and altricial mammals (relatively short gestation periods); but it is possible for this parameter to be modified in individual species with corresponding consequences for brain development. In fact, gestation period is just one of the parameters that combine to determine the level of maternal investment in offspring in any mammalian species. In recent years, it has become increasingly clear that differential reproductive strategies in mammals, including differential levels of maternal investment, can be interpreted with respect to the spectrum from r-selection to K-selection (MacArthur and Wilson, 1967; Pianka, 1970),

thus placing maternal investment firmly in a broad ecological context. In relatively unstable habitats or in habitats with extreme seasonal changes many animal species are subject to drastic mortality, and the theoretical carrying capacity (K) of the environment is rarely attained. Under such conditions, resources are usually not limiting and natural selection will tend to favor maximization of the intrinsic rate of natural increase (r_{max}) and rates of development (r-selection). In relatively stable habitats, by contrast, many animal species will exist for much of the time at or near carrying capacity and natural selection will favor increased efficiency of utilization of environmental resources, including limitation of reproductive turnover (K-selection). It is characteristic of K-selecting environments that competition, both within and between species, is intense, and the relatively few offspring that are produced are typically provided with enhanced parental investment of some kind. There is obviously a close correspondence between the r-selection/K-selection distinction and the altricial/precocial neonate difference among mammals, in that the reproductive features of altricial mammals (e.g., large litter-size) are related to high reproductive turnover, whereas those of precocial mammals (e.g., relatively long gestation period) are indicative of increased parental investment in individual offspring. The primates, with their precocial offspring, fit the K-selection category very well, as might be expected from the fact that they have typically been inhabitants of tropical and subtropical forests for the last 50 million years at least. Correspondingly, primates have relatively long gestation periods compared with other mammals and this relative extension is found in other key parameters of the life-cycle, such as age of attainment of sexual maturity and maximum lifespan. But with the order Primates there is also scope for special adaptation of reproductive strategies in individual species. The lorisines (lorises, potto, angwantibo), for example, are characterized by low basal metabolic rates and sluggish locomotion to match, yet the adults end up with relative brain sizes comparable to those of their fast-moving relatives, the galagines (bushbabies), because the gestation period is relatively longer in lorisines and allows for more foetal brain growth, thus offsetting the limiting effect of the mother's low metabolic turnover. Such particular adaptations of individual species are common,

as is apparent from analysis of the differential partitioning of brain growth between foetal and postnatal life (see later) and it is here that one might seek special adjustments for specific behavioral requirements. Although primates as a group appear to be K-selected compared with certain other mammals (e.g., most rodents and insectivores), some degree of variation is to be expected since some primate species inhabit relatively K-selecting tropical rainforest while others occur in drier, more open environments which are likely to exert some r-selecting effect. The picture is further confused by the fact that different strategies can be followed within the same environment, but as far as primates are concerned the situation can be simplified into four alternative outcomes in terms of overall energy budgets (fig. 14). In tropical rainforest, which is probably the typical environment to which most primates have been adapted during their evolution, K-selection has generally led to restriction of the proportion of the energy budget available for reproduction, but because of enhanced investment in individual offspring, gestation periods are long and brain size is therefore usually quite large in both neonates and adults. Under K-selecting conditions, competition is fierce and this may well explain why certain forest-living primate species (e.g., lorisines, owl-monkeys, and possibly colobines) have developed a strategy of lowering basal metabolic rates. This permits them to feed on certain foods (e.g., some arthropods; leaves) which are protected by toxic substances, though at the cost of reducing overall metabolic turnover. (Maximum metabolic turnover is directly related to basal metabolic rate: McNab, 1980.) Mammals with low basal metabolic rates are sluggish, at least in part because the proportion of body weight devoted to muscle decreases with decreased metabolic turnover (McNab, 1978) and the energy available for reproduction is even more curtailed. Hence, such species can only possess relatively large brains if gestation periods are extended to offset the effect of low maternal metabolic rate on foetal brain growth.

Should a forest-living primate species subsequently become adapted for living in open country, the relative r-selecting effect of this environment may have a number of possible outcomes (fig. 14). In any event, since food availability is not usually a pronounced limiting factor as it is in rainforest, constraints on the overall energy

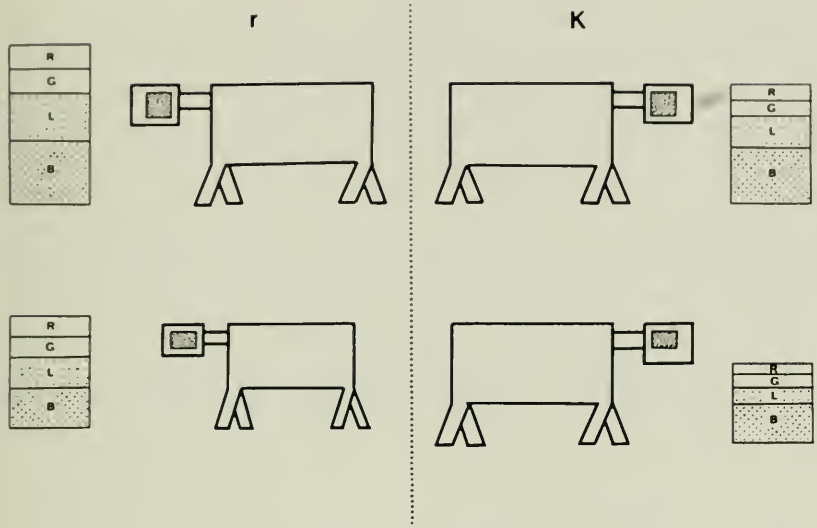

FIG. 14. Schematic illustration of possible effects of K-selection vs. r-selection with respect to overall metabolic turnover and brain size. A relatively K-selected species with a typical mammalian basal metabolic rate (top right) will have a moderate energy budget. A large part of this budget will be represented by basal metabolism (B), with moderate locomotor expenditure (L) generating through food-aquisition the energy required for maintenance, growth and repair (G) and reproduction (R). Under the intensive competition typical of K-selecting conditions, some species may adopt a "low-energy strategy" (bottom right), involving reduced metabolic rate (B) and limitation of energy available for locomotion (L), growth (G) and reproduction (R). Unless special adaptations are developed (e.g., extension of gestation period), such a low-energy strategy will result in a relative limitation of brain size, as in colobine monkeys. Under r-selecting conditions, a mammal species of the same body size (top left) will typically devote a greater proportion of its energy budget to reproduction (R) and faster growth processes (G). Since basal metabolic rate is unlikely to change, a large brain size can only be maintained if a "high-energy strategy" is adopted, involving greater investment of locomotor energy (L) to permit increased harvesting of food. An alternative outcome under r-selecting conditions is relative reduction of body size which will lead (among other things) to increased reproductive potential. Again, brain size can only remain relatively large if a "high-energy strategy" is adopted.

budget are relaxed to some extent. For this reason, it is unlikely that a strategy of feeding on toxin-rich foods and lowering basal metabolism will develop, and certainly no open-country primate species seems to have adopted such a strategy. On the other hand, open-

country primates must to some extent respond to the pressure exerted by r-selection toward increased reproductive output. In mammals, an increase in reproductive potential can be achieved in various ways, such as by an increase in litter-size (usually accompanied by a reduction in gestation period) or through earlier attainment of sexual maturity, and the latter mechanism seems to be predominant among open-country primates. Hence, primates exposed to r-selecting conditions can increase their energy budgets (in comparison to their forest-living counterparts), but they are also constrained to invest more in reproductive turnover. One of the easiest ways for the latter to be achieved is through reduction in body size, which is also likely to entail a reduction in gestation period and other parameters, though it is theoretically possible for a species to remain the same size after shifting from forest to more open country and for the greater energy budget to allow for increased reproductive output without requiring any reduction in parameters such as brain size. Hence, a primate species living under open-country conditions can have the same brain and body size as a forest-living counterpart, though it will theoretically have a higher overall metabolic throughput and a higher reproductive potential. It is clear from figure 13 that open-country cercopithecines do not tend to have larger brains than their forest-living counterparts and fully overlap with them. As noted above, the largest relative brain size is found in the forest-living talapoin among the cercopithecine monkeys.

These considerations present certain problems for the prevailing theory of human evolution, according to which the definitive changes are related to a shift from forest to open-country conditions (the so-called "savanna theory"). In terms of general ecological pressures, such a shift would not have favored development of the particular human combination of a very large brain size with extremely slow reproductive turnover. For, when body size is taken into account, it is found that all the critical parameters of the human reproductive life-cycle (age of attainment of sexual maturity; gestation period; longevity) are greater than in any other primate species (or, indeed, any other mammal species). In other words, the combination of large brain size and slow reproductive turnover in *Homo sapiens* is indicative of the operation of an extreme form of K-selection, not

of exposure to r-selecting conditions. It could, of course, be argued *post hoc* that human cultural attributes permit our species to create relative stability in environments which to other species are unpredictable, but it is difficult to understand how *gradual* increase in human brain size (see later), and hence gradual increase in the overall intellectual capacity required for cultural developments, could have taken place under relatively r-selecting conditions out in the savanna. Whereas relative brain size may well be maintained in K-selected species which move from forest to open country, as seems to have been the case with savanna-living cercopithecine monkey species, it is difficult to see how r-selecting environmental conditions could favor any further increase in brain size (see also Rudder, 1979).

THE SPECIAL FEATURES OF HUMAN BRAIN EVOLUTION

The foregoing comparisons have demonstrated that *Homo sapiens* shares a number of general features of brain size and its development with the other primates, most notably in producing precocial offspring and in the shift to a distinctive relationship between brain size and body size during foetal development (fig. 8). But human beings also exhibit a number of special features which set them apart from other primates, or at least from their closest relatives the great apes. These may be listed as follows:

(i) The remarkably large size of the adult brain relative to body size.
(ii) The rapid development of both brain and body during foetal development, resulting in a distinctively large brain and body size at birth, compared to great apes.
(iii) The greater degree of postnatal growth of the brain, accomplished by continuation of foetal brain : body relationships for at least one year after birth and associated with the "secondary altricial condition."

The distinctiveness of *Homo sapiens* with respect to the last two features is somewhat obscured because of variation between primate species in the partitioning of brain growth between foetal and post-

natal stages. For instance, the degree of postnatal brain growth in humans is greater than in any other primate species, but there is considerable scatter about the best-fit line in a plot of adult brain size against neonatal brain size (fig. 7). Similarly, there is some variation among primate species in the degree to which the brain develops *in utero*. However, it is to be expected that overall there should be an inverse relationship between the two phenomena, since species which have a relatively large degree of brain development *in utero* are likely to have less postnatal brain growth. This relationship can be further explored by calculating indices for both foetal and postnatal brain growth. The *foetal brain growth index* can be calculated using the empirical allometric formula determined for the relationship between neonatal brain size and adult body weight in primates (N = 30):

$$\log_{10}E_N = 0.83 \cdot P_A + 1.46 \qquad (r = 0.96) \qquad (19)$$

For each species, the "expected" brain size of the neonate can be calculated from the adult body weight using this formula and the ratio of actual to expected neonate brain size provides an index of the amount of foetal brain growth compared to the norm for primates. Since total postnatal growth of the brain is isometric relative to neonatal brain size, the *postnatal brain growth index* can be calculated by simply dividing adult brain size by neonatal brain size. As mentioned above, the average value for the ratio of adult to neonatal brain size is 2.3 in primates (see also fig. 7). These two indices can then be plotted against one another to examine the partitioning between foetal and postnatal growth in primates. When this is done (fig. 15) it emerges that there is indeed a negative relationship between the postnatal brain growth index (PI) and the foetal brain growth index (FI):

$$PI = 3.07 - 0.78 \cdot FI \qquad (r = -0.60) \qquad (20)$$

In other words, as expected, species which have a relatively high degree of foetal brain development typically have relatively little postnatal brain development and vice versa. When the data are analyzed in this way, it emerges that *Homo sapiens* is quite distinctive in the combination of greater than expected foetal brain

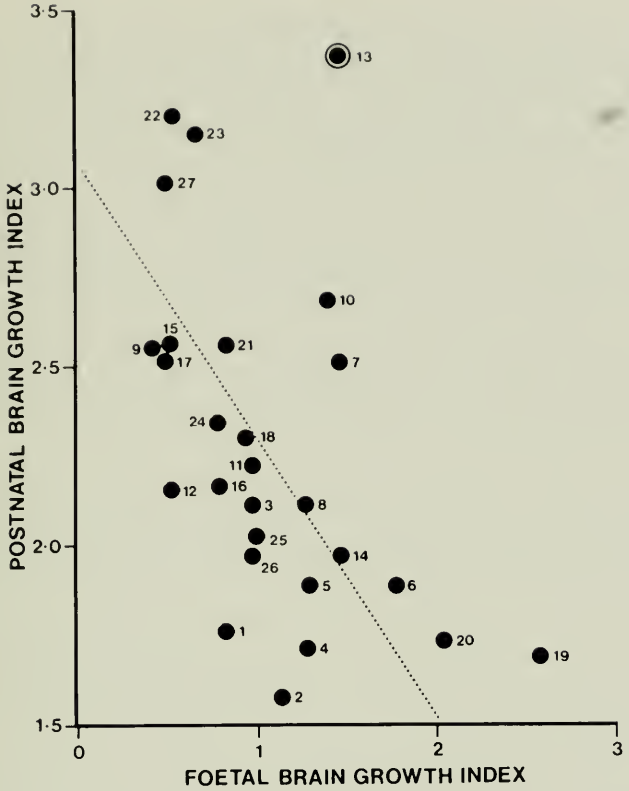

FIG. 15. Plot of postnatal growth index (PI) against foetal growth index (FI) for the brain in 27 primate species. FI is calculated with respect to equation (19) and indicates, for each primate species, the degree to which the brain has developed at birth in comparison to the typical primate condition (FI = 1). PI is simply calculated by dividing adult brain weight by neonatal brain weight to indicate the degree of postnatal brain development (average PI for primates = 2.3). Man has the highest value for PI and one of the highest values for FI; since there is an overall negative correlation between PI and FI (dotted line = major axis excluding *Homo sapiens*), this combination is quite unique.

Key:

1. *Alouatta palliata*
2. *Aotus trivirgatus*
3. *Arctocebus calabarensis*
4. *Ateles geoffroyi*
5. *Callimico goeldii*
6. *Callithrix jacchus*
7. *Cebus capucinus*
8. *Colobus polykomos*
9. *Galago crassicaudatus*
10. *Galago demidovii*
11. *Galago senegalensis*
12. *Gorilla gorilla*
13. *Homo sapiens*
14. *Hylobates lar*
15. *Lemur catta*
16. *Lemur fulvus*
17. *Lepilemur mustelinus*
18. *Loris tardigradus*
19. *Macaca mulatta*
20. *Macaca nemestrina*
21. *Microcebus murinus*
22. *Nycticebus coucang*
23. *Pan troglodytes*
24. *Papio cynocephalus*
25. *Pongo pygmaeus*
26. *Saguinus oedipus*
27. *Varecia variegata*

growth with the maximum observed degree of postnatal brain enlargement. *Homo sapiens*, with a foetal brain growth index value of 1.48, is surpassed only by three primate species among those surveyed: *Callithrix jacchus*, *Macaca nemestrina*, and *Macaca mulatta*; and all of these species exhibit conspicuously low values (1.66–1.88) for the postnatal brain growth index. When the human value for the foetal brain growth index is used to calculate an expected value for PI from equation (20), it emerges that the human brain grows by a factor of 1.8 more than expected for a typical primate species during the postnatal period. This enhancement of postnatal brain growth is doubtless attributable largely or exclusively to the special extension of foetal brain : body relationships through the first year of postnatal life (fig. 11).

As a general rule, it is presumably more efficient in energetic terms for brain growth to take place during foetal life as far as possible, since the mother's metabolic capacity is considerably greater than that of her neonate. Postnatal brain growth requires the developing infant (operating at a high metabolic rate per unit body weight because of its small body size) to convert material supplied in the mother's milk into brain tissue, and this is undoubtedly less efficient. It is therefore striking that so much of human brain growth takes place after birth, but this is because of the constraints of pelvic dimensions in the human female (as was suggested by Portmann, 1941, though he later discarded this interpretation). The human foetus does in fact grow very rapidly compared with that of a great ape, reaching approximately twice the size for both brain and body in a gestation period which is only slightly longer. By that stage, however, the human infant has reached the limit imposed by the mother's pelvis and birth must take place. Hence, the extension of the foetal pattern of postnatal brain growth into the first year of postnatal life in humans represents a special mechanism to circumvent the limitation on neonatal head size imposed by the pelvis. That this is so is confirmed by examination of the relationships in odontocete cetaceans, which have very large relative brain sizes (fig. 3) but only a rudimentary pelvis that is unlikely to limit head size of the neonate at birth. The bottle-nosed dolphin (*Tursiops truncatus*) has an adult body weight of about 155 kg and a gestation

period of about 11 months; it produces a neonate weighing 20 kg with a brain weight of 770 g, which approximately doubles through postnatal growth to reach the adult brain weight of 1600 g (Sacher and Staffeldt, 1974). Reference to equation (11) shows that this is a relatively small amount of postnatal brain growth for a precocial mammal, whereas from equation (8) it can be seen that the neonatal brain size is unexpectedly large (by a factor of about 4) for a precocial mammal. Hence, the evidence is that *Tursiops truncatus* achieves a large adult brain size by enhancement of foetal brain growth, rather than through increased postnatal brain growth, as would be expected in the absence of any maternal pelvic constraint at birth. It therefore seems reasonable to accept the interpretation that pelvic constraints require considerable postnatal development of the brain in *Homo sapiens* (Jordaan, 1976a; Gould, 1977; Leutenegger, 1982).

Continuation of the foetal pattern of brain and body growth into the first year of postnatal life in human beings also poses special problems with respect to lactation, since it is quite clear that a pattern of early postnatal brain growth that is unique among mammals must require a unique milk to supply the needs of the developing human infant. It is, of course, possible that the great degree of postnatal brain development in human beings merely requires the provision of standard nutrients in greater quantities. However, it is also possible that human breast milk contains components which are not normally present in significant quantities in the milk of other precocial mammals with a normal pattern of postnatal brain growth, such as the cow. The widespread use of modified or unmodified cow's milk formulae as a substitute for human breast milk therefore deserves special attention from the point of view of early postnatal brain development. It has been shown that human milk differs from cow's milk in numerous respects (Gaull, 1979; Gaull et al., 1982) and some of the differences may well be specifically relevant to brain development. In particular, human milk differs markedly in its lipid constituents in that long-chain unsaturated fatty acids (especially oleic acid) predominate and there are several differences in amino acid and protein content. The whey protein : casein ratio is inversed in human milk compared to cow's milk and human milk has a considerably greater availability of non-protein nitrogen. In human

milk free amino acids are present in far greater concentrations and in quite different proportions, and the free "amino acid" taurine is particularly noteworthy in that it has been specifically implicated in brain development (Gaull, 1979) and is more than 30 times more concentrated in human than in cow's milk.

In view of these pronounced biochemical differences between human and cow's milk and the special requirements of the developing human brain, it is pertinent to ask whether substitution of cow's milk for human milk leads to deficits in early human brain development. This question does not seem to have been asked very often and it is hence significant that there is some evidence for such deficits (Menkes, 1977; Rodgers, 1978). Rodgers, in particular, took great care to exclude the effects of possible confounding variables (e.g., social class, family size, birth order, etc.) and still detected a significantly greater degree of intellectual impairment in bottle-fed children compared with breast-fed children. This is all the more remarkable in that almost all the children involved (2424 individuals in the 1946 birth cohort included in the U.K. National Survey of Health and Development) were weaned from milk before the age of 12 months (82.2 percent of breast-fed children and 57.5 percent of bottle-fed children in fact received no further milk after 10 months of age). Such early weaning itself presents problems, since typical foetal relationships between the growing brain and body weight persist for at least 12 months after birth in human infants (fig. 11) and there was actually a bias *against* breast-fed infants in the sample, since they were generally weaned earlier. In addition, some of the apparent confounding variables identified in Rodgers's analysis may actually be secondary effects related to breast feeding; for instance, children that were born first in the birth order were also more likely to have been breast fed. Overall, it is clear from Rodgers's analysis that there is *some* link between breast feeding and subsequent intellectual development, though it has not yet been demonstrated that this link is a direct one between milk biochemistry and brain development. Further, it must be remembered that artificial milk formulae have been considerably modified since 1946 (the date of birth of the cohort studied by Rodgers) and that the present-day situation could be rather different. Nevertheless, Ounsted (1982) has reported

significant differences between neurobehavioral test scores of breast-fed versus bottle-fed infants where modern artificial milk formulae were used and, given the peculiar features of early postnatal brain development in human beings outlined above, the relationship between breast feeding and brain maturation obviously deserves more detailed examination.

THE FOSSIL RECORD OF HUMAN BRAIN SIZE

Even a superficial comparison of modern man and the great apes reveals that there are three particular features which involve marked morphological differences in humans: the very large brain, bipedal striding, and dental restructuring. These three features are all clearly connected in that locomotion and food processing underlie the provision of energy for the development and maintenance of a large brain. In terms of the approach adopted here, it can be argued that the uniquely large relative size of the human brain (compared with other primates) requires a relatively high energy flow through the mother, whereas the relatively slow reproductive turnover of modern *Homo sapiens* implies that this strategy required comparative stability in the availability of food resources for its evolution. A further perspective on the evolutionary background to these special human characteristics is provided by the fossil evidence for human evolution (Tobias, 1971) and this permits us, in particular, to ask extremely pertinent questions about the timing and rate of human brain size evolution.

There are now numerous fossil hominid skulls for which cranial capacities have been determined (Tobias, 1971; Holloway, 1973a, 1973b, 1978) and it is possible to interpret these in phylogenetic terms through comparisons with *Homo sapiens* and other primates. Because the great apes are man's closest relatives, it has been traditional to compare hominid fossil cranial capacities particularly with the great apes and modern humans. However, two problems have bedeviled attempts to interpret quantitative data on hominid fossil cranial capacities. In the first place, earlier authors frequently did not take body size and accompanying scaling effects into account,

and this led to an underestimation of the degree of brain development in *Australopithecus africanus,* the earliest well-documented species in hominid evolution. It is generally accepted that *A. africanus* was smaller in body size than any of the modern great apes and man and it is therefore misleading to state, without any proviso, that cranial capacities of gracile australopithecines fall within the range of the modern great apes. The scaling effect of body size on australopithecine brain size has been taken into account only relatively recently (Schaeffer, 1962; Stephan, 1972; Holloway, 1973a; Jerison, 1973; Pilbeam and Gould, 1974) and there are still many authors who continue to imply that the evolutionary expansion of the human brain postdated the australopithecine level and was confined to the last two million years of human evolution (via *Homo habilis* and *Homo erectus* to *Homo sapiens*). Of course, calculations which take into account the effect of body size as a factor in hominid brain evolution depend upon reliable estimates of body weight in fossil hominids, but increasing attention has now been paid to this (Schaeffer, 1962; Stephan, 1972; Kinsey, 1972; Jerison, 1973; McHenry, 1974a, 1974b, 1976; Pilbeam and Gould, 1974; Steudel, 1980; Cronin et al., 1981) and a consensus is slowly emerging. Certainly, we are now moving away from the previous unsatisfactory situation where hominid brain size was considered in relation to geological time with no reference at all to body weight (e.g., see Lestrel and Read, 1973; Lestrel, 1975). Once estimates of body size are taken into account for *Australopithecus africanus,* it emerges that brain size was, at the very least, 30 percent larger than would be expected for a modern great ape of the same body size (see later). But even this is likely to be an underestimate of the evolutionary advancement of the brain in gracile australopithecines because of a second problem which has been given virtually no mention in the literature. Comparison of hominid fossils with modern great apes (and other primates) involves the hidden assumption that relative brain size in modern primates can be equated with the ancestral condition from which great apes and man diverged. Since there has been a general trend toward brain size expansion throughout the mammals (Jerison, 1973; Martin, 1973), such a "living fossil" approach represents no more than a crude approximation to the real

situation. In fact, it is quite likely that there has been some expansion of the brain, relative to body size, in all the lineages which diverged from the common ancestor of the great apes and man (viz., the ancestral hominoid), with the modern forms differing only in the degree to which this has occurred. Hence, if we were able to compare *Australopithecus africanus* with the ancestral hominoid, rather than with modern great apes, its relative brain size would doubtless be found to be even more advanced. Thus, as recognized by Stephan (1972) and by Jerison (1973), evolutionary expansion of the human brain began prior to the earliest known australopithecines in which cranial capacity is measurable. Hence, attempted explanations of human brain size evolution must take into account the fact that brain expansion began prior to known dates for the first appearance of definite stone tools and therefore prior to any hard evidence for subsistence activities (e.g., hunting) dependent upon such implements. Hypotheses which link human brain size expansion directly to large-scale hunting activities (and perhaps to associated features of social organization) are accordingly extremely suspect.

In searching for an explanatory framework to account for the remarkable degree of evolutionary expansion of the human brain, it is also important to determine from the fossil record whether such expansion has taken place uniformly throughout human evolution or whether there have been marked discontinuities. All authors who have taken body size into account in examining the fossil evidence for human brain size evolution are agreed that expansion has been progressive, rather than limited to a short period of geological time, but the exact pattern of rates of brain expansion over time (e.g., uniform versus irregular) remains to be clarified. Such an undertaking will require analysis of data on cranial capacity, estimated body weight and geological age for a large sample of individual hominid fossil specimens. In the interim, one can at least obtain a general picture by considering average values for cranial capacity, body weight and dating for the following taxa: *Australopithecus africanus*; *Homo habilis*; *Homo erectus*; *Homo sapiens* (table 2).

As in other cases, any attempt to "eliminate" the effect of body size through allometric analysis of hominid brain size encounters the problem of defining which is the appropriate level for compar-

TABLE 2

Data on Cranial Capacities and Body Weights for Great Apes, Fossil Hominids and Modern Man

Species	Cranial Capacity (cc[a])	Body Weight (kg[a])	Geological Age (mya)	EQ	EQ_{ow}
1. GREAT APES					
Pan paniscus	325[b] (N = 8)	35	—	1.94	1.27
Pan troglodytes	385[c] (N = 363)	40	—	2.08	1.39
Gorilla gorilla	495[c] (N = 668)	126	—	1.12	0.90
Pongo pygmaeus	405[c] (N = 442)	53	—	1.77	1.24
2. FOSSIL HOMINIDS					
Australopithecus africanus	442[b] (N = 6)	30[a–f]	2.8[e]	3.29	1.90
Homo habilis	642[b] (N = 3)	40[b,d,e]	2.0[e]	3.47	2.32
Homo erectus	941[b] (N = 14)	50[a–f]	1.1[e]	4.29	2.98
3. MODERN MAN					
Homo sapiens	1230[d]	57[d]	—	5.08	3.60

[a] Cranial capacities and body weights averaged for males and females.

Sources: [b] Holloway, 1978. [c] Tobias, 1971. [d] Pilbeam and Gould, 1974. [e] Cronin et al., 1981. [f] McHenry, 1976.

ison. Pilbeam and Gould (1974), for example, chose to use the allometric relationship for great apes as the baseline for assessing relative brain size in fossil and modern hominids. As is usual with relatively small taxonomic units (in this case, the family Pongidae), a relatively low value was determined for the allometric exponent ($\alpha = 0.34$ from the major axis). However, this may not be a very appropriate comparison because the largest great ape, the gorilla, is predominantly folivorous and may therefore be expected to have both a relatively low metabolic rate and a relatively small brain size, thus depressing the value determined for the allometric exponent. The data in table 2 have therefore been used to calculate first standard encephalization quotient (EQ) values in comparison to mammals generally, using equation (4), and then Old World simian encephalization quotient (EQ_{ow}) values, using equation (18), in order to assess the change in hominid brain size from two different perspectives (fig. 16). When EQ values are plotted against time for fossil

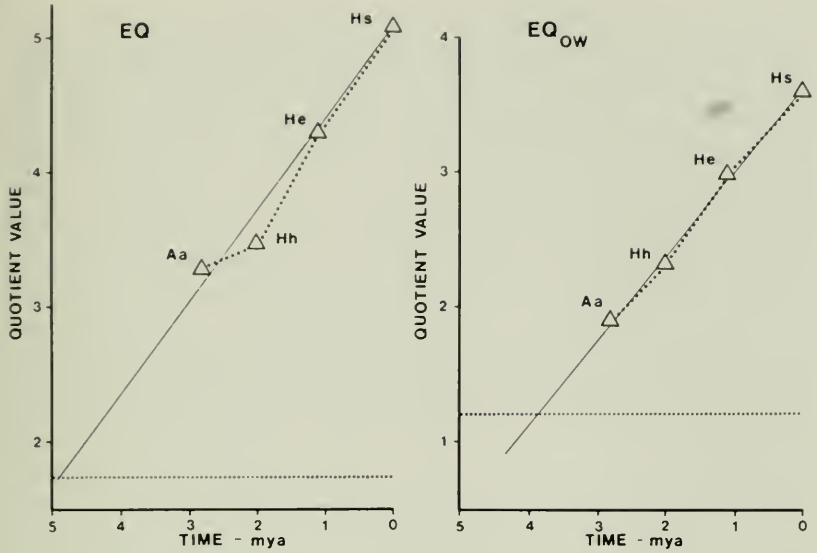

FIG. 16. Plot of encephalization quotient values against time for hominids, using the average values listed in table 2 for cranial capacity, body weight and geological age. EQ values, relating hominid brain sizes to a general placental mammal standard, are calculated according to equation (4) (see also fig. 3). EQ_{ow} values, relating hominid brain sizes to the standard condition among Old World monkeys and apes, are calculated according to equation (18) (see also fig. 12). In both cases, the minimal value for modern great apes is indicated by a horizontal dotted line, while the general trend in the hominid values has been extrapolated back along the best-fit line. [N.B. The lines joining the hominid species need not imply any direct evolutionary continuity; they may merely reflect an overall trend.]

Key: Aa = *Australopithecus africanus*; Hh = *Homo habilis*; He = *Homo erectus*; Hs = *Homo sapiens* (modern).

hominids, it can be seen that *Australopithecus africanus* lies well above both the average condition for mammals (for which EQ = 1.0) and the average condition for great apes (EQ = 1.73), showing a 90 percent increase over the latter. Relative brain size increases progressively above the gracile australopithecine level, but from this perspective there is a suggestion that there could have been some acceleration in brain size expansion following the transition from *Australopithecus* to *Homo*. The plot of EQ_{ow} values, however, shows no such evidence of acceleration in brain size expansion; the data

yield an almost perfect straight line. Since EQ_{OW} values take into account the flatter slope of the Old World simian allometric relationship ($\alpha = 0.60$, as opposed to 0.76 for mammals generally), the quotient value for *Australopithecus africanus* is not so markedly different from that for modern pongids ($EQ_{OW} = 1.20$), but it is still significantly above it and shows an increase of 58 percent over the average great ape value. In both cases (i.e., with EQ and EQ_{OW}) it is possible to extrapolate back in time to estimate when hominid brain size expansion might have started, assuming departure from the minimal condition for modern pongids and no marked acceleration at any stage. The estimates are 5.8 and 4.4 million years ago, respectively, giving an average of about five million years (as was suggested by Jerison, 1973, as a rough estimate). Of course, it is possible that there were in fact significant changes at times in the rate of human brain size evolution, relative to body size, and only additional fossil evidence for the earlier stages of human evolution can resolve this point. For the time being, the following firm conclusions may be drawn:

1. Relative brain size in the earliest well-documented hominid, *Australopithecus africanus*, was already significantly increased compared with modern great apes and therefore considerably advanced over the (doubtless) even smaller-brained common ancestor of great apes and man.
2. Expansion of relative brain size in human evolution has been a progressive phenomenon, though there was possibly some acceleration at the time of transition from *Australopithecus* to *Homo*.
3. Expansion of human brain size, relative to body size, probably began about five million years ago (if not earlier) and therefore antedated all the available fossil evidence of any substance (i.e., anything more than isolated fragments of dubious affinity).

These observations are particularly important in that it is clear that any explanatory framework for the evolution of man's remarkably large brain must account both for the early onset of brain expansion and for its progressive nature. Many discussions of human brain size evolution have been phrased in terms of a direct comparison of modern great apes and *Homo sapiens* and the hypothetical

explanations advanced have tended to imply some relatively abrupt transition associated with the emergence of some special human characteristic. Further, it must be noted that evolutionary expansion of human brain size seems to have petered out about 200,000 years ago, and it has often been noted that classic neanderthalers (*Homo sapiens neanderthalensis*) had a larger average cranial capacity than modern man (*Homo sapiens sapiens*). Hence, at a time when human control over environmental resources was presumably moving into its most impressive phase of development, brain size apparently stabilized. This provides additional reason for believing that the progressive expansion in human brain size which took place between five million and 200,000 years ago was a response to relative predictability of specific habitat conditions rather than to man's increasing control over them.

As a final point relating to the fossil evidence for human evolution, it is worth noting that pelvic limitation on increased foetal brain development was probably reached about one and a half million years ago, just prior to the emergence of *Homo erectus*, as currently recognized in the fossil record. Prior to that time, increase in relative brain size above the great ape level could probably have been achieved by modification of the rate and/or extent of foetal growth without any need for significant postnatal postponement of a foetal brain growth pattern. However, subsequent to the attainment of a cranial capacity of about 850 cm^3, increasing development of the "secondarily altricial condition," was probably involved as postnatal continuation of foetal growth patterns became progressively more necessary. Thus, it seems likely that increasingly elaborate parental care was required in *Homo erectus* and then still more in *Homo sapiens* to cater for the increasingly helpless condition of the infant during the first months of postnatal life.

CONCLUSIONS

The approach in this discussion of human brain evolution is essentially dependent upon three basic tenets. Firstly, it is taken as axiomatic that no understanding of brain size can be reached without

a consideration of the effects of scaling to body size. Secondly, it is held that only a broad comparative study of brain size in mammals can provide an adequate perspective for reliable interpretation of human brain size evolution. Finally, it is maintained that the obvious heavy energetic cost of brain tissue requires some discussion of the general ecological background to brain size evolution.

Once body size is considered, it emerges that *Homo sapiens* is indeed outstanding among mammals in terms of relative brain size (though the odontocete cetaceans come a close second) and appropriate examination of the available fossil evidence shows that man's very large brain developed progressively over a period of about five million years. To some extent, the pre-eminent position of *Homo sapiens* in terms of relative brain size can be attributed to our primate heritage. We belong to an order of mammals which is marked out by relatively large brains overall, associated with a specific pattern of foetal development in which the proportion of brain tissue at all stages has been increased in comparison to all other mammals. This, in turn, relates to the fact that primates as a group seem to be relatively K-selected and accordingly have precocial, rather than altricial, young.

But *Homo sapiens* has gone far beyond other primates in terms of brain size evolution over the past five million years or more. During this period, we developed a particularly rapid pattern of foetal brain and body development, ultimately complemented by a one-year extension of foetal growth rates into postnatal life, accompanied by the emergence of the "secondarily altricial" condition of the human neonate. We are, in this, unique among the mammals and this should be carefully borne in mind when we consider nutrition during pregnancy and during the first year of postnatal life in comparison with other species. In particular, future improvement in substitutes for human breast milk could well result from specific study of the relationship between milk constituents and early development of the foetal brain. Evidence of possible deficits in brain development associated with the use of milk substitutes deserves particularly close attention.

One enormous question still remains unanswered: Why did this rapid and far-reaching evolutionary expansion of the human brain

take place at all? There is, at present, widespread acceptance of the "savanna hypothesis" of human evolution and a common corollary to this has been the postulate that the large human brain evolved due to specific selection pressures associated with hunting, tool-use and/or social organization. Holloway (1973a), for example, sees an important feedback relationship between social organization and human brain evolution: "The human brain is both the product and cause of the evolution of human social behaviour." Yet consideration of the energetic requirements associated with the evolution of the brain, in terms of both the level and reliability of resource availability, must surely place particular emphasis on early human subsistence patterns. *Homo sapiens,* as the most K-selected of the mammal species, must have evolved in response to a rather unusual combination of environmental factors which made available a relatively steady, predictable supply of food lacking in significant toxin levels. Unfortunately, evolution of all the major distinctive morphological attributes of man (large brain; bipedal adaptation; remodeling of jaws and teeth) was well under way some time prior to the earliest known substantial australopithecine remains, so the key evidence is still lacking. However, it can at least be said that an additional, pressing question has now been formulated which will require an answer in future examination of the fossil record of human evolution: "How could hominids afford the energetic cost of developing such a large brain?"

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