Brain Evolution: New Light on Old Principles

Abstract. *The fossil evidence on the evolution of brains and bodies in mammals shows that there has been a progressive increase in relative brain size accompanied by and correlated with increased diversity among species in relative brain size. Small-brained species have also evolved, but more large-brained species have appeared in successive epochs.*

Among the oldest principles in quantitative evolutionary biology is Lartet's observation about changes in relative brain size. His statement, in translation, was:

> The further back that mammals went into geological time, the more was the volume of their brain reduced in relation to the volume of their head and to the overall dimensions of their body (*1*).

Lartet's principle is extended in this report by analyzing the change in diversity in relative brain size during 60 million years of the evolution of carnivorous and ungulate (hooved) mammals of the Northern Hemisphere.

We define relative brain size as the ratio between actual and expected brain size, and we define "expected" brain size by the regression equation in which brain size is predicted from the body size:

$$\log E = 2/3 \log P + \log 0.12 \quad \text{(1a)}$$

where E and P are brain and body weights, respectively, in grams. The equation is usually analyzed as an example of an allometric relationship (*2, 3*) and is written as a power function:

$$E = 0.12\, P^{2/3} \quad (1)$$

We may now define our measure of relative brain size as the encephalization quotient EQ_i for species i, the ratio of its brain size E_i to the expected brain size E_e in a living mammal of the same body size P_i. This is expressed as

$$\mathrm{EQ}_i = E_i/E_e \quad (2)$$

In the case of a particular body size P_i, we may use Eq. 1 to give us expected brain size in cgs units:

$$E_e = 0.12\, P_i^{2/3} \quad (3)$$

Substituting Eq. 3 in Eq. 2, we obtain

$$\mathrm{EQ}_i = E_i/0.12\, P_i^{2/3} \quad (4)$$

This defines EQ for any species in which brain and body size are known (*4*).

We can now analyze the history of brain size in Tertiary mammals and their living descendants. The Tertiary began about 65 million years ago (m.y.) and ended about 2 or 3 m.y. (*5*), and our comparisons involve mammals of the Northern Hemisphere during that period: the "archaic" ungulates and carnivores that were entirely replaced in their niches and the "progressive" orders that replaced them. In the fossils, brain size was considered as equal to the volume of the endocast (*6*), and body size was estimated from the regression of body weight on body length in living animals (*7*).

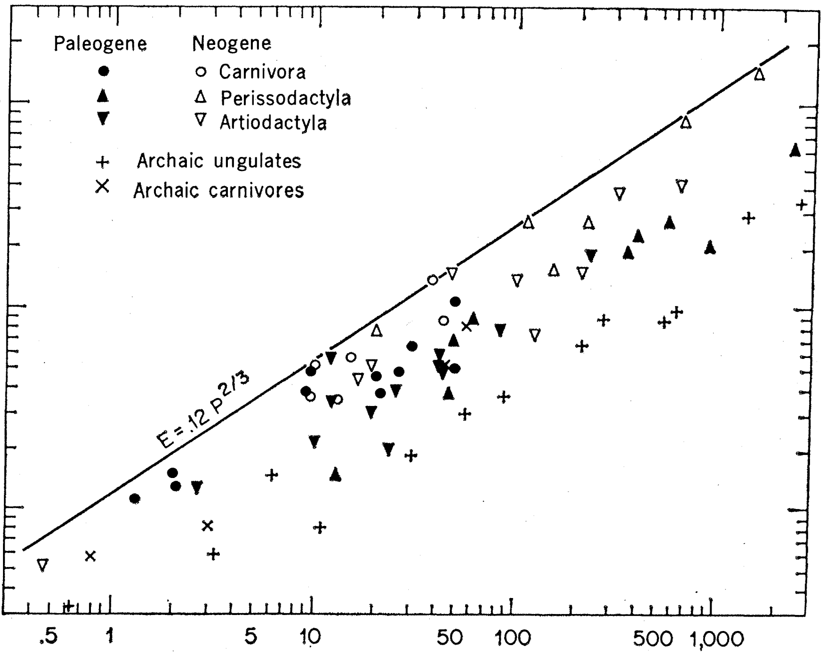

Fig. 1. Brain size (endocast volume) as a function of body size in 69 fossil ungulates and carnivores, logarithmic scale. The line is Eq. 1a, the "average" for living mammals fitted to a large and diverse set of species.

The assemblages for the present report were differentiated according to the statistically "significant" comparisons that could be made (*8*). For example, Eocene and Oligocene assemblages could not be distinguished in the progressive orders with respect to EQ; these were therefore combined as Paleogene assemblages. The same was true of the artiodactyls and the perissodactyls of each epoch; these were therefore combined as (progressive) ungulates. The following are brief descriptions of the assemblages (*9*):

1) *Archaic ungulates.* Orders Condylarthra and Amblypoda, 13 species; middle Paleocene to late Eocene, 60 to 40 m.y.

2) *Archaic carnivores.* Order Creodonta, 4 species; mid-Eocene to lower Oligocene, 50 to 35 m.y.

3) *Paleogene ungulates.* Order Perissodactyla (10 species) and order Artiodactyla (12 species); lower Eocene to upper Oligocene (11 Eocene and 11 Oligocene species), 55 to 22.5 m.y.

4) *Paleogene carnivores.* Order Carnivora, 11 species; Oligocene, 35 to 22.5 m.y.

5) *Neogene ungulates.* Orders Perissodactyla and Artiodactyla, 13 species; Miocene and Pliocene, 22.5 to 2.5 m.y.

6) *Neogene carnivores.* Order Carnivora, 6 species; Miocene and Pliocene, 22.5 to 2.5 m.y.

7) *Recent ungulates.* There are 25 living species, more or less matched in niche and in body size to the fossil samples. Because only a few perissodactyls have survived to our time (horses, rhinoceroses, and tapirs), data on only five species could be assembled from the literature. The remaining 20 species are artiodactyls.

8) *Recent carnivores.* There are 15 species, more or less matched in niche and in body size to the fossils.

Brain and body size measures for

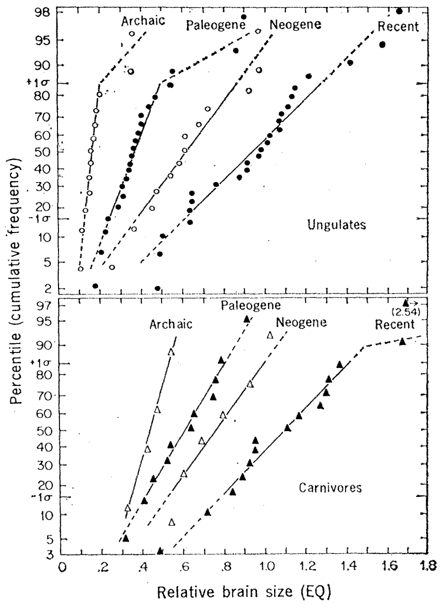

Fig. 2. Cumulative frequency distributions of relative brain size as measured by the encephalization quotient (EQ) in fossil and Recent carnivores and ungulates (plotted on probability paper). Lines were fitted within the range of ± 1 S.D., and dashed extensions indicate representativeness of normal distributions for extreme cases.

our 69 fossil species are presented as individual data points in Fig. 1. Equation 1a is also graphed in Fig 1. Two results are apparent. First, the parallel orientation of the line and the array of points is notable, especially in view of their independent origin. The orientation (represented by the exponent of 2/3 in Eq. 1) may represent the action of an important biological constant. Second, with a single exception, the fossil data points fell below the line of Eq. 1a, verifying Lartet's principle for this assemblage.

How do the fossil samples differ from one another, and how do they differ from their living descendants? The answers are in the cumulative frequency distributions of EQ in our assemblages, which are presented in Fig. 2.

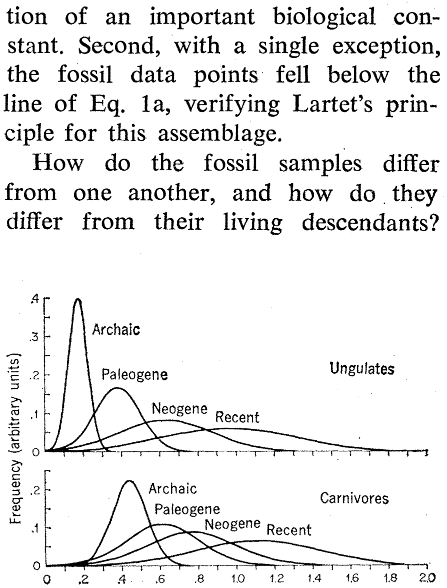

Fig. 3. Changing distributions of relative brain size as the brain evolved. Means and variances are based on fitted functions of Fig. 2.

Inspection of Fig. 2 shows that the underlying distributions were approximately normal for all of the groups (the linear fits are reasonable), although there were extended right-hand tails in a few assemblages. The solid lines in Fig. 2 are least-squares fits to the data between the 16th and 84th percentiles (± 1 S.D.).

A number of interesting comparisons can be made among the groups. A continuing increase in relative brain size as measured by EQ is clearly shown, and we also see that the carnivores had relatively larger brains than their ungulate contemporaries. It is also apparent that the groups became more diversified with the passage of time. Thus, the range of EQ in archaic ungulates was between 0.1 and 0.4, whereas in living ungulates it was from about 0.5 to 1.6.

The most intriguing result of this analysis is in the information about diversity shown by the changing slopes of the lines fitted to the data of Fig. 2. To appreciate the changing diversity in brain size in the temporal succession of species that we have sampled, let us reconstruct the populations that they represent. By using the parameters determined from the lines in Fig. 2, a set of frequency distributions of EQ in each population was determined; these are shown in Fig. 3. The normal curves are equal in area, and they may be viewed as probability distributions for EQ in the populations. These curves are our best guess about how the evolution of brain size in carnivores and ungulates actually occurred.

Two conclusions about diversity of brain size are inescapable. First, diversity evolved just as average size evolved. In the evolution of our mammal groups these evolutionary trends were correlated. Second, despite the evident general trend toward increase in average brain size, there is an interesting and important overlap in the region of low brain size, which indicates the presence of at least some small-brained species at all times. The evolution of enlarged brains, though generally a route to success and survival of new species, was apparently not universal even among progressive orders.

The key factor is probably that the brain in mammals has evolved in ways appropriate to behavior within particular niches. As more diversified niches were invaded, more diversified brain adaptations evolved.

HARRY J. JERISON
Departments of Psychiatry and
Psychology and *Mental Retardation*
Center, School of Medicine,
University of California,
Los Angeles 90024

References and Notes

1. ". . . plus les mammifères remontent dans l'ancienneté des temps géologiques, plus le volume de leur cerveau se réduit par rapport au volume de leur tête et aux dimensions totales de leur corps" [E. Lartet, *C. R. Acad. Sci. Paris* **66**, 1120 (1868)]. This is more often remembered as one of Marsh's "laws" [first mentioned by O. C. Marsh, *Amer. J. Sci. Arts* **8**, 66 (1874)] and popularized by Marsh in many other publications of that period, including *Science* **6**, 360 (1885). A quantitative verification of the "law" as an average effect was presented by H. J. Jerison (*2*).
2. H. J. Jerison, *Science* **133**, 1012 (1961).
3. S. J. Gould, *Biol. Rev.* **41**, 587 (1966); G. von Bonin, *J. Gen. Psychol.* **16**, 379 (1937).
4. For further discussion of gross brain indices and a summary of the literature, see H. J. Jerison, in *The Primate Brain* (vol. 1 of *Advances in Primatology*), C. R. Noback and W. Montagna, Eds. (Appleton-Century-Crofts, New York, 1970).
5. Cenozoic dating from W. A. Berggren, *Nature* **224**, 1072 (1969).
6. R. Bauchot and H. Stephan, in *Problèmes actuels de la paléontologie: évolution des vertébrés* (Centre National de la Recherche Scientifique, Paris, 1967), pp. 575–587.
7. H. J. Jerison, *The Evolution of the Brain* (Appleton-Century-Crofts, New York, in preparation).
8. The statistic from the Kolmogorov-Smirnov test for unequal samples was used because it is sensitive to differences in both means and dispersions; see P. J. Kim and R. I. Jennrich, in *Selected Tables in Mathematical Statistics*, D. B. Owen and H. L. Harter, Eds. (Markham, Chicago, 1970), vol. 1. The analysis will be included in the full publication of these results (now being prepared for submission to the *American Naturalist*).
9. More complete description of most of the fossils are in T. Edinger, *Evolution of the Horse Brain, Memoir* 25 (Geological Society of America, New York, 1948); L. Radinsky, *J. Comp. Neurol.* **134**, 495 (1968); *Ann. N.Y. Acad. Sci.* **167**, 277 (1969); C. Dechaseaux, *Ann. Paleontol. Paris* **55**, 195 (1969); J. Piveteau, *Traité de Paléontologie* (Masson, Paris, 1957–1961), vol. 6 (parts 1 and 2) and vol. 7; D. E. Russell and D. Sigogneau, *Mem. Mus. Nat. Hist. Natur. Paris* **16**, 1 (1965); D. Sigogneau, *Ann. Paleontol. Paris* **54**, 39 (1968). Data on living forms are mainly from E. W. Count, *Ann. N.Y. Acad. Sci.* **46**, 993 (1947).
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