BRAIN SIZE, ADAPTATION AND HETEROCHRONY IN GEOMYOID RODENTS

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Of the many unusual morphological features that characterize mammals, perhaps the most intriguing and least understood is the enlarged brain. Among mammals, brain weight and body weight are allometrically related and follow the equation *brain weight = k(body weight)$^\alpha$*, where k is the allometric coefficient and α is the allometric exponent. The allometric exponent (regression coefficient) on a double logarithmic plot of brain weight on body weight across the Mammalia is estimated to be .74 (Eisenberg and Wilson, 1978; Martin, 1981; Armstrong, 1983); that is, larger mammals tend to have proportionately smaller brains. However, within groups of mammals, certain lineages show unusually enlarged brains; in such cases, brain mass far exceeds that predicted based on body mass alone. Examples of highly encephalized species are found in disparate mammalian lineages and at different taxonomic levels: pteropodid bats and humans exhibit greater encephalization than do other families in their respective orders (Jerison, 1973; Eisenberg and Wilson, 1978); certain porpoises and dolphins (Delphinidae), including *Tursiops, Grampus,* and *Orcinus,* stand out as the most encephalized cetaceans (Jerison, 1973, 1981; Osborne and Sundsten, 1981); opossums of the genus *Caluromys* seem to have larger brains in proportion to body size than do other didelphid marsupials (Eisenberg and Wilson, 1981); and relative brain size in certain species of white-footed mice (e.g., *Peromyscus crinitus, P. truei,* and *P. pectoralis*) exceeds that seen in other species of the genus (Mace and Eisenberg, 1982).

Hypotheses designed to account for these unusually encephalized species of mammals are of two basic types. The first, which we term "eco-ethological specialization," is founded on the assumption that increased specialization of a function (motor, sensory, or cognitive) requires increased brain mass to control that function (the "principle of proper mass"; Jerison, 1973). According to this view, relative brain size is a reliable index of both a species' trophic behavior and the complexity of the species' habitat (Findley and Wilson, 1982). This hypothesis directs one to search for eco-ethological specializations in large-brained species to better understand the evolution of encephalization (for examples see Mann, 1963; Stephan and Pirlot, 1970; Pirlot and Pottier, 1977; Eisenberg and Wilson, 1978, 1981; Clutton-Brock and Harvey, 1980; Lemen, 1980; Mace et al., 1981; Roth and Thorington, 1982; Meier, 1983). The second hypothesis, articulated most recently by Gould (1977), suggests that the unusually enlarged brain may have originated through time shifts in an ancestral developmental sequence (heterochrony) resulting in a paedomorphic descendant possessing the proportionately large brain characteristic of the juvenile ancestor. According to the "heterochrony" hypothesis, then, one might search for evidence of ontogenetic perturbations in large-brained species to better understand the evolution of brain size. It is important to observe that these ideas are not directly competitive. The eco-ethological specialization hypothesis focuses on present use of the enlarged brain (with extrapolations as to its ori-

gin), whereas heterochrony is concerned solely with the origin of the enlarged brain (irrespective of its present use).

In this study we examine patterns of encephalization in a group of mammals, the rodent superfamily Geomyoidea, that shows both extreme eco-ethological diversity and obvious paedomorphosis (Hafner and Hafner, 1983). Patterns of encephalization in geomyoid rodents have not been examined previously, and selection of this assemblage of mammals provides an opportunity to examine both encephalization hypotheses using a single, well-defined taxon (Hafner, 1982). This group is autochthonous in North America and contains two extant families: the Heteromyidae (kangaroo rats, kangaroo mice, pocket mice), which includes both scansorial and bipedal granivores (seed eaters); and the Geomyidae (pocket gophers), which includes quadrupedal, fossorial herbivores. Further, two genera in the Heteromyidae, *Dipodomys* (kangaroo rats) and *Microdipodops* (kangaroo mice) are paedomorphs. No equivalent group of mammals contains species so different in body plan (Fig. 1), life style, or mode of locomotion. Herein, we analyze brain size in species representing all recognized genera and subgenera of geomyoid rodents. Brain-size data are combined with information on the gross structure of the brain to facilitate investigation of brain evolution in this group.

MATERIALS AND METHODS

Gross brain size in 222 specimens representing 31 species of geomyoid rodents was assayed by volumetric measurement of cleaned skulls. The endocranial cavity of each skull was filled with No. 12 lead shot. The shot was weighed and the weight was then converted to a volumetric value, endocranial volume (Eo), using an empirically derived calibration (Eisenberg and Wilson, 1981). The assumption that gross endocranial volume is directly related to both brain weight and brain neuron density in mammals is supported by a large body of evidence reviewed by Jerison (1973). To minimize the degree
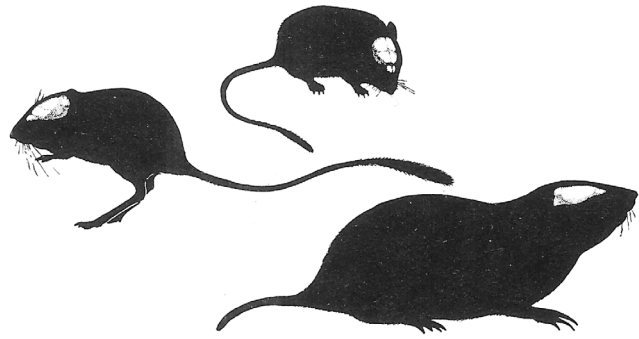

FIG. 1. Silhouettes of three principal geomyoid rodent morphotypes illustrating the relationship between brain size, body size, and morphotype in this group. Brain size in the morphologically generalized pocket mouse (*Chaetodipus* or *Perognathus*; upper) is generally typical for a mammal of this body size (8–35 g). Brain size in the morphologically specialized kangaroo rat (*Dipodomys*; left) is larger than would be predicted based on body size (40–150 g) alone. The fossorial pocket gopher (e.g., *Thomomys* or *Pappogeomys*; right) has a small brain relative to body size (90–640 g). See text for discussion.

of intraspecific variation, only adult male specimens were examined in this study. Regression analyses of log endocranial volume on log body mass were performed using all 31 species as well as treating the data on heteromyids and geomyids separately. We also examined functional relationships using log grand mean endocranial volume on log grand mean body mass across the 11 geomyoid genera. These ancillary regressions were run as a check for over- or under-representation of species in individual genera, which could lead to a bias in the original regression analysis. Table 1 presents the list of species examined and sample sizes used (localities are available on request).

Latex rubber endocasts were made from cleaned skulls following the method of Radinsky (1968). Cranial endocasts yield a faithful and detailed record of the brain's surface (cf. Dressler, 1979) and were used to examine gross brain structure. Size of the three principal brain regions (cerebrum, cerebellum, and olfactory bulbs) was assessed by measuring dorsal surface area of each structure. The square root of total dorsal surface area was highly correlated with the cube root
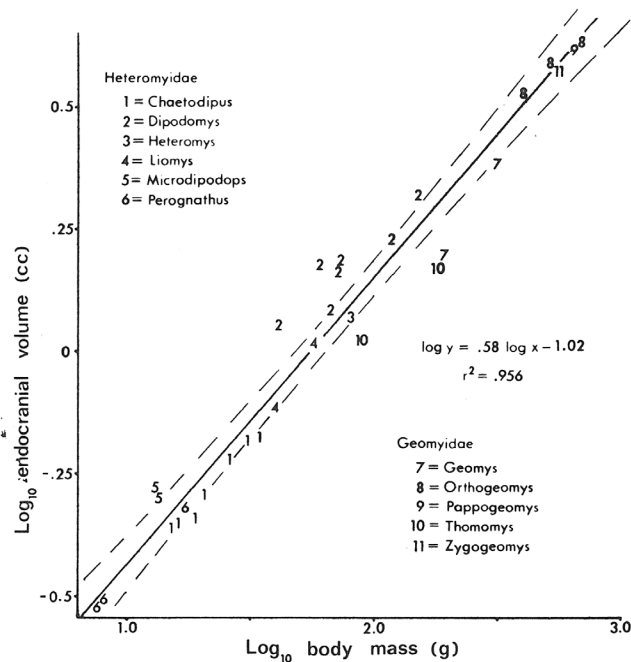
FIG. 2. Brain size/body size relationships in 31 geomyoid rodent species. Dashed lines are 95% confidence bands.

of total endocranial volume ($r = .982$; $P \ll .01$; $d.f. = 22$) indicating that surface area measures are a reliable index of brain volume. Nevertheless, the inference of brain volume from surface area measurements should be viewed with some caution because of the possibility of slight distortions in the latex endocast and possible errors in measuring the surface area of these small and complex structures.

RESULTS AND DISCUSSION

Encephalization in Geomyoid Rodents

Brain size (endocranial volume) and body size (mass in grams) in the Geomyoidea are functionally related by a positive linear trend (Fig. 2). Similar size-related patterns of encephalization have been reported for every group of mammals studied to date (Jerison, 1973; Armstrong, 1983 and included references). The allometric exponent describing the functional trend for geomyoid rodents ($\alpha = .58$; $P < .01$) is considerably less than the exponent value for brain size: body size scaling across the Mammalia ($\alpha = .74$), but its magnitude seems appropriate given the taxonomic levels

(within a superfamily) considered (see Lande, 1979).

The allometric exponent for the Geomyoidea ($\alpha = .58$; Fig. 2) is based on a regression analysis involving all 31 species examined. Allometric exponents for the separate families are calculable (α [Heteromyidae] = .66; α [Geomyidae] = .76), but we have pooled the data for all geomyoids because the allometric exponents for the separate families are not significantly different from one another ($F_s = 1.57$; $F_{.05[1,27]} = 4.21$). Further, although over-representation of species in individual genera (e.g., *Dipodomys* and *Chaetodipus*) might theoretically bias the overall functional relationship for the Geomyoidea, this was found not to be the case; regression analysis on log grand mean data for the genera yielded virtually identical results (α falls slightly from .58 to .57). Thus, the functional relationship described in Figure 2 appears to provide a reliable estimate of α for the Geomyoidea.

The association between log endocranial volume and log body mass among the geomyoids is quite strong ($r^2 = .956$) with only a few species departing significantly from the regression line (Fig. 2). Importantly, kangaroo rats (*Dipodomys*) and kangaroo mice (*Microdipodops*) have significantly large brains relative to other geomyoids. Figure 2 also reveals that pocket gophers of the genera *Thomomys* and *Geomys* fall below the 95% confidence band and, hence, have small brains relative to their body sizes.

Table 1 presents encephalization quotients (*EQ* values) for all geomyoid species examined. The *EQ* is a ratio between observed (*Eo*) and expected (*Ev*) brain size following Jerison (1973). *Ev* was calculated using mean body mass (Wt_b) in the formula $Ev = .055(Wt_b)^{.74}$ (Eisenberg and Wilson, 1981). This formula is derived from a regression of brain size against body size for more than 300 species of mammals and is used in evaluating the mammalian encephalization quotient, $EQ(M)$. An intra-geomyoid EQ value, $EQ(G)$, was calculated by substituting the

TABLE 1. Body size, brain size, and encephalization quotients in geomyoid rodents.

Species	N	Mean body mass g ± SD	Mean endocranial volume cc ± SD	Encephalization quotient (EQ) EQ(M)	EQ(G)
Kangaroo mice					
Microdipodops megacephalus	8	13.6 ± .8	.50 ± .02	1.32	1.16
Microdipodops pallidus	10	12.9 ± 1.6	.53 ± .03	1.45	1.26
Kangaroo rats					
Dipodomys deserti	8	114.7 ± 19.2	1.68 ± .08	.91	1.13
Dipodomys heermanni	10	71.3 ± 4.9	1.45 ± .06	1.12	1.28
Dipodomys merriami	10	41.0 ± 2.8	1.11 ± .08	1.29	1.36
Dipodomys microps	10	65.7 ± 9.6	1.18 ± .06	.97	1.10
Dipodomys ordii	4	60.2 ± 4.1	1.46 ± .11	1.28	1.43
Dipodomys panamintinus	8	74.0 ± 8.4	1.54 ± .11	1.16	1.34
Dipodomys spectabilis	9	146.6 ± 14.0	2.08 ± .12	.94	1.21
Pocket mice					
Chaetodipus baileyi	10	31.2 ± 5.4	.65 ± .03	.93	.93
Chaetodipus californicus	10	26.0 ± 2.0	.60 ± .03	.98	.95
Chaetodipus fallax	9	20.3 ± 1.8	.52 ± .06	1.02	.96
Chaetodipus formosus	10	15.3 ± 2.5	.43 ± .02	1.04	.93
Chaetodipus hispidus	10	35.2 ± 9.0	.66 ± .06	.86	.88
Chaetodipus penicillatus	10	16.5 ± 2.0	.44 ± .03	1.00	.91
Chaetodipus spinatus	8	19.1 ± 2.7	.46 ± .03	.94	.87
Perognathus flavus	10	8.0 ± 1.0	.30 ± .02	1.17	.95
Perognathus longimembris	6	8.0 ± .5	.31 ± .01	1.21	.98
Perognathus parvus	7	17.3 ± 2.4	.47 ± .02	1.04	.95
Spiny pocket mice					
Heteromys desmarestianus	6	77.1 ± 11.6	1.13 ± .02	.82	.96
Liomys irroratus	5	57.7 ± 7.7	1.02 ± .06	.92	.98
Liomys pictus	9	40.2 ± 6.8	.75 ± .03	.89	.89
Pocket gophers					
Geomys bursarius	7	192.4 ± 51.2	1.56 ± .18	.58	.78
Geomys pinetis	3	313.5 ± 56.6	2.42 ± .12	.62	.91
Orthogeomys cherriei	1	405	3.35	.72	1.08
Orthogeomys heterodus	2	630	4.16	.64	1.04
Orthogeomys hispidus	1	542.1	3.84	.66	1.05
Pappogeomys gymnurus	8	637.0 ± 92.9	4.04 ± .36	.62	1.00
Thomomys bottae	7	185.2 ± 27.6	1.48 ± .04	.56	.75
Thomomys talpoides	3	90.6 ± 6.9	1.06 ± .04	.69	.82
Zygogeomys trichopus	3	545.0 ± 32.8	3.81 ± .09	.65	1.04

value $Ev = .095(Wt_b)^{.58}$; this Ev value is based on the regression illustrated in Figure 2. EQ values less than 1.00 denote relatively small brains, and values greater than 1.00 describe relatively large brains. Among the geomyoids (Table 1), *Microdipodops pallidus* has the largest mammalian encephalization quotient, $EQ(M) = 1.45$, indicating that this kangaroo mouse has a brain nearly one-half again larger than predicted based on body mass. However, in comparison with other big-brained mammals, this value may seem diminutive: man's lofty $EQ(M) = 6.3$; the bottlenosed dolphin (*Tursiops truncatus*) has an $EQ(M) = 4.5$; and the killer whale's (*Orcinus orca*) $EQ(M) = 2.3$ (Jerison, 1973; Osborne and Sundsten, 1981). Based on intra-geomyoid comparisons, i.e., considering $EQ(G)$ values, kangaroo mice and kangaroo rats have brains that are from 10% to 43% larger than predicted from body size alone, and the smaller pocket gophers have brains only three-quarters of the predicted size (Table 1).

Recently, Martin (1981) and Armstrong (1983) demonstrated a relationship between brain size and metabolic rate in mammals. According to Martin, the metabolic rate of the mother may constrain the brain size of her neonate and, hence, the eventual size of the adult brain (i.e., brain size tracks metabolic rate). In contrast, Armstrong suggests that the adult mammal requires a particular basal metabolic rate to support its brain (i.e., metabolic rate tracks brain size). Both of these hypotheses would predict that large-brained geomyoids should have relatively high basal metabolic rates and small-brained species should have relatively low metabolic rates. Using geomyoid metabolic rate data provided by McNab (1966, 1979a, 1979b), and MacMillen (1983), we regressed basal metabolic rate values for 12 taxa (representing eight genera) against their $EQ(M)$ values. Basal metabolic rate was expressed as percent expected based on body mass ("% Kleiber"; Kleiber, 1932, 1961). The relationship between relative brain size and relative metabolic rate was non-significant (Spearman $r_s = -.1049$; $P = .373$). In fact, the species with the highest metabolic rate relative to body mass (*Heteromys*; McNab, 1979b; MacMillen, 1983) has the lowest $EQ(M)$ value of all heteromyids (Table 1). Certain large-brained geomyoids (e.g., *Microdipodops pallidus, Dipodomys merriami,* and *Perognathus longimembris*) have basal metabolic rates ranging from 18% to 46% below values predicted based on body mass. These findings do not reveal a link between brain size and metabolic rate in geomyoids and, hence, are not consistent with the hypotheses of Martin (1981) and Armstrong (1983). It appears that the relatively small brain in adult *Heteromys* is not the result of constraints placed on neonate brain size by low metabolic rate of the mother (cf. Martin, 1981), and enlargement of the brain in many other heteromyids has not been accompanied by increases in basal metabolic rate (cf. Armstrong, 1983). Although more data are needed, both

on brain size and metabolic rates, these preliminary results suggest that evolutionary changes in brain size and metabolic rate are decoupled in the Geomyoidea.

The Eco-ethological Hypothesis

The eco-ethological specialization hypothesis predicts correlations between degree of encephalization and degree of motor or sensory specialization. Although we found motor/sensory specialization difficult to assess, much less quantify, we selected two mensural variables to serve as indirect indices of specialization in the 31 geomyoid taxa. The first measure, breadth of the auditory bulla (or bullar expansion, BE), was chosen as an index of auditory specialization; extreme expansion of the bulla in *Dipodomys* is believed by many to reflect auditory-sensory specialization (Webster and Webster, 1980). The second variable, length of the hind foot (HF), was chosen as an index of locomotory specialization; the elongated hind feet of the bipedal species is clearly indicative of locomotory specialization (Bartholomew and Caswell, 1951; Fig. 1). We examined these two variables plus a third variable, brain volume (*Eo*), in a partial correlation analysis controlling for body size. Results of the partial correlation analysis revealed that both indices of specialization were correlated in a highly significant manner with brain volume: *Eo* with BE, partial $r = .84$; *Eo* with HF, partial $r = .80$; $P < .01$ in both cases). These correlations indicate that, independent of body size, as bullar inflation increases, brain size increases; and as hind foot lengthens, brain size increases.

Although able to document statistically significant relationships among these variables, we have not demonstrated that the variables are causally related. In other words, it is premature to conclude (based on these correlations) that the enlarged brain in kangaroo rats (for example) has evolved to assimilate increased amounts of neural input and coordinate complex auditory-sensory and locomotory func-

tions. Importantly, however, these correlations allow us to make predictions about the gross structure of the geomyoid brain. Examination of the brain should provide evidence to either refute or support explanatory statements based on the correlations.

Gross Structure of the Brain

In general, the mass of neural tissue controlling a particular function is proportional to the amount of information processing involved in performing that function (Jerison, 1973). Accordingly, we should expect that species with increased auditory specialization (as purported for kangaroo rats and kangaroo mice by virtue of their enlarged auditory bullae) should possess a relatively large cerebrum, with particular enlargement of appropriate auditory-sensory regions of the neocortex. Similarly, species showing increased locomotory specialization (again, the bipedal kangaroo rats and kangaroo mice) should show enlargement of appropriate motor regions of the neocortex plus general enlargement of the cerebellum. Finally, in species that are predominantly olfactorily oriented, we should expect to find relatively large olfactory bulbs. These predictions can be assessed by examining relative size of the three major components of the brain (cerebrum, cerebellum, and olfactory bulbs) using endocranial casts.

Examination of cerebrum size relative to body size (Fig. 3a) reveals that kangaroo rats and kangaroo mice show general enlargement of the cerebral cortex. More importantly, ventral displacement of the rhinal fissure and general posterior expansion of the neocortex (Fig. 4) may reflect enhanced auditory-sensory perception in both kangaroo rats and kangaroo mice. These observations are in accord with predictions based on the eco-ethological specialization hypothesis. For reasons that are unclear, certain species of small pocket mice (*Perognathus*) and small pocket gophers (*Thomomys* and *Geomys*) have unusually small cerebral hemispheres, whereas the larger pocket
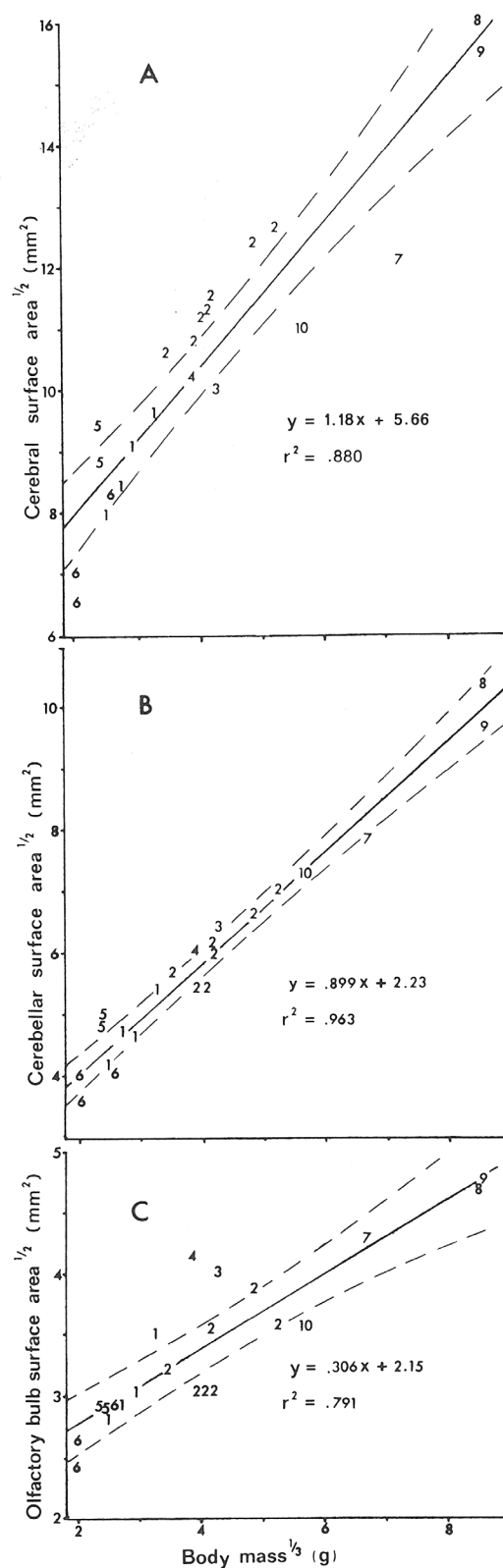

FIG. 3. Relationships between size of major brain components and body size in geomyoid rodents. Species as per Figure 2. Dashed lines are 95% confidence bands.

mice (*Chaetodipus*) and larger pocket gophers (*Orthogeomys* and *Pappogeomys*) have cerebra appropriate for their body size.
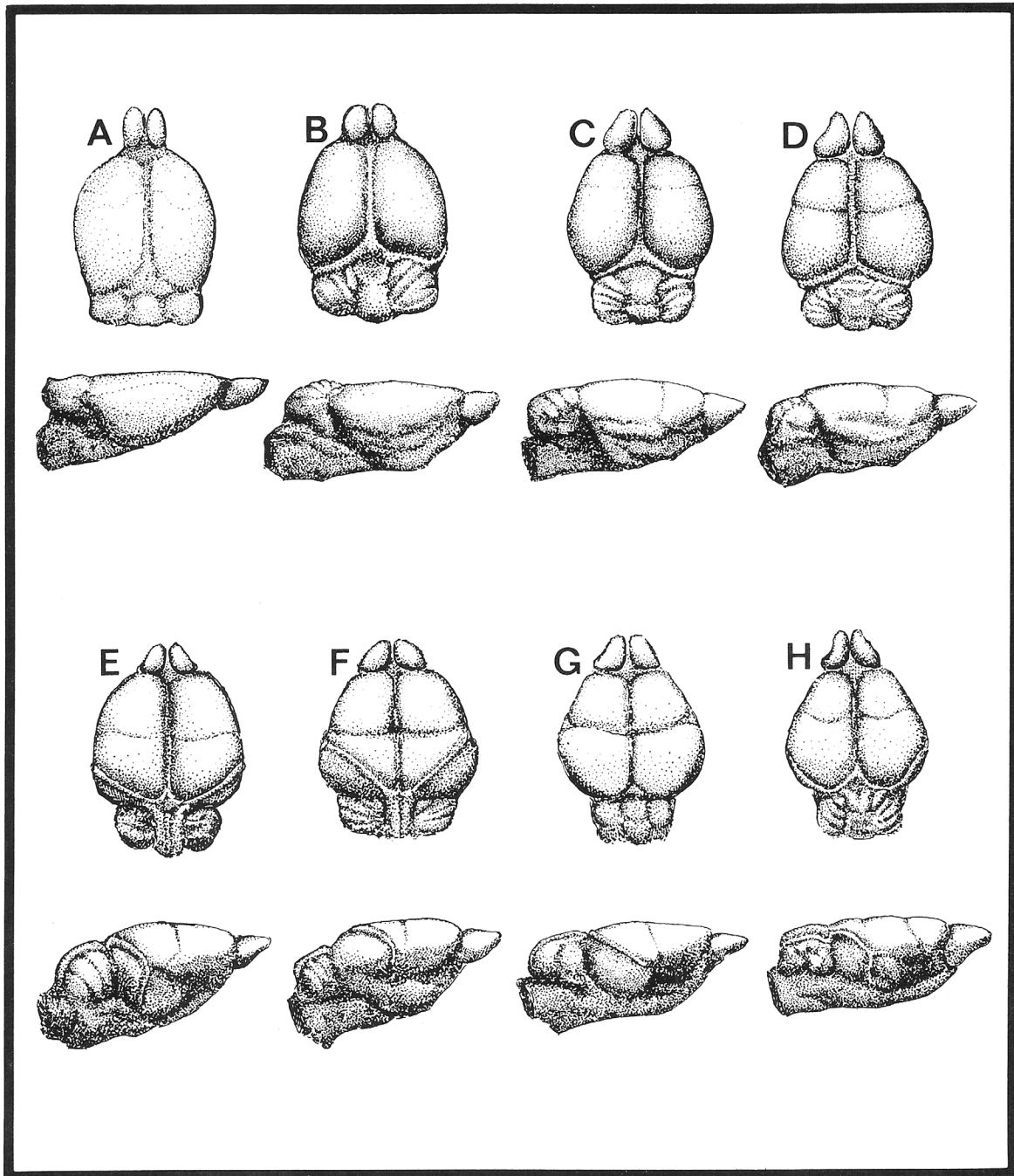
FIG. 4. Dorsal and lateral views of endocranial casts of representative geomyoid rodents. A = *Pappogeomys gymnurus*; B = *Thomomys bottae*; C = *Heteromys desmarestianus*; D = *Liomys irroratus*; E = *Dipodomys merriami*; F = *Microdipodops pallidus*; G = *Perognathus longimembris*; H = *Chaetodipus hispidus*. Brains are not drawn to scale.

Analysis of cerebellum size relative to body size (Fig. 3b) shows that kangaroo mice, in particular, have unusually enlarged cerebella (Fig. 4). Again, this is in accord with predictions of the eco-ethological specialization hypothesis; specialized locomotion (in this case, bipedality) should be accompanied by cerebellar enlargement. Note, however, that kangaroo rats, which are known to exhibit an even higher degree of bipedality, do not show the predicted cerebellar expansion; they simply fall along the trend-line with the generalized, scansorial forms such as *Chaetodipus* and *Perognathus*.

Comparison of the relative size of the olfactory bulbs (Fig. 3c; Fig. 4) reveals that the two genera of spiny pocket mice, *Liomys* and *Heteromys*, have unusually

TABLE 2. Size relationships among the major regions of the brain based on dorsal surface area measurements.

Species	Total dorsal surface area (mm^2)	Percent total dorsal surface area		
		Cerebrum	Cerebellum	Olfactory bulbs
Kangaroo mice				
Microdipodops megacephalus	110.9	70.15	22.09	7.75
Microdipodops pallidus	120.9	73.86	19.02	7.11
Kangaroo rats				
Dipodomys deserti	212.8	72.41	20.54	7.05
Dipodomys heermanni	179.4	71.79	21.18	7.02
Dipodomys merriami	155.3	72.57	20.73	6.70
Dipodomys microps	165.6	76.39	18.06	5.56
Dipodomys ordii	156.4	75.00	19.12	5.88
Dipodomys panamintinus	179.4	74.36	20.51	5.13
Dipodomys spectabilis	222.5	72.13	22.11	5.75
Pocket mice				
Chaetodipus californicus	113.8	72.76	19.16	8.08
Chaetodipus fallax	102.0	69.90	21.67	8.43
Chaetodipus formosus	89.6	71.88	19.20	8.91
Chaetodipus hispidus	135.3	69.10	21.80	9.09
Perognathus longimembris	61.0	69.84	20.66	9.51
Perognathus parvus	93.5	73.69	17.11	9.20
Spiny pocket mice				
Heteromys desmarestianus	158.7	63.77	26.09	10.14
Liomys irroratus	158.4	66.22	22.98	10.80
Pocket gophers				
Geomys bursarius	228.6	64.87	27.08	8.09
Orthogeomys heterodus	386.0	66.32	27.98	5.70
Pappogeomys gymnurus	356.4	67.62	26.01	6.37
Thomomys bottae	188.3	64.80	28.41	6.80

large olfactory bulbs. This observation leads us to predict that these animals may have enhanced olfactory abilities relative to other geomyoid species. However, present knowledge of the life history of these forms is insufficient to test this prediction.

Information on the percent contribution of cerebrum, cerebellum, and olfactory bulbs to total dorsal surface area of the brain is presented for 21 geomyoid species (Table 2). In all heteromyids except *Heteromys* and *Liomys,* the cerebrum contributes more than 69% to the total dorsal surface area of the brain, whereas the olfactory bulbs contribute less than 10%. In the four pocket gopher species examined, the cerebellum has an unusually large contribution to overall brain size. Finally, *Heteromys* and *Lio-*

mys have olfactory bulbs that are proportionately large relative to those of other geomyoids (see also Fig. 3c). Although these data allow for direct comparison of relative size of brain regions, regardless of the absolute size of the brain or body, proportional values can be misleading. For example, the cerebella in pocket gophers, which are proportionately large relative to those of other geomyoids when considering percentage of total brain (Table 2), are actually no larger than would be expected for geomyoids of these body sizes (see Fig. 3b). Similarly, the proportionately small cerebra in *Orthogeomys* and *Pappogeomys* (Table 2) are really appropriate in size for large-bodied geomyoids (Fig. 3a). The principal focus in studies of the allometry of different brain regions should be the relationship be-

tween the size of the brain region and the size of the body mass controlled by the brain, rather than relative size of the parts of the brain.

Developmental Heterochrony

Certainly, the evolution of brain size is a complex phenomenon and analyses based on single measures such as body size, metabolism, or simple indices of eco-ethological specialization will tend to oversimplify the issue (see also Lande, 1979). Nevertheless, we have shown that examination of the gross structure of the brain provides evidence in support of the eco-ethological specialization hypothesis in some, but not all, cases (see also Roth and Thorington, 1982). Although this method may provide insight into the functional significance of the enlarged brain, it is also clear that present-day function may provide few clues as to the evolutionary origin of the enlarged brain (see Gould and Vrba, 1982; Vrba, 1983).

Recently, two genera of geomyoid rodents, *Microdipodops* (kangaroo mice) and *Dipodomys* (kangaroo rats), were recognized as paedomorphs (Hafner and Hafner, 1983). These forms possess essentially all the classical features of the paedomorphic syndrome (for review see Gould, 1977), including enlarged head and eyes, elongated hind feet, delayed or truncated maturation, poorly ossified skeleton, weakly fused cranial sutures, and retarded development of molar roots (Hafner and Hafner, 1983). Importantly, we do not regard it as mere coincidence that the paedomorphic geomyoids—kangaroo mice and kangaroo rats—also show the most extreme degree of encephalization. Far from coincidence, enlargement of the brain is a classical paedomorphic feature, just as it is in humans (Gould, 1977). If we look, we see this syndrome of features appearing together commonly in group after group of living mammals (DeBeer, 1958; Gould, 1977). Clearly, we are in need of manipulative embryological studies to determine if, in fact, these features are developmentally linked. Recent advances in our knowl-

edge of the biochemistry and endocrinology of development (e.g., see Caplan et al., 1983; Zagon and McLaughlin, 1983) suggest that such experiments may soon be possible. In the interim, however, we cannot afford to discount the possible influence that heterochronic shifts in ontogeny may have had in the origin of highly encephalized forms.

Clearly, it is more parsimonious to suppose that the suite of juvenilized features shared by kangaroo rats and kangaroo mice, including the enlarged brain, originated together through developmental heterochrony, rather than to suppose that each trait originated independently through natural selection. It should be kept in mind that selection acting at any age results in associated effects at all other ontogenetic stages. Hence, morphological differentiation among adult forms may be the end result of evolutionary changes at earlier ontogenetic stages (for review see Gould, 1977; Cheverud et al., 1983). The original developmental shift(s) resulting in paedomorphosis (and, thus, encephalization) may have been advantageous to the organism for any number of reasons not directly involving the enlarged brain (Gould, 1977). As Williams (1966) and Vrba (1983) note, the process of adaptation by natural selection may yield incidental effects that are not a direct consequence of the selective process; macroevolutionary trends involving encephalization may represent such a case. The grossly enlarged brains of certain mammal species may be of great adaptive value or be largely neutral—an interesting question in its own right. However, when we consider the origin (as opposed to present function) of the enlarged brain, we must consider the possibility that it may have been developmentally mandated. We conclude that encephalization in certain geomyoid rodents, particularly kangaroo rats and kangaroo mice, may have been an incidental byproduct of heterochronic developmental changes in an ancestral lineage. Whether or not brain enlargement was originally a direct object of nat-

ural selection will never be known; however, there appears to be some evidence that the enlarged brain now functions to enhance eco-ethological specialization in certain living geomyoid species.

SUMMARY

The rodent superfamily Geomyoidea, heretofore unstudied with respect to brain-size evolution, contains species of widely differing morphologies and ecologies and provides an unusual opportunity to evaluate two current hypotheses concerning the evolution of mammalian encephalization: the eco-ethological specialization hypothesis and the heterochrony hypothesis. An analysis of encephalization in geomyoid rodents reveals that the highly encephalized forms, kangaroo mice (*Microdipodops*) and kangaroo rats (*Dipodomys*), also show unusual eco-ethological specializations. Examination of gross brain structure indicates that, in some cases, a causal link may exist between the enlarged brain and particular motor or sensory specializations. However, the most highly encephalized geomyoids are also paedomorphs, and it is suggested that the evolutionary origin of the enlarged brain in these forms may have been developmentally mandated and not originally the direct object of selection. It is concluded that the coevolution of mammalian brain size and body size is a complex phenomenon that may be greatly influenced by the evolution of ontogenies. Encephalization, per se, may or may not reflect long-term selection for increased eco-ethological specialization.

ACKNOWLEDGMENTS

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