From: HETEROCHRONY IN EVOLUTION
Edited by Michael L. McKinney
(Plenum Publishing Corporation, 1988)

Chapter 12

Heterochrony in Rodents

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1. Introduction

The mammalian order Rodentia is by far the largest order of mammals (approximately 1700 species), and rodents show ranges in body size, body plan, and ecological diversity that far exceed those seen in any other group of mammals, including bats and cetaceans. Living rodents inhabit all continents except Antarctica, and they are found in nearly every terrestrial habitat throughout their geographic range. Rodents usually play integral roles in the terrestrial ecosystems they inhabit, and they are often the most abundant and diverse of all vertebrates in a terrestrial community.

For these reasons and others, the order Rodentia seems the obvious mammalian group in which to examine patterns of morphological and ecological differentiation (usually termed evolutionary trends) in an effort to reveal causal evolutionary processes that generate organismal diversity. To be recognized as such, a higher order evolutionary trend must cut across phyletic boundaries (i.e., be lineage-independent), and it must generate predictable results in the groups it

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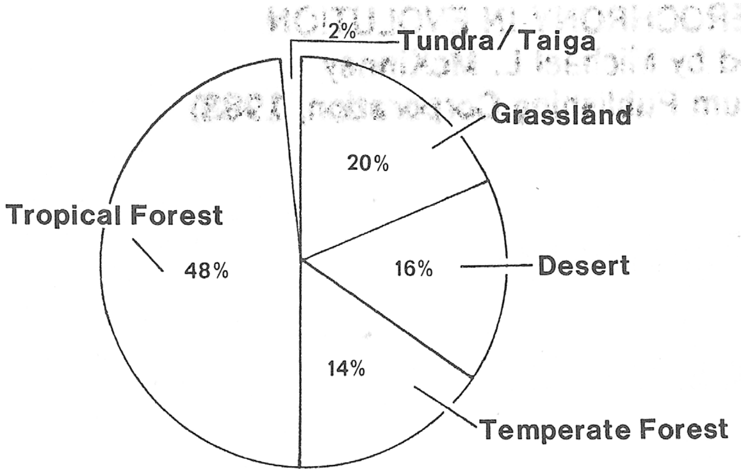

Figure 1. Distribution of 370 genera of living rodents among five general biomes.

affects. For example, the evolutionary trend leading to the many cases of gigantism in normally small mammals inhabiting oceanic islands and the trend toward reduction (or loss) of lateral digits in cursorial mammals are both lineage-independent phenomena that lead to predictable morphological consequences. Once the evolutionary trend is identified, one begins the search for an underlying causal factor, the elucidation of which is generally the major focus of interest in any evolutionary study.

The initial sections of this chapter focus on the identification of higher order evolutionary trends within the Rodentia. The remaining sections focus on the much more difficult (but infinitely more interesting) challenge of explaining the observed trends. In the latter effort, we find that we are only partially successful; but we do offer hypotheses to be tested and potential avenues for fruitful research that may bring future workers closer to understanding the higher order evolutionary principles that orchestrate broad patterns of mammalian differentiation.

2. A General Overview of Rodent Diversity

2.1. Ecological Diversity

Figure 1 provides a broad overview of ecological diversity among the 370 genera of living rodents recognized by Nowak and Paradiso (1983). Although subdivision of the earth's habitats into tropical forest, temperate forest, desert, grassland, and tundra/taiga is necessarily crude, it is clear that almost half of all living rodent genera inhabit tropical forest environments. This same pattern is evident when rodents are considered at the species level; for example, approximately 41% of 1673 living species of rodents inhabit tropical forest environments. Approximately equal numbers of rodent taxa, whether considered by genus or species, inhabit grassland, desert, and temperate forest environments. Finally, only 2% of all rodent genera (also 2% by species) inhabit the combined tundra/taiga habitat. Importantly, each ecological group contains rodents from distantly related lineages (i.e., the pattern is not lineage dependent), and the pattern could not have been predicted solely from the relative abundance of habitat types on earth. Thus, a higher order evolutionary trend is evident, and this trend has been

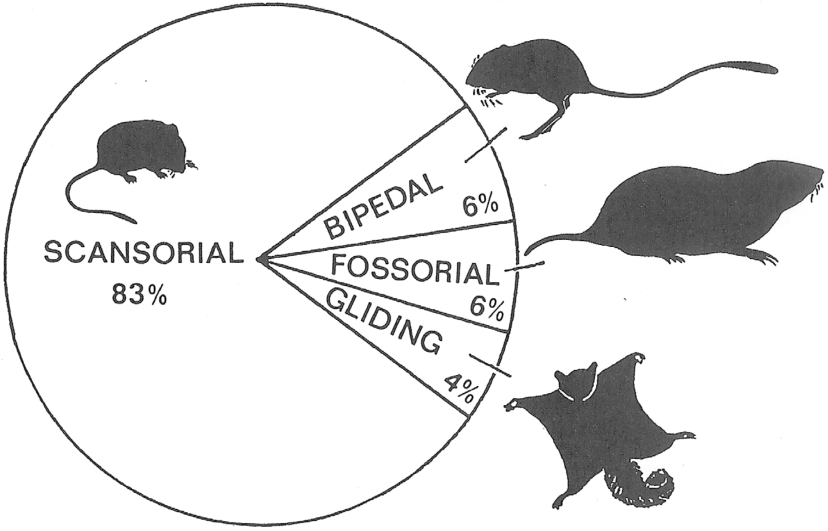

Figure 2. Diversity in body plan among extant genera of rodents.

explained in adaptive terms by zoogeographers such as Darlington (1957) and Keast (1972).

2.2. Diversity in Body Size

Living rodents range in body size from approximately 6 g (e.g., the mouse genera *Micromys* and *Delanymys*) to more than 60 kg (the capybara, *Hydrochaeris*). This range spans four orders of magnitude and exceeds the size range of any other mammalian order, including even the cetaceans. Not surprisingly, the distribution of individual rodent taxa within this vast size range is heavily skewed to the right; the median body size (by mass) among 370 genera of living rodents is approximately 80g, and 75% of all rodents (whether considered by genus or species) weigh less than 240 g. Given that the earliest rodents were also generally small (Romer, 1966), it is reasonable to conclude that there has been a major evolutionary trend toward retention of small body size in most rodent lineages. The adaptive explanation for this trend has involved a mixture of metabolic, trophic, and reproductive considerations (see Eisenberg, 1981, and references therein).

2.3. Diversity in Body Plan

Living rodents are easily subdivided into four discrete body plan categories (*Baupläne*): scansorial (= scampering); bipedal (= hopping); fossorial (= obligate burrowing); and gliding (= modified for nonpowered flight). Based on comparison with nonrodent mammals and vertebrates in general, the scansorial body plan is both generalized and primitive within the Rodentia. The three remaining categories (bipedal, fossorial, and gliding) include highly specialized and derived body plans that appear to represent evolutionary commitments to novel ways of life.

Figure 2 illustrates the distribution of rodent genera among the four body plan categories. Not surprisingly, most taxa (83%) are scansorial (or typically

TABLE I. Relationship between Habitat and Three Specialized Body Plans in Rodents

<table>
<tr><th rowspan="3">Specialized body plan</th><th colspan="10">Habitat[a]</th></tr>
<tr><th colspan="2">Desert</th><th colspan="2">Grassland</th><th colspan="2">Tropical forest</th><th colspan="2">Temperate forest</th><th colspan="2">Tundra/ taiga</th></tr>
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<tr><td>Bipedal</td><td>4</td><td>18</td><td>5</td><td>3</td><td>12</td><td>1</td><td>3</td><td>2</td><td>0</td><td>0</td></tr>
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<tr><td>Fossorial</td><td>4</td><td>4</td><td>5</td><td>12</td><td>12</td><td>2</td><td>3</td><td>6</td><td>0</td><td>0</td></tr>
<tr><td>Gliding</td><td>2</td><td>0</td><td>3</td><td>0</td><td>7</td><td>11</td><td>2</td><td>4</td><td>0</td><td>0</td></tr>
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[a] Exp, Expected frequency based on a survey of 370 genera of rodents. Obs, observed. An asterisk denotes a significant departure from expectation.

mouselike in body plan), whereas only 6% are bipedal, 6% are fossorial, and 4% are gliders. These same patterns hold when taxa are analyzed by species.

None of the three specialized body plan categories is restricted to a single rodent lineage. For example, the bipedal rodents include representatives from the distantly related superfamilies Muroidea, Dipodoidea, and Geomyoidea; the fossorial rodents include representatives from distinct rodent groups (e.g., caviomorphs, geomyoids, bathyurgids); and gliding species are found in the distantly related families Sciuridae and Anomaluridae. This survey indicates, therefore, that each of these specialized body plan categories is lineage independent, which suggests that each may represent a higher order evolutionary trend. Although trends, such as these, which lead to morphological or ecological similarity among distantly related taxa are generally termed evolutionary convergence, it should be recognized that "convergence" merely describes the trend; it does not explain it in causal terms.

The most striking and best-studied example of locomotory specialization among rodents is bipedality (e.g., Bartholomew and Caswell, 1951; Hatt, 1932; Howell, 1932). Bipedal rodents include 24 genera representing eight families, and all are remarkably similar morphologically and ecologically. Table I shows that bipedal rodents are not distributed randomly among the five habitat types, but occur more often than expected in desert habitats and less often than expected in tropical forest habitats.

In addition to elongated hindlimbs and reduced forelimbs, many bipedal rodents possess unusually large auditory bullae (the boney capsule housing the middle ear). Our examination of rodent crania [plus additional information provided in Nowak and Paradiso (1983)] reveals that roughly 40 of 370 rodent genera have grossly enlarged auditory bullae. If this character (bullar enlargement) were distributed randomly among rodents irrespective of body type, only two bipedal genera (6% of 40; see Fig. 2) would be expected to possess the feature. Our survey reveals, however, that 12 of the 40 rodent genera with enlarged auditory bullae are also bipedal forms ($\chi^2 = 54.4$; d.f. $= 3$; $p < 0.001$). Thus, there appears to be a nonrandom association among bipedality, enlarged auditory bullae, and desert habitation in rodents. Whether or not this association is biologically meaningful (i.e., whether or not the factors are causally linked) remains to be seen.

3. Functional Descriptions and Causal Explanations

Conventional explanations for the existence of novel body plans, such as those seen in certain rodents, focus on the adaptive aspects (advantages) of the functional design [e.g., see review by Eisenberg (1975)]. For example, gliding rodents [including sciurid "flying" squirrels (e.g., *Glaucomys*), and anomalurid scaly-tailed squirrels (e.g., *Anomalurus*)] have "wing" membranes because these small airfoils are selectively advantageous in that they allow for protracted leaps and thus may aid in predator avoidance. Fossorial rodents [e.g., tucu-tucos (*Ctenomys*), pocket gophers (*Thomomys*), and mole rats (*Spalax*)] have massive bodies equipped with powerful forelimbs and rugose, dense skulls because this morphology is adaptive in burrowing through the soil. Bipedal rodents [e.g., jerboas (*Dipus*) and kangeroo rats (*Dipodomys*)] have delicate, gracile bodies with long hindlimbs and long tails because natural selection seems to favor this "antipredator morphology" (Kotler, 1985) in rodents inhabiting open desert environments. Suffice it to say, the adaptive significance of the novel morphologies seen in certain rodents has received much attention from several generations of biologists. The emphasis on the current use (immediate adaptive significance) of the novelties has been so overwhelming that few workers have sought to understand the evolution of the novelties. Actually, the extreme adaptationist tradition has been so alluring in its simplicity that most workers have assumed (usually implicitly) that they are explaining the evolution of a feature when they explain its present use (see also Gould and Vrba, 1982, p. 13). In this tradition, morphological evolution is often explained as the result of long-term, directional selection (orthoselection) wherein natural selection favors certain adaptations present in ancestral species in response to long-term selective pressures on individual characters of atomized individuals. Caution should be exercised when viewing morphology from this kind of adaptationist perspective, inasmuch as it may lead to pseudoexplanatory inferences about morphological evolution [for review, see Gould and Lewontin (1979), Mayr (1983)].

A distinction should be made here between two kinds of perspectives which are important in evolutionary morphology: functional descriptions and causal explanations. Functional descriptions, such as those discussed above, explain morphology in terms of its purpose to the animal; prior morphological states of the feature are irrelevant in this context. Causal explanations, however, focus on prior morphological states and attempt to predict future states from earlier ones. Hence, functional descriptions address the current use (adaptive significance) of a feature, whereas causal explanations seek to address only the evolution of a feature, regardless of its present use. It is important to note that functional descriptions and causal explanations are not directly competitive. Conversely, the two must not be automatically treated as one and the same; functional descriptions that entail unwarranted extrapolations as to a character's origin (i.e., scenarios of adaptation) may belie the actual historical genesis of the feature.

It seems that virtually all of the explanations for the extreme morphological variation among rodents stem from functional descriptions. As noted by Brookfield (1982), an emphasis on present function may obfuscate our attempts to understand the evolution of evolutionary novelties. Our intent in the remainder of this chapter, then, is to focus on the evolution of the novel body plans seen in

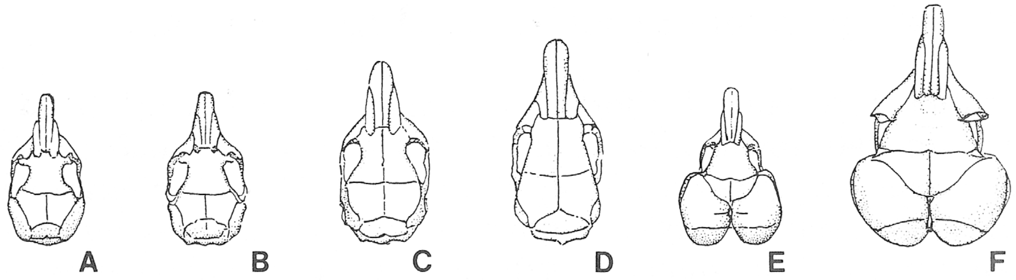

Figure 3. Representative crania of the Heteromyidae, showing diversity of morphological types. (A) *Perognathus*; (B) *Chaetodipus*; (C) *Liomys*; (D) *Heteromys*; (E) *Microdipodops*; (F) *Dipodomys*.

certain rodents. As such, we seek causal explanations for the evolution of morphological features, regardless of their present adaptive significance.

4. Geomyoid Rodents As a Case Study

4.1. Morphological and Ecological Breadth

We have shown that rodents, as a whole, show extreme morphological diversity (Fig. 2). Even so, one rodent group in particular, the superfamily Geomyoidea, provides an exceptional opportunity for studies in evolutionary morphology; three of the four major rodent body plans (Fig. 2) are found in this one superfamily (no gliding forms). No other mammalian superfamily, extant or extinct, is known to have the high degree of morphological differentiation of the geomyoids.

The history of geomyoid rodents is restricted to the New World, and extant forms include two families: the Heteromyidae (includes scansorial and bipedal forms) and the Geomyidae (all are fossorial forms). Although this superfamily is geographically restricted when compared with most other major rodent groups, geomyoids occupy virtually all kinds of terrestrial habitats, from sea level to well over 3000 m. For example, certain geomyoids, such as spiny pocket mice (*Heteromys*), inhabit moist, tropical forests. Other geomyoids, including kangaroo mice (*Microdipodops*) and certain species of kangaroo rats (*Dipodomys*), are restricted to extremely xeric, sand dune habitats in the desert.

The Heteromyidae (an appropriate epithet meaning "different mice") shows a surfeit of morphological types (Fig. 3) when compared to the typical range of morphological diversification seen in most other rodent families. Four of six heteromyid genera represent varied types of quadrupedal (scansorial) rodents: the pocket mice (*Perognathus* and *Chaetodipus*) and the spiny pocket mice (*Liomys* and *Heteromys*). This scansorial *Bauplan* is generalized for the Geomyoidea, as well as for the Rodentia (and also the Mammalia). Extreme morphological diversity is seen in the bipedal forms: kangaroo mice (*Microdipodops*) and kangaroo rats (*Dipodomys*). These bipedal ricochetors (saltators) are highly derived in morphology; notable features include large head (in proportion to body size) with greatly expanded auditory bullae (see Fig. 3) and extremely elongated hindlimbs. Kangaroo mice are tiny, bipedal rodents (approximately 10 g) and kangaroo rats are large, bipedal animals (approximately 40–170 g).

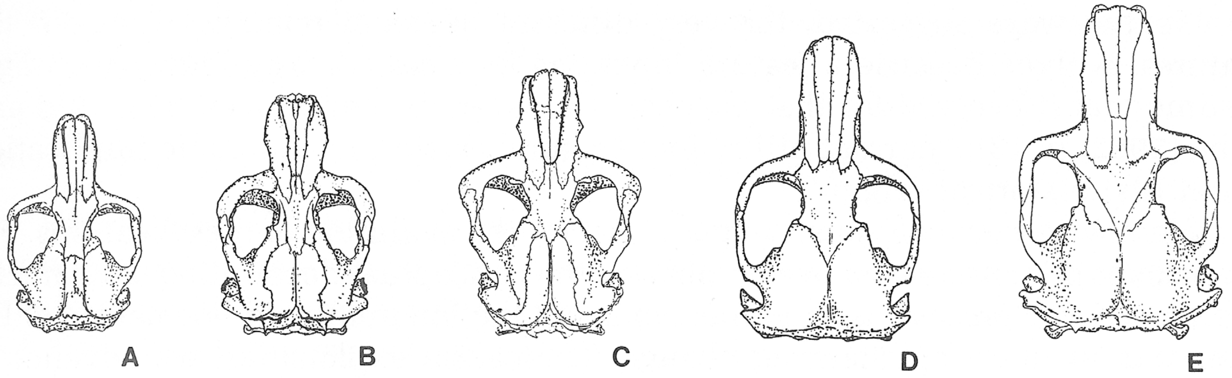

Figure 4. Representative crania among the Geomyidae. Note the general similarity in shape. (A) *Thomomys*; (B) *Geomys*; (C) *Pappogeomys*; (D) *Zygogeomys*; (E) *Orthogeomys*.

The geomyoids (literally ''earth mice'') also show a *Bauplan* that is highly derived in relation to the generalized scansorial condition. The geomyoids, or ''pocket gophers,'' include five genera: *Thomomys, Geomys, Pappogeomys, Zygogeomys,* and *Orthogeomys*. In marked contrast to the heteromyids, the geomyids are remarkably similar morphologically. With the exception of size differences, all pocket gophers look basically alike (see Fig. 4).

Together, these two families form a cohesive superfamily; all members of the Geomyoidea are united by the presence of externally opening, fur-lined cheek pockets. While many other rodents have internal cheek pouches for storing food, the geomyoid cheek pockets are unique in that they are positioned outside the buccal cavity [for review, see Hill (1937), Ryan (1986)]. Long (1976) hypothesized that the cheek pockets of the geomyoids represent a radical morphological shift that may have been caused by a simple developmental change. Hence, this key innovation suggests a discontinuous, macroevolutionary origin of the entire superfamily (see also Gould, 1980).

4.2. Scenarios of Adaptation and Morphological Evolution

It is indeed a challenge to explain the evolution of these extreme and conspicuous body plans found in the Geomyoidea. Among all geomyoid rodents, the bizarre morphology of the bipedal kangaroo mice and kangaroo rats has attracted the greatest amount of attention from biologists. These forms, like their Old World counterparts (e.g., *Jaculus, Dipus, Salpingotus,* and others), are considered by many to be the epitome of desert specialization (Mares, 1983). The evolution of the enormous head, huge hindfeet, large eyes, and long tail in kangaroo mice and kangaroo rats is explained conventionally in terms of the adaptive aspects of their morphology. The common opinion among biologists is, for example, that the large head serves as a counterbalancing organ during bipedal saltation, the huge hindfeet serve as sand paddles on sandy substrates, the large eyes are extreme adaptations for nocturnal vision, and the long tail serves as a midair rudder during ricochetal locomotion [for review, see Hafner (1988)]. Virtually all of these scenarios of adaptation focus on what is termed the ''antipredator morphology'' of *Microdipodops* and *Dipodomys* (Kotler, 1985). Whether or not these features function in the ways suggested, the very different question remains: how did the features evolve? Because a feature functions in a certain way today, we might assume that it evolved for that purpose. However, as emphasized by Gould and Vrba (1982, p. 13), "current utility [of a feature] carries no automatic implication about [its] historical origin."

Here we focus on a causal explanation for the evolution of these features. For the sake of this discussion, we emphasize the conceptual decoupling of character evolution from present use and thereby avoid the inherently *ad hoc* nature of the scenarios in inferring character change. The causal explanation we advance to account for macroevolution in the Geomyoidea focuses on the mechanisms of heterochrony (mutations that effect changes in developmental programs) as a broad, unifying explanation to account for the evolution of the wide variety of morphological novelties that occur in this group.

4.3. Hypothesized Heterochronic Transformations

The hypothesis that morphological evolution is the result of regulatory changes in development has been promoted by many workers (e.g., de Beer, 1930, 1958; Goldschmidt, 1940; Waddington, 1957, 1962; Gould, 1977). Both Waddington (1957, 1962) and Alberch (1980) noted that morphologies do not appear in a random or continuous manner in a group, but that there is a repetition of several distinctive body plans. Such is the case in rodents in general (Fig. 2) and with geomyoid rodents in particular. An examination of both fossil and extant geomyoids reveals that virtually all forms fit into one of three general *Baupläne*: scansorial mice, hopping (kangaroo-like) rats and mice, and fossorial forms (see Fig. 2). As pointed out by Alberch (1980), epigenetic interactions may reduce the spectrum of potential novel morphologies and impose a sense of order in morphological transformations through phylogeny; as a consequence, we should expect to see developmental constraints effecting phyletic parallelism. The observation that the Geomyoidea is rife with phyletic parallelism (Wood, 1935; Hafner and Hafner, 1983) is consistent with this view.

Geomyoid rodents contain genera that are morphologically generalized (the four genera of pocket mice and spiny pocket mice), others that appear to be generally paedomorphic, or juvenilized (kangaroo mice and kangaroo rats), and still others that seem to be hypermorphic, or developed beyond the generalized condition (pocket gophers). Both paedomorphism and hypermorphism are predictable consequences of heterochronic change, which leads us to deduce that developmental heterochrony may explain macroevolutionary diversification in geomyoid rodents [for review, see Hafner, J. C., Hafner (1983), Hafner, M. S., Hafner (1984), and Hafner (1988)]. Below, we use simplified phenomenological descriptions to illustrate how regulatory changes in ontogeny may, in affecting the timing of gene action and rates of morphogenesis and growth, explain morphological transformations in geomyoid phylogeny [for review see Gould (1977), Alberch *et al.* (1979), Alberch (1980), Løvtrop (1981a,b), and Rachootin and Thomson (1981)]. We will attempt to confirm our deductive conclusion that heterochrony explains macroevolutionary diversification in the Geomyoidea by independent inductive investigations within geomyoid rodents. We will thus examine indirectly the heterochrony hypothesis of morphological change, a hypothesis that is impossible to falsify directly because it treats unique, historical events.

4.3.1. The Pocket Mouse: A Generalized Geomyoid Rodent

Pocket mice, including *Perognathus, Chaetodipus, Liomys,* and *Heteromys,* exhibit a generalized rodent *Bauplan* (Eisenberg, 1981, p. 90) and probably represent a reasonable approximation of the ancestral geomyoid condition. An animal with this ancestral morphology (i.e., a pocket mouse) is likely to have conserved the developmental patterns of the geomyoid ancestor. As the pocket mouse ages from conception, its size and shape will change, following the ancestral ontogenetic growth curve. Perturbations of "control parameters," including the onset of growth, cessation of development, and rate of growth, may deform the ancestral ontogenetic trajectory and lead to morphological transmutations [for review of this model, see Alberch *et al.* (1979)]. We hypothesize that morphological diversification in the Geomyoidae is explicable from this ontogenetic perspective. Moreover, as we shall demonstrate, the novelties that are produced as end products of heterochrony include life history attributes and morphological features that are consistent with the heterochrony model [for review, see Gould (1977)].

4.3.2. The Kangaroo Mouse: A Progenetic Rodent?

Kangaroo mice (*Microdipodops*), like kangaroo rats (*Dipodomys*), are paedomorphic, or juvenilized, rodents. We suggest that paedomorphosis, merely a gross shape phenomenon, is shared between these genera as a result of phyletic parallelism. The obvious juvenile traits shared between the genera include the large head, large brain, large eyes, and long hindfeet (Hafner, J. C., Hafner, 1983; Hafner, M. S., Hafner, 1984; Hafner, 1988). In addition, adults of both *Microdipodops* and *Dipodomys* retain the complete stapedial canal and artery (Howell, 1932; Webster and Webster, 1975; Lay, 1988); these features are lost at an early ontogenetic stage or are incompletely developed in other geomyoids. Kangaroo rats and kangaroo mice, unlike other geomyoids, also have very light, delicate skeletons whose osseous elements show a low degree of fusion; weak fusion of skeletal elements is characteristic of juvenile mammals.

The crania of both *Microdipodops* and *Dipodomys* are peculiar because of their enormous size and the presence of hypertrophied auditory bullae (Fig. 3). The general perception is that cranial enlargement is due solely to bullar inflation. It is not clear how and why the auditory bullae have become so inflated in these forms (Hafner, 1988; Lay, 1988), but bullar hypertrophy alone does not account for the huge crania of kangaroo mice and kangaroo rats. Actually, condylonasal length of the skull (a measure of skull size excluding bullar swelling) and precaudal vertebral length (a measure of body size excluding tail) are allometrically related. The allometric exponent of skull (condylonasal) length on precaudal vertebral length across the Rodentia is estimated to be 0.65 (Fig. 5; $r = 0.97$, $p \ll 0.01$). It is this general rodent trend of negative allometry that explains in part why kangaroo mice and kangaroo rats have large heads; they have short precaudal vertebral lengths and therefore have proportionately large heads. However, both of these bipedal forms have skulls that are approximately twice as large as would

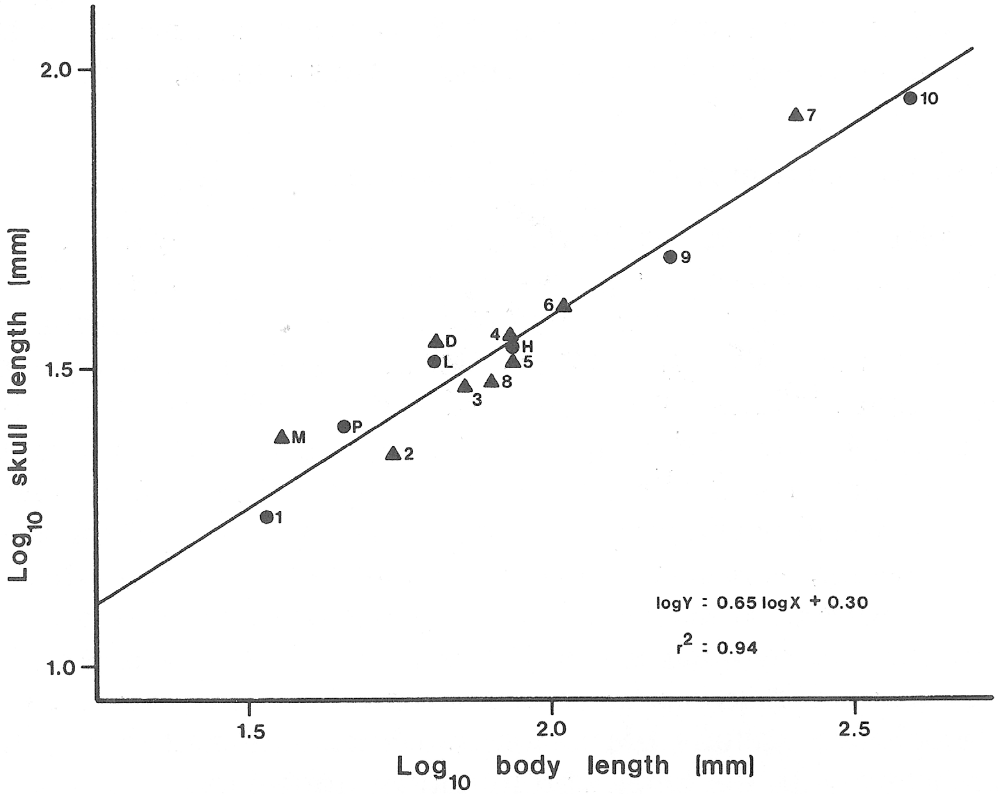

Figure 5. Relationship of skull size (condylonasal length) and body size (precaudal vertebral length) for various genera of (▲) bipedal and (●) quadrupedal rodents [data from Hatt (1932)]. (M) *Microdipodops*; (P) *Perognathus*; (D) *Dipodomys*; (L) *Liomys*; (H) *Heteromys*; (1) *Sicista*; (2) *Zapus*; (3) *Scirtopoda*; (4) *Jaculus*; (5) *Dipus*; (6) *Allactaga*; (7) *Pedetes*; (8) *Notomys*; (9) *Rattus*; (10) *Paramys*.

be predicted from their precaudal lengths alone. Functional constraints associated with bipedality do not seem to account for this disparity; indeed, Fig. 5 shows that some bipedal rodents have heads that are larger that those predicted by the regression (e.g., *Pedetes* and *Jaculus*), while other bipedal rodents have heads that are smaller than those predicted by the allometric trend (e.g., *Scirtopoda* and *Notomys*).

Despite the many paedomorphic characters shared between the bipedal heteromyids, *Microdipodops* differs from *Dipodomys* by many trenchant morphological and life history characteristics [for review, see Hatt (1932), Howell (1932), Wood (1935), and Hafner (1978, 1988)]. These differences suggest that the juvenilized morphology of kangaroo mice may have evolved in a manner that is fundamentally different from that in kangaroo rats; in short, juvenilization in *Microdipodops* may be the result of progenesis (Hafner and Hafner, 1983; Hafner, 1988). Progenesis is a heterochronic process in which somatic development is truncated because reproductive maturation is abbreviated. It involves a negative perturbation (truncation) in the ancestral ontogenetic trajectory (Alberch *et al.*, 1979) and results in a small, rapidly maturing paedomorph. Kangaroo mice, in comparison with other geomyoids, show retention of juvenile morphology and are also small.

In general, progenesis seems to be associated with animals near the *r* end of the *r*–*K* spectrum of life-history strategies [for review, see Gould (1977); see also McKinney (this volume)]. In comparison with other geomyoids, kangaroo mice possess many of the classical attributes of a more highly *r*-selected organism; small

Figure 6. Comparison of (A) a kangaroo rat, age 10 days, with (B) a pocket mouse, age 9 days. Drawings modified from Lackey (1967) and Hayden and Gambino (1966). See text for discussion. Scale is 10 mm.

body size, reduced longevity (Hall and Lindsdale, 1929; Egoscue *et al.*, 1970; and personal observation), and larger litter size (Hall, 1941; O'Farrell and Blaustein, 1974; Fleming, 1977); in addition, kangaroo mice subsist on an ephemeral resource base (insects and seeds) (Hall, 1941). Kangaroo mice also inhabit ephemeral (semistabilized) sand-dune habitats in the Great Basin Desert [a cold desert, (steppe) that is characterized by an abbreviated growing season]. It follows, then, that the adaptive significance of this kind of heterochronic perturbation (progenesis) may be attributable not to the juvenilized morphology per se, but to the suite of life-history characteristics [especially small body size and rapid and precocious maturation (Wootton, 1987)] brought about by the developmental change. From this viewpoint, the juvenilized morphology of kangaroo mice may be an incidental by-product of progenesis that persists because it was not egregiously maladaptive in its initial form. Subsequent periods of natural selection, acting on developmental variability, may have refined this juvenilized morphology into the finely tuned adaptive unit we see today.

Several other features of kangaroo mouse morphology support the hypothesis of progenesis. Kangaroo mice have only 24 caudal vertebrae [the fewest number of caudal elements of all heteromyids (Hatt, 1932; J. C. Hafner, unpublished data)]. Inasmuch as ossification occurs craniocaudally in heteromyids (Van De Graaff, 1973), the reduced number of caudal elements is a predicted result of progenetic truncation of the ancestral ontogeny. In addition, certain cheek teeth of kangaroo mice contain closed roots, whereas kangaroo rats show the opaeodont (open root) condition. In accord with the progenetic hypothesis, the molar roots of kangaroo mice appear late in ontogeny and are greatly reduced in comparison with the ancestral (e.g., pocket mouse) condition (Merriam, 1891; Wood, 1935; Hall, 1941).

4.3.3. The Kangaroo Rat: A Neotenic Rodent?

The kangaroo rat and pocket mouse, although very different in body plan and body size as adults, are surprisingly similar in appearance during early stages of development. Moreover, at approximately 9 or 10 days after birth, both rodents look remarkably like *adult* kangaroo rats in that they possess large heads and large hindfeet in relation to their body size (Fig. 6). While the body proportions of the animals are basically the same at this stage (Fig. 6), the pocket mouse changes radically over time; in contrast, the gross shape of the kangaroo rat changes very little from this point onward and retains its juvenile shape. Specifically, the rate of change in shape during development seems to be retarded in the kangaroo rat in comparison with the ontogeny of the pocket mouse. Assuming that the pocket mouse retains the developmental pattern of the ancestor, then we may deduce from this comparison that a retardation of the ancestral ontogenetic shape trajectory leads to neotenic morphology. This retardation plus a longer overall growth period (delay in the termination signal of growth) leads to a descendant that is both neotenic and large. We suggest that the juvenilization of kangaroo rats occurred in this manner (see also Hafner, 1988).

It appears that neoteny is a common occurrence in both plants and animals and it is often associated with organisms near the *K* end of the *r*–*K* spectrum of life-history strategies (Gould, 1977). Kangaroo rats, which we hypothesize to be neotenic, are *k*-selected by rodent standards: they have a long life span (Egoscue *et al.*, 1970; and personal observation); show slow development (Chew and Butterworth, 1959; Butterworth, 1961; Eisenberg and Isaac, 1963; Hayden and Gambino, 1966; Lackey, 1967; Fleming 1977); have long gestation periods (Eisenberg and Isaac, 1963; Fleming 1977); have enlarged brains (Hafner and Hafner, 1984); and have small litters (Hall, 1946; Butterworth, 1960; Eisenberg and Isaac, 1963; Fleming, 1977).

According to the retardation model, features that appear late in the ancestral ontogeny would be expected to be absent or reduced in size (and retain the juvenile shape) in the neotenic descendant. There is evidence that both the distal phalanges (Van De Graaff, 1973) and the roots of molars (Zakrzewski, 1981) are features that appear late in ontogeny. Thus, the reduction and/or loss of the hallux in adult kangaroo rats and the generally opaeodont (open-rooted) condition of the molars argue forcefully for retardation. Conversely, two characters appear discordant with the neoteny hypothesis: enlarged auditory bullae and elongated tail. Kangaroo rats, like kangaroo mice, have hypertrophied bullae and elongated tails. In both rodents, bullar inflation may be due to peramorphosis (*sensu* Alberch *et al.*, 1979; McNamara, 1986); that is, the bullae may have developed beyond the ancestral condition. The high number of caudal vertebrae in kangaroo rats (Hatt, 1932) also seem to argue that tail elongation in kangaroo rats (but not kangaroo mice; see above) may result from peramorphosis. Hence, tail elongation in kangaroo rats and kangaroo mice may have been achieved in two different ways: additional caudal vertebrae in the former, and longer, yet fewer, caudal vertebrae in the latter. As such, these rodents may represent a natural parallel to the replicate selection experiments with mice (*Mus*) by Rutledge *et al.* (1975). Thus, kangaroo rats, although generally juvenilized in appearance, may be the end product of different heterochronic processes (i.e., paedomorphosis and peramorphosis) that acted concurrently. The simultaneous action of different heterochronic processes was also described for an Eocene echinoid (McKinney, 1984) and for human evolution (Gould, 1977).

4.3.4. The Pocket Gopher: A Hypermorphic Rodent?

The adult pocket gopher, unlike other geomyoids, possesses a heavily ossified skeleton; the skull, in particular, is exceptionally rugose and shows a high degree of fusion among cranial elements. These features (skeletal rugosity and fusion) are characteristic of later stages of mammalian ontogeny. This, coupled with the

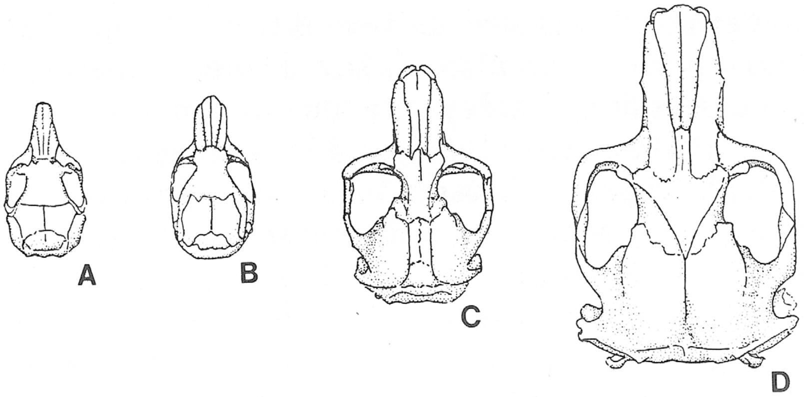

Figure 7. Comparison of (B) a neonatal pocket gopher (*Thomomys*) with (A) an adult pocket mouse (*Chaetodipus*) and (C,D) adult pocket gophers of different genera (*Thomomys* and *Orthogeomys*, respectively). Note the similarity between the juvenile pocket gopher (B) and the adult pocket mouse (A).

fact that neonatal pocket gophers look remarkably like mature pocket mice (Fig. 7), leads us to suggest that hypermorphosis is involved in the morphological evolution of pocket gophers.

Hypermorphosis is a process wherein there is a positive perturbation (delay) in the signal for cessation of growth in the ancestral ontogeny; the hypermorphic descendant is termed a peramorph (Alberch *et al.*, 1979). This developmental perturbation allows prolongation of the development of somatic features and permits pocket gophers to surpass or extend the ancestral ontogenetic trajectory; this is recapitulation through hypermorphosis. Hence, juvenile levels of morphological differentiation in the pocket gopher may be adult features of the ancestor. In the developing pocket gopher, the "pocket mouse" morphotype is attained at the same size of the adult ancestor, but the pocket gopher is still juvenile at this size; adult pocket gophers are large geomyoids. It is for this reason that we reject recapitulation by acceleration as the process leading to peramorphosis in pocket gophers.

4.3.5. Conclusions on Geomyoid Heterochrony

We have hypothesized that heterochronic disturbances during development have resulted in morphological evolution in the rodent superfamily Geomyoidea. Heterochronic changes in the generalized (ancestral) pocket mouse ontogeny may have effected both recapitulation and reverse recapitulation in geomyoids. Recapitulation, as seen in pocket gophers, may have been achieved through hypermorphosis. Although kangaroo rats and kangaroo mice are both paedomorphic, reverse recapitulation appears to have resulted via different heterochronic processes: neoteny in kangaroo rats and progenesis in kangaroo mice. If we are correct, the kangaroo mouse [or "dwarf kangaroo rat," as it was originally called by Merriam (1891)] is not merely a scaled-down version of the neotenic kangaroo rat, but is a separate, unique progenetic form.

It should be emphasized that the epigenetic interactions effecting these morphological transformations are probably much more complex than the simple heterochronic changes that we have outlined. For example, the kangaroo mouse appears to be mainly progenetic, but its enlarged auditory bullae may be the result of acceleration. Similarly, the gross morphology of the kangaroo rat is hypothesized to be mainly a result of neoteny and a longer overall growth period, but it is possible that the hypertrophied auditory bullae and elongated tail resulted from hypermorphosis [see above and Lay (1988)]. Morphogenesis is a complex process and "pure" examples of, say, neoteny unaccompanied by other heterochronic processes are probably very uncommon [for discussion, see Gould (1977), Alberch *et al.* (1979), Fink (1982), and McKinney (1984)]. Before one can understand fully morphological differentiation in the Geomyoidea, much more complete data are needed on growth and development, longevity, age at maturation, litter sizes, food habits, and many other crucial natural history parameters.

Over the past decade or so, it has become increasingly clear that evolutionary changes in shape and size arise from evolutionary change in developmental programs. For the geomyoids, we propose that their disparate morphological modifications evolved through heterochronic shifts in ontogeny. Our emphasis here on developmental heterochrony stems from the recent realization that a single heterochronic perturbation (i.e., a point mutation affecting development) may cause sweeping morphological changes when its effects are amplified by the myriad of pleiotropic and epigenetic effects that occur during development. All developmental processes that are genetically correlated with those that are directly affected by the heterochronic event will, in turn, be altered [for discussion, see Atchley (1987)]. What, then, is the role of natural selection in geomyoid macroevolution? It is most parsimonious to postulate that natural selection acts on developmentally integrated character complexes that are affected by heterochronic changes in ontogeny. This explanation is much simpler than one that views natural selection as acting on each morphological feature independently. The evolution of each novel morphological trait, then, might not be attributable to the direct, "fine-tuning" action of natural selection, but may occur largely as an inseparable and highly interdependent subunit of a developmentally integrated character complex that is, in turn, governed by various hierarchical developmental processes. The study of heterochrony seems to be an epistemologically sound way of probing the causal underpinnings of phylogenetic transmutation, or macroevolution (*sensu* Simpson, 1944, 1953), in this group. Moreover, the trends noted here may explain not just geomyoid patterns of differentiation, but the distinct body plans seen in other rodent groups as well.

5. Selective and Developmental Constraints

5.1. Adaptive Significance

As was stated at the outset, the intent of this chapter is to focus on patterns of morphological differentiation in rodents in an attempt to gain insight into the causal evolutionary processes that may be responsible for effecting macroevolution. In any discussion of macroevolution, however, it is difficult to maintain a proper perspective on the subject of adaptation. While our emphasis is on the evolution and not the present adaptive significance of the rodent *Baupläne*, it is important here to remark briefly on the relevance of the adaptationist program to the study of rodent biology.

The adaptationist program, when correctly implemented, is a profitable method of scientific research because it is of heuristic value [for review, see Mayr

(1983)]. However, Gould and Lewontin (1979) are correct in criticizing those studies of adaptation that ignore the integrated aspect of the phenotype and atomize the individual in an attempt to determine the adaptive significance of a specific trait. A more holistic approach, advocated by Gould and Lewontin (1979), and the classical adaptationist approach are both important in studies of adaptation. Actually, there is no reason why both approaches cannot be pursued simultaneously; the research programs are not mutually exclusive.

To date, the adaptationist approach has dominated the study of rodent morphological evolution. Indeed, consider the generally accepted scenarios of adaptation for each of the three novel body plans in rodents: a "flying" squirrel has gliding membranes because gliding is adaptive in predator avoidance; a fossorial rodent has a heavy, excessively rugose skull because it is advantageous for an animal burrowing (often chewing) its way through the soil; and a bipedal rodent has long hindlimbs because rapid bipedal locomotion aids in predator avoidance. These adaptationist explanations may or may not be true; this is not the issue here. The point is, once a convincing explanation has been proffered, it quickly becomes dogma. Once dogma is firmly entrenched, competing hypotheses (adaptationist or otherwise) are rarely considered and few, if any, attempts are made actually to test hypotheses about the functional descriptions of characters (Hafner, 1988). On the whole, the adaptationist program has not produced testable functional hypotheses for most of the novel morphologies seen in rodents. Accordingly, it now seems appropriate to consider more holistic approaches to the study of adaptation. In so doing, it might be profitable to investigate the adaptive significance of the *Bauplan* in its entirety (including life-history features), as opposed to the conventional method of focusing on the adaptiveness of individual morphological traits.

5.2. Selective or Developmental Constraints?

It is important to recognize the distinction between developmental and selective constraints in the study of morphological evolution [for review, see Maynard Smith *et al.* (1985)]. However, at any particular instance, it may be exceedingly difficult to resolve the relative contributions of developmental and selective constraints in shaping macroevolutionary patterns. Although Maynard Smith *et al.* (1985) suggest several ways of distinguishing between selective and developmental constraints, they also note that no method is absolutely foolproof.

Ultimately, it may be impossible to identify unambiguously the constraints that are responsible for producing the evolutionary novelties we see in rodents. The main problem is that the production of an evolutionary novelty itself is a unique event that is unlikely to be duplicated; hence, macroevolution is generally not amenable to direct investigation. In rodents, however, if heterochrony can be shown to be the underlying mechanism responsible for the production of similar novel body plans in several unrelated phyletic groups (see below), then it would be proper to conclude that developmental constraints are of at least some importance in effecting macroevolutionary patterns. We hasten to add, however, that even if heterochrony is implicated in the morphological differentiation of the major rodent body plans, the nonrandom association between environment and the body plans (see Section 2.3) makes it impossible to factor out environmental considerations in the course of macroevolution. With these problems in mind, and in consideration of our present level of understanding of the role of development in evolution, it seems that our best hope is to attempt to identify what mechanism or combination of mechanisms is most likely responsible for the origin of morphological novelties.

6. Prospectus and Directions for Future Study

Our hypotheses concerning heterochrony are based largely on the patterns of morphological differentiation seen in adult specimens of geomyoid rodents. These hypotheses predict that developmental programs of the derived forms (e.g., kangaroo rats, kangaroo mice, and pocket gophers) are altered in a specific fashion relative to the generalized (ancestral) condition. Moreover, these heterochronic hypotheses may have relevance beyond the taxonomic boundary of the Geomyoidea; we propose that much of the morphological differentiation seen in the rodents may be explained by heterochronic perturbations in development. In particular, we suggest that morphological convergence associated with two of the major rodent body plans, bipedality and fossoriality, is explicable by the heterochrony model.

Our hypotheses concerning the morphological transformations in geomyoid rodents are testable with the accumulation of new, comparative data on growth and development. We predict, for example, that the growth and development of the neotenic kangaroo rat is retarded relative to that of the generalized (pocket mouse) condition; existing data, although scanty, seem to support this. Our hypothesis also predicts developmental truncation in kangaroo mice; however, nothing is known about growth and development of kangaroo mice. If future work demonstrates that the ontogeny of the kangaroo mouse is *not* truncated relative to the generalized pattern, then our hypothesis of the progenetic origin of the kangaroo mouse is falsified. Similarly, our hypothesis concerning hypermorphosis in pocket gophers is amenable to direct falsification by comparative data on growth and development.

We predict that the convergent evolutionary trends toward bipedality and fossoriality seen in rodents may have been caused largely by heterochronic changes in development. For example, bipedality in the dipodid and murid rodents may be associated with paedomorphosis. In this regard, we hypothesize that the dipodid genus *Salpingotus* (dwarf jerboa), the ecological equivalent to the kangaroo mouse, is a progenetic form and should show truncated development; nothing is known about the growth and development of *Salpingotus*. We also predict that the Old World counterparts to the kangaroo rat (e.g., jerboas, including *Dipus* and *Jaculus*) are neotenic. Interestingly, Kirmiz (1962) reports that the development of *Jaculus* is retarded relative to that of the rat (*Rattus*); in this case, the developmental information is consistent with our heterochrony model. Other striking examples of convergence are provided by the fossorial rodents; hypermorphosis may be involved in the trend toward fossoriality. Comparative developmental studies should reveal whether forms such as the tucutuco (*Ctenomys*) or the various kinds of mole rats (e.g., *Spalax*, *Tachyoryctes*, and *Bathyergus*) are hypermorphic relative to the generalized condition.

Future work exploring the evolution of ontogenies may prove to be a profitable way of understanding morphological evolution in rodents. Future workers interested in macroevolution in rodents should seek to gather the kinds of data on growth and development that can be brought to bear on these hypotheses of heterochrony. In this regard, Atchley's (1987) developmental quantitative genetics model stressing genetic variance–covariance structure seems most appropriate. Basic descriptive data (e.g., postnatal growth curves) are currently lacking for most species of rodents. Accordingly, we encourage other workers to investigate the embryological and postnatal ontogeny of rodents, as was done recently in neotomine–peromyscine rodents (Creighton and Strauss, 1986). Manipulative embryological studies (e.g., DuBrul and Laskin, 1961) and studies of developmental integration (character correlation) are also needed to evaluate fully the role of developmental perturbation in morphological evolution. While the omnipresent force of natural selection serves ultimately as the arbitrator in determining the success or failure of evolutionary novelties, we should not overlook the possible importance of developmental heterochrony in the evolution of morphological trends in the Rodentia.

ACKNOWLEDGMENTS. Appreciation is extended to D. J. Hafner and R. W. Thorington, Jr. for their critical comments on early drafts of this material and for invaluable discussion during the course of this work. We thank S. Warschaw and S. Muth for their clerical assistance. This research was supported in part by research grants from the National Science Foundation BSR-8600644 (J.C.H.) and BSR-8607223 (M.S.H.).

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