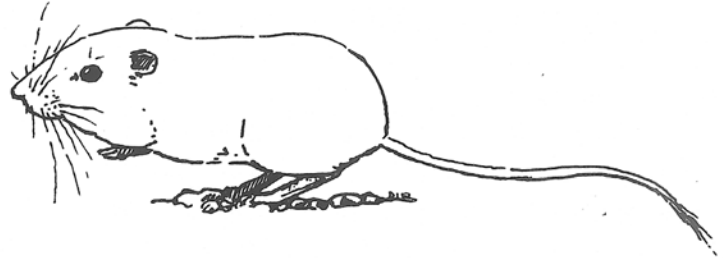# MACROEVOLUTIONARY DIVERSIFICATION IN HETEROMYID RODENTS: HETEROCHRONY AND ADAPTATION IN PHYLOGENY

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Introduction

Macroevolution, although variously defined and redefined (e.g., Bock, 1979; Dobzhansky, 1937; Goldschmidt, 1940; Mayr, 1963; Rensch, 1959; Simpson, 1944, 1953; Stanley, 1979), is probably best considered to be a phenomenological description of the large-scale morphological change that usually accompanies transpecific evolution (cladogenesis at the species level and higher taxonomic categories). Importantly, this large-scale morphological differentiation includes the eventual production of a macroevolutionary novelty: a unique morphology or *Bauplan* that, when considered in retrospect, seemingly allowed the bearer (a new taxon) to enter a new adaptive zone (sensu Simpson, 1944). One of the most exciting tasks in evolutionary biology is that of providing a convincing explanation, attendant with testable propositions, for the macroevolutionary novelty. To provide a thorough explanation of macroevolution in a taxonomic group, one must carefully consider three separate aspects of the problem:

1) phylogenetic relationships among the taxa; 2) adaptive significance of novel morphologies; and, 3) the causal mechanism(s) responsible for morphological diversification.

The intent of this contribution is to provide a preliminary assessment of macroevolution in the rodent family Heteromyidae (pocket mice, kangaroo rats, and their allies). This family is a morphologically and ecologically diverse group whose extant members display an array of adaptive types from scansorial, mesic-adapted genera to bipedal, xeric-adapted genera. Although differences at the generic level are generally considered to be at the lower end of the scale of macroevolutionary divergence (e.g., Bock, 1979), the high degree of structural divergence among the heteromyid genera provides an unusual opportunity to investigate major evolutionary change.

The evolutionary and taxonomic history of the Heteromyidae is intimately associated with that of the Geomyidae (pocket

gophers; all extant members are fossorial). Together, these two families form a cohesive superfamily, the Geomyoidea, whose members are united by the presence of externally opening, fur-lined cheek pockets (among other features). The superfamily Geomyoidea is autochthonous in continental North America and is an old, monophyletic lineage that is distantly related to other rodent groups (Wood, 1935; Hafner, 1982). The geomyoids experienced major phyletic diversification in the Oligocene to Pliocene coincident with the climatic trend towards increasing coolness and aridity (Flint, 1971) and the development of the Madro-Tertiary Geoflora (Axelrod, 1950, 1958, 1976). Due to marked similarities in heteromyid and geomyid biogeographic histories and their close phyletic association (for review, see Hafner, 1982; Hafner and Hafner, 1983), relevant geomyid information will be presented in this review to facilitate a more thorough understanding of macroevolutionary divergence within the Heteromyidae.

Evolutionary Relationships of Heteromyid Rodents

During the past one-half century a tremendous volume of literature pertaining to heteromyid evolution has accumulated. The most recent statement of the evolutionary relationships of the Heteromyidae was provided by Hafner and Hafner (1983); that study integrated the classic morphological treatises of the 1930s (e.g., Hatt, 1932; Howell, 1932; Wood, 1935) with the more recent systematic treatments (e.g., *Chaetodipus*: Patton, 1967a; Patton et al., 1981; *Perognathus*: Patton, 1967b; Williams, 1978; *Dipodomys*: Johnson and Selander, 1971; *Microdipodops*: Hafner, 1978, 1981; Hafner et al., 1979; *Liomys*: Genoways, 1973; *Heteromys*: Rogers and Schmidly, 1982). The following account is a current synopsis of the patterns of supraspecific relationships within the extant Heteromyi-

dae. I use as my point of departure Hafner and Hafner (1983) and included references.

Hafner's (1982) molecular study indicated that the divergence between the heteromyids and geomyids occurred in the early Eocene (approximately 50 my before present); this estimate was based on an average of 90 immunological distance (*ID*) units measured between the families and molecular clock calculations available at that time. As Hafner noted, his time estimate for the heteromyid-geomyid split predates the earliest geomyoid fossil (*Heliscomys*; early Oligocene) by 10 to 15 my. I have re-evaluated Hafner's (1982) immunological data using Sarich's (1985) revised calibration for the molecular clock. This new calibration rectifies some recently discovered miscalibrations and resets the molecular clock for albumin immunological studies (for discussion see Sarich, 1985:429–433). Accordingly, the time, t, of separation between two lineages may be estimated by the relation $t = k(100 - QP)$, where k is the new calibration factor (0.67–0.71) relating the difference in albumin cross-reaction to time (in millions of years) and QP is the quantitative precipitin value for micro-complement fixation data ($QP = 100 - [ID/2]$). This corrected time calibration places the initial geomyoid radiation in the early Oligocene (approximately 30–32 mybp); hence, the molecular data are in accord with the paleontological evidence (see also Wahlert, this volume).

Figure 1 summarizes current views on heteromyid relationships. The extant heteromyids comprise three principal lineages (including six genera) that diverged in the Oligocene: 1) subfamily Heteromyinae (*Liomys* and *Heteromys*); 2) subfamily Perognathinae (*Perognathus* and *Chaetodipus*); and, 3) subfamily Dipodomyinae (*Dipodomys* and *Microdipodops*). The Heteromyinae (spiny pocket mice) form the most distinct and internally cohesive lineage within the family and have experienced a long evolutionary history independent of the other subfamilies (Fig. 1). The spiny
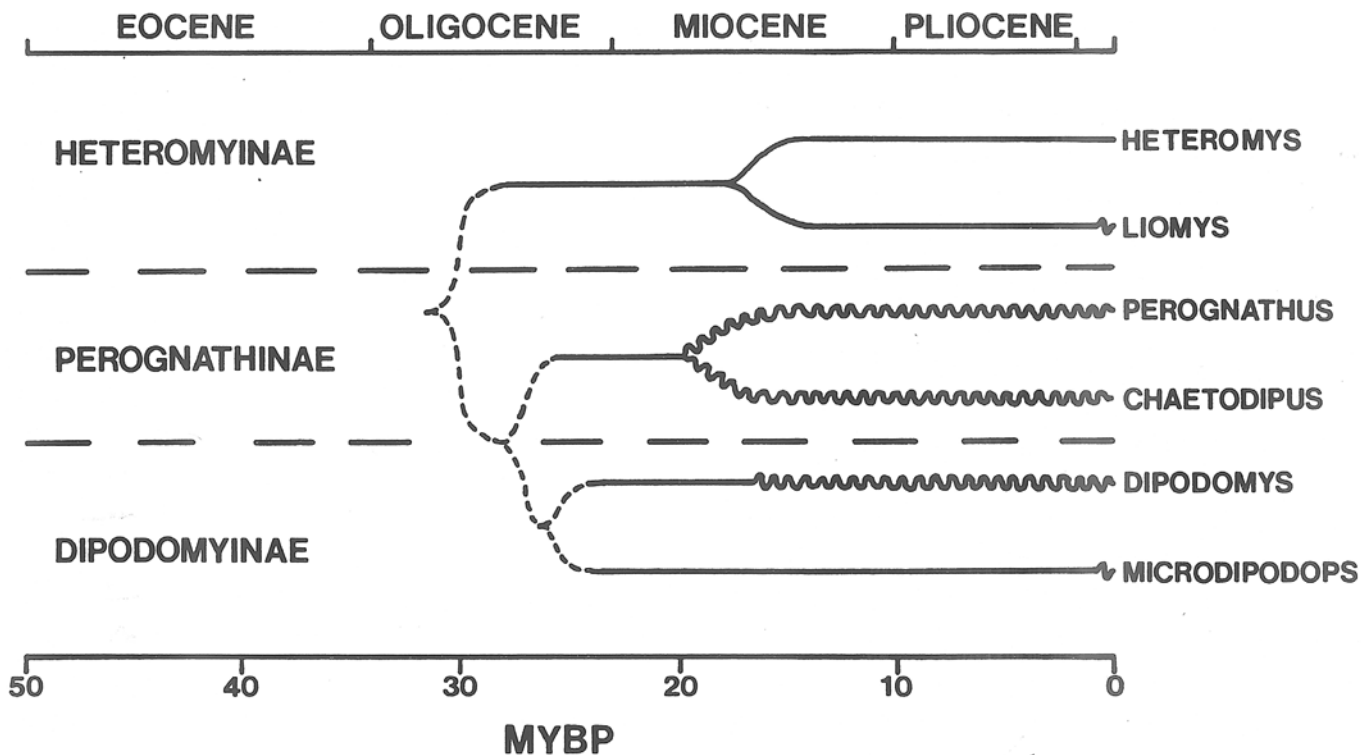
FIG. 1.—Phylogeny of the extant Heteromyidae indicating supraspecific relationships. Solid lines indicate probable affinities, sinuous lines relate the fossil record (the paleontological literature does not distinguish between *Perognathus* and *Chaetodipus*), and the dashed lines signal areas in need of further investigation. The time scale is based on fossil evidence (Lindsay, 1972; Wood, 1935) and immunological and allozymic data (Hafner, 1982; see text for molecular clock calibration).

pocket mice show generalized (mouse-like) rodent morphology and, unlike the other heteromyids, show a marked ecological propensity for tropical to subtropical environs. The Perognathinae (pocket mice) are also morphologically conservative in body plan, yet these pocket mice inhabit a broad spectrum of arid environments (e.g., sandy deserts, arid grasslands, chaparral and thornscrub forests). The Dipodomyinae includes the morphologically aberrant kangaroo mice, *Microdipodops,* and kangaroo rats, *Dipodomys*. The kangaroo mice are narrowly adapted to xeric, sandy habitats, whereas the kangaroo rats show a broad tolerance to generally arid environments (e.g., arid grasslands, chaparral, and desert habitats).

The subfamilial affinity of *Microdipodops* has plagued heteromyid systematists virtually since its discovery and description a century ago (for review, see Hafner and Hafner, 1983). Over the years, the taxonomic placement of kangaroo mice has vacillated between the Perognathinae and the Dipodomyinae, but it is now recognized that kangaroo mice may represent an independent lineage with no close relatives in the extant fauna (Hafner, 1978; Hafner and Hafner, 1983). However, recent biochemical evidence (Hafner, 1982; Hafner and Hafner, 1983) indicates that *Microdipodops* may be genetically slightly more closely related to *Dipodomys* than to extant perognathines. More detailed biochemical analyses are needed to confirm or refute the hypothesized alignment of kangaroo mice with kangaroo rats, but for now *Microdipodops* is placed provisionally in the Dipodomyinae (Fig. 1). It is important to recognize, however, that kangaroo mice, although sharing with kangaroo rats obvious superficial traits (e.g., large head and long hind feet), are not merely scaled-down versions of kangaroo rats; kangaroo mice are physiologically, ecologically and morphologically quite different from kangaroo rats.

The family Heteromyidae, including morphologically disparate scansorial and ri-

cochetal forms, has undergone flamboyant morphological diversification by rodent standards; *Microdipodops* and *Dipodomys* clearly represent evolutionary novelties (but see Mares, this volume). In marked contrast to the heteromyids, members of the closely related family Geomyidae (pocket gophers) are remarkably conservative morphologically. With the exception of size differences, the extant pocket gophers are nearly uniform in morphology. Presumably, stringent selective constraints associated with the fossorial habitus restricted the realm of possible morphologies in the Geomyidae. Nevertheless, pocket gopher morphology is also a novel (derived) body plan when compared with the generalized (mouse-like) rodent condition. If macroevolution is considered as large-scale morphological change, then it seems that macroevolutionary diversification in the superfamily has resulted in several distinct evolutionary novelties among the extant taxa: kangaroo rats, kangaroo mice and pocket gophers.

Adaptation and the Evolution of Novel Features

The tremendous breadth of morphological differentiation seen in the Geomyoidea provides an exceptional opportunity for studies in evolutionary morphology. Although this superfamily is geographically restricted when compared with most other major rodent groups, geomyoids inhabit both desert and tropical environments and show remarkable modifications attendant with fossoriality (pocket gophers) as well as scansorial (pocket mice) and ricochetal (kangaroo rats and kangaroo mice) habits. It is indeed a challenge to explain the evolution of these extreme and conspicuous morphological modifications.

The remarkable morphological features characteristic of the ricochetors (*Dipodomys* and *Microdipodops*) are a popular case in point. Conventional explanations for the morphological novelties shown by these

forms focus on the adaptive aspects (advantages) of the functional design (for example, see review by Eisenberg, 1975). Inherent in these explanations is the assumption that random mutation produces sufficient variation in form such that natural selection will continually shape the morphological features into a better adapted form. For kangaroo mice and kangaroo rats, one's attention is drawn immediately to the enormous head (due, in part, to inflation of the auditory bullae) and huge hind feet, as well as the large eyes and long tail. There are many opinions as to the function of each of these features (see Table 1), and virtually all of these adaptive explanations focus on what is termed the "anti-predator morphology" of *Microdipodops* and *Dipodomys* (e.g., Kotler, 1985). These explanations demonstrate "the enormous power of the principle [of natural selection] as a weapon of explanation" (Waddington, 1975: 41). Morphological evolution in the Heteromyidae is usually explained as a result of long-term, directional selection (orthoselection): natural selection favors certain adaptations present in ancestral species and these adaptations are accentuated in descendant species in response to the same selective pressures. For example, Hall (1946: 406) remarked on "evolution towards perfecting rapid locomotion by use of the hind limbs in *Dipodomys* . . .", while Grinnell (1922:23) wrote, "The reduction of the toes [in *Dipodomys*] is, then, a sort of orthogenetic tendency inherent in the group as a whole, but it is no less, in the writer's view, an adaptational process. . . ." The question of adaptation is, of course, central to our understanding of morphological evolution in the Geomyoidea. However, previous attempts to address this topic have relied on an oversimplified accounting of the mechanism of evolution. Evolution involves more than simply natural selection acting on a "genetic system" and, as Waddington (1975: 58) observes, we must consider at least two other crucial components: the "exploitive system" and the "epigenetic system." A

TABLE 1.—*Adaptive explanations for certain conspicuous morphological features of kangaroo mice (*Microdipodops*) and kangaroo rats (*Dipodomys*).*

Morphological feature	Adaptive function	Source
Enlarged auditory bullae	1) delicate balance in ricochetal locomotion	Seton (1928); Hatt (1932); Setzer (1949)
	2) highly specialized acoustic sense	Howell (1932); Setzer (1949)
	3) sounding boards to monitor vibrations through the ground	Howell (1932)
	4) low-frequency hearing sensitivity for predator avoidance	Webster (1962); Webster and Webster (1971, 1975, 1980)
Large eyes	1) good nocturnal or crepuscular vision	Hall and Linsdale (1929)
Long tail	1) counterbalancing organ	Hatt (1932); Howell (1932); Hall (1941); Bartholomew and Caswell (1951)
	2) support prop or "third leg" for animal at rest	Hatt (1932); Howell (1932); Bartholomew and Caswell (1951)
	3) mid-air rudder for trajectory control	Hatt (1932); Howell (1932); Bartholomew and Caswell (1951)
	4) protection: misdirection of enemy's attack to terminal tuft (*Dipodomys* only)	Howell (1932); Hatt (1932); Mares (1983)
Long hind feet	1) "sand paddles" for locomotion on sandy soils	Hall and Linsdale (1929); Hall (1941)
	2) richochetal locomotion for rapid dodging and quick escape from predators	Howell (1932); Hall (1946); Bartholomew and Caswell (1951); Kotler (1985)
	3) bipedal saltation for an energetically efficient mode of locomotion and successful exploitation of a hyperdispersed resource base	Howell (1932); Reichman and Oberstein (1977); Price (1978)

more thorough understanding of adaptation is possible when one takes this more eclectic view of the evolutionary process.

Functional Significance of Novel Features

There are two types of explanations in biology: functional and causal explanations. Functional explanations explain morphology in terms of its purpose to the animal and disregard prior states, whereas causal explanations focus on prior morphological states and attempt to predict future states from earlier ones. It is important to observe that functional and causal explanations are not directly competitive and, in fact, address different sets of questions. Functional explanations focus on present use of a feature, whereas causal explanations are concerned solely with the evolution of the feature (regardless of its present use). Both kinds of explanations are important, but it seems that problems arise when functional explanations are used to make unwarranted extrapolations as to the evolution of a feature. Until recently, explanations for the extreme morphological variation found among the heteromyids were all of the functional (or adaptationist) type (see Table 1). These functional explanations, unfortunately, often infer evolution and, therefore, obfuscate the other important set of questions that needs to be addressed (see also Brookfield, 1982). Clearly, some of these oft-cited explanations may pertain to actual "aptations" (either adaptive or exaptive characteristics; Gould and Vrba, 1982), but functional explanations are epistemologically unsatisfactory hypotheses for the evolution of a novel feature. Below I address in detail several cases that are relevant to

this discussion of adaptation and the evolution of novel features.

Large auditory bullae.—Evidence indicating that the enlarged bullae in *Microdipodops* and *Dipodomys* function to facilitate low-frequency hearing and represent an adaptation to avoid predatory strikes by owls and snakes (Webster, 1962; Webster and Webster, 1971, 1972, 1975, 1980) has been received with virtually universal acceptance. Not surprisingly, the enlarged bullae of kangaroo rats are now cited as a textbook example of vertebrate adaptation (e.g., Gunderson, 1976:331–332; Stebbins, 1983: 84; Vaughan 1978:467–468; Willson, 1984: 158). Nonetheless, this hypothesized antipredator adaptation deserves critical evaluation (see Lay, this volume). Webster (1962) originally determined that in *Dipodomys* hypertrophy of the middle-ear cavity is associated with unusually sensitive cochlear microphonic responses between 1,000 and 3,000 Hz and that experimental reduction of middle-ear volume dramatically reduces this sensitivity. Webster (1962) further showed that the predatory strikes of owls and rattlesnakes have pre-strike sounds that contain these same (1,000 to 3,000 Hz) frequencies. The conclusion drawn from these studies, coupled with predator-prey experiments (Webster, 1962; Webster and Webster, 1971), is that the enlarged middle ear of the kangaroo rat facilitates low-frequency reception, which is particularly adaptive for nocturnal animals in open areas and, therefore, plays an adaptive role in predator avoidance. Importantly, it is not generally recognized that the heightened reception of key frequencies within the 1,000 to 3,000 Hz range originally reported by Webster (1962) was later "regarded as an artifact of the method of analysis" by Webster and Webster (1972:50). Subsequent data by Webster and Webster (1975, 1980) indicate that the auditory sensitivity curves for various species of heteromyids (including *Perognathus, Microdipodops, Liomys, Heteromys,* and *Dipodomys*) do not exhibit a pronounced peak between 1,000 to 3,000

Hz, but show rather flat sensitivity curves from low (≈ 100 Hz) to high ($\approx 30,000$ Hz) frequencies. Further, although *Microdipodops* and *Dipodomys* are said to have more sensitive cochlear microphonics than do other heteromyids with smaller middle-ear cavities (Webster and Webster, 1980), no statistical tests were performed to document that significant differences in sensitivity actually exist. From the available data (Webster and Webster, 1980:252) it is clear that all genera of heteromyids are actually more sensitive between 300 to 1,000 Hz than in the "predatory range" of 1,000 to 3,000 Hz; hence, the validity of this predator-avoidance hypothesis is questionable. Most significantly, and contrary to the predictions of their model, Webster and Webster (1971: 314) have demonstrated that kangaroo rats with experimentally reduced middle-ear volume were still able to avoid the predatory strikes of the rattlesnake (see below). Moreover, if enlarged middle ear cavities do indeed function to facilitate low-frequency hearing for predator avoidance in open desert environments, it is not clear why there is no demonstrated relationship between auditory bullar size and environment within the family (Grinnell, 1922; Setzer, 1949; Webster and Webster, 1975).

Large eyes.—Kangaroo rats and kangaroo mice are nocturnal rodents that have large eyes. If enlargement of the eyes is an adaptation for enhanced nocturnal vision, then it is necessary to document that the large eyes of the kangaroo rats and kangaroo mice facilitate more keen vision than do the smaller eyes of other rodent genera with which they are sympatric. So far, no such tests have been undertaken. One must be cautious in assuming that the large eyes represent a special adaptation for enhanced nocturnal vision; actually, the antelope ground squirrel (*Ammospermophilus*), commonly found sympatric with the heteromyid ricochetors, also has large eyes, yet is a diurnal rodent.

Elongated tail.—Kangaroo mice and kangaroo rats have long tails relative to body

length (for comparative rodent data, see Hatt, 1932). The tails of *Microdipodops* and *Dipodomys* undoubtedly function to some degree in maintaining balance during locomotion; this locomotory function of the tail (and a thermoregulatory function as well) applies to rodents in general (for review, see Thorington, 1966). But if the long tails of *Microdipodops* and *Dipodomys* represent adaptations for the richochetal mode of locomotion (Bartholomew and Caswell, 1951; Hall, 1941; Hatt, 1932; Howell, 1932), one would expect that tail length and hind foot length would be correlated across ricochetal taxa. Importantly, Grinnell (1922) and Setzer (1949) have determined that such a relationship does not exist among heteromyid species. Also, if natural selection has acted to perfect the ricochetal mode of locomotion, it is unclear why kangaroo rats hurl through the air "in a more or less lopsided fashion" (Howell, 1932:386), and often land off-balance "owing apparently to clumsy use of the tail" (Howell, 1944:40). In a rigorous examination of tail function, Bartholomew and Caswell (1951) cut off the tail of a kangaroo rat to test the importance of the tail in the maintenance of equilibrium during bipedal locomotion. Their experiment determined that "removal of the tail had no apparent effects despite frequently heard statements to the contrary" (Bartholomew and Caswell, 1951:165). Coupled with this experimental result is Howell's (1923) and my personal observations that short-tailed kangaroo rats (those whose tails have been shortened presumedly by accidental injury) frequently occur in nature. It also seems incongruent that the tail of *Microdipodops* is "relatively less flexible" than that of pocket mice (Hatt, 1932:646) if it is adapted to serve as a counterpoise and a mid-air rudder during saltation. Actually, the unusual tail of kangaroo mice, being thickened in the mid region, is a site of fat deposition and storage and probably serves important physiological needs of the animal. In sum, the arguments that the elongated tail was shaped by natural selection to function specifically in ricochetal locomotion seem unconvincing.

Long hind feet.—Certain heteromyids have long hind feet and are able to move rapidly in open environments. However, the assumption that the long hind foot of kangaroo rats and kangaroo mice is an adaptation that has been finely tuned by natural selection to facilitate ricochetal locomotion in open habitats remains unchallenged. The argument would be stronger if all bipedal forms inhabited open environments. However, Grinnell (1922) and Setzer (1949) concluded that there is no relationship between saltatorial specialization and habitat type in species of *Dipodomys*. Indeed, kangaroo rats inhabit both xeric grasslands and coastal (often fog-shrouded) chaparral hillsides, as well as sparsely vegetated sand dunes; thus, the explanation that the ricochetal mode of locomotion is a finely tuned adaptation specifically for life in open environments appears incorrect. Further, recent studies have shown, contrary to conventional opinion, that bipedal saltation does not impart kangaroo rats an energetic advantage over quadrupedal locomotion (MacMillen, 1983; Thompson et al., 1980) and energy saving by elastic storage (in tendons and muscle fibers) appears to be unimportant in animals of this size (Biewener et al., 1981). With respect to the explanation that bipedal saltation is a special adaptation for predator avoidance, I point out that both the bipedal kangaroo rats and the quadrupedal pocket mice rely on the same escape response (long, erratic leaping) to avoid predation (Bartholomew and Cary, 1954; Price and Brown, 1983; personal observations).

Questioning adaptationist explanations.—The ad hoc adaptationist explanations designed to account for the existence of the unusual morphological features discussed above may themselves be impediments to a clear understanding of morphological evolution in the Heteromyidae. Surprisingly, however, only a few workers have questioned these functional explanations. Wood (1935:143) remarked, "There

is a strong relation among rodents between a highly inflated auditory region and ricochetal locomotion, though the reason for this correlation is obscure." Also, Bartholomew and Cary (1954:391), in observing that the food habits, food-gathering style, habitat preferences, and escape responses were similar in both kangaroo rats and pocket mice, posed the question, "Why should one be bipedal and the other quadrupedal?" Pye (1965:169), in an analysis of the auditory apparatus of the Heteromyidae, observes, "The possible functional significance of these modified cochlear structures has been discussed by Webster, but more ecological and physiological work needs to be carried out before any firm conclusions can be reached." More recently, Thompson et al. (1980:224) asked, "If there is no energetic advantage for small animals to hop, why do they do so?" These questions and many others prompt critical reconsideration of these functional explanations. Functional (or adaptationist) explanations are important in biology, but one must keep in mind that the theory of natural selection does not necessarily legitimize ad hoc functional explanations for each smallest component of an atomized organism (for discussion see Brookfield, 1982; Mayr, 1983). Future workers should evaluate critically these long-accepted explanations as well as consider other explanations for the evolution of these features.

Predator-prey Studies: an Evaluation

Most of the functional explanations that have been proffered (Table 1) argue that the novel morphology of ricochetal heteromyids is, in one way or another, adaptive in predator avoidance. If we are to understand the present utility of these novel morphologies, then it is crucial that these adaptive hypotheses be evaluated and tested thoroughly. Several important studies have been conducted that were designed to test

the view that kangaroo mice and kangaroo rats have particularly adaptive "anti-predator morphology" (Kotler, 1985, Webster, 1962; Webster and Webster, 1971). A critical review of these predator-prey studies follows.

Predator-prey experiments with kangaroo rats.—Webster's (1962) experimental study of Screech Owl (*Otus asio*) and Sidewinder (*Crotalus cerastes*) predation on the kangaroo rat (*Dipodomys merriami*) was the first investigation of the functional significance of the "anti-predator morphology." Webster's (1962) studies focused on the function of the inflated auditory bullae. Having first reported that normal kangaroo rats have unusually sensitive cochlear microphonics between the range of 1,000 to 3,000 Hz (a finding later dismissed as erroneous; see above), Webster compared the ability of kangaroo rats with experimentally reduced middle-ear volume (and reduced microphonic response) with normal kangaroo rats in avoiding the predatory strikes of owls and rattlesnakes. Eight kangaroo rats (four unoperated and four with reduced middle-ear volumes) were tested for their ability to avoid predation by screech owls: two of four normal individuals avoided the owls' attacks, but none of the animals with reduced middle-ear volume was able to avoid capture. Six kangaroo rats (three normal and three with reduced middle-ear volumes) were used in the Sidewinder experiments: all three normal kangaroo rats avoided strikes and all three operated individuals were struck and killed by the rattlesnake. Webster (1962) further reported that sounds of an attacking owl and rattlesnake contained frequencies of 1,200 Hz and 2,000 Hz, respectively. Webster (1962) concluded from these experiments that the hypertrophied bullae confer to the kangaroo rat a special auditory sensitivity at low frequencies that enables the detection of predators.

In a more extensive study, Webster and Webster (1971) carried out observation sessions to test kangaroo rat (*D. merriami*)

avoidance of the predatory strikes of the Sidewinder. The predator-prey sessions involved kangaroo rats in six different physical conditions: 1) normal (unoperated); 2) operated (plasticene placed in bullae to reduce middle-ear volume); 3) control (plasticene placed between skin and bullae); 4) blinded; 5) control and blinded; and, 6) operated and blinded. These predator avoidance experiments demonstrated that kangaroo rats with experimentally reduced middle-ear volumes were, in fact, *able* to avoid the strikes of the Sidewinder, contradicting Webster's (1962) earlier findings. Actually, kangaroo rats in five of the six test states (involving 18 forty-minute observation sessions) were routinely able to avoid the predatory strikes of the Sidewinder; only those kangaroo rats that were both surgically blinded and had their middle-ear volumes reduced were occasionally struck and killed (three of eight such encounters resulted in the rattlesnake striking and killing the kangaroo rat).

Webster and Webster (1971) concluded from their studies that natural selection should favor individuals with good low-frequency hearing (for predator avoidance) and that the enlarged bullae evolved in response to those selection pressures (see also Fleischer, 1978; Lay, 1972). However, the predator-prey experiments conducted by Webster (1962) and Webster and Webster (1971) do not support the idea that the hypertrophied bullae endow the possessor with an enhanced ability to avoid predation. It is now known that kangaroo rats (and kangaroo mice) have a broad range of hearing sensitivity (Webster and Webster, 1980) but do not exhibit the peaks of sensitivity in the "predatory frequencies" of 1,000 to 3,000 Hz (see discussion above). Also, a recent study of hearing in other small mammals (Heffner and Heffner, 1985) contradicts the idea that small mammals require enlarged auditory bullae to hear low frequencies. It seems that the predator-prey experiments conducted by Webster (1962) and Webster

and Webster (1971) are inconclusive and more experiments are needed to gain a more thorough understanding of the functional significance of the enlarged auditory bullae.

Natural selection experiments.—Webster and Webster (1971) live-trapped 27 kangaroo rats (*D. merriami*) for an experiment to determine whether animals with reduced middle-ear volume showed reduced survivorship in the wild compared with those individuals with normal, unoperated bullae. The kangaroo rats were divided into three groups of nine: 1) normal, unoperated; 2) operated (plasticene placed in bullae to reduce middle-ear volume); and, 3) control (plasticene weights placed above middle-ear cavities). The kangaroo rats were released on the study site (approximately 7 ha) and survivorship was estimated by mark-and-recapture censusing methods involving 136 live traps set out approximately once very four nights. Individuals were presumed dead if they were not recaptured during four consecutive nights of trapping at the end of the study (approximately one month after the initiation of the experiment). At the conclusion of the study, 14 kangaroo rats were recaptured: two of the operated kangaroo rats and six individuals each from the normal and control groups. Webster and Webster (1971) concluded from these data that fewer operated animals were retrapped because these kangaroo rats, having reduced middle-ear volume, were more vulnerable to predation by the Sidewinder (the only kangaroo rat predator observed on the study site) than were those animals without middle-ear reduction.

The results of Webster and Webster's (1971) natural selection study are provocative but, given the design of the study and the nature of the animals themselves, there are important considerations that should be addressed before meaningful conclusions can be drawn. For example, a *G*-test for goodness of fit performed on Webster and Webster's (1971) survivorship data reveals that the observed frequencies of recaptured

individuals do not depart significantly from random expectation ($G = 2.64$; $P \gg 0.05$). Thus, Webster and Webster (1971) were not justified in concluding that the apparent disappearance of the operated animals during the study resulted from their increased vulnerability to predation relative to normal animals. Their conclusion, in addition to being statistically unwarranted, seems to be inconsistent with their own predator-prey experiments that demonstrated that kangaroo rats with reduced middle-ear volume and normal kangaroo rats were equally able to avoid the strikes of the Sidewinder (also in Webster and Webster, 1971). Webster and Webster's (1971) experiments do *not* demonstrate that the enlarged middle-ear cavities in kangaroo rats, as opposed to the reduced condition in many other rodents, represent a special adaptation for predator avoidance.

Predator selectivity studies.—Kotler (1985) stated that *Microdipodops* and *Dipodomys* exhibit conspicuous "anti-predator morphology" and he pointed out that the genera possess many morphological characteristics (e.g., hyperinflated auditory bullae and elongated hind legs) that are beneficial in avoiding predation. He reasoned that bipedal heteromyids, by virtue of their "anti-predator morphology," should suffer lower rates of predation than coexisting species that were quadrupedal and lacked such adaptive morphology. To assess this, Kotler (1985) studied predation by long-eared owls (*Asio otus*) on desert rodents in a sand-dune community. Densities of rodent species were determined by census trapping and those values were compared with the proportional occurrence of rodent species in regurgitated pellets found beneath a nearby roost of long-eared owls. Prey selectivity indices were calculated (proportion of a rodent species in pellets divided by the proportional density of that rodent) and selectivity values for "bipedal species" (*Dipodomys* and *Microdipodops*) were compared with "quadrupedal species" (*Perognathus, Peromyscus, Reithrodontomys*) over six sample time periods. Kotler (1985) concluded that the owls

did not capture rodents in the proportion in which they occurred on the sand-dune site but, instead, selectively preyed upon the quadrupedal rodents because of their lack of anti-predator adaptations. Although the results of his study are consistent with the premise that bipedal heteromyids possess "anti-predator morphology," the conclusions are suspect because of problems in the experimental design and analysis of data.

The experimental design rests on a tenuous assumption that the desert rodents can be partitioned into two locomotory categories: bipedal and quadrupedal rodents. While it is fashionable to categorize *Dipodomys* and *Microdipodops* as bipedal rodents (essentially everyone does this as a kind of shorthand for describing their curious, kangaroo-like morphology), in the present study that seeks to explore whether bipeds are superior to quadrupeds in predator avoidance this categorization cannot pass without careful scrutiny. Despite the fact that nearly everyone refers to kangaroo mice as being bipedal, Eisenberg (1963:29) states that, "Analysis of several films and observation of *Microdipodops* for long periods of time reveal that a quadrupedal ricochet is the predominant mode of locomotion". Also, most workers have seemingly overlooked Seth Benson's observation of a pocket mouse running bipedally on a lengthy (15-foot) dash (see Hatt, 1932:629–630). In view of what is known about the locomotion of kangaroo rats, kangaroo mice and pocket mice, it is incorrect for Kotler (1985) to lump kangaroo rats and kangaroo mice together as "bipeds" and compare them to other "quadrupeds" in this predator selectivity study.

The experimental design of the study assumes that the owls hunted for rodents in the same area (or at least in the same habitats) as that censused by live trapping; this is a basic assumption upon which the accuracy of the selectivity indices are dependent. Given that there is no assurance that the owls restricted their hunting activities to the semi-stabilized dune area, it is incorrect to report selectivity values that are

based on the comparison of the proportion of rodents in owl pellets with the density of rodents on the dunes. Although Kotler was careful to raise this caveat (Kotler, 1985: 826), the fact that several rodent species that never occurred on the sand dunes were recovered in the owl pellets strongly suggests that the owls hunted in a variety of habitats. Although Kotler eliminated the non-dune species from his analysis, it is, nevertheless, impossible to disentangle this sampling bias from the selectivity indices.

In analyzing the selectivity information, Kotler (1985) compared the pooled data for bipedal species with pooled data for quadrupedal species. Pooling the species based on locomotory morphology may have obscured important information on the selectivity of long-eared owls for individual prey species. While the categorical division of the rodents into bipedal and quadrupedal species was designed to represent those species that do and do not possess the "anti-predator morphology," this subdivision reflects, more realistically, body size differences between the two categories. The so-termed bipedal group includes four species of kangaroo rats (ranging in body size from 41 g to 100 g) and one species of kangaroo mouse (13 g), whereas the quadrupedal group includes one pocket mouse (8 g) and two cricetids (13 g and 26.5 g; body mass data from Burt and Grossenheider, 1952; Jones, 1985). Thus, the typical animal in the bipedal group was considerably larger than the typical quadrupedal animal. Body size is an important criterion of prey vulnerability (see Craighead and Craighead, 1969) and, in a separate study, Kotler (1984) noted that large size helps reduce the vulnerability of kangaroo rats to predators. It seems that Long-eared Owl prey selectivity in Kotler's (1985) study may simply reflect this owl's preference for small-sized prey and has little or nothing to do with the morphological conformation of the prey species. Hence, there is no control for the owl's predatory behavior, which may well be biased toward one functional prey type for reasons unrelated to the prey themselves. Inasmuch as both

bipedal and quadrupedal heteromyids exhibit the same predator escape response (Bartholomew and Cary, 1954), prey size may be of paramount importance to the hunting owl; the morphological conformation of the prey may be a minor consideration. Such an interpretation is supported by other predator-prey studies that show that a different species of owl, the Great Horned Owl (*Bubo virginianus*), preys selectively on larger desert rodents (Longland, 1983; Longland and Jenkins, 1987).

Conclusions on predator-prey studies. — The kind of research that seeks to demonstrate the adaptedness of individuals and their features, termed the "adaptationist program" (Gould and Lewontin, 1979; Mayr, 1983), has proven itself to be of fundamental importance in many areas of biology. The adaptationist program, doubtless, can also be of great heuristic value in the study of the Heteromyidae. This is because there is much need for a clearer understanding of the functional significance of the novel morphologies seen in the heteromyid species.

Experimental predator-prey studies would seem to offer the most promising avenue for future research designed to investigate the adaptedness of individuals and their features. Such studies, by the nature of their design, are able to eliminate the confounding variables that often plague natural predation and selection studies. Future studies should be more comparative in nature, involving nonricochetal heteromyids as experimental controls against which the predator avoidance success of species with the hypothesized "anti-predator morphology" is compared. It is important to approach future studies with the purpose of attempting to refute the "anti-predator morphology" hypothesis rather than to embark on a study of adaptation with the premise that the hypothesis is already known to be correct (for philosophical perspective on scientific research, see Wenner and Wells, 1990). It is in this manner that rigorous studies can be designed and executed to provide unambiguous answers to tedious ques-

tions pertaining to the functional significance of morphological features.

Heterochrony and Macroevolution in Geomyoid Rodents

Among all geomyoid rodents, the bizarre morphology of the ricochetal kangaroo mice and kangaroo rats has attracted the greatest amount of attention from biologists and these forms are considered by many to be the epitome of desert specialization (e.g., Mares, 1983). The evolution of the enormous head, huge hind feet, large eyes, and long tail in kangaroo mice and kangaroo rats is explained conventionally in terms of the adaptive aspects of their morphology (see discussion above and Table 1). Despite how these features may function in their present context, the very different question remains: how did they evolve? Because a feature functions in a certain way today, we might assume that it originated for that purpose. However, as emphasized by Gould and Vrba (1982:13), "current utility [of a feature] carries no automatic implication about [its] historical origin."

The proper alternative to a functional explanation is a causal explanation for the evolution of a feature. Causal explanations decouple evolution from present use and thereby avoid the inherent ad-hoc nature of functional explanations that have been misappropriated to infer evolution. The causal explanation that seems to account for macroevolution in the Geomyoidea focuses on the mechanisms of heterochrony (mutations that effect changes in developmental programs). Heterochrony provides a general, unifying explanation to account for the evolution of the wide variety of morphological novelties evident in this group (Hafner and Hafner, 1983, 1988; Hafner and Hafner, 1984).

Several years ago I observed that many of the obvious morphological features of kangaroo rats and kangaroo mice, most notably the large head and eyes and the long hind feet, were traits commonly attributable to a paedomorph. This initial observation, coupled with the subsequent discovery that young pocket gophers (approximately two weeks of age) look remarkably like mature pocket mice, prompted further investigation and culminated in the hypothesis that evolutionary epigenetics might resolve the riddles of morphological transformation in geomyoid rodents (Hafner and Hafner, 1983, 1988; Hafner and Hafner, 1984). Below, I rely on phenomenological descriptions to demonstrate how regulatory changes in ontogeny may, in affecting the timing of gene action and rates of morphogenesis and growth, lead to morphological phyletic evolution (for review see Alberch, 1980; Alberch et al., 1979; Gould, 1977; Løvtrup, 1981a, 1981b; Rachootin and Thomson, 1981).

The view that morphological evolution is the result of regulatory shifts in development has been championed by many workers, most notably by Goldschmidt (1940), Waddington (1957, 1962), and Gould (1977). Waddington (1957, 1962) and, more recently, Alberch (1980), observed that morphologies do not appear in nature in a random or continuous manner, but that there is a repetition of several distinctive morphotypes. Such is the case with geomyoid rodents. A perusal of both fossil and extant forms reveals that virtually any geomyoid rodent fits into one of three general morphological categories (*Baupläne*): generalized mice, kangaroo-like rats and mice, and the fossorial, pocket gopher morphotype (Fig. 2). As pointed out by Alberch (1980), epigenetic interactions may reduce the scope of potential novelties and impose a sense of order in morphological transformations through phylogeny; as a consequence, we see developmental constraints effecting phyletic parallelism. The Geomyoidea is rife with phyletic parallelism (Hafner and Hafner, 1983; Wood, 1935) and, indeed, the bipedal pocket gopher ancestor, *Schizodontomys*, from the Miocene is an excellent case in point.

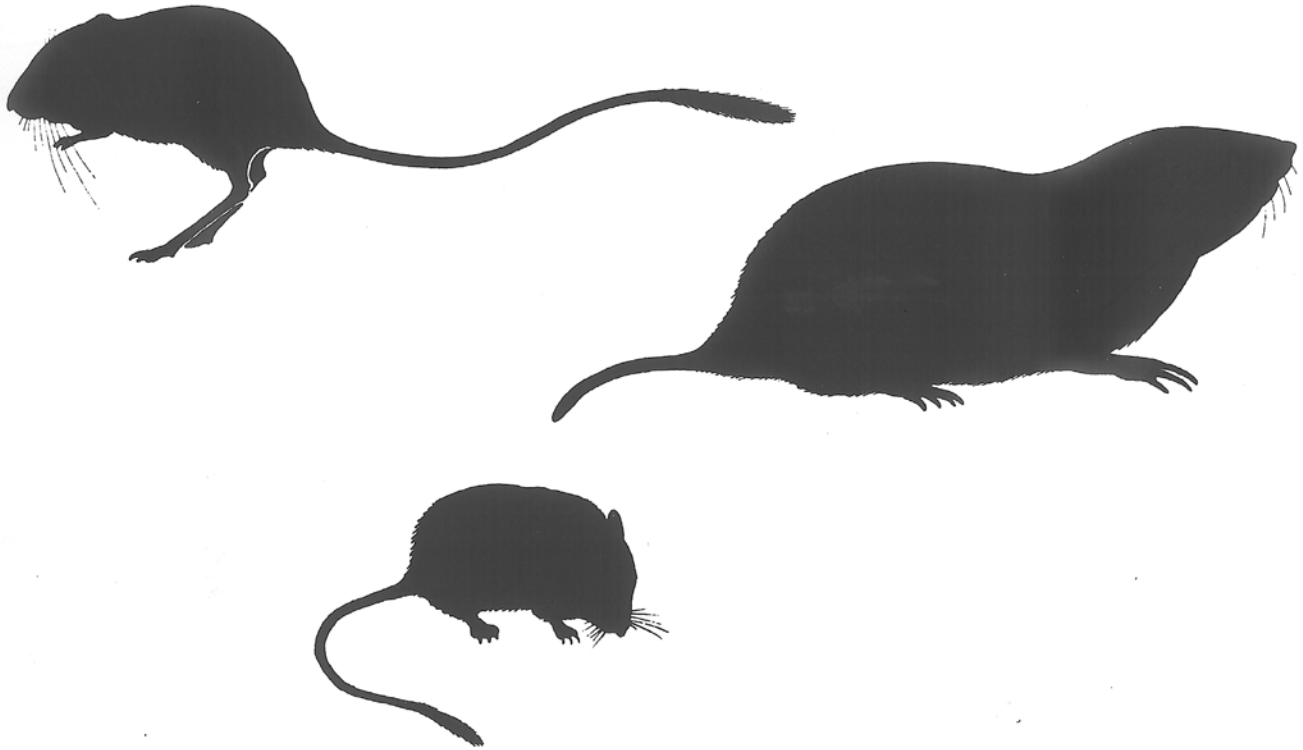*The paedomorphs.*—*Microdipodops* and *Dipodomys* share a variety of features that

FIG. 2.—Silhouettes of the three principal morphotypes found in the extant Geomyoidea. The body form of the pocket mouse (*Perognathus, Chaetodipus, Liomys, Heteromys*; lower) represents the generalized rodent condition. The fossorial pocket gopher (*Thomomys, Geomys, Pappogeomys, Orthogeomys, Zygogeomys*; right) is a robust, large-bodied form. The kangaroo-like form (*Dipodomys, Microdipodops*; left) is highly specialized with a large head, long hind feet, small fore feet, and long tail (the tail of *Microdipodops* [not shown] is thick at the midsection and lacks the terminal tuft). See text for discussion.

are characteristic of the juvenile state, or paedomorph (Hafner and Hafner, 1983, 1988; Hafner and Hafner, 1984). The obvious traits include the large head, large eyes, and long hind feet; these are among the endearing qualities of kangaroo mice and kangaroo rats and, doubtless, have contributed to the popularity of the heteromyids. As Gould (1977:350) observes, "Our concept of 'cute' is strongly determined by the common traits of babyhood: relatively large eyes, short face, smooth features, bulbous cranium." The manifestation of this character complex (plus other features) in the adults of *Microdipodops* and *Dipodomys* argues strongly for paedomorphosis.

The large heads of *Microdipodops* and *Dipodomys* have attracted much comment from biologists. At first glance, extreme inflation for the auditory bullae appears singularly responsible for the large crania of these ricochetal rodents. While it is unclear

how and why the bullae have become so greatly hypertrophied, bullar expansion alone does not seem to account for the large crania of these forms. As noted by Hafner and Hafner (1988), precaudal vertebral length (a measure of body size excluding tail) and condylonasal length of skull (a measure of skull size excluding bullae) are allometrically related and follow the equation *skull length* = *k* (*precaudal vertebral length*)$^{\alpha}$, where *k* is the allometric coefficient and α is the allometric exponent. The allometric exponent (regression coefficient) on a double logarithmic plot of skull length on precaudal vertebral length across the Rodentia is estimated to be 0.65 (Fig. 3; $r = 0.97, P \ll 0.01$). Hence, animals with shorter precaudal vertebral lengths (heteromyids in general) have, necessarily, proportionately larger heads. It is this allometric relationship (Fig. 3) that explains, in part, the large heads of kangaroo mice and kangaroo
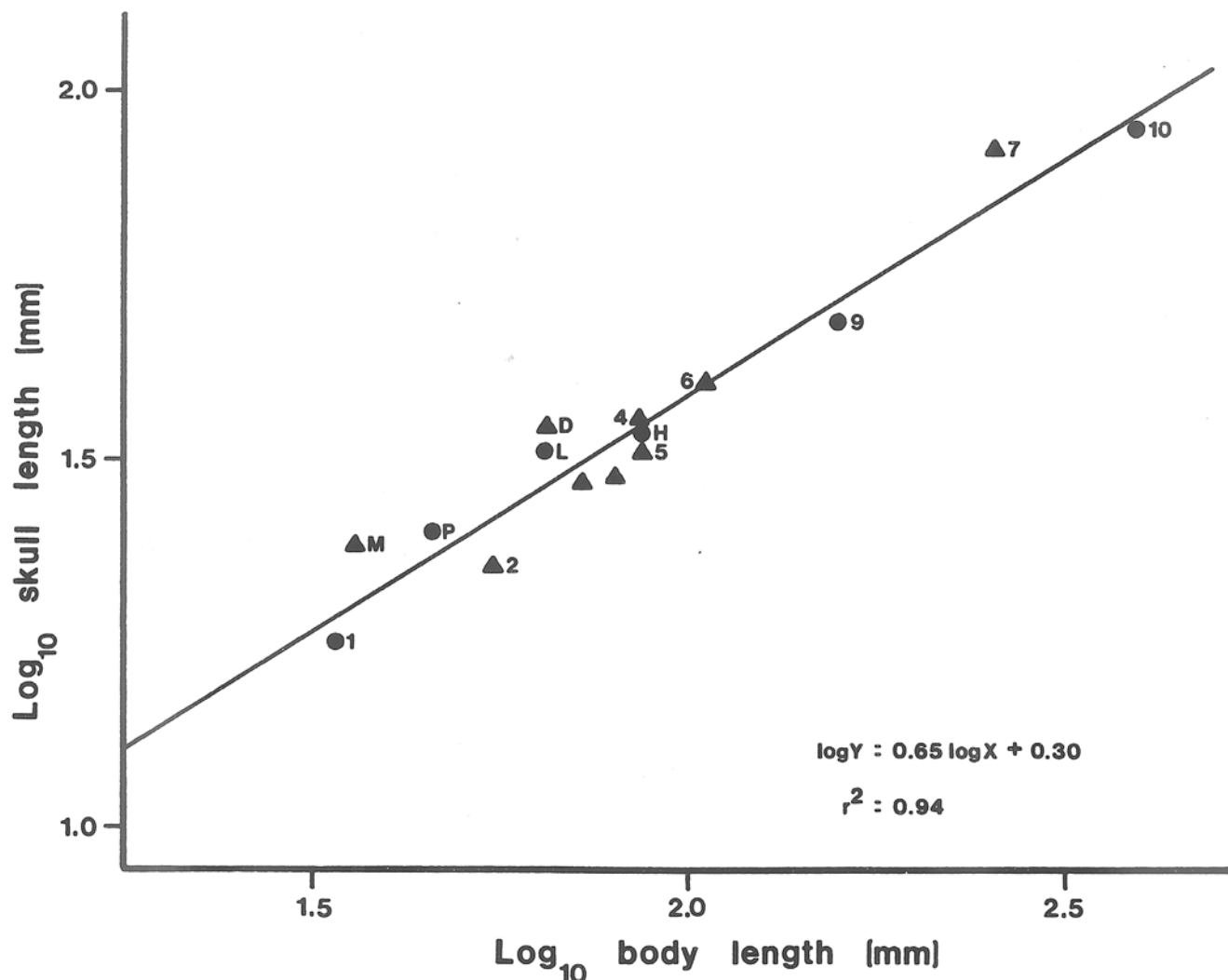
FIG. 3.—Relationship between skull (condylonasal) length and body (precaudal vertebral) length for 15 genera of ricochetal and nonricochetal rodents (data from Hatt, 1932:722). Ricochetors are indicated with triangles and nonricochetors by dots. Genera are as follows: M, *Microdipodops*; P, *Perognathus*; 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*.

rats. Note, however, that the regression of skull length against precaudal vertebral length (Fig. 3) reveals that *Microdipodops* and *Dipodomys* have skulls that are 135% and 125% larger, respectively, than predicted from precaudal vertebral length alone. Apparently, functional constraints associated with locomotion do not explain this deviation. Inspection of Fig. 3 shows that there is no relationship between the ricochetal habitus and proportionate head size in rodents; that is, some bipedal rodents have heads that are larger than predicted (e.g., *Jaculus* and *Pedetes*), whereas other bipedal rodents have heads that are smaller than predicted (e.g., *Scirtopoda* and *Notomys*).

The large heads of kangaroo mice and

kangaroo rats may also be due to their relatively large brains (see Table 2; Hafner and Hafner, 1984). Enlargement of the brain seems to be a common result of paedomorphosis (Gould, 1977). The relatively large brains of kangaroo mice and kangaroo rats may result from time hypermorphosis, as is well established for human encephalization (for discussion see Shea, 1988). Time hypermorphosis here results in a relatively enlarged brain by allowing for a protracted fetal period of high relative growth of the brain; as a consequence, time hypermorphosis yields a high brain/body ratio that is characteristically paedomorphic.

Kangaroo rats and kangaroo mice share several other paedomorphic features. Both

TABLE 2.—*Selected morphological and life-history characteristics of heteromyids.*

Genus	Mean adult body mass (g)[a]	Mean brain EQ value[b]	Mean rear foot in percentage head and body[c]	Mean tail in percentage head and body[c]	Mean number of caudal vertebrae[c]	Mean litter size[a]	Mean gestation time (days)[d]
Perognathus	10.6	0.96	28	107	—	4.2	25.1
Chaetodipus	22.6	0.92	28	121	26[e]	4.3	27.0
Liomys	43.8[f]	0.94	25[e]	118[e]	26[e]	4.0[g]	26.5
Heteromys	74.4[h]	0.96[i]	27[e]	128[e]	27.5	3.0[j]	27[i]
Microdipodops	12.5	1.21	36	130	24	3.9	—
Dipodomys	76.1	1.26	37	143	29.9	3.1	29.4

[a] Means for genera (except *Liomys* and *Heteromys*) calculated from species data in Jones (1985) and included references.

[b] Means for intra-geomyoid encephalization quotients (*EQ* values) calculated from species data in Hafner and Hafner (1984). *EQ* values less than 1.00 denote relatively small brains, whereas values greater than 1.00 describe relatively large brains.

[c] Hatt (1932).

[d] Means for genera calculated from species data in Jones (1985) and included references.

[e] Value based on one specimen.

[f] Mean calculated from species data in Burt and Grossenheider (1952), MacMillen and Hinds (1983) and Jones (1985). When a range was given instead of a mean, the average of the range limits was used. Also, several estimates available for the same species were averaged.

[g] Mean calculated from data for species in Eisenberg (1963) and Fleming (1977); several estimates for the same species were averaged.

[h] Mean calculated from data on *H. desmarestianus* in MacMillen and Hinds (1983) and Jones (1985).

[i] Data from a single species.

[j] Mean calculated from data for species in Eisenberg (1963) and Fleming (1977). When a range was given instead of a mean for a species, the average on the range limits was used. Also, several estimates available for the same species were averaged.

Microdipodops and *Dipodomys* retain the stapedial canal and artery (Howell, 1932). The stapedial artery, derived from the second aortic arch, is likely present in all mammals at some stage of development, yet in many mammals it commonly disappears at an early ontogenetic stage. Importantly, Howell (1932:503–504) observes that, among the geomyoids, only *Microdipodops* and *Dipodomys* have a complete stapedial canal and artery, whereas species of *Perognathus*, *Liomys* and *Thomomys* show various degrees of degeneration of the artery and canal. Lastly, kangaroo mice and kangaroo rats, in comparison with other geomyoids, have very light, delicate skeletons whose osseous elements are smooth and paper thin, and show a low degree of fusion. Unfused and/or definitive sutures are commonplace in the skulls of *Microdipodops* and *Dipodomys* and this reduced level of ossi-fication further describes a paedomorphic condition.

Kangaroo mice and kangaroo rats do, however, differ by a vast number of fundamental morphological features (e.g., see Hafner, 1978; Hatt, 1932; Howell, 1932; Wood, 1935), despite the many shared paedomorphic characters. Indeed, the entire natural history of *Microdipodops* is unlike that of *Dipodomys*; the genera differ markedly in body size, life-history strategy, locomotion, ecology, physiology, and geographic distribution. Paedomorphosis is a gross morphological expression (a shape phenomenon) that appears to be shared between these genera as a result of phyletic parallelism. As hypothesized by Hafner and Hafner (1983, 1988), two separate heterochronic processes may be involved in the juvenilization of kangaroo mice and kangaroo rats.
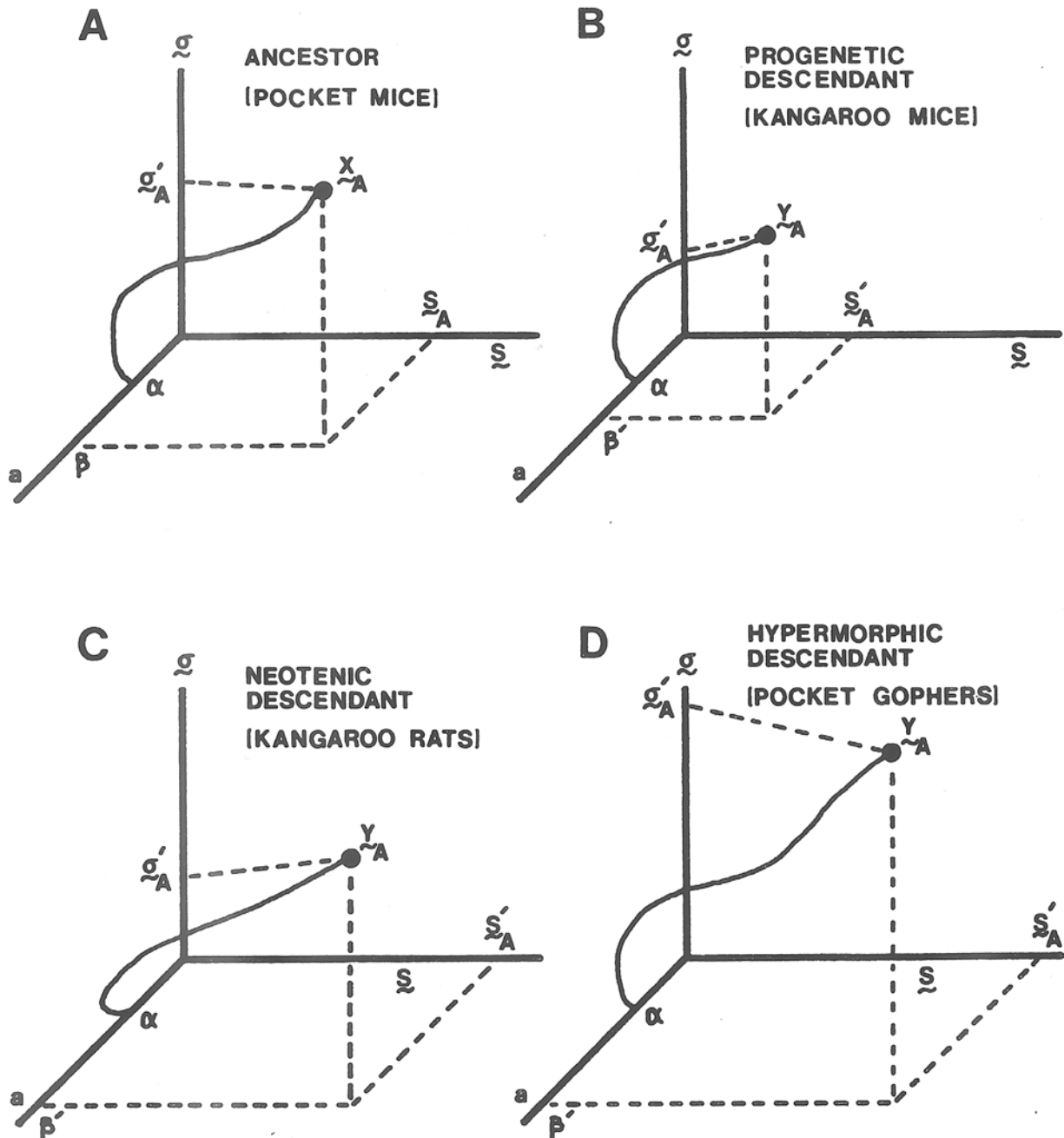
FIG. 4.—Morphological transformations through ontogeny and phylogeny in the Geomyoidea. Ancestral ontogenetic trajectory is altered producing phylogenetic transmutation of morphology. A hypothetical development event is mapped on an age axis (a) and form coordinates, size (S) and shape (σ). The onset (α) and cessation of development (β) are indicated along the age axis. As an animal ages, an ontogenetic trajectory is traced out leading to the adult ancestor, X_A or adult descendant, Y_A. Terminology follows Alberch et al. (1979). See text for discussion.

The ancestral ontogenetic trajectory.— Pocket mice, including *Perognathus, Chaetodipus, Liomys* and *Heteromys,* exhibit a generalized rodent *Bauplan* (Eisenberg, 1981:90) and probably represent a reasonable approximation of the ancestral geomyoid condition. It is difficult to specify the exact size of the ancestral *Bauplan,* but it was probably moderately small (and not moderately large as suggested by MacMillen

[1983] and MacMillen and Hinds [1983]); the paleontological evidence (e.g., Reeder, 1956; Wahlert, this volume; Wood, 1935) shows that the earliest geomyoids (including *Heliscomys, Proheteromys* and *Mookomys*) varied from small rodents approximately the size of *Perognathus longimembris* (8 g; Jones, 1985), to medium-sized forms such as *Chaetodipus californicus* (23 g; Jones, 1985) and *Liomys* (43.8 g; Burt and Gros-

senheider, 1952; Jones, 1985; MacMillen and Hinds, 1983). An animal with this ancestral morphotype is likely to have conserved the developmental patterns of the geomyoid ancestor. As the animal ages from conception, its size and shape will change, following the ancestral ontogenetic trajectory. In Figure 4, I use the formalism proposed by Alberch et al. (1979) to analyze the morphological transformations through ontogeny and phylogeny in the Geomyoidea. This method describes ontogeny using a three-axis system: a, the age axis that details the timing of differentiation events; S, the size axis; and σ, the shape axis (Fig. 4). The ontogenetic-trajectory method is used here to represent the overall ontogeny of an individual and to illustrate the general effects of possible heterochronic changes. It is an idealized representation which describes a myriad of hypothetical structures and organs on a single pair of size and shape coordinates (for discussion see Alberch, 1980; Alberch et al., 1979). Perturbations (δ) of the "control parameters," including the onset of growth (α), cessation of development (β), size growth rate (k_S) and rate of change in shape (k_σ), deform the ancestral ontogenetic trajectory and lead to phylogenetic transmutations (Fig. 4). Much of the morphological diversification in the Geomyoidea is explicable from this ontogenetic perspective and the morphological novelties that are produced are predictable end products of heterochronic perturbations.

Kangaroo mice: the progenetic descendant. —Kangaroo mice, in comparison with other geomyoids, show retention of juvenile morphology and are very small in body size. It is hypothesized, then, that kangaroo mice represent a paedomorphic version of a somewhat larger (though still moderately small) geomyoid ancestor (see also Hafner and Hafner, 1983, 1988). Importantly, Shea (1983, 1988) and McKinney (1988) note that two different heterochronic events may lead to a small-sized paedomorph: time progenesis (= time hypomorphosis) and rate progenesis (= rate hypomorphosis). Time progenesis is a process in which ontogeny is truncated because the time required for reproductive maturation is abbreviated. This involves a negative perturbation ($-\delta\beta$) in the ancestral ontogenetic trajectory (Fig. 4B) and results in a small, rapidly maturing paedomorph. Rate progenesis, however, involves a reduction in size growth rate ($-\delta k_S$) and leads not only to a small descendant, but one that is also a paedomorph; this is true because change in size is inextricably associated with change in shape and few traits change isometrically with size. It is important to distinguish between these two kinds of progenesis, because these heterochronic mechanisms, though producing similar results, suggest different selective environments and adaptive scenarios. As noted by Shea (1988), the ecological correlates of the diminutive paedomorph would be expected to be different if the heterochronic mechanism involved truncated growth time (time progenesis) or reduced growth rate (rate progenesis). For time progenesis, selection may act mainly for reduced growth duration in an environment where early maturation and increased reproductive output are advantageous. Alternatively, if rate progenesis is involved, selection may act principally on reduced growth rate and smaller size as a means of reducing interspecific competition by exploiting an alternative food resource (e.g., insects).

Both Gould (1977) and McKinney (1986) observe that the key to understanding the immediate significance of heterochrony lies in the theory of r and K selection (life-history strategies). Gould (1977:293) predicts that "*progenesis will be associated with r strategies and neoteny with K strategies*" (italics his). Interestingly, *Microdipodops* inhabits an obvious r-selected environment (ephemeral sand-dune habitats in the Great Basin Desert) and, while the data are scanty, it seems to possess the attributes of an r strategist when compared to most other geomyoids. In addition to showing small body size, kangaroo mice seem to have somewhat reduced longevity (Egoscue et al., 1970) and subsist on insects (an ephemeral resource

base) as well as seeds (Hall, 1941); they do not, however, seem to show larger litter sizes as was previously reported (cf., Hafner and Hafner, 1988; see Table 2). It should also be kept in mind that the genus is autochthonous in the Great Basin Desert (Hafner, 1978, 1981) and through its evolutionary history has faced the rigors of cold (high elevation), desert habitats that are characterized by a shortened growing season.

Given the complete lack of information on the growth and development of *Microdipodops,* it is impossible to identify which of the two mechanisms of progenesis may be involved (for discussion see McKinney, 1988). Indeed, future workers must gather the kinds of data for kangaroo mice that will allow for the distinction between these heterochronic processes (as well as a consideration of other possibilities including postdisplacement or even neoteny) that may be responsible for paedomorphosis here. However, the small body size and obvious paedomorphosis suggest that either form of progenesis is the favored heterochronic hypothesis for *Microdipodops.* If time progenesis is involved in the evolution of kangaroo mice, then they may represent a parallel to New World callitrichid monkeys where precocious maturation as a life-history strategy may have been the principal object of selection (see Shea, 1988). Alternatively, selection favoring small body size and dietary specialization on insects may be the underlying effectual aspect of evolution involving rate progenesis; a parallel here may be the Old World talapoin monkeys (see Shea, 1988). In either case, it seems that the juvenilized morphology of kangaroo mice (a necessary byproduct of progenesis) may be entirely incidental.

The kangaroo mouse, as a progenetic descendant, harbors several morphological characters not seen in the kangaroo rat (a neotenic descendant, see beyond). Wood (1935:112) was first to notice that the enamel of the incisors of adult *Microdipodops* is white to very pale yellow in color and he suggested that this is a juvenile characteristic (enamel tends to darken with age). In contrast, adults of most other species of geomyoids usually have dark, yellow-colored enamel on their incisors. Kangaroo mice, despite having a relatively long tail, also possess the fewest caudal vertebrae (24) of all heteromyids (see Table 2). According to Hatt (1932:644) "*Microdipodops* then, has achieved a fairly long tail through lengthening of the units, while *Dipodomys* has its long tail, at least in part, by virtue of units added." Inasmuch as ossification occurs craniocaudally in heteromyids (Van De Graaff, 1973), this reduction in the number of vertebral elements may simply be due to the truncation of the size/shape pattern of the ancestral ontogeny that results from either time or rate progenesis (early offset signal of development or reduced rate of overall weight growth prevents further ossification of tail vertebrae). As discussed above, kangaroo mice have relatively large heads because they have short precaudal lengths (Fig. 3). However, kangaroo mice do have greatly inflated auditory bullae. It seems that the extremely enlarged bulla is a result of the unique development of an additional bullar lobe. Wood (1935:112, 242) determined that the "swelling" of the anterior lobe is due to the anterior migration of the temporalis muscle which carries the delicate squamosal up on the dorsum of the skull. Wood (1935:242) described this modification as "the most striking action of muscle on bone detected within the family . . . ." Lastly, the cheek teeth of kangaroo mice seem not to have fully developed roots when compared to those of pocket mice; the cheek teeth of *Microdipodops* possess molar roots that are irregularly present, greatly reduced in size and appear late in ontogeny (for discussion see Hall, 1941; Merriam, 1891; Wood, 1935).

Kangaroo rats: the neotenic descendant.—A retardation in the rate of change in shape of the ancestral ontogenetic trajectory $(-\delta k_a)$ will lead to the production of a neotenic descendant. The juvenilization of kangaroo rats may have occurred in this manner (Hafner and Hafner, 1983, 1988; see Fig. 4C). Neoteny occurs often in nature

and may result from direct selection for juvenile features and/or larger body sizes in *K*-selected environmental regimes (Gould, 1977). Slow development may produce a descendant of the ancestral adult size but one retaining juvenile features. This decrement in the shape growth rate, coupled with a delay in β (Fig. 4C) is sufficient to explain the observed variety of medium- to large-sized kangaroo rat species. *Dipodomys,* in comparison to other geomyoids, possesses many of the classical features associated with the neotenic syndrome: moderate to long life span (Egoscue et al., 1970); slow development (Butterworth, 1961; Chew and Butterworth, 1959; Eisenberg and Isaac, 1963; Fleming, 1977; Hayden and Gambino, 1966; Lackey, 1967); long gestation period (Eisenberg and Isaac, 1963; Fleming, 1977); enlarged brain (Hafner and Hafner, 1984); and generally small litters (Butterworth, 1960; Eisenberg and Isaac, 1963; Fleming, 1977; Hall, 1946). This associated complex of characters (see Table 2) suggests that the kangaroo rats are near the *K* end of the *r-K* spectrum of life-history strategies. That some species of kangaroo rats inhabit desert regions does not contradict this hypothesis. Actually, several of the more strictly desert-dwelling species (e.g., *D. microps, D. spectabilis* and *D. deserti*) subsist almost entirely on leaves, flower heads and seeds from perennial species (a largely nonfluctuating resource base as compared with seeds of annuals and insects) and, strictly speaking, many other kangaroo rat species are not found in the desert at all (e.g., *D. californicus, D. heermanni, D. stephensi, D. venustus*). Gould's (1977) hypothesis that neoteny may result from direct selection for larger body size and/or juvenile features seems worthy of serious consideration here; Kotler (1984) observed that larger kangaroo rats were less vulnerable to predation by owls and canids and better able to forage in open habitats than smaller species of rodents (see also above discussion and Kotler, 1985).

Several morphological features unique to *Dipodomys* are germane to this discussion

of neoteny: the reduction and/or loss of the hallux, the generally opaeodont (open-rooted teeth) condition of the molars, and the high number of caudal vertebrae (kangaroo rats, with generally 31 caudal elements, have the highest number of caudal vertebrae in the family; Hatt, 1932; Table 2). 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. Most interestingly, 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. Conversely, the high number of caudal vertebrae (Hatt, 1932) suggests that, although terminal ossification occurs relatively late (but probably earlier than the above two features), the retention and prolongation of fetal growth tendencies allow for the continued progressive development of caudal vertebrae.

Pocket gophers: the hypermorphic descendant.—It has been hypothesized that the process of hypermorphosis may be largely responsible for the gross shape and size of pocket gophers (Hafner and Hafner, 1983, 1988). Hypermorphosis leads not only to a descendant whose shape transcends that of the ancestral form (technically, peramorphosis), but one that is also large in size. Hypermorphosis can be achieved by two separate processes: time hypermorphosis and rate hypermorphosis (for discussion see Shea, 1983, 1988; McKinney, 1988). Time hypermorphosis is a process wherein there is a positive perturbation in the signal for cessation of growth $(+\delta\beta)$ in the ancestral ontogeny (Fig. 4D) that produces a hypermorphic individual (also termed a peramorph; Alberch et al., 1979); that is, lengthened period of growth allows for the extension of the ancestral allometric trajectory. In contrast, rate hypermorphosis involves an increase in size growth rate $(+\delta k_s)$ and also produces a large, peramorphic descendant. As noted by Shea (1988), increased rate of overall weight growth will result in extension of the size/shape pattern

of the ancestor, but without changing the ancestral allometry or maturation time. Most of the general morphological attributes of pocket gophers seem to support this hypothesis of hypermorphosis. The adult pocket gopher possesses a heavily ossified skeleton, the cranial elements of which show a high degree of fusion; these are classical attributes of later mammalian ontogeny. Further, pocket gophers are large-sized geomyoids.

While peramorphosis may be produced by several other processes (e.g., acceleration and predisplacement; see Alberch et al., 1979), the marked similarities in size and shape between very young pocket gophers and adult pocket mice (Hafner and Hafner, 1988) suggest that hypermorphosis is involved in the morphological evolution of pocket gophers. This heterochronic perturbation allows pocket gophers to "go beyond" or extend the ancestral ontogenetic trajectory (Fig. 4D). Hence, juvenile levels of morphological differentiation in the pocket gophers may be adult features of the ancestor (recapitulation). 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 a juvenile at this size. It is for this reason that I favor hypermorphosis (as opposed to recapitulation by acceleration) as the process leading to the peramorphosis in this case.

Gould (1977) notes that there is usually a link between K-selective regimes and hypermorphosis. In accord with Gould's observation, it seems that pocket gophers inhabit a relatively nonfluctuating environment (the subterranean niche), subsist on a stable food (primarily roots and tubers), are large in body size (relative to heteromyids), exhibit strong intra- and interspecific competitive abilities (e.g., Miller, 1964), and may be long lived (Howard and Childs, 1959). However, recent information available for *Thomomys,* the smallest of the pocket gopher genera, shows high annual population turnover and suggests that it may be a more *r*-selected strategist (Daly and Patton, 1986).

Clearly, much more data are needed (particularly for the larger genera such as *Orthogeomys* and *Zygogeomys*) before any conclusions can be made on the possible relationship between hypermorphosis and life-history strategies among the pocket gophers.

Conclusions on ontogeny and phylogeny. — It has been hypothesized that heterochronic disturbances during development have been involved in macroevolution (sensu Simpson, 1944, 1953) in the Geomyoidea. To clarify a description of the observed phenomena, I have incorporated the "ontogenetic-trajectory" formalism of Alberch et al. (1979). Figure 5 summarizes these views concerning morphological transformations through ontogeny and phylogeny in geomyoid rodents by focusing on one structural complex: the cranium. Deformations in the ancestral (mouse-like) ontogenetic trajectory (Fig. 4) results in recapitulation (through hypermorphosis) and reverse recapitulation (through progenesis or neoteny). Adult descendants that are particularly large in size (e.g., the pocket gopher, *Orthogeomys grandis,* or the kangaroo rat, *D. deserti*; Fig. 5), but show the same shape as smaller relatives, may result from proportioned giantism.

One of the principal aims of this review is to emphasize the possible role of heterochrony (mutations that cause altered developmental programs) in morphological evolution of heteromyid (and geomyid) rodents. The focus here on heterochrony, of course, is intended not to mitigate the role of natural selection in macroevolution. Clearly, the omnipresent force of selection serves ultimately in judging the success or failure of any evolutionary novelty. But by emphasizing heterochrony, I want to encourage a more eclectic view of morphological evolution in these rodents; specifically, a view that does not ignore the recent realization that evolutionary changes in size and shape arise from evolutionary change in developmental programs (see Atchley, 1987).
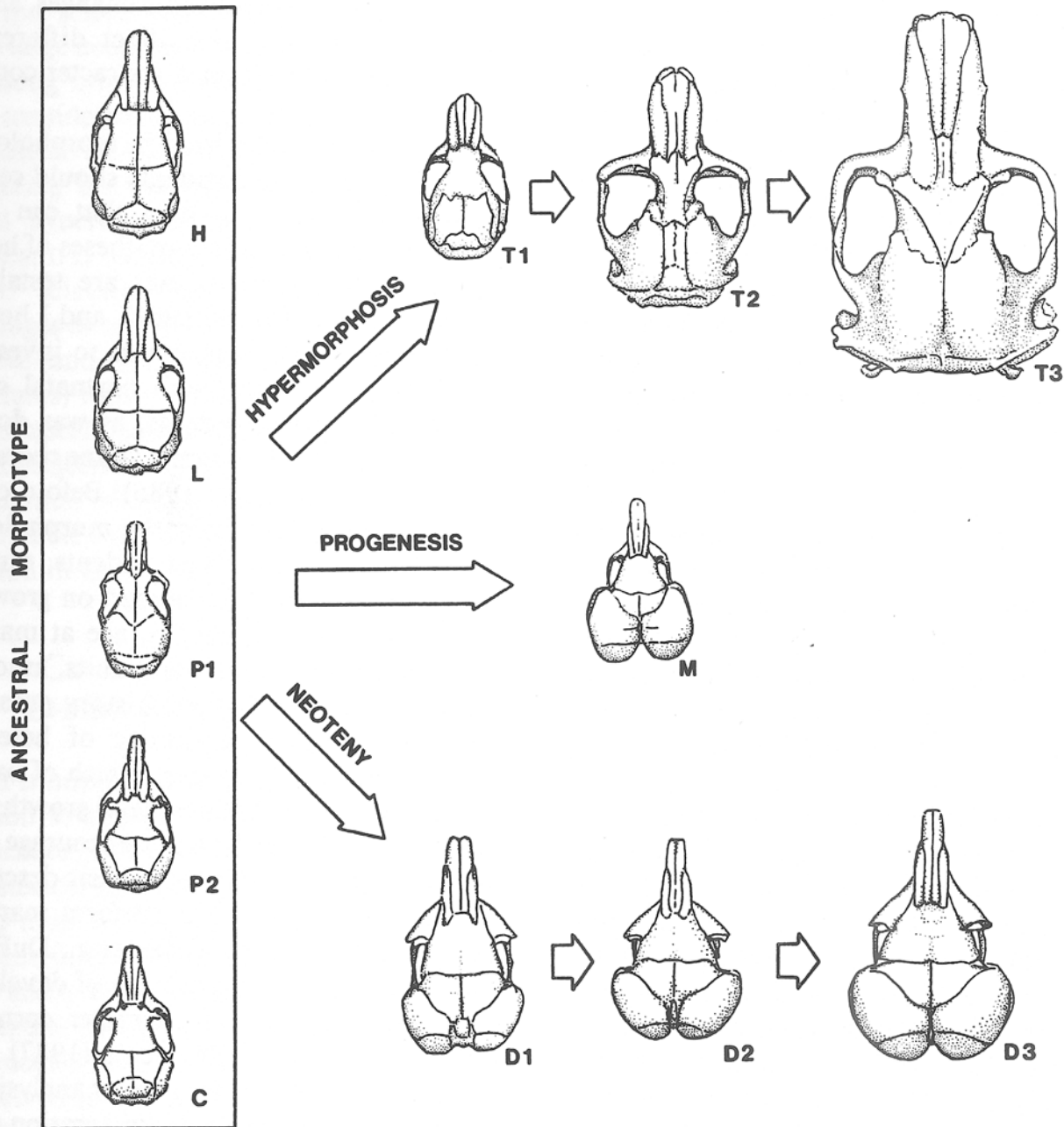
FIG. 5.—The evolution of geomyoid cranial differentiation based on the hypothesized heterochronic disturbances during development. Five genera illustrate the presumed ancestral ("mouse-like") morphotype: *Heteromys desmarestianus* (H), *Liomys irrortaus* (L), *Peromyscus truei* (P1), *Perognathus parvus* (P2), *Chaetodipus penicillatus* (C). Other crania are as follows: young *Thomomys monticola* (T1), *Thomomys umbrinus* (T2), *Orthogeomys grandis* (T3), *Microdipodops megacephalus* (M), *Dipodomys compactus* (D1), *Dipodomys merriami* (D2), and *Dipodomys deserti* (D3). All crania are drawn from adult individuals except for T1. Note the similarity between the young pocket gopher (T1) and the ancestral morphotype. Figures modified from Hall (1946, 1981), Setzer (1949), and Genoways (1973).

The hypotheses presented here (see also Hafner and Hafner, 1988) are based mainly on patterns of morphological differentiation seen in adult specimens. These hypotheses predict that the ontogenies of the derived novel forms, such as kangaroo mice and kangaroo rats, were altered in a specific fashion relative to the ancestral condition. It should be pointed out, however, that the epigenetic interactions affecting these morphological transformations are much more complex than the simple heterochronic changes that are outlined. The intent here is to suggest that a substantial portion of the

morphology of each derived form represents an intercorrelated set of traits that may be produced by a single heterochronic perturbation. As such, I hypothesize that the kangaroo mouse is *mainly* progenetic, the kangaroo rat is *mainly* neotenic, and the pocket gopher is *mainly* hypermorphic. One must keep in mind that morphogenesis is a complex process and examples of "pure" types of heterochronic changes unaccompanied by other basic heterochronic events are probably very rare (for discussion see Alberch et al., 1979; Fink, 1982; Gould, 1977; McKinney, 1984). It follows then that not everything about these derived creatures would be expected to be consistent with a strict (global) interpretation of the heterochrony hypotheses that are presented. Indeed, not all traits are going to show the same heterochronies inasmuch as trait dissociation (mosaic evolution) is very common (for discussion see McKinney, 1988). For example, the short tail of pocket gophers seems to be truncated (only 16–18 caudal vertebrae [Hill, 1937]; cf. Table 2), but an obvious prediction from a global interpretation of the above hypothesis is that the peramorph should have a high number of caudal vertebrae (and, thus, a long tail). Also, the kangaroo mouse has greatly enlarged auditory bullae (perhaps the result of acceleration), but the animal is hypothesized to be mainly progenetic. Additionally, the large auditory bullae and elongated tail of kangaroo rats may be peramorphic, yet the form is hypothesized to be mainly neotenic. A single heterochronic perturbation may, but need not, cause rather global morphological changes when its effects are amplified by a myriad of pleiotropic and epigenetic effects that occur during development. More commonly, morphological patterns are produced by a combination of heterochronic events (Alberch et al., 1979), and individual traits evolve largely as a subunit of a developmentally integrated character complex that is, in turn, governed by various hierarchical developmental processes. Thus, it seems that dissimilar kinds of heterochronic changes, acting independently, may affect different developmentally integrated character complexes.

Future workers interested in morphological evolution in these rodents should seek to gather the kinds of data that can be brought to bear on these hypotheses of heterochrony. These hypotheses are testable (see Hafner and Hafner, 1988), and I hope that they will encourage others to investigate the embryological and postnatal ontogeny of geomyoid rodents, as was done recently in neotomine-peromyscine rodents (Creighton and Strauss, 1986). Before one is able to understand fully the morphological differentiation in these rodents, much more complete data are needed on growth and development, longevity, age at maturation, litter sizes, and food habits, among many other crucial natural history parameters. Despite the popularity of heteromyids, there is a surprising dearth of basic descriptive data on the postnatal growth for most species. Accordingly, I encourage future workers to perform these basic descriptive studies, as well as to perform manipulative embryological studies (e.g., DuBrul and Laskin, 1961) and studies of developmental integration and character correlation. In this regard, Zelditch's (1987) approach using confirmatory factor analysis in the study of developmental integration and Atchley's (1987) developmental quantitative genetics model stressing genetic variance-covariance structure seem to provide promising directions for future research.

In summary, I propose that much of the striking morphological modifications in the heteromyids may have resulted from heterochronic shifts in ontogeny. As such, the evolution of each trait might not be attributed solely to natural selection but, subsequent to the heterochronic event(s), each trait may have been modified by selection for its present utility. The novel features may have arisen in a rather serendipitous manner (nonadaptations), but later were available for cooptation in descendants by

further selection regimes; the long hind feet, the large head, and the delicate, gracile body (among other novelties), then, might best be considered as exaptations rather than adaptations (see Gould and Vrba, 1982). Considering the examples of paedomorphosis and hypermorphosis within the Geomyoidea, it is reasonable to postulate that natural selection acted on heterochronic changes in ontogeny to effect adaptive *Baupläne* (and, perhaps, associated life-history features) rather than generating each morphological feature independently through orthoselection. Future work exploring the evolution of ontogenies may prove to be a profitable way of understanding macroevolution in this unique group.

Current Utility Versus the Evolution of Novel Features

It is important in the study of macroevolution to consider both the functional significance (current utility) and the evolution (historical genesis) of a novel character; the two must not be automatically considered as one in the same, nor should these ideas be taken to be directly competitive. The adaptive significance of the novel morphologies seen in the Heteromyidae have received much attention from several generations of biologists. The emphasis on the current utility of the novelties has been so overwhelming that few workers have attempted to explore the evolution of the novelties. In fact, most prior workers have assumed (usually implicitly) that they are explaining evolution when they explain present use; thus, they have failed to see the distinction between the two concepts. Moreover, it should also be clear that the questioning (or even refutation) of any hypothesized functional explanation does not necessarily lend support to any particular model for the evolution of the feature.

Adaptive significance of evolutionary novelties. —The adaptationist program has sought to demonstrate the adaptedness of

novelties seen in the Heteromyidae by focusing on the functional significance of individual traits (e.g., the enlarged auditory bullae, the long hind feet, long tail, big eyes). Mayr (1983) stated repeatedly that a more holistic approach to the study of adaptation is appropriate only when all specific analyses of individual traits fail to determine an adaptive significance. I question this view because it is inappropriate, in principle, to dissect the phenotype into individual characters and concentrate on the adaptive significance of a trait (see Dobzhansky, 1956; Gould and Lewontin, 1979); the whole organism is always much more than the sum of its parts. However, I agree that the adaptationist program is a profitable method of scientific research, because of its great heuristic value (see Mayr, 1983). It is for this reason that the adaptationist question, "What is the function of a given trait?", is important in the biology of the Heteromyidae. Actually, there is no reason why the more atomistic and more holistic approaches cannot be pursued simultaneously. The research programs are not mutually exclusive and there is much promise for reciprocal illumination. The adaptationist approach in the Heteromyidae, however, has not yet produced convincing functional explanations for the various novel features. Accordingly, it is now appropriate to consider seriously more holistic approaches to explain the adaptiveness of the evolutionary novelties. 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 individual morphological traits.

Distinction between selective and developmental constraints. —If we are to understand the evolution of the novel body plans in the Heteromyidae, we must find ways of distinguishing between developmental and selective constraints. Unfortunately, given our present ignorance of the mechanisms of developmental regulation and our inadequate understanding of the role of development in evolution, it may be exceedingly

difficult to resolve this issue (for review, see Maynard Smith et al., 1985). Clearly, one of the principal tasks awaiting future generations of biologists is that of identifying the relative contribution of developmental and selective constraints in shaping macroevolutionary patterns.

Maynard Smith et al. (1985) suggest four possible ways to distinguish selective and developmental constraints in evolution: 1) testing quantitative predictions about the adaptive basis of certain traits; 2) direct measurement of the strength of selection; 3) direct assessment of heritable variation; and, 4) comparative analysis of variation (e.g., allometry). However, Maynard Smith et al. (1985) observed that none of these methods provides a foolproof means of distinguishing between developmental and selective constraints. They also noted that it will often be impossible to identify the constraints that are responsible for producing evolutionary patterns.

We will probably never be able to determine, unambiguously, the mechanism(s) responsible for the evolution of the novel forms because the production of a novelty, itself, is a unique event. Our best hope would be to identify what mechanism or combination of mechanisms is most likely responsible for the evolution of a particular trait or suite of characters. In the Heteromyidae, with obvious instances of paedomorphosis and peramorphosis, it seems clear that developmental constraints are involved (to some unknown extent) in effecting macroevolutionary patterns. As mentioned elsewhere (Hafner and Hafner, 1984), it is more parsimonious to suppose that the suite of juvenilized features of *Microdipodops* and *Dipodomys* evolved together through developmental heterochrony, rather than to suppose that each trait was shaped independently through natural selection. Clearly, we are in need of both descriptive and manipulative embryological studies to determine if, indeed, the suite of paedomorphic features of *Microdipodops* and *Dipodomys* are linked as has been hypothe-

sized. In the interim, though, we should not discount the possible influence that heterochronic changes in ontogeny may have had in the macroevolutionary diversification of the Heteromyidae.

Summary

The rodent superfamily Geomyoidea is a monophyletic lineage that is autochthonous in North America. Extant geomyoids are divisible into two groups: 1) the Heteromyidae, whose members display an adaptive array of bipedal and scansorial forms; and, 2) the Geomyidae, all members of which are fossorial. The Heteromyidae, with its morphologically heterogeneous forms, provides an excellent opportunity to investigate major evolutionary divergence. This study treats three aspects of macroevolution in the Heteromyidae: 1) evolutionary relationships among the taxa; 2) adaptive significance of the novel morphologies; and, 3) mechanism(s) responsible for the diversification of the evolutionary novelties.

The extant heteromyids comprise three principal lineages that diverged during the Oligocene: 1) subfamily Heteromyinae (*Liomys* and *Heteromys*); 2) subfamily Perognathinae (*Chaetodipus* and *Perognathus*); and, 3) subfamily Dipodomyinae (*Dipodomys* and *Microdipodops*). The heteromyine and perognathine rodents are generalized in morphology. In contrast, kangaroo mice, *Microdipodops*, and kangaroo rats, *Dipodomys*, are morphologically derived; these forms represent evolutionary novelties.

There are two ways to explain the evolutionary novelties seen in the Heteromyidae: 1) functional explanations that focus on the adaptedness and present use of a novel feature; and, 2) causal (mechanistic) explanations for the evolution of the novel morphology. Most functional (adaptationist) explanations pertaining to kangaroo mice and kangaroo rats focus on the hypothesized "anti-predator morphology". These adaptationist arguments are reviewed and evaluated and it is concluded that there is much

need for a clearer understanding of the functional significance of the novel morphologies. In addition, a model is presented to describe how heterochronic changes in ontogeny may explain the evolution of the morphological novelties seen in the superfamily. Thus, the initial evolution of each novel trait might not be attributed to the action of natural selection but, subsequent to its appearance, each nascent trait may have been modified by selection for its present utility.

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