Evolutionary and biogeographic histories in a North American rodent family (Heteromyidae)

Lois Fay Alexander
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EVOLUTIONARY AND BIOGEOGRAPHIC HISTORIES IN A
NORTH AMERICAN RODENT FAMILY (HETEROMYIDAE)

by

Lois Fay Alexander

Bachelor of Science
Oregon State University, Corvallis
1990

Master of Science
Oregon State University, Corvallis
1994

A thesis submitted in partial fulfillment
of the requirements for the

Doctor of Philosophy Degree in Biological Sciences
Department of Biological Sciences
College of Sciences

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Evolutionary and Biogeographic Histories in a North American Rodent Family (Heteromysidae)

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ABSTRACT

Evolutionary and Biogeographic Histories in a North American Rodent Family (Heteromyidae)

by

Lois F. Alexander

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Professor of Biological Sciences
University of Nevada, Las Vegas

The family Heteromyidae includes six genera of rodents traditionally placed in three subfamilies endemic to the Nearctic and northern Neotropical biogeographic regions. Although several of these taxa represent intensively studied members of North and Central American ecosystems (e.g., kangaroo rats, pocket mice), phylogenetic relationships within and among subfamilies, genera, and species-groups are poorly understood. Here, I used maximum likelihood (ML), Bayesian, and maximum parsimony (MP) analyses of sequence data from two mitochondrial DNA genes—COIII (699 bp) and cytochrome b (1140 bp)—to investigate phylogenetic relationships among 55 species-level taxa. I found robust support for monophyly of genera Dipodomys, Microdipodops, Chaetodipus, and Perognathus; sampling of Liomys and Heteromys was inadequate to evaluate their reciprocal status. All analyses converge on a phylogeny that robustly resolves several historically contentious issues, including monophyly of the subfamily Dipodomyinae (Microdipodops + Dipodomys), and a monophyletic Chaetodipus that includes C. formosus, C. baileyi, C. formosus, C. baileyi, C.
rudinis and C. hispidus. However, Perognathinae (Perognathus + Chaetodipus) is not supported, with no basal resolution among Perognathus, Chaetodipus, Dipodomyinae, and Heteromyinae. Many intrageneric clades receive strong support and are discussed herein.

I used the phylogenetic information to evaluate several hypotheses regarding the evolution of the Heteromyidae. I separately evaluated the evolution of morphological characters (body size, number of hind toes [Dipodomys only], and rump spines [Chaetodipus only]) and macroecological evolution by coding each taxon into classes (body size – very small, small, medium, large, or very large; number of toes – 4 or 5; rump spines – presence or absence) and biome-level categories (grassland steppe, chaparral, subtropical thornscrub, warm desert, or cold desert) and then tracing the history of the morphological characters and ecological transitions during radiation of extant groups using the Fitch optimization in MacClade. Because the mitochondrial DNA genes chosen for these analyses resulted in very limited resolution at the basal nodes of the Heteromyidae tree, recommendations for future directions of study are discussed.
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CHAPTER 1

INTRODUCTION

Taxonomic background

The family Heteromyidae is well established within the order Rodentia as a member of the superfamily Geomyoidea along with Geomyidae (DeBry and Sagel 2001; Montgelard et al. 2002). Historically, the members of Heteromyidae and Geomyidae have been recognized as either a single family (Geomyidae) in two subfamilies (Geomyinae and Saccomyinae or Heteromyinae) or more recently as two distinct families (Heteromyidae and Geomyidae) in the superfamily Geomyoidea (Ryan 1989; Williams et al. 1993). This family of deciduous thorn-scrub and arid-adapted rodents is comprised of six genera (Chaetodipus, Dipodomys, Heteromys, Liomys, Microdipodops, and Perognathus) including approximately 57 species that are distributed from southern Canada, throughout the aridlands of western North America, south through Mexico, Central America, and into northern South America.

Chaetodipus, Dipodomys, Microdipodops, Perognathus, and Liomys are found primarily in dry, arid habitats, whereas Heteromys occupies moist neotropical rainforest habitats (Schmidly et al. 1993).

Heteromyidae is currently divided into three subfamilies: Perognathinae containing Perognathus and Chaetodipus; Heteromyinae containing Heteromys and Liomys; and Dipodomyinae containing Dipodomys and Microdipodops (Hafner 1993;
Patton 1993; Wahlert 1993; Williams et al. 1993). The most controversial aspect of this arrangement has been the recent placement of *Microdipodops* within Dipodomyinae (Hafner 1978; Hafner and Hafner 1983; Reeder 1956; Ryan 1989; Wahlert 1985) instead of the previously accepted placement within Perognathinae (Hafner 1978; Hall 1981; Wood 1935). It is possible that this group represents an independent lineage with no close living relatives (Hafner 1978; Hafner 1993). In addition, it has been suggested that *Heteromys* is paraphyletic relative to *Liomyis* (Rogers 1990). My sampling of *Heteromys* and *Liomyis* is insufficient to address this question and is being addressed elsewhere (Duke Rogers, pers. comm. 2003).

Phylogenetic relationships among the 22 species of kangaroo rats (genus *Dipodomys*) also are in a state of confusion. Many attempts have been made to resolve this problem, but all were prior to the advent of modern molecular systematics. Several morphological comparisons have been attempted previously, but no satisfying conclusions can be drawn. Many researchers have attempted to arrange kangaroo rats into phylogenetic groups, but have generally failed partly because all 22 previously recognized species are morphologically similar (Stock 1974). The first comprehensive evaluation of relationships within the genus *Dipodomys* was that of Grinnell (1921) who based his analysis on external and cranial morphology. Many attempts have been made to revise the original groups suggested by Grinnell (1921). Kangaroo rats have been grouped by cranial and skeletal characteristics (Best 1993; Schnell et al. 1978), tooth characteristics (Nader 1966; Wood 1935), baculum (Best and Schnell 1974; Burt 1936), skeletal specialization and visceral measurements (Setzer 1949), protein variation (Johnson and Selander 1971), chromosomes (Patton and Rogers 1993; Stock 1993; Wahlert 1993; Williams et al. 1993). The most controversial aspect of this arrangement has been the recent placement of *Microdipodops* within Dipodomyinae (Hafner 1978; Hafner and Hafner 1983; Reeder 1956; Ryan 1989; Wahlert 1985) instead of the previously accepted placement within Perognathinae (Hafner 1978; Hall 1981; Wood 1935). It is possible that this group represents an independent lineage with no close living relatives (Hafner 1978; Hafner 1993). In addition, it has been suggested that *Heteromys* is paraphyletic relative to *Liomyis* (Rogers 1990). My sampling of *Heteromys* and *Liomyis* is insufficient to address this question and is being addressed elsewhere (Duke Rogers, pers. comm. 2003).

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1974), satellite DNA (Mazrimas and Hatch 1972), immunological distance (Hatch and Mazrimas 1977), and by attempting to combine several sources of information (including "field experience") to obtain groups (Lidicker 1960b). Analyses based strictly on cranial and skeletal morphology results in "clades" that are similar phenetically ("large" taxa grouped together; "small" taxa grouped together) but not necessarily evolutionarily related (Best 1993). Phylogenies resulting from these various analyses have significantly different groupings of species, and a consensus regarding phylogenetic relationships within the genus Dipodomys has not been reached.

A phylogenetic analysis using molecular techniques is needed to evaluate this problem. Once a reliable phylogeny is estimated, questions can be addressed regarding the evolutionary and biogeographic history of the group. Patterns and timing of genetic divergences can be used in conjunction with historical geologic events to evaluate the historical biogeography of the genus Dipodomys.

Biogeographic structure within this group is not likely to be all "deep history" (Miocene - Pliocene) or all "shallow history" (Pleistocene), but rather a combination resulting from the variety of processes operating at different scales. Phylogenetic history among species and species groups within the genus Dipodomys likely will reflect biogeographic pattern congruent with landscape evolution in the Miocene - Pliocene as well as more recent divergences in the Pleistocene.

Within particular species in the genus Dipodomys, many researchers have evaluated specific questions such as foot drumming behavior (Randall 1994; Randall 1995), population structure (Good et al. 1997), dispersal (Jones et al. 1988; Waser and
Elliott 1991), genetic structure (Hamilton et al. 1987; Waser and Elliott 1991) and survival and reproductive effort (Jones 1988; Waser and Jones 1991). With robust phylogenetic hypotheses regarding evolutionary relationships among species in this genus, many of the species-level questions that have been studied previously could be expanded to include evolutionarily related species groups or other relevant units of classification.

The phylogenetic relationships of subfamilies, genera, and species groups within the family Heteromyidae need comprehensive evaluation. My first set of objectives of this study was to estimate phylogenetic relationships among the six genera in the family Heteromyidae. This included a re-evaluation of the three proposed subfamilies, an evaluation of the phylogenetic relationships among the 22 species of kangaroo rats in the genus Dipodomys, and a review of the phylogenetic relationships within Chaetodipus and Perognathus. In order to accomplish these objectives, it is important to consider the historical framework in which Heteromyids evolved.

Landscape Evolution

Fossil records suggest that heteromyid rodents originated during the Oligocene in western North America; major lineages diversified within the Neogene (Wahlert 1993), during which time there was pronounced geological activity and landscape evolution. The development of the deserts of western North America began with the uplift of the Rocky Mountains in the United States, and the Sierra Madre Oriental in Mexico during the Eocene (Levin 1978). As large areas of the Rocky Mountain region were uplifted, enormous volumes of material eroded from the eastern slopes and filled intermontane basins to the east, thus contributing to the formation of the
Great Plains (Levin 1978). These crustal movements continued throughout the remaining epochs of the Cenozoic with additional uplift and erosion creating new sedimentary layers throughout the Oligocene, Miocene, and Pliocene. During the late Miocene and Pliocene, the Great Plains evolved from a woodland savanna to a grassland savanna to a grassland steppe.

Also beginning in the Eocene, a continuous subduction zone off the west coast created a parallel zone of volcanic activity in the area that later became the Sierra Madre Occidental in Mexico (Ortega-Gutiérrez and Guerrero-Garcia 1982). In the Oligocene and Miocene, hundreds of calderas and their resulting ash-flow tuff deposits, caused by the subduction of the pacific plate, combined to form the high plateau that makes up the Sierra Madre Occidental (Mexican Plateau; Swanson and McDowell 1984). Subsequent block faulting and erosion formed isolated basins on the eastern and western aspects of the Mexican Plateau. During the Miocene, the Coast and Cascade Ranges in southern Oregon began to uplift, causing a rainshadow that began to create drier climates and expanding grasslands on the east side of these ranges; this region makes up the northern Great Basin of today (Baldwin 1964).

From the Oligocene to the late Miocene, forests and savannas were gradually replaced with steppe and semi-desert habitats. This continued during the latest Miocene with expansion of regional deserts, grasslands and shrub-steppes. The remains of plants and animals in the sediments suggest that the Pliocene was cooler and drier than the Miocene (Levin 1978).

The Sierra Nevada Mountains were compressed and intruded during the Jurassic, but were steadily reduced by erosion throughout the Tertiary. The continental crust
east of the Sierra Nevada began to stretch in an east-west direction in the Miocene. The crust broke into a series of north-south-trending valleys and mountain ranges (Fiero 1986). Less than five million years ago, through a combination of uplift of the Sierran block and down-dropping of the area to the east, the Sierra Nevada rose again. Rising far more steeply to the east than the west, the entire Sierra Nevada tilted with a gentle slope westward to California's Central Valley and steep eastern slope (Levin 1978). During the late Pliocene, the continued continental crust expansion increased the northward extent of the Gulf of California; uplifted the Peninsular, Tehachapi, and Coast Ranges of Baja California and California; and drained California's Central Valley (Norris and Webb 1976).

The Cascade and Coast Ranges, the Sierra Nevada, the Transverse and Peninsular Ranges, and the Sierra Madre Occidental blocked the prevailing western storm tracks, whereas the Sierra Madre Oriental and the Rocky Mountains blocked the summer monsoon moisture moving north and west from the Gulf of Mexico. The combined effect of blocking the moisture from the Pacific Ocean to the west, and the summer moisture from the Gulf of Mexico, was the drying and gradual formation of the Great Basin, Mojave, Peninsular, Sonoran, and Chihuahuan Deserts. The Great Basin and northern Mojave deserts changed from woodland savannas to shrub steppe communities during the latest Miocene and early Pliocene. Similarly, the Mexican Plateau changed from a semi-arid savanna to a desert-scrub steppe woodland, and the Sonoran and southern Mojave deserts changed from semi-desert and subtropical thornscrub to desert scrub (reviewed in Riddle 1995).
A long history of dynamic geologic and climatic shifts certainly had a pronounced effect on the aridland biotas of western North America. Many pre-Pleistocene to late-Pleistocene alternative explanations for speciation events can be hypothesized and tested with the use of modern molecular techniques that are now available. By matching phylogenetic patterns of genetic diversity with biogeographic patterns of aridlands taxa and postulated geologic events, hypotheses regarding causal relationships between earth history and the evolutionary history of the biota can be evaluated. Analyses of evolution and biogeography at different taxonomic levels can help elucidate the biotic history of the deserts (generally) and the history of the Heteromyidae (specifically).

Fossil History

The first heteromyid fossils (*Proheteromys*) appear in the fossil record during the Oligocene (Wahlert 1993). *Proheteromys* may be an early member of the Heteromyinae (Wood 1935), but Heteromyinae and Perognathinae are not clearly distinguishable in the fossil record in the early Miocene (Wilson 1960). The earliest identifiable *Perognathus* / *Chaetodipus* fossils appear during the Hemingfordian North American Land Mammal Age (NALMA) of about 20 million years ago (Wahlert 1993), with representatives that are similar in size and dental morphology to extant *Perognathus* species as well as extant *Chaetodipus* species appearing in the late middle Miocene (Williams 1978). Therefore, *Perognathus* and *Chaetodipus* were possibly differentiated as early as the late middle Miocene (Williams 1978). Positively distinguishing between the two genera from fossils, however, has not been possible thus far. Also appearing during the Hemingfordian NALMA of the Miocene,
Cupidinimus previously was considered to be the earliest representative of the Dipodomyinae, but recently it has been suggested that it may have closer affinities with the Perognathines (Wahlert 1993). The earliest recognizable Dipodomys fossils appear during the early Barstovian age of the middle Miocene, whereas the earliest recognizable Microdipodops and Liomys fossils do not appear until the Rancholabrean age of the Pleistocene (Wahlert 1993). Thus, modern genera (with the possible exception of Microdipodops) were in place for the majority of the tectonic development of the west including the Basin and Range expansion and the uplifts of the Rocky Mountains, Colorado Plateau, Sierra Madre Oriental, Sierra Madre Occidental, Sierra Nevada, Peninsular Mountains, Coast Range, and the Cascade Mountains. This makes the family Heteromyidae a very interesting taxonomic group to use as a barometer of evolutionary development coinciding with development of a geologically dynamic region.

A Priori Hypotheses

Given that the fossil record places the first Heteromyid fossils in the Oligocene, but that the subfamilies and genera are not clearly distinguishable, this raises questions as to the timing of subfamily and generic diversification. For example, discerning the difference between Perognathus and Chaetodipus from the fossil record has not been possible; however, they have been treated as monophyletic groups, at least at the subgenus level, based on molecular analyses of extant taxa (Patton 1993; Patton et al. 1981; Williams et al. 1993). The extent to which genera cannot be discriminated from the fossil record may be extreme. For example, Microdipodops does not appear
in the fossil record until the Pleistocene, although it could represent a very deep lineage split if it is indeed the sister lineage of *Dipodomys*.

The three currently recognized subfamilies and previously proposed relationships among them are presented as testable hypotheses in Figure 1. Assuming monophyly of the three subfamilies, examples of other possible alternative hypotheses include: Perognathinae sister to Heteromyinae with Dipodomyinae basal; and Heteromyinae sister to Dipodomyinae with Perognathinae basal. Another set of testable hypotheses of relationships involves the genera and species within the traditional subfamilies. Notably, is *Microdipodops* related to Perognathinae (sensu stricto), some subset of Perognathinae, or Dipodomyinae? Additional relevant hypotheses of relationships include: inclusion of *formosus*, *baileyi*, and *hispidus* within a monophyletic *Chaetodipus* (*formosus* and *baileyi* have been considered somewhat intermediate morphologically between *Chaetodipus* and *Perognathus* [Patton et al. 1981]; with no reference to the elevation of *Chaetodipus* to generic rank by Hafner and Hafner [1983], Hoffmeister [1986] considered all of the Perognathinae to be genus *Perognathus* when he placed *hispidus* into its own subgenus, *Burtognathus*, based primarily on bacular and chromosomal characteristics); and an investigation of previously proposed species groups within *Chaetodipus* (Patton and Rogers 1993; Patton et al. 1981), *Dipodomys* (Best and Schnell 1974; Johnson and Selander 1971; Lidicker 1960b; Schnell et al. 1978; Stock 1974), and *Perognathus* (Williams 1978).
Fig. 1. Testable hypotheses of previously or currently proposed (dashed lines and boxes) relationships among the three currently recognized subfamilies (solid lines and boxes).
Morphological and macroecological evolution in the Heteromyidae

Within the family Heteromyidae there exists a large range of body sizes from the smallest pocket mouse (50 mm head and body length; 8 g) to the largest kangaroo rat (180 mm head and body length; 138 g). These rodents occur as far north as British Columbia and Saskatchewan and as far south as the Pacific coast of Columbia and the northern coast of Ecuador, South America (Schmidly et al. 1993). Heteromys inhabit more mesic environments than any of the other Heteromyids; they are found primarily in lowland rainforests and tropical cloud forests of Central and northern South America and tend to be large in body size (H. anomalus and H. australis are medium). Liomys is mostly confined to semi-arid habitats of Mexico and Central America and tend to be medium in size (L. spectabilis is large). It has been suggested that resource partitioning between Heteromys and Liomys has resulted in Heteromys occurring in the higher and wetter regions of their distribution and Liomys remaining in the lower, drier regions (Genoways 1973). Microdipodops are small bodied and are restricted to arid regions of the central Great Basin. Dipodomys occur throughout the arid or semi-arid regions of western North America including both warm and cold deserts, grasslands, and chaparral. Most Dipodomys are either medium (n=9) or large in size (n=9), but four are very large. The very small or small Perognathus occur in desert and grassland regions that extend north to British Columbia and Saskatchewan, east to the Mississippi River, and south into Mexico; Perognathus alticola and P. parvus are the only medium sized Perognathus and are found in two isolated populations in chaparral regions of California and the Great Basin, respectively. With two exceptions, Chaetodipus occurs in warm desert,
chaparral, subtropical thorn-scrub areas of the southern United States and northern Mexico and are small or medium in body size; *C. hispidus* ranges farther north (North Dakota) and east (Louisiana) than any other *Chaetodipus* (Schmidly et al. 1993) and *C. formosus* inhabits intermountain sagebrush areas more typical of cold desert microhabitats in spite of a primarily warm desert and chaparral distribution. My second set of objectives was to analyze morphological (body size and other genus-level traits) and ecological (macroecological habitats at a biome level) evolution within selected subsets of heteromyids from a phylogenetic context.
CHAPTER 2

METHODS

Phylogenetics of Heteromyidae

I applied maximum parsimony (MP), maximum likelihood (ML), and Bayesian methods using PAUP 4.0b (Swofford 1999) and MrBayes 2.01 (Huelsenbeck 2000) to analyze mitochondrial DNA sequences from nearly all species of Heteromyidae from the United States and Mexico as well as exemplars of the neotropical genera. Within Dipodomys, Microdipodops, Chaetodipus, and Perognathus, all species except for one of questionable taxonomic status (Chaetodipus lineatus, Williams et al. 1993) were sampled. I included 16 species-level taxa from the genus Chaetodipus; C. lineatus was not included, and C. arenarius was split into two species (arenarius1 and arenarius2) based on preliminary evidence indicating presence of a “cryptic” species that is provisionally assignable to C. dalquesti (Riddle et al. 2000b; Roth 1976; but see Best 1993). I included 11 species-level taxa from the genus Perognathus. I included 22 previously described taxa of Dipodomys, including 20 species-level taxa: D. venustus and D. elephantinus are now considered to be conspecific (Best et al. 1996) and preliminary evidence suggests that D. insularis, D. margaritae, and D. merriami from the southern Baja California peninsula also might be conspecific (Alexander et al. in litt.; Riddle et al. 2000b). I included both species of Microdipodops, one representative of Heteromys (H. desmarestianus), and two representative species of
Liomy (L. pictus and L. irroratus). Geomys breviceps, which belongs to the sister family Geomyidae, served as the outgroup taxon (Appendix).

Total genomic DNA was extracted from frozen tissue following a lysis buffer protocol (Longmire et al. 1991). A 705-bp fragment of mitochondrial DNA including the cytochrome oxidase subunit 3 (CO III) gene was amplified via polymerase chain reaction (PCR) with primers H8618 and L9323 (Riddle 1995). The cytochrome-b (cyt-b) region of the mitochondria was amplified via PCR with primers MVZ05 and MVZ14 (Smith and Patton 1993). PCR fragments were gel purified with a QBiogene Gene Clean kit following manufacturer protocols. The same primers that were used for PCR amplification of CO III and cyt-b were used to sequence both strands of every individual. In addition to the primers used for PCR, one more primer (15162) was used for sequencing the cyt-b gene (Taberlet et al. 1992). A total of 699-bp of the CO III gene and 1140-bp of the cyt-b gene were aligned with BioEdit (Hall 1999) and used in all analyses.

These gene regions are not independent estimates of phylogeny, but are evolving at a similar rate (Xia 1998) and therefore are being used in combination to increase numbers of informative characters available for analysis. These relatively rapidly evolving genes are likely to lose phylogenetic signal at the base of the heteromyid tree, but they should be informative for the intra- and intergeneric questions that are posed herein. Maximum parsimony analyses (heuristic search, random addition sequence, tbr branch swapping, 20 repetitions) were performed with equal weights, and because of differential probability of saturation relative to site positions in a coding sequence, I also weighted characters by site-specific transition-transversion ratios. Both of these
analyses were repeated with 500 bootstrap repetitions. With the assistance of
ModelTest 3.06 (Posada and Crandall 1998), I chose the Tamura-Nei model (Tamura
and Nei 1993), with a gamma distribution of rate heterogeneity among sites (0.6593)
and an assumption of some invariant sites (proportion = 0.4634), as the best
evolutionary model for the full, 2-gene set, and used the resulting likelihood settings in
the maximum likelihood analyses of the entire family Heteromyidae. A ML log-
likelihood ratio test was used to address whether the best ML tree is significantly more
likely than various alternative trees of interest.

For the bayesian analyses, I ran four Markov chain Monte Carlo (MCMC) chains
simultaneously using MrBayes for 1,000,000 generations sampling every 100
generations, resulting in 10,000 trees. The point at which likelihood scores stabilized
was noted and trees recorded prior to that point (1,000 trees) were discarded as the
‘burn-in’; posterior probabilities were generated from the remaining 9,000 trees. I
compared pruned bayesian trees from each of the three primary clades for which I had
good taxon sampling (Chaetodipus, Dipodomys, and Perognathus) to phylogenetic
hypotheses of previous studies with Kishino-Hasegawa (K-H) tests (which are more
appropriate if a priori hypotheses are available), as well as parallel likelihood tests in
the form of Shimodaira-Hasegawa (S-H) tests (which are more appropriate without a
priori hypotheses; Goldman et al. 2000; Shimodaira and Hasegawa 1999).

Morphological and macroecological evolution in the Heteromyidae

To examine the evolution of body size, I coded each taxon into body-size
categories (very small = 8-10 g, small = 11-16 g, medium = 20-60 g, large = 61-90 g,
or very large = 91-140 g) primarily based on published estimates of mean male body
mass (Best 1988; Best and Lackey 1985; Best and Thomas 1991; Jones 1985; Wilson
and Ruff 1999). Published weights were unavailable for 13 species but were
estimated by comparing head and body length of known-weight species and
developing an index to use for estimating weights directly from head and body data
(D. J. Hafner, pers. comm.). For Dipodomys, mass = (1.786*head+body) – 140.708;
for Chaetodipus, mass = (0.679*head+body) – 38.233; for Heteromys, mass =
(0.681*head+body) – 30.131, and for Liomys, mass = (1.286*head+body) – 97.857.
In the genus Dipodomys, some species have four toes on each of the hind feet and
others have five toes; in the genus Chaetodipus, some species have dorsal rump
spines, whereas others are smooth. These characters were coded as presence or
absence and traced onto phylogenetic hypotheses. In a separate analysis, I evaluated
macroecological evolution by coding each taxon into biome-level categories
(grassland steppe, chaparral, subtropical thorn-scrub, warm desert, or cold desert;
Appendix). I then traced the history of morphological and ecological transitions
during radiation of extant groups using the Fitch optimization in MacClade (Maddison
and Maddison 2000) onto the trees resulting from both the ML and Bayesian analyses.
CHAPTER 3

RESULTS

Phylogenetics of the family Heteromyidae

Regardless of method used for analysis (Figs. 2-4), I found robust support for the monophyly of genera Dipodomys, Microdipodops, Chaetodipus, and Perognathus; for a clade that includes Microdipodops and Dipodomys (i.e., Dipodomyinae); and for a clade that includes exemplars representing Liomys and Heteromys (i.e., Heteromyinae). Gamma-corrected distances among the genera are provided in Figure 5. The parsimony analysis (Fig. 2) offers weak support for a clade comprised of Chaetodipus and Perognathus, which is unsupported otherwise (Figs. 3, 4).

Generally, I found very little support for sister-group relationships at the base of the tree. Although the ML analysis shows a fully resolved tree with a basal Perognathus, grouped next with Chaetodipus, then Heteromyinae, then Dipodomyinae (Fig. 2-4; \(-\ln \text{ likelihood} = 36026.84165\)), this tree is not significantly better than one showing the traditional subfamilial topology (\(-\ln \text{ likelihood} = 36027.25254\); Shimodaira-Hasegawa test, \(p = 0.459\)).

Dipodomys

Kangaroo rats have been divided into six to nine different species groups primarily based on morphology (Best and Schnell 1974; Blair 1954; Davis 1942; Grinnell 1921; Lidicker 1960a; Lidicker 1960b; Schnell et al. 1978; Setzer 1949) and chromosomes.
(Johnson and Selander 1971; Stock 1974). Our analyses of the cyt-b and CO III regions of the mitochondrial DNA are consistent with many of the previous groupings, at least in terms of group membership (Figs. 2-4). We found support in all analyses for a Dipodomys agilis species group with an agilis plus simulans clade grouping with an elephantinus plus venustus clade. Dipodomys heermanni, panaminitinus and stephensi consistently group together with strong support in all analyses. Dipodomys gravipes, ingens, and microps exhibit affinities to the heermanni group, but do not have any support in their specific relationships. All of these taxa together form a clade that is moderately well supported and joins D. californicus.

I found robust support in all analyses for a Dipodomys merriami species group comprised of merriami, insularis, margaritae, and nitratoides that is sister to an elator plus phillipsii clade (D. phillipsii species group). A spectabilis plus nelsoni clade (D. spectabilis species group) is strongly supported in all analyses, as is the basal position of D. deserti. In all analyses except for the ML, we found some support (weak in the MP analysis) for a compactas plus ordii clade. We found very little resolution for the relationships among species groups. The MP analyses resulted in an unresolved polytomy amongst the heermanni plus agilis plus californicus clade, the merriami plus phillipsii clade, ordii, compactus, and a spectabilis plus nelsoni clade. Kishino-Hasegawa and Shimodaira-Hasegawa tests were performed to compare the mtDNA MrBayes Dipodomys clade with that generated from chromosomal data by Patton and Rogers (1993); the mtDNA tree generated in this study was significantly better than the chromosomal tree (K-H = p < 0.0001, mtDNA tree length = 2891, chromosome tree length = 3165; S-H = p < 0.0001; -lnL = 14113.069).
Fig. 2. MP tree with characters weighted by site-specific transition-transversion ratios (CI = 0.1795, RI = 0.4915, tree length = 10130.3, number of parsimony informative characters = 854, total number of characters = 1839). Numbers along branches summarize results of 500 bootstrap repetitions. All nodes with bootstrap support < 50 have been collapsed. The topology of the equally weighted MP tree was the same: tree length = 9047, CI = 0.1896, and RI = 0.1823.
Fig. 3. Bayesian tree generated from running 4 MCMC chains simultaneously for 1,000,000 generations and sampling every 100 generations. Numbers along branches summarize results of 95% probability values from 9,000 trees after discarding the first 1,000 trees as the burn-in. All nodes with support < 95 have been collapsed.
Fig. 4. Maximum-likelihood tree for all representatives of the family Heteromyidae included in these analyses (Tamura-Nei + I + gamma model).
Fig. 5. Gamma-corrected mean distance within genera (bold diagonal); gamma-corrected mean distance between genera (above diagonal) and corresponding standard error below diagonal.
Chaetodipus

Interspecific relationships within the monophyletic genus *Chaetodipus* remain the primary confusion. Sixteen species-level taxa were included in the analysis of *Chaetodipus*. Several convincing lines of evidence now have placed *C. formosus* solidly within the genus *Chaetodipus* rather than *Perognathus* (Patton et al. 1981). Previously described species-groups for this genus were based primarily on general morphologic similarities rather than actual relationship; the taxonomic breakdown has included a species group with moderately well developed rump spines (including *intermedius, nelsoni, fallax, artus*, and *goldmani*) and a species group without defined rump spines (including *penicillatus [eremicus], pernix*, and *arenarius*). Most of the remaining taxa (*californicus, spinatus, baileyi [rudinoris], hispidus*, and *formosus*) were placed in monotypic species groups (Patton et al. 1981).

Based on chromosome research summarized by Patton and Rogers (1993), *C. penicillatus, C. baileyi*, and *C. pernix* each have significant karyotypic variation that may reflect cryptic species. In the cases of *C. penicillatus* and *C. baileyi*, the previously embedded cryptic species are now recognized as *C. eremicus* and *C. rudinoris*, respectively (Lee et al. 1996; Riddle et al. 2000a).

*Chaetodipus formosus* and *C. baileyi (+ rudinoris)* traditionally have been described as somewhat intermediate in morphology between *Chaetodipus* and *Perognathus*. I consistently found robust support for a *baileyi plus rudinoris* group and strong (Bayesian – Fig. 3) to very weak support (MP – Fig. 2) for uniting this group with *formosus* prior to uniting with all of the rest of the *Chaetodipus*. They are
clearly basal lineages, but my results support their inclusion within a monophyletic *Chaetodipus*.

Morphologic and chromosomal characteristics traditionally have been used to separate *C. hispidus* from the rest of the genus; it has been placed into its own subgenus of *Chaetodipus, Burtognathus* (Hoffmeister 1986). In each of my analyses, *C. hispidus* consistently groups within the monophyletic *Chaetodipus* and is one step inside the basal *formosus-baileyi-rudinoris* subclade (Figs. 2-4).

I found some agreement with the two traditional, morphology-based species groups (Figs. 2-4). In all analyses, I found robust support for a *goldmani, artus, nelsoni* group and support (weak in the MP – Fig. 2) for the subsequent addition of *intermedius* to that group (but no support for the traditional inclusion of *fallax*). I found robust support for an *eremicus, pernix, penicillatus* group (but no support for the traditional inclusion of *arenarius*); the relationships at the tips differ slightly in the various analyses. I found solid Bayesian support (Fig. 3) that first unites these two groups (with ML agreement and concurrence with Riddle et al. 2000a), followed by an unresolved trichotomy with an *arenarius1, arenarius2, californicus, fallax* group and *spinatus* (all five taxa are grouped in the ML – Fig. 4). The MP analyses, however, result in an unresolved polytomy of these initial two groups along with *spinatus, fallax, californicus*, and a solidly supported *arenarius1* plus *arenarius2* group (Fig. 2).

Kishino-Hasegawa and Shimodaira-Hasegawa tests were performed to compare the mtDNA MrBayes *Chaetodipus* clade with a tree generated from chromosomal data by Patton and Rogers (1993) and a tree that was generated from allozyme data (Patton et al. 1981). The mtDNA tree generated in this study was significantly better than
both the chromosomal tree ($K-H = p < 0.0001$, mtDNA tree length = 3181,
chromosome tree length = 3508; $S-H = p < 0.0001$, -lnL = 14122.431) and the
alloyeme tree ($K-H = p < 0.0001$, mtDNA tree length = 3181, chromosome tree length
= 3374; $S-H = p < 0.0001$, -lnL = 14126.147).

**Perognathus**

Eleven species-level taxa were included in this analysis, including two species-
level taxa within *P. parvus* (based on the preliminary evidence of Riddle 1995).
Previously described species groups (Williams 1978) include a *longimembris* group
(*longimembris*, *amplus*, and *inornatus*), a *parvus* group (*parvus* and *alticolus*), a
*fasciatus* group (*fasciatus*, *flavescens*, and *apache*), and a *flavus* group (*flavus* and *merriami*). These species groups were supported with high levels of bootstrap support
in the analyses of Riddle (1995) and in the current study. I found strong parsimony
bootstrap support (Fig. 2) and high Bayesian probabilities (Fig. 3) for these species
groups as well as identical relationships within species groups, regardless of analysis
method. In the MP, ML and Bayesian analyses (Figs. 2, 3, and 4, respectively), the
only differences in the resulting phylogenetic hypotheses are the relationships among
the species groups. All three methods support a *longimembris* plus *flavus*
arrangement. The differences arise in the relationships between this *longimembris*
plus *flavus* clade and the remaining two species groups. Both the parsimony (Fig. 2)
and Bayesian analyses (Fig. 3) resulted in an unresolved trichotomy of the *parvus*,
*fasciatus*, and *longimembris* plus *flavus* species groups, although there is non-
significant indication (probability of 88) of a *fasciatus* plus *parvus* grouping in the
Bayesian analysis, which agrees with that found by Williams (1978). The ML
analysis (Fig. 4) arranged *longimembris* plus *flavus* with *fasciatus* and then the entire clade with *parvus*. The specific relationships among the four species groups remain unresolved.

Kishino-Hasegawa and Shimodaira-Hasegawa tests were performed to compare the mtDNA MrBayes *Perognathus* clade to previously suggested relationships based on chromosomal data (Williams 1978) and mitochondrial DNA data from cyt-b and CO III (Riddle 1995). The MrBayes tree generated in this study was identical to the relationships described by Williams (1978) and by Riddle (1995) except for the placement of the *parvus* group. Williams (1978) placed the *parvus* group with the *fasciatus* group, whereas Riddle (1995) placed the *parvus* group with the *longimembris* plus *flavus* groups. Because the current Bayesian analysis placed these groups in an unresolved trichotomy, both of the previously published trees were somewhat better than my bayesian tree, but neither of them were significant in the Shimodaira-Hasegawa tests. The mtDNA tree generated by Riddle (1995) was better than the bayesian tree (K-H = $p < 0.0001$, Riddle mtDNA tree length = 2186, bayesian mtDNA tree length = 2210; S-H = $p < 0.093$, $\text{-lnL} = 10933.630$); the tree generated from chromosomal data by Williams (1978) also resulted in a somewhat better tree (K-H = $p < 0.0001$, chromosome tree length = 2192, mtDNA tree length = 2210; S-H = $p < 0.272$, $\text{-lnL} = 10941.316$). If the two previously published studies are compared, the mtDNA tree of Riddle (1995) is shorter, but not significantly better (K-H = $p < 0.3547$, Riddle mtDNA tree = 2186, chromosome tree length = 2192; S-H = $p < 0.117$, $\text{-lnL} = 10933.631$) than that provided by Williams (1978).
Morphological and macroecological evolution in the Heteromyidae

Morphological characters were mapped onto both the bayesian and the maximum likelihood trees from my phylogenetic analyses. Body size (mass) was mapped onto bayesian and ML trees for the entire family Heteromyidae, but is shown one clade at a time (Figs. 6-11). Number of hind toes was mapped onto the Dipodomys clade (Figs. 6, 7) and the presence or absence of rump spines was mapped onto the Chaetodipus clade (Figs. 8, 9). Because the base of the parsimony and bayesian trees are unresolved polytomies, tracing the history of the transitions of body size during the radiation of the family Heteromyidae remains ambiguous; the ambiguity does not improve when mapped onto the fully resolved ML tree. Dipodomys, Chaetodipus, and Perognathus were examined separately and are summarized below.

In a separate analysis, I evaluated macroecological evolution by coding each taxon into biome-level categories (grassland steppe, chaparral, subtropical thorn-scrub, warm desert, or cold desert; Appendix), which I then mapped onto the bayesian and ML phylogenetic trees (Figs. 3, 4). Because of the unresolved nature of the basal node in the bayesian phylogeny, the ancestral condition for the family Heteromyidae was equivocal between a warm desert and a subtropical thorn-scrub origin. A warm desert origin is indicated in Perognathus, Chaetodipus, and Dipodomyinae, whereas the subfamily Heteromyinae is entirely subtropical thorn-scrub. When the biome categories were mapped onto the fully resolved ML tree, the family maintained its warm desert origin. Similar to the body size analysis, each of the four groups is examined separately (Figs. 6-11).
Fig. 6. A) Body size, B) number of toes on hind foot, and C) biome characters for *Dipodomys* mapped onto the bayesian tree.
Fig. 7. A) Body size, B) number of toes on hind foot, and C) biome characters for *Dipodomys* mapped onto the ML tree.
Fig. 8. A) Body size, B) presence of rump spines, and C) biome characters for *Chaetodipus* mapped onto the bayesian tree.
Fig. 9. A) Body size, B) presence of rump spines, and C) biome characters for Clastodontus mapped onto the ML tree.

- **A**
  - C. goldmani
  - C. artus
  - C. nelsoni
  - C. intermedius
  - C. eremicus
  - C. perimix
  - C. penicillatus
  - C. arenarius
  - C. califomicus
  - C. fallax
  - C. spinatus
  - C. hispidus
  - C. baileyi
  - C. rudinoris
  - C. formosus

- **B**
  - C. goldmani
  - C. artus
  - C. nelsoni
  - C. intermedius
  - C. eremicus
  - C. perimix
  - C. penicillatus
  - C. arenarius
  - C. califomicus
  - C. fallax
  - C. spinatus
  - C. hispidus
  - C. baileyi
  - C. rudinoris
  - C. formosus

- **C**
  - C. goldmani
  - C. artus
  - C. nelsoni
  - C. intermedius
  - C. eremicus
  - C. perimix
  - C. penicillatus
  - C. arenarius
  - C. califomicus
  - C. fallax
  - C. spinatus
  - C. hispidus
  - C. baileyi
  - C. rudinoris
  - C. formosus

- **Legend**
  - medium
  - small
  - spiny
  - smooth
  - equivocal

- **Biomes**
  - grassland steppe
  - cold desert
  - warm desert
  - chaparral
  - subtropical thornscrub
  - equivocal
Fig. 10. (A) Body size and (B) home characters for *Perognathus* mapped onto the Bayesian tree.
Fig. 11. (A) Body size and (B) home characters for *Perognathus* mapped onto the ML.
CHAPTER 4

DISCUSSION

Phylogenetics of the family Heteromyidae

In all analyses I found robust support for the monophyly of all genera as well as for clades that support Dipodomyinae and Heteromyinae. The lack of resolution for the basal nodes within the family Heteromyidae is most likely caused by the use of mitochondrial genes that saturate fairly quickly (Simon et al. 1994). More conservative nuclear genes might offer better resolution of the deeper nodes on this tree; I am currently evaluating a suite of nuclear genes to address this problem.

Dipodomyinae

One of the most significant findings of these phylogenetic analyses is corroboration of the position of Microdipodops within the subfamily Dipodomyinae rather than within the Perognathinae. Based primarily on fossil dental characteristics, Reeder (1956) suggested that Microdipodops is more closely related to Dipodomys than any other extant taxa. He stated: “although it is not recently derived from similar stock, it is probably the remnant of the flourishing Cupidinimus-Perognathoides complex of the late Tertiary” (Reeder 1956:416). In the extent of hypsodonty and the pattern of cusps, the dentition of Microdipodops is nearly identical to that of Cupidinimus and very similar to that of Perognathoides (Reeder 1956).

The deep divergence between Dipodomys and Microdipodops in my
data indicates that *Microdipodops* diverged at least 10 million years earlier than its first appearance in the fossil record (Pleistocene). *Dipodomys* first appears in the fossil record during the Barstovian age of the middle Miocene and radiated thereafter. The phylogenetic split between the ancestors of the *Dipodomys* and *Microdipodops* lineages must therefore have occurred no later than the early-middle Miocene. Early *Microdipodops* tooth-only fossils may have been misidentified as *Cupidinimus* or *Perognathoides*. The xeric, sandy habitat to which *Microdipodops* is specifically adapted may not have assumed its current distribution until the interpluvial periods of the Pleistocene. *Microdipodops* tends to occur along shorelines of pluvial lakes, but *M. megacephalus* also occupies somewhat gravelly soils. If the ancestral form of Dipodomyinae had a warm desert origin as our data suggests, it is possible that the ancestral *Microdipodops* remained ecologically tied to sandy areas of the warm deserts and tracked the sandy habitats northwards during the geological evolution of the Great Basin. This, however, does not explain their absence from sandy habitats in the southern deserts. We know that the areas that are now warm deserts were not warm deserts at the base of the Dipodomyinae radiation in the Miocene. The warm desert origin for the ancestral Dipodomyinae is most likely an artifact of the way that the Fitch parsimony algorithm processes nodes in MacClade (Maddison and Maddison 2000). Specific substrates, instead of general biomes, might be less plastic through the duration of a lineage and therefore, might be a more informative character to map once a well supported phylogeny is obtained.
Perognathinae

These analyses corroborate the complete phylogenetic separation of Chaetodipus and Perognathus. In fact, I have found no support for the historical inclusion of both genera (Perognathus and Chaetodipus) in the subfamily Perognathinae. Levels of interspecific divergence in both Chaetodipus and Perognathus within the cytochrome b gene are considerably higher than other genera of rodents (Johns and Avise 1998). The conservative nature of their morphology is in stark contrast to their molecular divergence (Modi 2003). Even though paleontologists have been unable to distinguish the two genera based on fossils, they are highly divergent lineages within the family Heteromyidae. It would be interesting to revisit the fossil specimens now that this generic dichotomy is robustly established and ask whether they can be assigned to genus with confidence. Morphometric data presented by Hafner (Fig. 3 in Hafner 1978) demonstrated that Chaetodipus and Perognathus are not particularly similar in morphometric space. Hafner presented phenograms representing phenetic relationships (Fig. 2 in Hafner 1978) that place Microdipodops in a position that implies paraphyly of the genus Perognathus; this paraphyletic arrangement is removed when we consider that in current taxonomy the Perognathus that Hafner (1978) referred to includes both Perognathus and Chaetodipus. Interestingly, if we consider modern taxonomy, Hafner (1978) found that Microdipodops is morphologically more similar to Perognathus than Perognathus is to Chaetodipus. My analyses show no evidence for a subfamily Perognathinae containing Perognathus and Chaetodipus.
Morphological and macroecological evolution in the Heteromyidae

Examining morphological and macroecological evolution at the basal nodes was problematic because of the general lack of resolution at the base of the tree. The ancestral condition of the early heteromyids will be better evaluated after I am able to resolve the basal relationships within the Heteromyidae. In the biome analyses it is possible that the implied warm desert ancestry is an artifact of the way the Fitch parsimony algorithm processes nodes in MacClade (Maddison and Maddison 2000). If Heteromyinae were the basal subfamily, for example, subtropical thornscrub would be the ancestral state. Some intriguing results emerged, however, from examination of each major clade.

Dipodomys

Even with an equivocal origin of Dipodomys having large or very large body size, the body size evolution of kangaroo rats is relatively straightforward (Figs. 6, 7); Dipodomys is, on average, medium to large-bodied (20-90 g). Very large bodies (> 90 g) have evolved independently at least twice, but remained very limited (the basal D. deserti + D. spectabilis + D. nelsoni, and the very recent speciation of D. ingens). The lack of resolution at the base of the tree makes the precise number of separate events ambiguous. Smaller kangaroo rats (20 – 60 g, "medium" sized Heteromyids as classified in this study) appear to have evolved three or four times; the lack of resolution at this point in the tree also makes this determination ambiguous. Two of three clades of kangaroo rats that are joined in an unresolved trichotomy contain all but two of the medium sized Dipodomys; which may represent one or two separate events. D. microps and D. simulans have very recently achieved smaller sized bodies.
in separate evolutionary events. *D. elator* is the only large-bodied member of an otherwise medium-sized group, representing a recent attainment of increased size.

Five toes on each of the hind feet is undoubtedly the ancestral condition within Heteromyidae. It appears from these analyses that the ancestral *Dipodomys* lost a toe on each hind foot; this was followed by at least two subsequent reversals to the five toed condition. *D. compactus* and *D. ordii*, which form a clade in the bayesian analysis, and clade containing the *D. heermanni* + *agilis* species groups represent all of the five toed *Dipodomys*.

Within *Dipodomys*, species groups frequently have been based on many different morphological criteria (Best 1993; Burt 1936; Grinnell 1921; Lidicker 1960b; Setzer 1949; Wood 1935). According to Stock (1974:514) “use of indices of specialization without attention to different habitat preferences has obscured phyletic relationships.” We have tried to combine macroecological and body size evolution with the phylogenetic hypotheses generated in this study. In an attempt to define the early origins of the *Dipodomys* species groups, Stock (1974:519) stated that “The occurrence of only 2N = 72 forms, except for *D. merriami*, throughout most of the geographic range of the genus suggests that kangaroo rats may have first evolved in the semiarid grasslands of northern Mexico and the central United States and may have developed the evolutionary trends toward bipedal locomotion in response to open, semiarid grassland situations rather than in response to true desert conditions as is usually held to be the case.” He also suggests that the “ancestral condition” of *Dipodomys* is one that possesses “brush-dwelling” characteristics (Stock 1974).
Contrary to the idea that *Dipodomys* evolved in the semi-arid grasslands as suggested by Stock (1974), our analyses indicate that the subfamily Dipodomyinae (along with the *Chaetodipus* and *Perognathus*) had a warm desert origin (Figs. 6-11). This result will need further evaluation after the achievement of a more fully resolved phylogenetic hypothesis. Within *Dipodomys*, *D. deserti*, which is restricted to the warm desert, is basal to the rest of the genus. The root of the next branch, the *D. spectabilis* plus *D. nelsoni* clade, is equivocal between a warm desert and a grassland steppe origin because *D. spectabilis* tends to be found in grassland areas, whereas *D. nelsoni* is found in warmer and drier desert areas. The ancestor of *D. ordii* and *D. compactus* appears to have moved into the grassland steppes and cold desert regions of western North America. The *D. merriami* species group is currently restricted to the warm deserts, whereas their sister group, the *phillipsii* species group, is more restricted to the eastern grasslands, but does occur in some dry aridlands. The habitat affinity of the ancestral form of both species groups (*merriami* plus *phillipsii*) remains equivocal between a warm desert and a grassland steppe origin. With four exceptions (*D. ingens, gravipes, panamintinus*, and *microps*), the remaining *Dipodomys* are restricted to chaparral areas; it appears as though *Dipodomys* evolved chaparral affinities only once with several subsequent reversals. *D. ingens, gravipes, and panamintinus* reverted back to a warm desert ecological type, whereas *D. microps* adapted to the cold desert areas of the Great Basin from a chaparral ancestor. It therefore appears that different lineages of *Dipodomys* have adapted to warm desert habitats as many as six times independently. The *D. merriami* species group and its sister clade (*elator* and *phillipsi*) suggest a separation of habitat types (warm desert and grassland steppe).
that may have chronologically coincided with the separation of the eastern grasslands and the western deserts. The *D. agilis* species group (*agilis* + *simulans* + *venustus* + *elephantinus*) and *D. californicus* are restricted to chaparral. Other than the *D. merriami*+ group and the *D. agilis*+ group, the remaining kangaroo rats seem to demonstrate significant amounts of plasticity in habitat association. The *D. heermanni* group, including *heermanni, panamintinus, stephensi, microps, gravipes*, and *lings*, have adapted to three different biomes in as many as four different events (Fig. 6, 7).

The *D. spectabilis* species group, including only *spectabilis* and *nelsoni*, have adapted to moderately different habitat niches. Similarly, *D. ordii* and *D. compactus*, which are weakly grouped together as a species group, have adapted to two different biomes. It is possible that the plasticity demonstrated at the tips of the *Dipodomys* tree suggest that it would not be possible to identify the ancestral condition of this group even if the phylogenetic relationships were clearly resolved. There has been repeated reinvasion of biomes over time; biome ecology is clearly not a conservative character.

**Chaetodipus**

*Chaetodipus* historically has been split into species groups based on external morphology, primarily the presence or absence of rump spines. Generally, this genus was split into two species groups; those with moderately well developed rump bristles (*C. intermedius, nelsoni, fallax, artus*, and *goldmani*), and those without defined rump bristles (*C. penicillatus* [+ *eremicus*, *pernix*, and *arenarius*]), with the remaining species left in monotypic species groups (*C. californicus, baileyi* [+ *rudinoris*, *hispidus, formosus*, and the very bristly *spinatus*]. *C. dalquesti* (*arenarius*2, herein) was not separated from *C. arenarius* in spite of the presence of rump bristles. These
species groups have little to do with actual phylogenetic relationship. A smooth pelage was most likely the ancestral condition (Figs. 8, 9). Rump bristles either evolved twice (the very spiny *C. spinatus* and *C. fallax*, along with the moderately bristly *C. californicus* and *C. arenarius* at one time, and the *C. goldmani* group including *C. goldmani*, *artus*, *nelsoni* and *intermedius* at a later date), or only once with a subsequent return to the smooth pelage in the *C. penicillatus* group (including *C. penicillatus*, *pernix*, *eremicus*, and *arenarius*). Spines seem to be a relatively good indicator of species groups and also tend to be a good indicator of specific microhabitat; spiny *Chaetodipus* occur in rocky habitat, whereas smooth *Chaetodipus* tend to occur in more sandy habitats.

Most of the species of *Chaetodipus* currently are either small or medium-bodied (Figs. 8, 9). The ancestral *Chaetodipus* probably was a medium sized species; all three members of the basal clade and the following branch currently are medium-bodied. With the exception of four medium-sized species that evolved recently, but separately (*C. californicus*, *C. fallax*, and *C. goldmani* + *C. artus*), all of the remaining species are small-bodied.

The genus *Chaetodipus* appears to have had a warm desert origin (Figs. 8, 9). Under this interpretation, *C. hispidus* secondarily evolved adaptations to the grassland steppes, *C. californicus* and *C. fallax* developed chaparral tendencies, and three other species have recently adapted to subtropical thornscrub areas in two different evolutionary events (*C. goldmani* plus *C. artus*, and *C. pernix*).
Perognathus

The size of the ancestral Perognathus is equivocal between small (11–16 g) and very small (8-10 g), but it seems likely that the genus had a very small-bodied ancestral form (Figs. 10, 11). If Perognathus began as a very small-bodied form, the small forms evolved twice (P. amplus and P. fasciatus) and the medium forms evolved once (P. alticola and P. parvus).

Perognathus historically has been split into four species groups: a longimembris species group (longimembris, amplus, and inornatus); a flavus species group (flavus and merriami); a fasciatus species group (fasciatus, flavescens, and apache); and a parvus species group (parvus and alticola). Whether or not this genus had a warm desert origin, each of the four species groups has adapted to different conditions (Figs. 10, 11). The longimembris species group has maintained its affinities for the warm deserts of the southwest while its sister species group (flavus species group) has adapted to the grassland steppe of the southeast. The other two species groups have adapted to more northerly habitats. The fasciatus species group has adapted to cold desert grassland areas of the upper Great Plains, whereas the parvus species group is restricted to the cold desert areas of the Great Basin (parvus) and California chaparral (alticola). Perognathus clearly demonstrates the ecological plasticity found within the family Heteromyidae.

Summary

From the Oligocene to the late Miocene, subtropical thorn forests and woodland savannas were gradually replaced with steppe and semi-desert habitats. This continued during the latest Miocene with expansion of regional deserts, grasslands and
shrub-steppes. The early to middle Miocene experienced a tremendous radiation of Heteromyid rodents (Korth 1994; Savage and Russell 1983). *Perognathus* (including *Chaetodipus*) and *Dipodomys* were well established by the middle Miocene (Wahlert 1993). The remaining three genera (*Microdipodops*, *Liomys*, and *Heteromys*) have such a poor fossil record that we are unable to identify their initial appearance from fossils. My data suggests, however, that the four primary clades (Dipodomyinae [including *Dipodomys* and *Microdipodops*], *Perognathus*, *Chaetodipus*, and Heteromyinae [including *Heteromys* and *Liomys*]) all have had a similar amount of time since lineage divergence. The initial diversification of all of these groups probably coincided with the middle Miocene formation and expansion of steppe and semi-desert habitats into at least three provinces (Riddle et al. 2000a): eastern grasslands and savannas (occupied by *Chaetodipus hispidus*, and the ancestors of the *Perognathus fasciatus*, *Dipodomys spectabilis*, and *D. ordii* species groups); semi-deserts and woodlands of the Basin and Range (occupied by *D. deserti*, *Microdipodops*, and the ancestors of the *C. formosus* and *P. parvus* species groups); and semi-deserts and subtropical thorn-scrub in western Mexico (occupied by the ancestors of the *C. baileyi* and *D. merriami* species groups). Subsequent diversification events within each genus took place in response to continuing isolation of the regional deserts throughout the late Miocene, early Pliocene, and into the recent glacial-interglacial cycles of the Pleistocene.

The subfamily Heteromyinae is the only subtropical lineage in the family Heteromyidae and has the most primitive morphology. *Liomys* is restricted to the arid and semi-arid regions of Central and South America. This genus is apparently limited
in its distribution by extreme aridity and high moisture; they have an apparent requirement of at least 250 mm of rainfall per year, but *Liomys* is replaced by *Heteromys* in the more mesic areas (Schmidly et al. 1993). If the subfamily Heteromyinae is approximately as old as the Dipodomyinae, *Perognathus*, and *Chaetodipus* as it appears in these analyses, this group of rodents could have evolved in southern North America, moved south into Central America, and then on into South America after the rejoining of Panama and Columbia as part of the Great American Interchange (Webb 1985) during the Pliocene (~3 mya). They probably were restricted to several refugia in Central America during the glacial periods of the late Pleistocene when climatic conditions became colder and drier. The Pleistocene refugia may have provided the isolation necessary for speciation within each of these genera.

**Future Work**

Two mitochondrial gene regions were evaluated for this study. Even though they are not independent estimates of phylogeny, they are evolving at a similar rate, and therefore, combining the two increased the numbers of informative characters available for analysis. These relatively rapidly evolving genes did, however, lose phylogenetic signal at the base of the family-level and genus-level trees. Additional loci need to be examined to resolve the relationships among genera within Heteromyidae and among species groups within the genus *Dipodomys*.

The family relationships within the order Rodentia have remained largely unresolved in spite of a significant amount of work done on this group of mammals (including morphological, paleontological, and molecular studies); three clades above
the family level, however, have been consistently supported: suborder Hystricognathi, superfamily Geomyoidea, and superfamily Muroidea (DeBry 2003). Several nuclear genes recently have been used as independent estimates of phylogeny in many different groups of mammals. The nuclear gene that codes for the interphotoreceptor retinoid-binding protein (IRBP) has been used to study interordinal (Stanhope et al. 1992; Stanhope et al. 1998; Stanhope et al. 1996), interfamilial (DeBry and Sagel 2001; Huchon et al. 2002), and intergeneric (DeBry 2003) relationships within mammals. Mercer and Roth (2003) have demonstrated that third base position substitutions in IRBP behave in a good clock-like rate of evolution. These IRBP studies have been able to resolve relationships that were previously ambiguous with mitochondrial DNA. As more studies are completed with nuclear genes, and IRBP in particular, they become more useful as comparative datasets for future research. The IRBP dataset for Rodentia is extensive and now includes at least 22 genera (DeBry and Sagel 2001).

In addition to IRBP, two other nuclear genes have been used with success at deeper nodes in phylogenetic trees. The recombination activating gene 2 (RAG2) is an intronless coding gene that has been used to resolve deep nodes among bats (Teeling et al. 2002), needlefishes (Lovejoy and Collette 2001), as well as the early placental mammal radiation (Murphy et al. 2001a). The gene that codes for cannabinoid receptor type I (CB1) is another intronless region of the nuclear DNA and has been useful for evaluating relationships among mammal orders (Murphy et al. 2001a; Murphy et al. 2001b). Other nuclear gene sequences have been used successfully at
deeper phylogenetic levels as well (e.g. Type I STS Markers; Koepfli and Wayne 2003).

At this time, I am proposing additional research and analyses of the relationships within the family Heteromyidae using the IRBP, RAG2, and CB1 genes of the nuclear DNA. Because these genes have been successful at resolving previously problematic deep nodes in a wide variety of taxa, they are good candidate genes for resolving both the currently ambiguous deep nodes within the family Heteromyidae and the relationships of species within the genus *Dipodomys*. In a recent multigene analysis of rodents, DeBry (2003) found strong support for the Geomyoidea plus Castoridae – Pedetidae clade sister to a Muroidea plus Dipodidae clade. I will conduct the next phase of this research in two stages. I will include representatives of 4 genera within the family Heteromyidae (two *Perognathus*, two *Chaetodipus*, two *Microdipodops*, and two *Dipodomys*; *Liomys* and *Heteromys* currently are being evaluated by other researchers – Duke Rogers, pers. comm.) as well a representative *Geomys* (Geomyoidea), *Zapus* (Dipodidae), and *Peromyscus* (Muroidea). After confirming that these genes are in fact useful in resolving the deeper nodes that have been problematic, and that Geomyoidea consists of Geomyidae plus Heteromyidae, the second stage of this research will include all Heteromyidae species within the genera *Perognathus*, *Chaetodipus*, *Dipodomys*, and *Microdipodops* and representatives of *Heteromys* and *Liomys*. *Geomys*, *Zapus*, and *Peromyscus* will be used as outgroups.

Previous researchers have found that third position sites of IRBP can demonstrate variation in nucleotide composition, whereas RAG2 is homogeneous (DeBry 2003; Huchon et al. 2002). I will evaluate the phylogenetic signal of each gene and each
codon position separately as well as in combined analyses. By partitioning the data, it will be possible to conduct MP, ML, and Bayesian analyses using only the data with useful phylogenetic signal.
LITERATURE CITED


sampling using three nuclear genes. Molecular Biology and Evolution 19:1053-1065.

Huelsenbeck, J. P. 2000. MrBayes: Bayesian inference of phylogeny. Distributed by the author, Department of Biology, University of Rochester.


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Molecular Ecology 1:27-36.

Molecular Biology and Evolution 10:512-526.


Evolution 45:935-943.


Appendix - Catalog reference numbers; taxa; biome classification (some taxa occur in more than 1 biome category and are indicated with both); body size classification, abbreviated as follows: very small (VS), small (S), medium (M), large (L), and very large (VL); bristle status, abbreviated as follows: smooth (SM), spiny (SP), and very spiny (VSP); localities; and GenBank accession numbers for (COIII, cyt-b) specimens included in these analyses.

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<td>California: Kern County; Naval Petroleum Reserve No. 2</td>
<td>XXXXXXXXX, XXXXXXXX</td>
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<td>LVT 2043 / TLB 11018</td>
<td>Mexico: Baja California Sur; Isla San José</td>
<td>XXXXXXXXX, XXXXXXXX</td>
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<td>LVT 2042 / NK 2158</td>
<td>Mexico: Baja California Sur; Isla Santa Margarita</td>
<td>XXXXXXXXX, XXXXXXXX</td>
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<td>LVT 1023</td>
<td>California: San Bernadino County; Kelso Dunes</td>
<td>XXXXXXXXX, XXXXXXXX</td>
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<td>LVT 3610</td>
<td>Mexico: Baja California Sur; 30 km N Todos Santos</td>
<td>XXXXXXXXX, XXXXXXXX</td>
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<td>LVT 4935</td>
<td>Nevada: Nye County; 9 mi N Beatty, Oasis Valley</td>
<td>XXXXXXXXX, XXXXXXXX</td>
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<td>LVT 1107</td>
<td>Mexico: Durango; 7 mi NNW La Zarca</td>
<td>AY009253, XXXXXXXX</td>
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<td>LVT 2045 / TLB 10241</td>
<td>California: Kern County; 6 mi W Buttonwillow</td>
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<td>LVT 1108</td>
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<td>Xxxxxxxxxx, Xxxxxxxxxx</td>
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<td>LVT 4672</td>
<td>California: San Bernadino County; 9 mi NNE Johannesburg</td>
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<td>LVT 2056 / NK 16072</td>
<td>Mexico: San Luis Potosí; Las Cabras, 4.6 mi NW Bledos</td>
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<td>LVT 2036 / TLB 10993</td>
<td>Mexico: Baja California; 3 km SE Colonia Vicente Guerrero</td>
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<td>LVT 2470</td>
<td>New Mexico: Socorro County; San Mateo Mts., Nogal Canyon</td>
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<td>LVT 2061 / TLB 10775</td>
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<td>LVT 2046 / TLB 10292</td>
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<td>LVT 5499 / FN31848 (ROM)</td>
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<td>LVT 1253</td>
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<td>LVT 1573</td>
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<td>LVT 403</td>
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<td>LVT 3703</td>
<td>New Mexico: Socorro County; Rio Salada</td>
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<td>LVT 2525</td>
<td>Wyoming: Carbon County; 10 mi S Seminole</td>
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<td>LVT 2527</td>
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<td>LVT 702</td>
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<td>LVT 601 / MSB-553</td>
<td>California: Madera County</td>
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<td>LVT 2191</td>
<td>Mexico: Baja California; 27 km S Punta Prieta</td>
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<td>LVT 603</td>
<td>Texas: Val Verde County</td>
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<td>LVT 1816</td>
<td>Utah: Wayne County; 9 mi S, 2 mi W Hanksville</td>
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<td>LVT 1920</td>
<td>Washington: Adams County; 4 mi S, 6 mi E Ritzville</td>
<td>Xxxxxxxxxx, Xxxxxxxxxx</td>
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<td>MVZ 197329</td>
<td>California: Kern County; Cameron Creek, Tehachapi Mtns.</td>
<td>Xxxxxxxxxx, Xxxxxxxxxx</td>
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<td>LVT 5500 / DLM 003</td>
<td>Arkansas: Little River County; 3 mi, NW Alieene</td>
<td>Xxxxxxxxxx, Xxxxxxxxxx</td>
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</tbody>
</table>
VITA

Graduate College
University of Nevada, Las Vegas

Lois Fay Alexander

Home Address:
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Boulder City, NV 89005

Degrees:
Bachelor of Science, Wildlife Science, 1990
Oregon State University, Corvallis

Master of Science, Wildlife Science, 1994
Oregon State University, Corvallis

Special Honors and Awards:
2003 Travel Award, BIOS, Dept. Biological Sciences, University of Nevada, Las Vegas, $200.00

2002 Travel Award, BIOS, Dept. Biological Sciences, University of Nevada, Las Vegas, $200.00

2001 Juanita Greer White Travel Award, Dept. Biological Sciences, University of Nevada, Las Vegas, $350.00

2001 Graduate Research Training Assistantship, University of Nevada, Las Vegas, $3267.00

2000 Elizabeth Horner Award, American Society of Mammalogists, $200.00

2000 Grant-in-Aid of Research, American Society of Mammalogists, $1000.00

2000 Graduate Student Association Research Grant, University of Nevada, Las Vegas, $500.00

1999 American Museum Natural History, Theodore Roosevelt Fund Grant-in-Aid of research, $1000.00
1999  Graduate Student Association Research Grant, University of Nevada, Las Vegas, $500.00
1998  Grant-in-Aid of Research, American Society of Mammalogists, $1000.00
1998  Grant-in-Aid of Research, Sigma Xi, $700.00
1998  Graduate Summer Session Scholarship, University of Nevada, Las Vegas, $2000.00
1998  Graduate Student Association Research Grant, University of Nevada, Las Vegas, $500.
1998  Graduate Student Association Research Grant, University of Nevada, Las Vegas, $400.00
1998  Graduate Research Training Assistantship, University of Nevada, Las Vegas, $1500.00
1997  Outstanding Woman in Science, Women in Science and Engineering, University of Nevada, Las Vegas
1997  Graduate Student Association Research Grant, University of Nevada, Las Vegas, $495.00
1996  Proposal Writing Seminar Award, University of Nevada, Las Vegas, $250.00
1996  Graduate Student Association Research Grant, University of Nevada, Las Vegas, $380.00
1993  Oregon State University, Merit Award, $3500.00
1993  Henry Mastin Fund Award for Graduate Research, Dept. Fish. & Wildlife, Oregon State University, $300.00
1992  Outstanding Teaching Assistant Award, Dept. Fish. & Wildlife, Oregon State University

Publications:
Alexander, L. F., and B. R. Riddle. in review. Phylogenetics of and trait evolution within the family Heteromyidae. Journal of Mammalogy

Alexander, L. F., B. R. Riddle, and D. J. Hafner. in review. Evolution and phylogeography of the Dipodomys merriami (Merriam's kangaroo rat) species
group: shallow geographic structuring of an abundant and widespread mammal in the North American warm deserts.


Professional Presentations:


Dissertation Title: Evolutionary and biogeographic histories in a North American rodent family (Heteromyidae).

Dissertation Examination Committee:
  Chairperson, Dr. Brett R. Riddle, Ph. D.
  Committee Member, Dr. Daniel Thompson, Ph. D.
  Committee Member, Dr. Peter Starkweather, Ph. D.
  Committee Member, Dr. David J. Hafner, Ph. D.
  Graduate Faculty Representative, D. Steven Rowland, Ph. D.