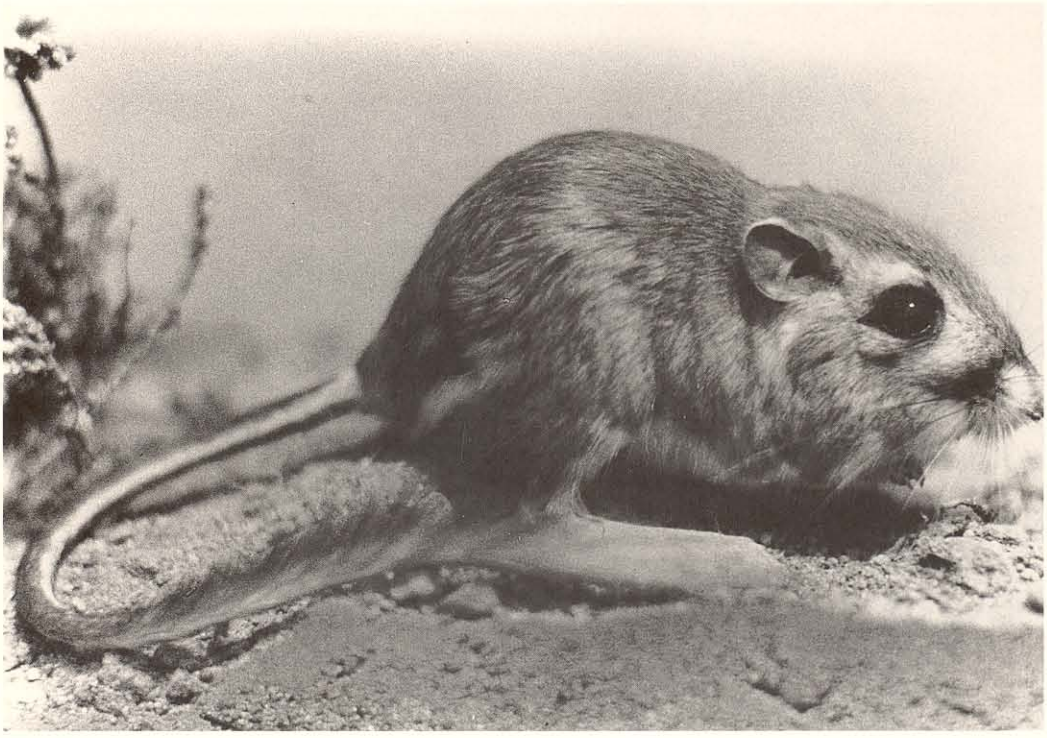
Biology of the Heteromyidae

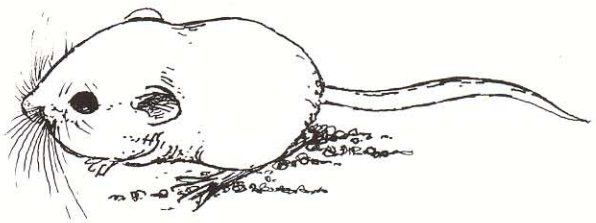
HUGH H. GENOWAYS
AND
JAMES H. BROWN
Editors



SPECIAL PUBLICATION NO. 10 ◇ THE AMERICAN SOCIETY OF MAMMALOGISTS

PATTERNS OF MORPHOLOGIC AND MORPHOMETRIC VARIATION IN HETEROMYID RODENTS

TROY L. BEST



Introduction

Studies of morphologic variation in heteromyids historically have centered on delineating taxonomic relationships and rarely contained quantitative information beyond the cursory presentation of measurements of type specimens (e.g., Dice, 1929; Grinnell, 1919; Merriam, 1894, 1902, 1904, 1907; Stephens, 1887). Descriptions such as "mastoid bullae more fully inflated" (Goldman, 1923:139), "mandible small for size of skull" (Merriam, 1894:110), or "outline of the skull is more nearly that of an equilateral triangle" (Huey, 1951:241) were used to describe morphologic differences among taxa. Later, descriptions of morphology became oriented toward use of standard statistical descriptions, that is, mean, range, and standard deviation (e.g., Hooper and Handley, 1948; Huey, 1951; Setzer, 1949). As the need for more detailed taxonomic assessments became apparent, partially because of the larger numbers of specimens from a larger number of collecting localities, so did the need for analyses with greater discriminating abilities. In the past 20 years there has been a trend toward quantifying morphologic variation using a variety of univariate and multivariate statistical techniques. In addition to their use as tools in taxonomic studies, these techniques have provided the basis for detailed studies of patterns of morphologic variation within and among species.

Although assessments of morphologic variation in heteromyids once centered on taxonomic implications, other aspects of these rodents' lifestyles have been addressed by studying morphologic traits. For example, information on morphologic variation within this family has led to assessments of predator avoidance and detection (e.g., Dice and Blossom, 1937; Kotler, 1985; Webster, 1962; Webster and Webster, 1971), movement and locomotion (e.g., Bartholomew and Cary, 1954; Bartholomew and Caswell, 1951; Biewener and Blickhan, 1988; Biewener et al., 1988; Hatt, 1932; Howell, 1933, 1944; Williamson and Frederick, 1977), functional anatomy and behavior (e.g., Dressler, 1979; Forman and Phillips, 1988; Hafner and Hafner, 1984; Kenagy and Trombulak, 1986; Nikolai and

Bramble, 1983; Pfaffenberger et al., 1985; Reichman, 1983; Ryan, 1986, 1989; Rylander, 1981; Thompson, 1985; Tibbitts and King, 1975; Van De Graaff, 1973; Vimtrup and Schmidt-Nielsen, 1952), water balance and physiology (e.g., Lawler and Geluso, 1986; MacMillen, 1983; Schmidt-Nielsen and Schmidt-Nielsen, 1951, 1952), seed-husking abilities (Rosenzweig and Sterner, 1970), resource partitioning and community structure (e.g., Bowers and Brown, 1982; Munger et al., 1983; Price, 1983, 1984; Price and Brown, 1983; Price and Heinz, 1984), integumentary modifications (e.g., Quay, 1965; Westerhaus, 1983), fossil history (e.g., Dalquest and Carpenter, 1986; Reeder, 1956; Voorhies, 1975; Wood, 1935), effects of long-term environmental changes (Roth, 1976*a*), life-history variables (Jones, 1985), and burrow structure (Best, 1982; Best et al., 1988). Morphologic studies also have addressed pelage and coloration, bacula, geographic variation, and environmental-morphologic relationships, which are discussed below.

Heteromyids occupy a range that extends over western North America and into northern South America. The 57 species within this family occupy a wide variety of habitats and are morphologically diverse (Fig. 1). Gray (1868), Coues (1875, 1877), and Elliot (1901) provided early summaries of what was known about this family. However, Wood (1931) was the first to review the fossil history and phylogeny, and he provided an interpretation of the evolutionary relationships of various taxa. Later, he presented a detailed review of evolutionary relationships among the extinct and extant forms of heteromyids (Wood, 1935). In the interim, Hatt (1932) and Howell (1933) presented interpretations of evolutionary relationships of heteromyids. Reeder (1956), employing mainly dental characters, performed an extensive review of fossil and Recent heteromyids. Hafner (1978) examined evolutionary relationships of *Microdipodops* using phenetic characteristics of four genera of heteromyids. Hafner (1982) and Hafner and Hafner (1983) compared heteromyids and geomyids to ascertain phylogenetic relationships among these families, and Wahlert (1985) presented an interpretation of relationships among extinct and extant forms of Geomyoidea. Wahlert (1993) reviewed the fossil record of heteromyids and suggested a classification of Recent and fossil genera.

To assess patterns of morphologic variation within heteromyids, a variety of morphologic traits have been studied including color (e.g., Benson, 1933; Dice and Blossom, 1937; Lidicker, 1960*a*), hair structure (Homan and Genoways, 1978), cheek pouch capacity (Morton et al., 1980), internal anatomy (Setzer, 1949), bacula (e.g., Best, 1981*a*; Best and Schnell, 1974; Burt, 1936, 1960; Genoways, 1973; Hoffmeister, 1986; Lidicker, 1960*b*), spermatozoa (Genoways, 1973; Hafner and Hafner, 1983), skeletons (Best, 1978; Schnell et al., 1978; Shaver, 1973), interparietal bones (e.g., Beer, 1965; Thompson, 1969), middle and inner ear structure (e.g., Webster and Webster, 1975, 1980), and crania (e.g., Baumgardner, 1989; Best, 1983*a*, 1983*b*, 1987; Best and Janecek, 1992; Engstrom et al., 1987; Grinnell, 1922; Hoffmeister, 1986; Kennedy and Schnell, 1978; Lidicker, 1960*a*; Morales and Engstrom, 1989; Rogers and Schmidly, 1982; Setzer, 1949; Smith, 1986). These studies have centered on variation within populations (e.g., Desha, 1967; Schitoskey, 1968; Schmidly, 1971; Webster and Jones, 1985), species (Best, 1987; Best and Janecek, 1992; Best et al., 1986; Dale, 1939; Engstrom et al., 1987; Hall and Dale, 1939; Hartman, 1980; Hoffmeister and Lee, 1967; Kennedy and Schnell, 1978; Lidicker, 1960*a*; Weckerly and Best, 1985; Williams, 1978; Williams and Genoways, 1979), or genera (e.g., Baumgardner, 1989; Genoways, 1973; Hafner, 1981; Hall, 1941; Schnell et al., 1978).

The purposes of this chapter are to provide a summary of studies related to pelage and coloration, bacula, geographic variation, and environmental-morphologic relationships, and to present new data regard-

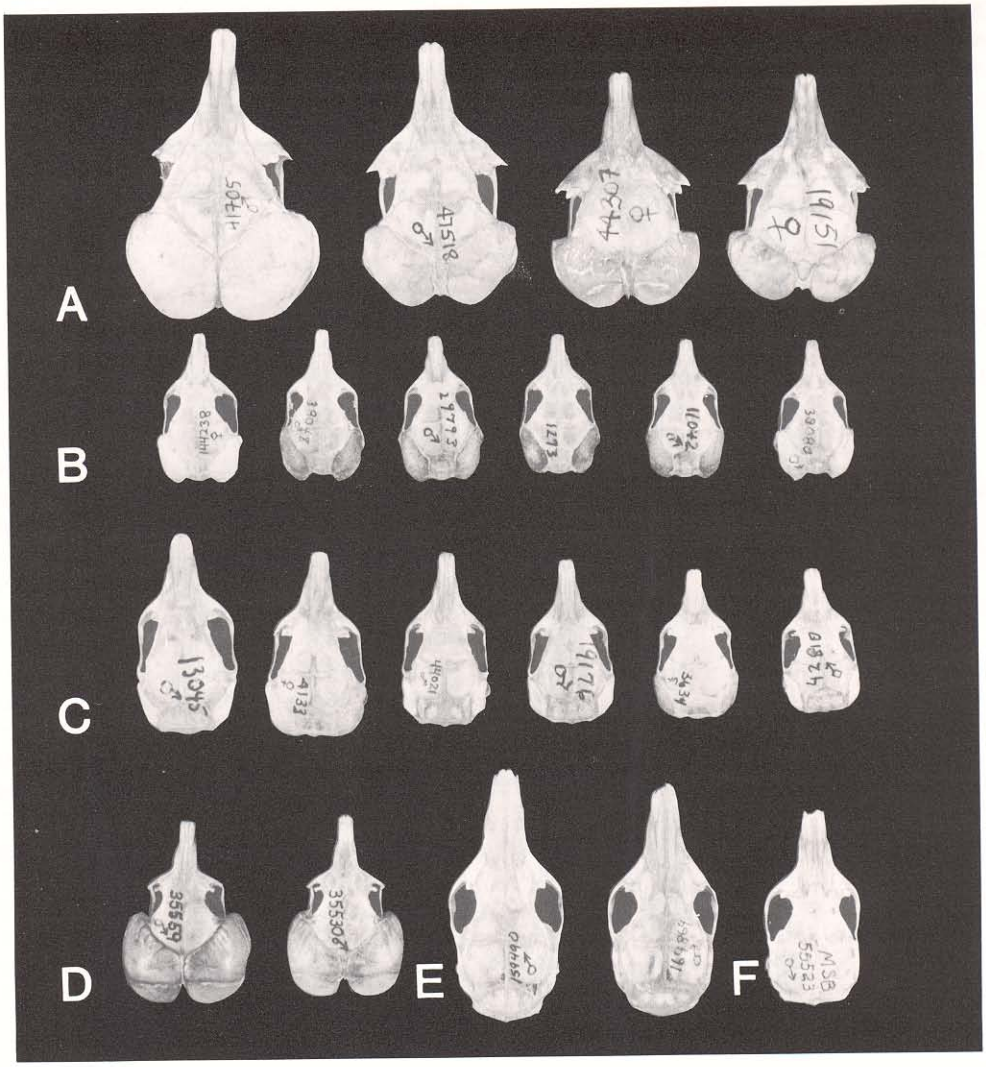


FIG. 1.—Crania of 21 species of the six genera of heteromyid rodents: A) *Dipodomys deserti* (Museum of Southwestern Biology 41705), *D. agilis* (MSB 47518), *D. insularis* (MSB 44307), *D. phillipsii* (MSB 19151); B) *Perognathus inornatus* (Museum of Vertebrate Zoology 144238), *P. amplus* (MSB 38048), *P. fasciatus* (MSB 29793), *P. flavus* (MSB 1273), *P. flavescens* (MSB 11042), *P. longimembris* (MSB 38080); C) *Chaetodipus hispidus* (MSB 13045), *C. baileyi* (MSB 4133), *C. spinatus* (MSB 44021), *C. nelsoni* (MSB 19176), *C. intermedius* (MSB 3634), *C. arenarius* (MSB 42810); D) *Microdipodops pallidus* (MSB 35559), *M. megacephalus* (MSB 35530); E) *Heteromys nelsoni* (MVZ 154490), *H. oresterus* (MVZ 164864); F) *Liomys pictus* (MSB 55523).

ing sexual dimorphism in size and phenetic patterns of morphologic variation among the 57 species of heteromyids. No attempt has been made to cover all aspects of these topics or of non-geographic variation, although authors have addressed these topics further (e.g., age variation is assessed by Anderson, 1964; Best and Schnell, 1974; Engstrom et al., 1987; Hoffmeister and Lee, 1967; Nader, 1978; Reeder, 1953; Rogers and Schmidly, 1982; Schitoskey, 1968; Webster and Jones, 1985).

TABLE 1.—*Secondary sexual dimorphism*[a] *in size of 19 external and skeletal characters of 20 species of kangaroo rats (*Dipodomys*). Minimally significant sexual dimorphism was assumed where* $P \leq 0.05$ *(one asterisk) and* $P \leq 0.01$ *(two asterisks). Measurements are mean values (mm).*

		Character							
Dipodomys	Sex	1	2	3	4	5	6	7	8
agilis	♂♂	288.8**	116.1**	172.8**	42.1**	15.3**	22.0**	39.4**	20.9**
	♀♀	283.9	114.0	169.9	41.6	15.0	21.8	39.0	20.7
californicus	♂♂	307.3	119.5	187.9**	44.1	15.8	22.4	38.9	22.6
	♀♀	304.8	120.5	184.3	43.9	16.0	22.3	38.7	22.6
compactus	♂♂	234.4	112.5	121.9	37.7*	12.5	21.3	37.1	19.8
	♀♀	231.9	110.6	121.3	36.8	12.4	21.2	36.9	19.9
deserti	♂♂	342.4**	141.2**	201.1**	53.7**	15.9	24.7**	45.8**	23.9**
	♀♀	330.7	135.5	195.2	52.6	15.5	24.0	44.7	23.1
elator	♂♂	306.2	124.3	182.0	45.7	13.4	23.7*	40.4*	23.7**
	♀♀	303.0	124.0	178.9	45.4	13.7	23.5	40.2	23.4
elephantinus	♂♂	326.2	129.0	196.7	46.7	19.2	24.2	42.6	22.8
	♀♀	322.5	128.9	192.6	46.8	19.5	24.3	42.5	22.8
gravipes	♂♂	306.8**	130.6**	176.1	44.8**	13.3	23.0	41.6*	23.6
	♀♀	300.0	127.1	173.2	44.1	13.5	22.9	40.6	23.4
heermanni	♂♂	300.4**	121.6**	178.8**	43.3**	15.0*	22.6**	40.2**	22.4**
	♀♀	295.1	119.4	175.6	42.6	14.6	22.4	39.7	22.2
ingens	♂♂	333.2	147.6*	185.7	50.2*	15.9	25.6*	45.2*	26.9
	♀♀	328.9	144.5	184.4	49.2	15.5	25.3	44.5	26.6
insularis	♂♂	258.2	108.2**	150.0	40.1	13.0	20.8	36.4	20.7
	♀♀	243.9	97.3	146.6	38.4	13.5	20.7	36.0	20.9
merriami	♂♂	245.7**	100.6**	145.7**	37.9**	12.6	19.6**	36.0**	19.6**
	♀♀	241.2	99.2	142.7	37.4	15.9	19.4	35.5	19.3
microps	♂♂	273.0*	113.5	159.6*	42.0**	12.9	22.2	39.0	19.3*
	♀♀	268.4	111.8	156.6	41.3	12.7	20.8	36.4	19.1
nelsoni	♂♂	318.9**	128.3	190.6**	66.6	23.1	24.6*	42.6**	23.1*
	♀♀	311.8	127.1	184.7	62.0	20.9	24.4	42.1	22.8
nitratoides	♂♂	240.0**	97.1	140.7**	35.3**	12.1	18.8**	34.4**	18.8**
	♀♀	235.1	98.1	137.0	34.9	11.9	18.6	34.0	18.7
ordii	♂♂	242.6	114.2	128.5**	39.1**	12.5	22.1**	39.4**	21.3*
	♀♀	241.5	114.0	127.3	38.6	12.4	21.9	39.1	21.3
panamintinus	♂♂	292.4**	120.2	172.3**	44.5**	14.0	22.7**	39.9**	23.1**
	♀♀	287.8	121.1	169.6	43.8	13.9	22.5	39.4	22.8
phillipsii	♂♂	276.0*	105.0	171.0*	41.4**	14.7	21.4	36.9*	21.5
	♀♀	271.4	104.2	167.2	40.7	14.6	21.2	36.5	21.5
spectabilis	♂♂	342.2**	142.3	199.2*	52.1	15.8	26.5**	45.7**	26.5**
	♀♀	338.0	142.0	195.9	51.8	15.7	26.2	45.2	26.2
stephensi	♂♂	284.2	115.7	168.4	41.7	13.8	22.1	39.1	22.6
	♀♀	281.8	115.8	166.0	41.3	13.8	22.1	39.0	22.6
venustus	♂♂	318.2*	128.7	192.9	45.8*	18.6	23.6**	41.6**	22.1**
	♀♀	313.5	122.9	190.7	45.1	18.2	23.3	41.0	21.7

[a] Sample sizes for *Dipodomys* used in these analyses are: *agilis* (1,741 adult males, 1,425 adult females), *californicus* (191, 150), *compactus* (48, 29), *deserti* (254, 204), *elator* (120, 86), *elephantinus* (38, 32), *gravipes* (56, 54), *heermanni* (474, 366), *ingens* (55, 47), *insularis* (9, 16), *merriami* (433, 397), *microps* (156, 174), *nelsoni* (112, 87), *nitratoides* (276, 200), *ordii* (691, 662), *panamintinus* (467, 385), *phillipsii* (93, 77), *spectabilis* (296, 232), *stephensi* (81, 70), *venustus* (65, 73).

TABLE 1.—*Continued.*

Character										
9	10	11	12	13	14	15	16	17	18	19
10.6**	14.2**	7.4**	4.9	3.6	4.9**	5.7**	13.2**	24.5**	19.1**	3.8**
10.5	14.1	7.3	4.9	3.6	4.9	5.6	13.2	24.3	19.0	3.7
10.8	15.0	7.4	5.1*	4.3	5.5	5.7	12.9	23.6	20.2	4.2*
10.7	14.9	7.4	5.1	4.3	5.5	5.7	12.9	23.5	20.1	4.1
10.4	14.4	7.0	5.0	3.8	4.9	5.1	11.9	22.2	17.8	3.8
10.3	14.3	6.9	5.0	3.9	4.9	5.0	11.8	22.1	17.6	3.8
12.4**	17.1**	8.3**	6.0	4.3**	4.8**	6.6**	15.2**	30.6**	21.7**	4.2**
12.2	16.6	8.1	5.9	4.2	4.6	6.5	14.9	29.9	21.2	4.1
11.6	16.0	7.9	5.6*	4.4*	6.4**	5.7**	13.4	24.8**	19.8**	4.3
11.6	15.9	7.8	5.5	4.3	6.3	5.5	13.4	24.5	19.6	4.2
11.0	15.7	7.9	5.4	3.9*	5.2	6.1*	14.0	25.9	20.5	4.5
11.0	15.6	7.8	5.5	4.1	5.2	5.8	14.0	25.9	19.9	4.6
10.9	14.8*	7.9	5.3	4.5	6.1	6.2*	13.7	26.0	21.2	4.0*
10.8	14.6	8.0	5.3	4.5	6.1	6.1	13.6	25.7	20.9	3.9
11.1**	14.8**	7.6*	5.3	4.2	5.2*	5.9**	13.5**	24.9**	20.4**	4.0**
11.0	14.6	7.6	5.3	4.1	5.2	5.8	13.3	24.6	20.1	3.9
12.3	16.7	8.5	5.7	5.0	6.4	6.8*	15.1*	29.2*	24.4	4.7*
12.3	16.6	8.5	5.7	4.8	6.3	6.6	14.9	28.7	24.0	4.6
11.1	13.4	7.4*	4.9**	3.5	5.7	4.7	11.6	22.8	17.8	3.6
11.2	13.7	7.2	4.6	3.6	5.7	4.7	11.5	22.7	17.6	3.5
11.1*	13.3**	7.0*	4.6	3.2*	5.2**	4.9**	11.9**	22.9**	17.0**	3.2**
11.0	13.1	7.0	4.6	3.2	5.1	4.8	11.8	22.6	16.8	3.1
10.0**	13.0**	6.8	4.8	3.7	3.7	5.6*	12.6*	23.5	18.3*	3.6*
9.8	12.7	6.7	4.7	3.7	3.7	5.5	12.5	23.3	18.1	3.5
11.9*	15.1*	7.7	5.8	4.3	5.2*	6.3**	14.5*	27.2**	21.9	4.1**
11.7	15.0	7.6	5.8	4.2	5.1	6.2	14.4	27.0	21.8	4.0
10.7	12.3*	6.8	4.5*	3.1	4.7*	5.2**	11.7**	22.4**	16.1	3.1**
10.6	12.2	6.8	4.4	3.1	4.7	5.1	11.5	22.1	16.0	3.0
13.2	14.6**	7.7	5.4	3.9	5.0*	5.7**	13.1*	24.7**	18.6*	3.9
13.1	14.5	7.7	5.5	3.9	5.0	5.7	13.0	24.6	18.5	3.9
11.5	15.5**	7.8**	5.3	4.2*	5.4	5.7**	13.1**	24.3**	20.6**	4.0**
11.5	15.2	7.7	5.2	4.2	5.3	5.6	12.9	24.0	20.3	3.9
11.7	13.7	7.4	5.2*	3.7	5.9	5.2	12.4	23.0	17.9	3.6
11.8	13.6	7.4	5.1	3.7	6.0	5.1	12.4	22.9	17.9	3.6
13.1	16.6	8.5	6.3*	5.0	5.7**	6.7**	15.3**	29.3**	24.9**	4.7**
13.1	16.5	8.5	6.2	5.0	5.6	6.7	15.2	29.0	24.7	4.5
11.1	14.3	7.5	5.2	4.1	5.8	5.5	13.5*	25.1	20.4	4.0
11.1	14.4	7.5	5.1	4.1	5.8	5.5	13.4	25.0	20.3	4.0
11.0	15.6	7.7	5.3	3.8	5.3*	6.0	13.7**	25.1**	20.6**	4.2
11.0	15.4	7.6	5.3	3.7	5.2	6.0	13.5	24.7	19.9	4.2

Methods

To assess patterns of morphologic variation and secondary sexual dimorphism in size, >19,500 specimens of the 57 species of heteromyid rodents were examined. Only the 12,563 adult specimens were used in statistical analyses. Examination of patterns of sexual dimorphism in size among taxa included assessment of 20 adult males and 20 adult females of each species. The only species with smaller samples were: *Dipodomys insularis* (9 males, 16 females); *D. margaritae* (3, 1); *Chaetodipus lineatus* (16, 10); *Heteromys goldmani* (14, 20); *H. nelsoni* (3, 6); *H. oresterus* (10, 9); and *Liomys spectabilis* (8, 12). For more detailed analyses of interspecific variation in sexual dimorphism, larger numbers of *Dipodomys* were examined (Table 1). Five external and 14 cranial measurements were analyzed (for description of characters, see Best, 1978). External characters were recorded to the nearest mm (from specimen tags) and cranial measurements were made to the nearest 0.1 mm using dial calipers. *Dipodomys* were aged according to the criteria of Best and Schnell (1974), and other genera were considered to be adult if the first premolar exhibited wear.

Character heterogeneity between sexes of each species was tested using a one-way analysis of variance, and mean values of each character for males and females of each species were used in multivariate procedures. Characters were standardized and correlation and distance matrices were calculated (Sneath and Sokal, 1973). Clusters of species and characters were obtained with the unweighted pair-group method using arithmetic averages (UPGMA). Principal components were calculated from a correlation matrix among characters, and projections of species were plotted on the first two components. A shortest minimally-connected network was computed from the matrix of distances between taxa. To elucidate correlations among characters, dendrograms were constructed from correlation matrices of the 19 standardized characters for males and for females of the genera *Dipodomys, Perognathus, Chaetodipus, Heteromys, Liomys,* and for the 57 species of Heteromyidae. Multivariate assessment was not conducted within *Microdipodops* since this genus is represented by only two species. However, *Microdipodops* is included in analyses of the family. Analyses were performed using an IBM mainframe computer and the programs UNIVAR (D. M. Power, unpublished) and NT-SYS (Rohlf et al., 1974).

Results

Character Correlations

For *Dipodomys,* most characters were highly correlated ($r > 0.88$). For both sexes, interorbital width, length of ear, and width of maxillary arch were not highly correlated with other characters ($r < 0.56$). Character correlations for *Perognathus* were slightly less than those for *Dipodomys.* Although most characters were highly correlated ($r > 0.83$), length of lacrimal, greatest width of cranium, and length of ear were the least correlated with other characters for either sex ($r < 0.75$). Females had lower correlations among characters than males. For *Chaetodipus,* characters grouped into two main clusters. In males, except for width of maxillary arch, which was not correlated highly with any other character ($r = 0.38$), one cluster contained the four external measurements obtained from specimen tags and the other contained the remaining characters. In females, maxillary arch width grouped with the four external characters and was well separated ($r = 0.64$) from the other cluster. For both sexes, the four external characters were not as highly correlated as were the other characters.

In *Heteromys,* all characters except interorbital width, basioccipital length, and lac-

rimal length were highly correlated ($r > 0.77$). For *Liomys,* characters were likewise highly correlated ($r > 0.80$). Characters for *Heteromys* and *Liomys* were the most highly correlated character sets, and those for *Perognathus* and *Chaetodipus* were the least correlated.

Character correlations within each sex for the 57 species of Heteromyidae were similar; both sexes had two large clusters. One contained total length, length of tail, length of body, nasal width, basal length of cranium, nasal length, alveolar length, basioccipital length, and length of ear. These characters were separated from those in the other cluster at a correlation of 0.78 for males and 0.79 for females. The most highly correlated pairs of characters in both sexes were total length with length of tail and basal length of cranium with nasal length.

Sexual Dimorphism

Means of characters and results of analyses of sexual dimorphism using large samples of 20 species of *Dipodomys* are presented in Table 1. For most characters males were larger than females, including those showing statistically significant differences between sexes. The sample of *D. margaritae* was inadequate for statistical analyses. Some species exhibited a large number of dimorphic characters (*D. agilis, D. deserti, D. heermanni, D. merriami, D. nelsoni, D. nitratoides, D. ordii, D. panamintinus,* and *D. spectabilis*), while others exhibited almost no difference between sexes (*D. californicus, D. compactus, D. elephantinus, D. insularis,* and *D. stephensi*). Species such as *D. elator, D. gravipes, D. ingens, D. microps, D. phillipsii,* and *D. venustus* exhibited significant sexual dimorphism in size in few characters. It was not surprising that so few characters showed dimorphism in *D. insularis* and *D. compactus* due to the small samples, but the nearly complete lack of differences in *D. californicus, D. stephensi,* and *D. elephantinus* was not expected. Qualitative examination of habitat differences, body size, or number of specimens used in analyses did not reveal any relationships with the number of sexually dimorphic characters.

When sexual dimorphism was assessed using only 20 males and 20 females of each species of *Dipodomys* (Table 2), results were different from those obtained with large samples. Little sexual dimorphism was evident using smaller samples. *D. deserti* showed sexual dimorphism in nine characters, *D. ingens* and *D. venustus* in five, and *D. spectabilis* in six. In the remaining species four or fewer characters exhibited differences between sexes. While there was little or no effect of sample size on detection of sexual dimorphism among the larger samples in Table 1, reduction to only 20 males and 20 females greatly affected detection of sexually dimorphic characters. However, mean values for each measurement remained similar for the two data sets.

Although detection of sexual differences appears to be sample-size dependent, it is of interest to see what patterns appeared among the other species and genera. In *Perognathus,* more than one-half of the characters for *P. alticola* and *P. parvus* were sexually dimorphic, as were seven characters for *P. amplus* and three for *P. inornatus* (Table 2). The remaining species had one or no sexually dimorphic characters. For *Chaetodipus,* four or more characters were dimorphic in *C. arenarius, C. artus, C. baileyi, C. goldmani, C. intermedius, C. lineatus, C. pernix,* and *C. spinatus.* No sexual differences were found in *C. formosus* or *C. hispidus.* The most sexually dimorphic species were *C. artus, C. goldmani, C. intermedius,* and *C. pernix.*

No sexual differences were detected in *Microdipodops.* For *Heteromys,* only *H. australis* and *H. nelsoni* were sexually dimorphic in four or more characters. One character was dimorphic in *H. desmarestianus* and two in *H. oresterus. L. irroratus* was dimorphic in four characters, *L. spec-*

TABLE 2.—*Secondary sexual dimorphism in size of 19 external and skeletal characters of 57 species of heteromyid rodents. Minimally significant sexual dimorphism was assumed where* $P \leq 0.05$ *(one asterisk) and* $P \leq 0.01$ *(two asterisks). Measurements are mean values (mm).*

Species	Sex	Character						
		1	2	3	4	5	6	7
Dipodomys								
1. *agilis*	♂♂	284.7	117.2	167.5	42.2	16.9*	21.7	39.3
	♀♀	285.1	116.1	169.0	42.2	17.6	21.7	38.3
2. *californicus*	♂♂	308.0	118.8	189.2	44.2	15.8	22.5	39.1
	♀♀	302.9	118.6	184.3	43.5	15.7	22.0	38.2
3. *compactus*	♂♂	233.6	113.6	120.0	38.1**	12.7	21.4	37.3
	♀♀	230.6	108.8	121.8	36.3	12.5	21.1	36.8
4. *deserti*	♂♂	334.9	141.8	193.1	54.2**	16.5	24.7*	45.8**
	♀♀	327.3	135.6	191.7	52.2	15.6	24.0	44.3
5. *elator*	♂♂	308.8	123.1	185.7	46.2	12.9	23.7	40.4
	♀♀	305.5	121.9	183.6	45.2	13.5	23.6	40.4
6. *elephantinus*	♂♂	327.2	129.7	197.5	46.8	19.4	24.4	42.8
	♀♀	320.7	130.3	190.4	46.7	19.5	24.3	42.5
7. *gravipes*	♂♂	299.1	127.4	171.7	44.5	13.1	22.7	41.1
	♀♀	298.0	126.0	172.0	44.0	13.4	22.7	40.7
8. *heermanni*	♂♂	298.1	119.1	179.0	43.1	14.2	22.4	39.6
	♀♀	291.8	119.5	172.3	42.6	14.5	22.4	39.5
9. *ingens*	♂♂	334.4	148.9	185.5	50.3	16.3	25.8*	45.6*
	♀♀	327.7	144.8	182.9	49.3	15.2	25.4	44.8
10. *insularis*	♂♂	258.2	108.2**	150.0	40.1	13.0	20.8	36.4
	♀♀	243.9	97.3	146.6	38.4	13.5	20.7	36.0
11. *margaritae*	♂♂	238.7	91.3	147.3	38.0	13.0	19.8	35.0
	♀♀	247.0	97.0	150.0	39.0	—	19.6	34.6
12. *merriami*	♂♂	240.8	97.7	143.1	37.5	11.2	19.4	35.8
	♀♀	244.5	101.2	143.3	38.3	11.7	19.6	35.9
13. *microps*	♂♂	276.7	116.4	160.4	42.6*	13.9	20.9	37.0*
	♀♀	270.9	115.6	155.3	41.3	13.1	20.6	36.0
14. *nelsoni*	♂♂	326.3	133.3**	193.0	46.3	16.8*	24.6	42.6
	♀♀	320.7	128.4	192.3	46.2	15.9	24.5	42.4
15. *nitratoides*	♂♂	240.6	101.4	139.2	35.2	12.4	19.0	34.7
	♀♀	241.7	102.2	139.5	35.2	11.8	18.9	34.6
16. *ordii*	♂♂	249.7	110.7	139.1	40.2	12.5	21.3	38.1
	♀♀	247.3	111.7	135.5	40.2	12.9	21.5	38.3
17. *panamintinus*	♂♂	291.3	119.1	172.2	43.9	14.0	22.4	39.4
	♀♀	286.5	119.5	167.1	44.0	14.4	22.6	39.4
18. *phillipsii*	♂♂	279.4	110.0	169.4	40.6	14.8	21.3	37.0**
	♀♀	276.4	109.3	167.1	39.9	14.8	21.0	36.3
19. *spectabilis*	♂♂	345.1	140.6	204.5	53.3	14.9*	27.0**	46.3**
	♀♀	339.1	141.9	197.2	49.7	16.2	26.0	45.1
20. *stephensi*	♂♂	284.4	116.3	168.1	41.4	14.2	22.2	38.9
	♀♀	282.6	116.6	166.0	41.3	13.9	22.2	39.0
21. *venustus*	♂♂	314.0	118.7	195.2	45.6	18.9	23.7*	41.6
	♀♀	316.2	123.0	193.3	45.4	19.2	23.3	41.0
Perognathus								
22. *alticola*	♂♂	163.6**	77.6**	86.0**	21.9**	5.9	15.3**	24.9**
	♀♀	149.5	72.5	77.1	20.7	5.6	14.6	23.8

TABLE 2.—*Continued.*

Character											
8	9	10	11	12	13	14	15	16	17	18	19
21.0	10.4	14.1	7.4	4.9	3.7	4.9*	5.5	13.2	24.6	18.9	3.6
21.1	10.5	14.0	7.5	5.1	3.7	5.1	5.5	13.2	24.5	18.9	3.6
23.0**	10.8	15.3	7.4	5.0	4.2	5.6	5.7	12.8	23.7	20.4	4.2
22.0	10.6	14.8	7.3	5.0	4.2	5.4	5.5	12.8	23.2	20.0	4.0
20.0	10.3	14.4	6.9	5.0	3.9	5.0	5.2	11.9	22.2	17.6	3.8
19.9	10.3	14.3	6.9	5.0	3.9	4.9	5.0	11.8	22.1	17.6	3.8
24.0**	12.2	17.1**	8.2	5.9	4.3	4.9*	6.5	15.2*	30.8**	21.6*	4.2
22.9	12.1	16.3	8.1	5.8	4.1	4.6	6.4	14.8	29.6	21.0	4.0
23.7	11.5	16.0	7.8	5.5	4.3	6.4	5.7	13.3	24.7	19.7	4.3**
23.4	11.5	15.7	7.8	5.4	4.2	6.3	5.6	13.3	24.5	19.5	4.1
22.9	11.0	15.8	8.0*	5.4	3.9	5.3	6.1	14.1	26.1	21.1	4.6
22.8	11.0	15.6	7.8	5.5	4.1	5.2	6.0	14.0	25.9	21.2	4.6
23.3	10.8	14.7	7.9	5.4	4.5	6.1	6.1	13.6	25.6	21.1	4.0
23.3	11.0	14.6	7.9	5.3	4.5	6.0	6.1	13.5	25.6	20.7	4.0
22.0*	10.9	14.6	7.6*	5.2	4.0	5.2	5.8	13.3	24.4	20.0	3.9
22.5	10.9	14.5	7.5	5.1	4.1	5.2	5.7	13.3	24.5	20.0	3.9
26.9	12.4	17.0	8.5	5.7	4.8	6.4	6.7	15.1*	29.3*	24.4	4.8**
26.5	12.2	16.9	8.5	5.7	4.8	6.3	6.7	14.9	28.7	24.0	4.6
20.7	11.1	13.4	7.4*	4.9**	3.5	5.7	4.7	11.6	22.8	17.8	3.6
20.9	11.2	13.7	7.2	4.6	3.6	5.7	4.7	11.5	22.7	17.6	3.5
19.4	11.2	13.2	7.0	4.9	3.3	5.3	4.6	11.4	21.9	17.6	3.3
19.3	11.0	12.9	7.0	4.8	3.2	4.9	4.4	11.7	21.5	17.5	3.0
19.7	11.3	13.2	7.0	4.6	3.2*	5.2	5.0	11.9	22.9	17.1*	3.2
19.4	11.3	13.5	7.0	4.5	3.0	5.2	4.9	11.8	22.8	16.7	3.1
19.3	10.0	12.9	6.7	4.6	3.5	3.8**	5.6	12.7*	23.6	18.2	3.5
19.1	9.8	12.5	6.7	4.7	3.5	3.5	5.5	12.5	23.3	17.9	3.5
23.2	12.0	15.2	7.8	5.8	4.2	5.1	6.4	14.4	27.1	21.6	4.1
23.2	12.1	15.1	7.7	5.7	4.1	5.2	6.3	14.5	27.2	21.8	4.0
19.0	10.9	12.4	6.9	4.4	3.0	4.8	5.1	11.7	22.5	16.1	3.1
18.8	10.7	12.3	6.9	4.4	3.1	4.7	5.1	11.7	22.4	16.2	3.0
20.8	10.5	14.1	7.3	4.9	3.7	4.6	5.5	12.7	23.9	18.0	3.8
20.7	10.9	14.1	7.4	5.1	3.8	4.7	5.5	12.7	24.0	18.0	3.8
22.9	11.4	15.2	7.7	5.2	4.0	5.4	5.5	12.9	23.9	20.2	3.8
22.7	11.4	15.1	7.7	5.2	4.1	5.3	5.6	13.0	24.0	20.2	3.8
21.0	11.2	13.8	7.5	5.1	3.7	5.9	5.0	12.4	22.9	17.8	3.6
20.9	11.2	13.7	7.5	4.9	3.6	5.9	5.0	12.4	22.7	17.5	3.5
26.6	12.9	16.9**	8.6	6.4	5.0	5.7	6.9	15.6	29.6*	25.1*	4.8
25.8	12.8	16.3	8.5	6.3	4.9	5.5	6.7	15.3	28.9	24.5	4.6
22.4	11.0	14.2	7.6	5.1	4.0	5.7	5.4	13.5	25.0	20.4	4.1
22.5	10.9	14.3	7.5	5.2	4.1	5.9	5.4	13.4	25.0	20.3	4.0
22.3**	11.1	15.4	7.7	5.3	3.7	5.3**	6.0	13.8	25.2*	20.4**	4.2
21.5	11.0	15.4	7.6	5.3	3.6	5.0	6.0	13.6	24.7	19.8	4.1
12.0**	6.1**	10.0**	4.7*	3.8*	1.6	1.2	3.9*	8.2**	12.9**	12.4**	2.6*
11.5	5.8	9.2	4.6	3.7	1.7	1.2	3.7	8.0	12.4	11.8	2.5

TABLE 2.—*Continued.*

Species	Sex	Character 1	2	3	4	5	6	7
23. *amplus*	♂♂	153.9	70.8	83.1*	20.7	7.2	14.8**	24.7**
	♀♀	149.1	70.1	79.1	20.3	6.7	14.3	23.9
24. *fasciatus*	♂♂	136.8	71.2	65.7	17.4	7.2	13.9	23.0
	♀♀	137.1	72.1	65.0	17.5	6.9	13.9	22.9
25. *flavescens*	♂♂	135.1	72.1	63.0	18.8	6.6	13.8	22.8
	♀♀	134.8	70.4	64.4	19.1	6.7	14.0	23.0
26. *flavus*	♂♂	113.2	59.0	54.2*	16.5	6.2	12.7	20.8
	♀♀	111.6	60.4	51.3	16.7	6.2	12.5	20.5
27. *inornatus*	♂♂	148.8	72.6	76.2	19.6	7.8	14.5	23.6
	♀♀	146.6	72.1	74.5	19.4	7.4	14.2	23.0
28. *longimembris*	♂♂	134.1	58.5	72.5	18.8	7.0	13.0	22.1
	♀♀	137.4	56.9	74.2	19.0	6.9	13.1	22.0
29. *parvus*	♂♂	178.7**	83.6**	95.1**	23.8**	9.5*	16.2**	26.3**
	♀♀	163.9	78.3	85.6	22.3	8.3	15.4	25.2
Chaetodipus								
30. *arenarius*	♂♂	155.8	69.5	86.3	21.3	7.9	13.9	22.9*
	♀♀	152.3	67.3	85.1	20.9	7.8	13.8	22.4
31. *artus*	♂♂	190.5**	92.1**	98.5	23.5*	10.8	16.7**	26.5**
	♀♀	180.0	85.9	94.1	22.9	10.9	16.3	25.7
32. *baileyi*	♂♂	209.9	94.5	115.4*	25.4*	10.1*	18.1	28.9
	♀♀	218.1	92.5	125.6	28.8	11.3	18.0	28.6
33. *californicus*	♂♂	218.3	88.5	125.2	26.5	13.1	17.1	27.9
	♀♀	213.8	85.3	124.1	26.3	13.7	17.0	27.7
34. *fallax*	♂♂	190.9	84.6	106.3	24.0	9.7	16.3	26.6
	♀♀	186.6	82.0	104.6	23.3	9.7	16.3	26.4
35. *formosus*	♂♂	193.7	82.7	106.7	25.1	11.6	16.4	27.0
	♀♀	189.5	79.0	106.4	24.8	11.5	16.4	27.0
36. *goldmani*	♂♂	197.9	81.4	107.5	24.2	11.3	16.7**	27.0*
	♀♀	189.4	83.7	105.8	23.4	10.4	16.1	26.0
37. *hispidus*	♂♂	205.1	101.5	97.9	24.6	11.3	19.6	30.7
	♀♀	201.2	106.9	94.3	23.7	11.4	19.8	30.7
38. *intermedius*	♂♂	166.6	74.0	92.6	21.5**	7.5	15.1*	24.6**
	♀♀	167.1	74.1	93.0	20.9	7.5	14.9	24.1
39. *lineatus*	♂♂	168.9	74.4	94.5	23.3	7.4	15.5**	25.0
	♀♀	163.2	73.0	90.2	22.3	7.5	14.8	24.3
40. *nelsoni*	♂♂	179.2	80.7	98.6	21.2	8.0	15.9	25.5
	♀♀	176.4	78.4	98.1	21.0	7.8	15.7	25.2
41. *penicillatus*	♂♂	167.7	76.6	91.1	21.6**	8.2	15.1	24.2
	♀♀	167.3	75.8	91.5	23.1	8.5	15.0	24.3
42. *pernix*	♂♂	162.1*	75.2	83.0	21.6	9.9*	15.3**	24.4**
	♀♀	152.5	68.9	80.1	21.3	9.1	14.6	23.2
43. *spinatus*	♂♂	198.7	85.0	113.7	23.8	10.1	16.1*	26.3**
	♀♀	198.1	82.6	115.4	23.7	10.2	15.6	25.5
Microdipodops								
44. *megacephalus*	♂♂	149.2	65.0	84.2	24.9	10.1	14.6	28.3
	♀♀	148.9	66.8	82.1	24.6	10.0	14.5	28.0
45. *pallidus*	♂♂	154.8	65.8	89.0	25.6	10.3	14.8	28.9
	♀♀	154.4	66.3	88.1	25.7	10.3	14.7	28.7

TABLE 2.—*Continued.*

Character											
8	9	10	11	12	13	14	15	16	17	18	19
11.6**	5.6	9.5**	4.3	3.5	1.8	1.0	3.9	8.1**	13.8**	12.4	2.4
11.2	5.5	9.1	4.3	3.4	1.6	1.0	3.8	8.0	13.4	12.1	2.4
10.7	5.3	8.5	4.5	3.3	1.4	1.0	3.9	8.2	12.9	12.3	2.3
10.6	5.2	8.6	4.4	3.3	1.4	1.0	3.9	8.1	12.9	12.3	2.4
10.5	5.4	8.4	4.3	3.4	1.6	0.9	3.9	7.9	12.6	11.6	2.4
10.5	5.3	8.5	4.4	3.4	1.6	0.9	3.9	7.9	12.8	11.9	2.4
9.9	4.6	8.0	4.0	3.2	1.4	0.9	3.4	7.3	12.0	10.9	2.1
9.8	4.6	7.8	4.0	3.2	1.5	0.9	3.4	7.3	11.9	10.8	2.2
11.7**	5.2	8.9**	4.2	3.4	1.7**	1.1	3.8	7.7	13.1	12.1	2.4
11.3	5.2	8.5	4.2	3.4	1.4	1.1	3.7	7.8	13.0	11.8	2.4
10.5	5.4	8.4	4.2	3.1	1.6*	1.0	3.5	7.6	12.7	11.3	2.3
10.4	5.5	8.4	4.3	3.2	1.3	1.1	3.5	7.5	12.4	11.2	2.3
12.6**	6.1**	10.6**	4.9	3.8	1.8	1.2	4.1	8.6	13.5	13.0	2.7
11.9	5.8	9.8	4.8	3.8	1.8	1.2	4.0	8.5	13.3	12.7	2.5
11.0*	6.1	8.8	4.3	3.3	1.6	1.3*	3.3*	7.6	12.1	11.5**	2.5*
10.5	5.9	8.7	4.3	3.3	1.5	1.2	3.1	7.5	11.8	11.1	2.4
13.0**	6.5*	10.0**	4.6	3.9	1.7	1.3	4.0**	8.6	13.4**	13.3*	3.1
12.5	6.3	9.6	4.6	3.8	1.6	1.2	3.7	8.5	12.9	12.9	3.1
13.4	6.9	11.7	4.9	4.3	2.2	1.8	4.4*	9.7	15.2	15.0	3.0
13.5	6.8	11.5	5.0	4.3	2.2	1.8	4.2	9.5	15.3	15.0	2.9
13.0	6.8	11.0	4.9	4.1	1.8	1.6	4.1	9.0*	14.1	14.3	3.2
13.0	6.8	11.1	4.9	4.1	1.9	1.6	4.1	8.8	13.9	14.3	3.1
12.4	6.4	10.3	4.9	4.0*	1.9	1.6	4.0	8.9	13.8	13.4	2.7
12.3	6.5	10.4	4.9	4.1	2.0	1.6	3.9	8.7	13.9	13.5	2.7
12.5	6.7	10.8	4.9	4.0	1.9	1.6	4.0	9.0	14.3	13.7	2.7
12.5	6.7	10.8	4.9	4.0	2.0	1.5	4.0	9.0	14.3	13.6	2.7
12.5**	6.2*	10.6*	4.6*	3.9*	2.0	1.4	4.3	8.6	13.6*	13.0**	3.3
11.8	6.1	10.0	4.5	3.7	1.8	1.4	4.1	8.5	13.2	12.6	3.1
14.9	7.4	12.3	5.4	4.6	2.0	1.2	5.0	10.2	15.7	15.5	3.5
15.1	7.3	12.2	5.3	4.7	2.1	1.3	5.0	10.3	15.6	15.6	3.5
11.3	6.3*	9.5	4.6	3.7	1.7	1.3	3.8**	8.2**	13.0	12.3*	2.7**
11.2	6.2	9.4	4.5	3.7	1.8	1.3	3.6	8.1	12.9	12.1	2.6
11.7**	6.2	9.7*	4.6	3.7	1.7	1.3	3.8	8.3	13.0	12.9*	2.7
11.2	6.2	9.3	4.6	3.7	1.7	1.3	3.7	8.2	12.7	12.4	2.6
11.8*	6.4	10.0	4.6	3.7	1.7	1.3	3.8	8.3	13.5*	13.1	2.8
11.5	6.4	9.7	4.6	3.7	1.8	1.4	3.9	8.3	13.2	12.8	2.7
11.1	5.8	9.1	4.4	3.5	1.7	1.3	3.9	8.0	12.5	12.3	2.9
11.2	5.9	9.2	4.4	3.6	1.7	1.4	3.9	7.9	12.5	12.2	2.8
11.9**	5.8*	9.4**	4.4	3.6	1.6	1.2	3.8*	8.0**	12.4**	12.4**	2.9*
11.4	5.6	8.6	4.3	3.5	1.6	1.2	3.6	7.7	11.9	11.8	2.7
11.9	6.6	10.4	4.4	3.8	1.7	1.4	4.0*	8.4	13.3	12.9	2.8**
11.7	6.5	10.0	4.4	3.7	1.7	1.3	3.8	8.3	13.1	12.7	2.6
11.5	6.6	10.4	5.3	3.5	1.4	1.4	4.1	9.7	18.6	11.2	2.3
11.3	6.4	10.1	5.2	3.5	1.4	1.4	4.0	9.6	18.7	11.2	2.3
12.1	6.8	10.1	5.3	3.5	1.3	1.5	4.0	10.1	19.9	11.5	2.3
12.0	6.8	10.0	5.4	3.5	1.3	1.5	4.1	10.0	19.9	11.6	2.3

TABLE 2.—*Continued.*

Species	Sex	Character 1	2	3	4	5	6	7
Heteromys								
46. *anomalus*	♂♂	289.6	133.8	155.8	34.1	19.2	22.9	36.1
	♀♀	279.1	128.9	150.2	33.9	19.2	22.3	35.4
47. *australis*	♂♂	267.5	127.5*	140.0	33.3	16.8*	21.5*	35.8*
	♀♀	256.7	120.3	136.4	33.0	15.9	21.1	35.1
48. *desmarestianus*	♂♂	281.1*	133.1	148.0	34.1	16.0	21.8	35.4
	♀♀	271.6	129.7	141.9	34.2	15.9	21.9	35.3
49. *gaumeri*	♂♂	276.6	125.3	151.3	34.1	15.9	21.4	34.7
	♀♀	269.3	123.4	145.9	33.2	16.3	21.5	34.7
50. *goldmani*	♂♂	336.8	148.5	188.2	37.1	19.1	24.3	38.9
	♀♀	335.1	143.6	190.9	36.0	17.9	23.6	38.0
51. *nelsoni*	♂♂	358.0*	161.5	196.5	43.3	22.0**	25.5	41.0*
	♀♀	336.4	150.6	185.8	41.5	20.3	24.8	39.3
52. *oresterus*	♂♂	334.0**	159.4*	174.6	40.4	18.3	24.2	39.2
	♀♀	309.9	141.1	168.7	40.3	18.8	24.2	38.7
Liomys								
53. *adspersus*	♂♂	253.5	126.9	126.6	30.8	15.5	22.9	35.4
	♀♀	248.8	123.4	125.4	30.3	15.2	22.7	35.0
54. *irroratus*	♂♂	254.8**	125.4**	129.4	31.9	—	21.9	33.7
	♀♀	246.1	118.6	127.6	30.9	—	21.6	33.2
55. *pictus*	♂♂	239.5	110.3	129.2	28.8	—	19.8	31.4
	♀♀	232.0	110.5	121.5	28.4	—	19.7	31.0
56. *salvini*	♂♂	226.7	114.2*	112.4	26.8	14.4	20.0	31.6
	♀♀	216.5	107.5	109.0	26.0	13.7	19.6	30.9
57. *spectabilis*	♂♂	267.6*	109.4	142.6**	30.6	16.4	21.4	33.7
	♀♀	244.8	101.5	123.0	30.7	16.7	21.0	33.5

tabilis in two, and *L. salvini* in one. Most of the dimorphic characters in *Liomys* were non-cranial measurements.

Patterns of Variation

To illustrate morphologic diversity among the six genera, crania of 21 species are shown in Fig. 1. Phenograms, constructed from correlation and distance matrices, for each sex of five genera and for the family Heteromyidae are presented in Fig. 2 through 5. For *Dipodomys,* each of the correlation phenograms can be divided into two primary clusters at a correlation of about −0.25 (Figs. 2A and 2C). In males, the upper cluster contains *D. agilis, D. elephantinus, D. venustus, D. deserti, D. microps, D. nelsoni, D. californicus,* and *D. heermanni,* and the remaining species compose the second cluster. Similarly for females, *D. agilis, D. elephantinus, D. venustus, D. microps, D. deserti,* and *D. nelsoni* are in the upper cluster, but *D. spectabilis* also is present, and *D. californicus* and *D. heermanni* are in the lower cluster. The most highly correlated pairs of species for both sexes are *D. elephantinus* with *D. venustus* and *D. insularis* with *D. phillipsii.*

Distance phenograms for *Dipodomys* may be interpreted as containing two clusters representing variation in size among species (Figs. 2B and 2D). For males, *D. deserti, D. ingens,* and *D. spectabilis* compose one cluster and the smaller species the other. Similarly for females, *D. ingens* and *D. spectabilis* make up one cluster and the remaining species make up the other. If the

TABLE 2.—*Continued.*

Character											
8	9	10	11	12	13	14	15	16	17	18	19
16.1	8.4	15.1	5.5	5.5	2.0	1.0	5.2	9.6	15.0	—	4.9
16.0	8.4	14.6	5.5	5.5	1.7	1.1	5.2	9.7	14.8	—	4.8
16.1*	9.1	14.5	5.4	5.3	1.9	1.0	5.5**	9.6	14.8	16.0	4.5*
15.8	9.0	14.3	5.4	5.4	1.9	1.0	5.2	9.5	14.7	15.9	4.3
16.2	9.4	14.5	5.4	5.4	1.5	1.0	4.9	9.5	15.1	—	4.4
16.2	9.3	14.3	5.4	5.5	1.6	1.0	5.0	9.6	15.0	—	4.3
15.7	8.6	14.0	5.3	5.3	2.0	1.0	5.1	10.1	15.6	15.3	4.0
15.8	8.5	14.3	5.3	5.3	1.8	1.0	5.0	10.0	15.4	15.4	4.1
17.6	9.9	16.4	5.9	5.8	2.0	1.3	5.5	10.5	16.2	17.4	4.8
17.1	9.7	15.8	5.9	5.8	2.0	1.2	5.4	10.4	16.1	17.1	4.7
18.2	9.5	16.1	6.5*	6.4	1.7	1.2	6.1	11.1	16.8	18.0	5.0
17.7	9.6	15.7	6.2	6.1	1.8	1.3	6.0	11.0	16.6	17.7	5.1
17.2	9.4	15.9	5.9	5.8	2.0	1.2	5.4	10.5	16.3	16.9	4.8
17.1	9.2	15.9	5.8	5.6	1.9	1.3	5.2	10.6	16.1	16.9	4.8
16.5	7.7	14.7	6.1	5.5	1.9	1.2	5.3	9.9	15.3	16.3	4.0
16.4	7.8	14.3	6.1	5.5	1.9	1.3	5.2	9.9	15.2	16.4	4.0
15.8	8.2	13.8*	6.2	5.5	1.5	1.2	4.9	9.9*	15.8	—	4.0
15.7	8.2	13.2	6.3	5.5	1.4	1.2	4.8	9.7	15.6	—	3.9
14.8	7.6	13.1	5.5	5.1	1.6	1.1	4.7	9.2	14.4	—	3.7
14.6	7.5	12.9	5.5	4.9	1.5	1.0	4.5	9.2	14.3	—	3.7
14.3	6.7	12.8	5.4	5.0	1.8	0.9	4.8	9.3	14.3	14.5	3.5
14.1	6.7	12.4	5.5	5.0	1.7	0.9	4.7	9.2	14.1	14.5	3.5
15.0	8.1	14.2	6.2	5.6	2.2	1.1	5.1	9.4	15.3	15.5	3.9
15.0	8.2	13.8	6.1	5.6	2.0	1.0	5.1	9.4	15.0	15.6	3.9

phenograms are considered to have three clusters, the general size separation for both sexes is still evident. The larger species are in the lower clusters for both sexes, the intermediate-sized species are in the upper cluster, and the generally smaller species are in the middle cluster.

Correlation and distance phenograms for both sexes of *Perognathus* are presented in Fig. 3. Because the correlations among species are low, it seems appropriate not to separate them into clusters (Figs. 3A and 3C). The species having the highest correlation for both sexes are *P. flavus* with *P. parvus*. The distance phenograms can be divided into two clusters (Figs. 3B and 3D). The phenogram for males has *P. alticola* and *P. parvus* in the same cluster separated from the other species (Fig. 3B). For females, *P. parvus* and *P. flavus* each form single-member clusters (Fig. 3D). The most similar species pairs for both sexes are *P. amplus* with *P. inornatus* and *P. fasciatus* with *P. flavescens*.

Also shown in Fig. 3 are correlation and distance phenograms for male and female *Chaetodipus*. In the correlation phenograms, there are two primary clusters (Figs. 3E and 3G). For males, the lower cluster contains *C. artus, C. pernix, C. hispidus, C. goldmani,* and *C. penicillatus*. For females, except for the inclusion of *C. hispidus* in the upper cluster, the same species occur in the lower cluster. The most highly correlated pairs of species for males were *C. baileyi* with *C. fallax* and *C. goldmani* with *C. penicillatus*; for females, they were *C. intermedius* with *C. nelsoni* and *C. goldmani* with

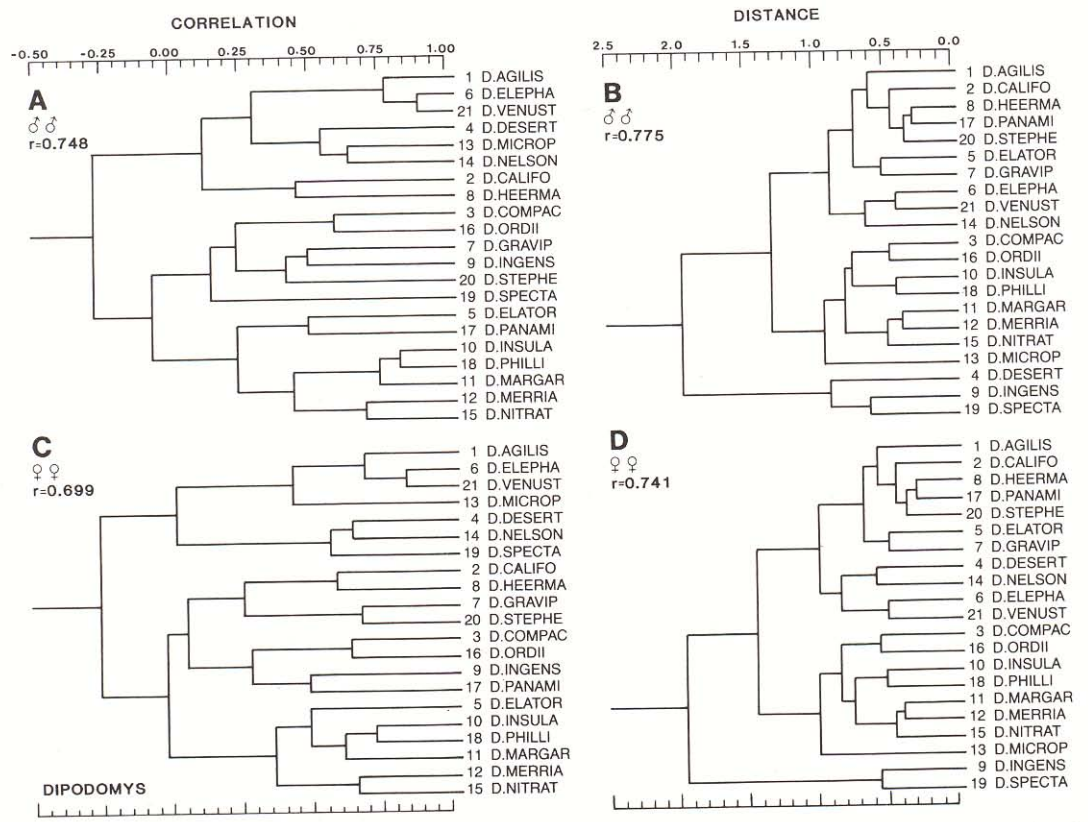


FIG. 2.—Phenograms constructed from correlation and distance matrices for the 21 species of male (A and B, respectively) and female (C and D, respectively) *Dipodomys*. Clusters were obtained using the UPGMA. Accuracy of the diagrams in depicting the relationships increases from left to right. Numerical identifications are the same as in Table 2. The cophenetic correlation coefficients (*r*) are indicated.

C. penicillatus. Distance phenograms for both sexes separated *C. hispidus*, the largest species of this genus, from other taxa (Figs. 3F and 3H). Remaining species are divided into two clusters for each sex. For males, *C. arenarius, C. intermedius, C. lineatus, C. nelsoni, C. penicillatus,* and *C. pernix* are separated from the other species, and for females, *C. baileyi, C. californicus, C. fallax,* and *C. formosus* form a separate cluster. This second cluster appears to be related to differences in body size because smaller species tend to group in the upper cluster for each sex.

Correlation and distance phenograms for both sexes of *Heteromys* are presented in Fig. 4. The correlations among species for both sexes are low (Figs. 4A and 4C). Thus, separation into clusters is not appropriate. The most highly correlated species pair for males is *H. desmarestianus* with *H. goldmani* and for females *H. desmarestianus* with *H. nelsoni*. Distance phenograms for both sexes are similar (Figs. 4B and 4D). One cluster contains *H. anomalus, H. australis, H. gaumeri,* and *H. desmarestianus,* and the second contains the larger-sized taxa, *H. goldmani, H. oresterus,* and *H. nelsoni*. The most similar pairs of species in the distance phenograms for males and females are *H. goldmani* with *H. oresterus* and *H. australis* with *H. gaumeri,* respectively.

For *Liomys*, correlation phenograms show less correlation among species than within *Heteromys* (Figs. 4E and 4G). The occurrence of *L. adspersus* with *L. salvini* is the

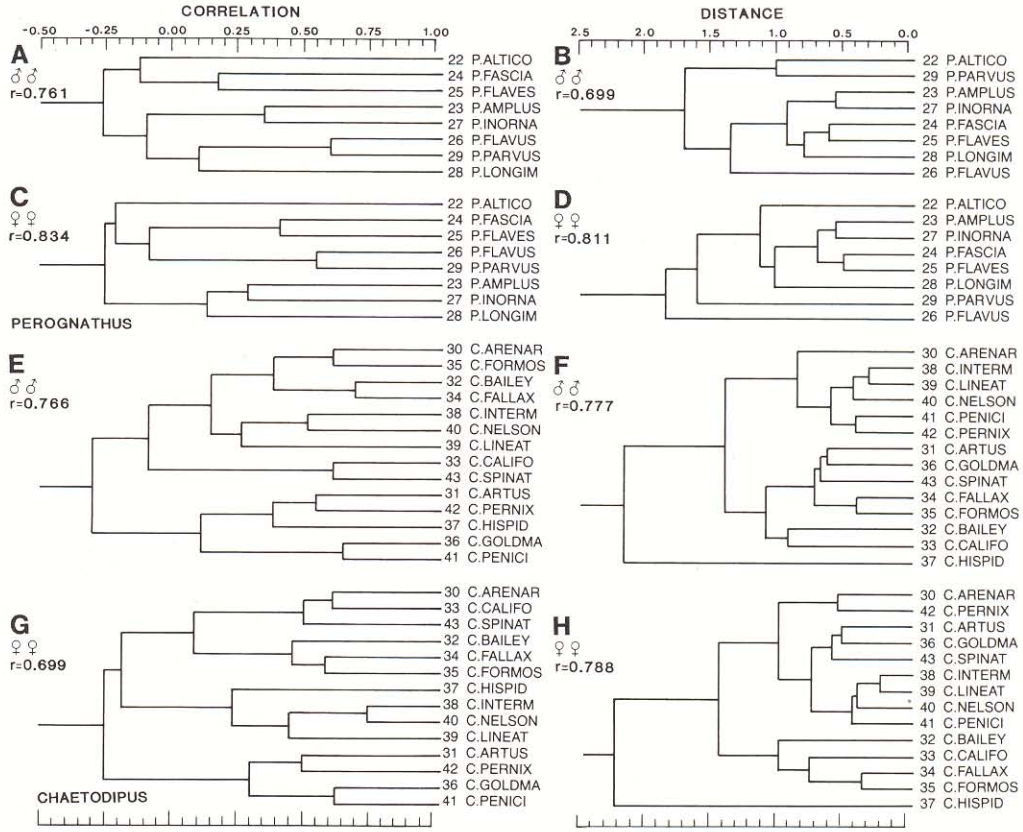


FIG. 3.—Phenograms constructed from correlation and distance matrices for the eight species of male (A and B) and female (C and D) *Perognathus*, and for the 14 species of male (E and F) and female (G and H) *Chaetodipus*. The format is the same as in Fig. 2.

only consistant pairing of species among correlation phenograms for males and females. Distance phenograms are similar between sexes (Figs. 4F and 4H); both have two clusters separated at a distance of about 1.6. For both sexes, *L. adspersus, L. irroratus,* and *L. spectabilis* form one cluster and *L. pictus* and *L. salvini* form the other. *Liomys pictus* and *L. salvini* are the smallest taxa in most measurements (Table 2).

Correlation and distance phenograms for both sexes of the 57 species of Heteromyidae are presented in Fig. 5. Each correlation phenogram can be divided into three clusters at a correlation of about zero (Figs. 5A and 5C). In males, the lower cluster contains *C. hispidus* and all the species of *Heteromys* and *Liomys,* the middle cluster contains *P. parvus, C. baileyi, C. artus, C. goldmani, C. penicillatus, C. pernix, C. californicus, C. spinatus, C. fallax,* and *C. formosus,* and the upper cluster contains *Dipodomys, Microdipodops,* and the remaining species of *Perognathus* and *Chaetodipus.* The most highly correlated species are *M. megacephalus* with *M. pallidus, D. merriami* with *D. nitratoides,* most of the *Heteromys* with each other, *L. adspersus* with *L. salvini,* and *L. irroratus* with *L. pictus.* For females, the same species are in the lower cluster as in the male phenogram, the middle cluster does not have *P. parvus,* and the upper is the same with the addition of *P. parvus.* The most highly correlated species are the same for females as for males.

Distance phenograms also show three major clusters for both sexes that generally

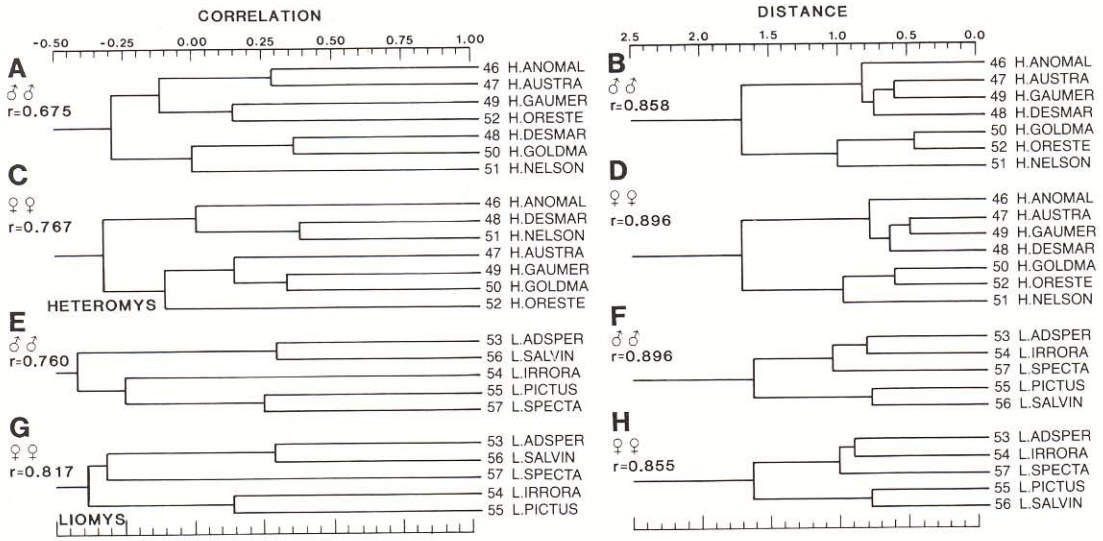


FIG. 4.—Phenograms constructed from correlation and distance matrices for the seven species of male (A and B) and female (C and D) *Heteromys,* and for the five species of male (E and F) and female (G and H) *Liomys.* The format is the same as in Fig. 2.

appear to represent size variation among species (Figs. 5B and 5D). For both sexes, *Dipodomys* are in the upper cluster, *Liomys, Heteromys,* and *C. hispidus* are in the middle cluster, and the remaining *Chaetodipus, Perognathus,* and both species of *Microdipodops* are in the lower cluster. For males, *Microdipodops* are not as close to *Perognathus* and *Chaetodipus* as in the female phenogram. Also, there are some differences in the arrangement of species in each of the primary clusters when male and female phenograms are examined. For example, within the upper cluster for males, *Dipodomys* generally is separated into small, medium, and large body size; for females, it is separated into medium-large, large, and small body size.

Loadings of characters on the first two principal component axes are presented in Table 3, and two-dimensional projections are depicted in Figs. 6 and 7. For *Dipodomys,* character correlations with principal component I for both males and females are >0.73 for all characters except length of ear and maxillary arch width. For both sexes, species 6 (*D. elephantinus*), 14 (*D. nelsoni*), 4 (*D. deserti*), 9 (*D. ingens*), and 19 (*D. spectabilis*) have the highest loadings along component I (Figs. 6A and 6B). This component accounts for about 80% of the phenetic variation (Table 3) and has separated larger species to the right side of the figures. In analyses of morphologic characters, this component may be taken to represent overall variation in size. On principal component II, which accounts for about 7% of the phenetic variation (Table 3), species 13 (*D. microps*) and 5 (*D. elator*) are widely separated for males and for females (Figs. 6A and 6B). The second component has its highest loading on length of ear and maxillary arch width for both sexes (Table 3).

Both sexes of *Perognathus* have loadings >0.70 on principal component I for all characters except length of ear (Table 3). For both sexes, species 26 (*P. flavus*) has the lowest loading along this component and species 29 (*P. parvus*) the highest (Figs. 6C and 6D). This component accounts for 82% of the phenetic variation in males and 77% in females (Table 3). Larger species are to the right side of Figs. 6C and 6D. On the second component, which accounts for 6

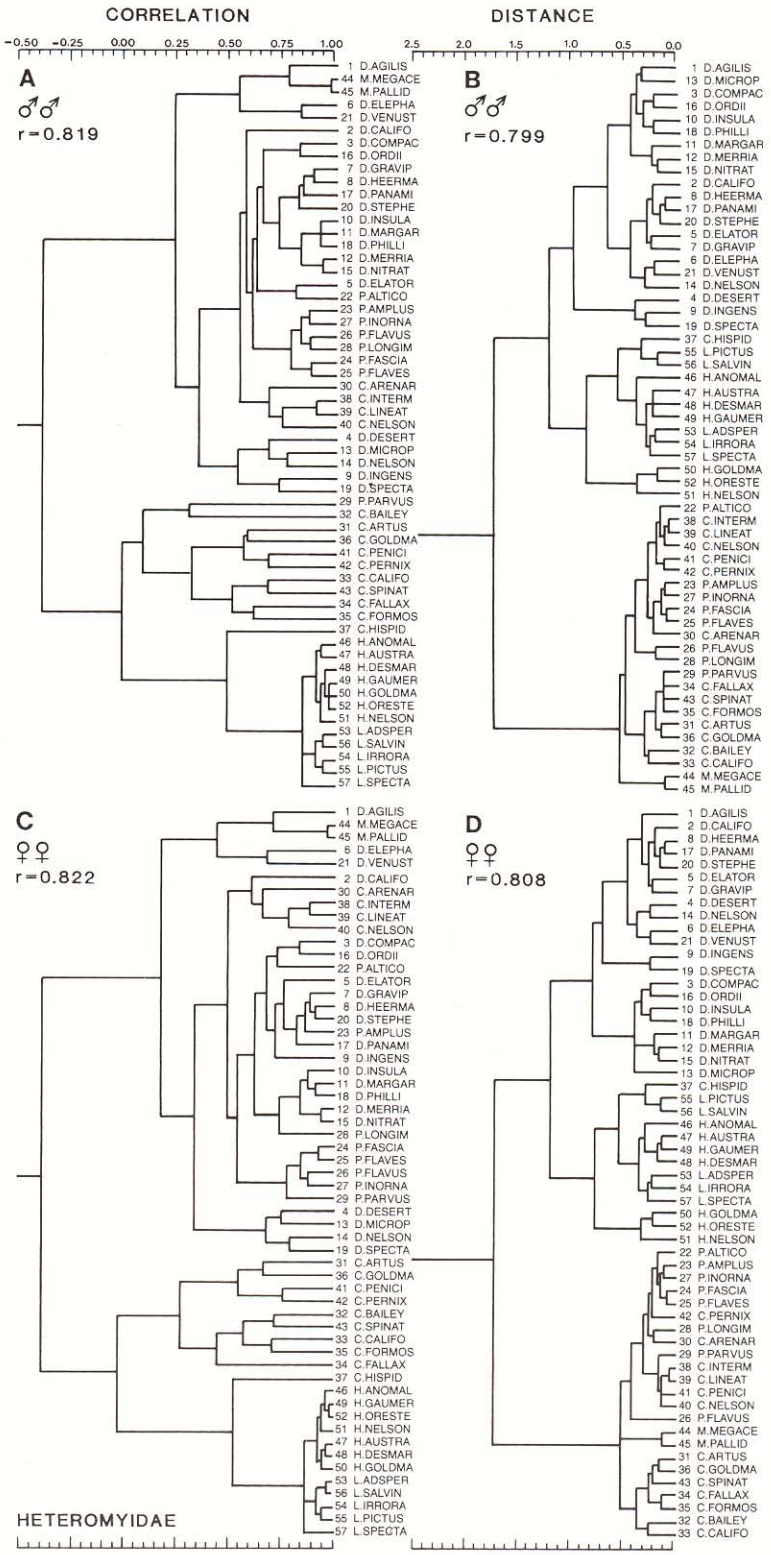


FIG. 5.—Phenograms constructed from correlation and distance matrices for the 57 species of male (A and B) and female (C and D) Heteromyidae. The format is the same as in Fig. 2.

TABLE 3.—*Character loadings*[a] *on the first two principal components of phenetic variation among 19 characters for five genera and the family Heteromyidae.*

Character	Char. no.	Sex	*Dipodomys* I	*Dipodomys* II	*Perognathus* I	*Perognathus* II	*Chaetodipus* I	*Chaetodipus* II	*Heteromys* I	*Heteromys* II	*Liomys* I	*Liomys* II	Heteromyidae I	Heteromyidae II
External														
Total length	1	♂♂	0.952	−0.157	0.994	−0.038	0.910	−0.299	0.986	−0.031	0.871	−0.436	0.958	−0.250
		♀♀	0.942	−0.201	0.958	−0.075	0.900	−0.345	0.961	−0.134	0.968	−0.013	0.965	−0.211
Length of body	2	♂♂	0.945	−0.109	0.914	0.167	0.930	0.154	0.955	−0.005	0.574	0.816	0.885	−0.433
		♀♀	0.962	−0.120	0.853	0.306	0.923	0.266	0.979	0.011	0.515	0.815	0.913	−0.376
Length of tail	3	♂♂	0.860	−0.172	0.945	−0.145	0.682	−0.646	0.964	−0.049	0.635	−0.680	0.965	−0.109
		♀♀	0.855	−0.233	0.866	−0.229	0.666	−0.687	0.933	−0.201	0.871	0.104	0.961	−0.088
Length of hind foot	4	♂♂	0.959	−0.119	0.956	−0.060	0.851	−0.395	0.937	0.021	0.939	−0.028	0.986	0.091
		♀♀	0.942	−0.183	0.914	−0.269	0.777	−0.532	0.922	0.086	0.928	−0.103	0.984	0.088
Length of ear	5	♂♂	0.613	−0.562	0.618	−0.544	0.732	−0.176	0.879	−0.190	0.802	−0.777	0.832	−0.462
		♀♀	0.601	−0.526	0.511	0.526	0.774	−0.220	0.816	0.476	0.743	−0.803	0.844	−0.443
Cranium														
Basal length	6	♂♂	0.984	−0.033	0.986	0.006	0.973	0.204	0.986	−0.104	0.935	0.280	0.962	−0.254
		♀♀	0.985	−0.003	0.988	0.055	0.975	0.197	0.979	0.043	0.946	0.232	0.963	−0.250
Greatest length	7	♂♂	0.984	−0.102	0.996	−0.037	0.996	0.070	0.993	−0.036	0.932	0.194	0.994	−0.043
		♀♀	0.984	−0.043	0.992	0.052	0.994	0.095	0.983	−0.077	0.961	0.011	0.993	−0.041
Maxillary arch spread	8	♂♂	0.961	0.235	0.962	−0.112	0.946	0.269	0.987	0.084	0.878	0.433	0.970	0.222
		♀♀	0.943	0.298	0.944	−0.138	0.953	0.243	0.988	−0.063	0.919	0.355	0.972	0.212
Interorbital width	9	♂♂	0.739	0.348	0.920	0.175	0.897	0.013	0.674	0.502	0.821	−0.301	0.960	0.182
		♀♀	0.732	0.345	0.859	−0.369	0.926	0.054	0.727	−0.349	0.843	−0.181	0.964	0.169
Nasal length	10	♂♂	0.945	0.057	0.974	0.043	0.985	0.014	0.917	−0.136	0.942	−0.011	0.960	−0.238
		♀♀	0.932	0.128	0.978	−0.132	0.986	−0.003	0.942	−0.223	0.912	−0.105	0.962	−0.228
Intermaxillary width	11	♂♂	0.949	0.190	0.889	0.355	0.913	0.134	0.971	0.077	0.946	−0.210	0.947	0.278
		♀♀	0.951	0.196	0.918	−0.126	0.916	0.154	0.990	0.050	0.918	−0.100	0.951	0.266
Alveolar length	12	♂♂	0.939	0.096	0.910	0.301	0.974	0.126	0.964	0.066	0.968	−0.182	0.914	−0.361
		♀♀	0.947	−0.017	0.898	−0.246	0.960	0.173	0.940	0.214	0.889	−0.305	0.906	−0.380
Lacrimal length	13	♂♂	0.898	0.261	0.752	−0.491	0.873	−0.136	0.017	−0.983	0.293	−0.667	0.851	0.489
		♀♀	0.879	0.263	0.703	−0.120	0.906	−0.139	0.499	−0.662	0.341	−0.773	0.850	0.489
Maxillary arch width	14	♂♂	0.435	0.781	0.824	0.104	0.437	−0.828	0.938	−0.103	0.909	0.247	0.779	0.601
		♀♀	0.395	0.784	0.803	−0.412	0.676	−0.652	0.963	0.059	0.914	0.384	0.786	0.591
Basioccipital length	15	♂♂	0.931	−0.212	0.874	0.019	0.913	0.291	0.831	−0.139	0.828	0.014	0.970	−0.069
		♀♀	0.928	−0.174	0.790	0.508	0.895	0.298	0.812	0.242	0.829	−0.243	0.967	−0.072

TABLE 3.—*Continued.*

Character	Char. no.	Sex	*Dipodomys* I	*Dipodomys* II	*Perognathus* I	*Perognathus* II	*Chaetodipus* I	*Chaetodipus* II	*Heteromys* I	*Heteromys* II	*Liomys* I	*Liomys* II	Heteromyidae I	Heteromyidae II
Greatest depth	16	♂♂	0.964	−0.166	0.903	0.166	0.975	0.092	0.909	−0.036	0.797	0.594	0.942	0.300
		♀♀	0.971	−0.136	0.946	0.219	0.975	0.173	0.945	−0.107	0.899	0.380	0.949	0.281
Greatest width	17	♂♂	0.926	−0.122	0.804	−0.412	0.966	0.023	0.911	−0.004	0.935	0.025	0.876	0.448
		♀♀	0.924	−0.075	0.752	0.479	0.972	0.014	0.917	−0.239	0.936	0.090	0.880	0.439
Zygomatic width	18	♂♂	0.967	0.054	0.934	−0.008	0.977	0.041	0.990	0.364	0.994	0.149	0.986	0.111
		♀♀	0.963	0.047	0.893	0.409	0.990	0.037	0.997	0.143	1.000	0.016	0.988	0.088
Nasal width	19	♂♂	0.922	0.030	0.940	0.232	0.733	0.417	0.820	−0.197	0.988	0.117	0.877	−0.441
		♀♀	0.907	−0.011	0.918	−0.136	0.760	0.415	0.856	0.469	0.983	−0.080	0.861	−0.476
Total[b]		♂♂	80.79	7.38	81.77	5.88	78.79	9.71	81.28	7.94	73.66	17.31	86.27	10.52
		♀♀	79.81	7.50	76.57	8.74	80.41	9.96	82.87	7.01	76.53	13.79	86.71	10.02

[a] Correlations of species mean values of individual characters with the component axes.

[b] Percent of total phenetic variance explained.

and 9% of the phenetic variation for males and females, respectively, the highest character loadings are for length of ear and greatest width of cranium for both sexes, plus lacrimal length for males and basioccipital length for females. Species 27 (*P. inornatus*), 23 (*P. amplus*), and 22 (*P. alticola*) are the most widely separated along this component for males (Fig. 6C), and species 28 (*P. longimembris*) and 24 (*P. fasciatus*) are the most divergent for females (Fig. 6D).

For *Chaetodipus,* loadings on principal component I are >0.70 for all characters, except length of tail and maxillary arch width for both sexes (Table 3). For both sexes the smallest taxon, species 30 (*C. arenarius*), has the lowest loading on this component and species 35 (*C. formosus*), 33 (*C. californicus*), 32 (*C. baileyi*), and 37 (*C. hispidus*) have the highest loadings (Figs. 6E and 6F). The largest species is *C. hispidus* (species 37). This component accounts for about 80% of the variation for both sexes. The second principal component, which represents about 10% of the variation in both sexes, has loadings $>\pm 0.50$ for length of tail and maxillary arch width for both sexes (Table 3). In addition, females have a high loading on length of hind foot for this component. Species 37 (*C. hispidus*) is the most widely separated taxon along this component for both sexes (Figs. 6E and 6F).

Heteromys has high loadings for all characters on principal component I, except lacrimal length (Table 3). About 82% of the variance is explained by this component. For both sexes, species 47 (*H. australis*) and 49 (*H. gaumeri*), which are the smallest taxa in this genus, have lowest loadings on this component. Species 52 (*H. oresterus*), 51 (*H. nelsoni*), and 50 (*H. goldmani*) have highest loadings (Figs. 7A and 7B). The second principal component, representing about 7% of the variation, has loadings $>\pm 0.50$ for lacrimal length for both sexes, and interorbital width for males (Table 3). Species 48 (*H. desmarestianus*) for males (Fig. 7A) and species 46 (*H. anomalus*) and 50 (*H. goldmani*) for females had the most divergent scores on this component.

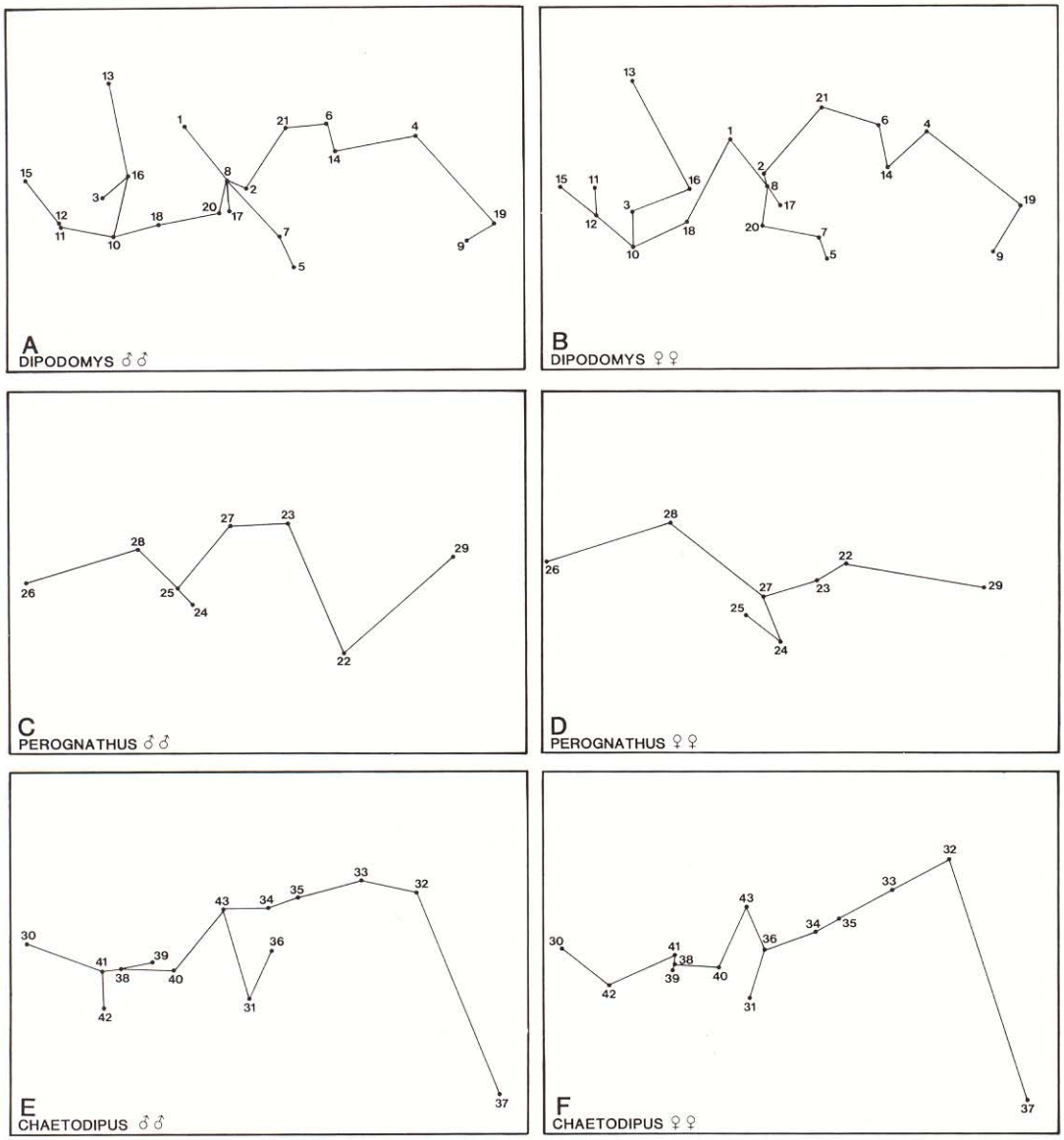


FIG. 6.—Projections of species onto the first two principal component axes of variation in the matrix of correlations of 19 morphologic characters for male (A) and female (B) *Dipodomys,* male (C) and female (D) *Perognathus,* and male (E) and female (F) *Chaetodipus.* The range of values along principal component I (horizonal axis) is from −1.5 to 2.0 (left to right), and for principal component II (vertical axis) from 1.0 to −1.0 (front to back). The shortest simply-connected networks, derived from the matrix of distance coefficients for the same character, are drawn between the species. Numbers correspond to the species listed in Table 2.

In *Liomys,* all characters except length of body and lacrimal length for both sexes and length of tail for males had loadings >0.74 on principal component I (Table 3), which accounted for about 75% of the variation. Species 56 (*L. salvini*) and 55 (*L. pictus*) had the least loadings on this component. These two species are smaller than the others. The

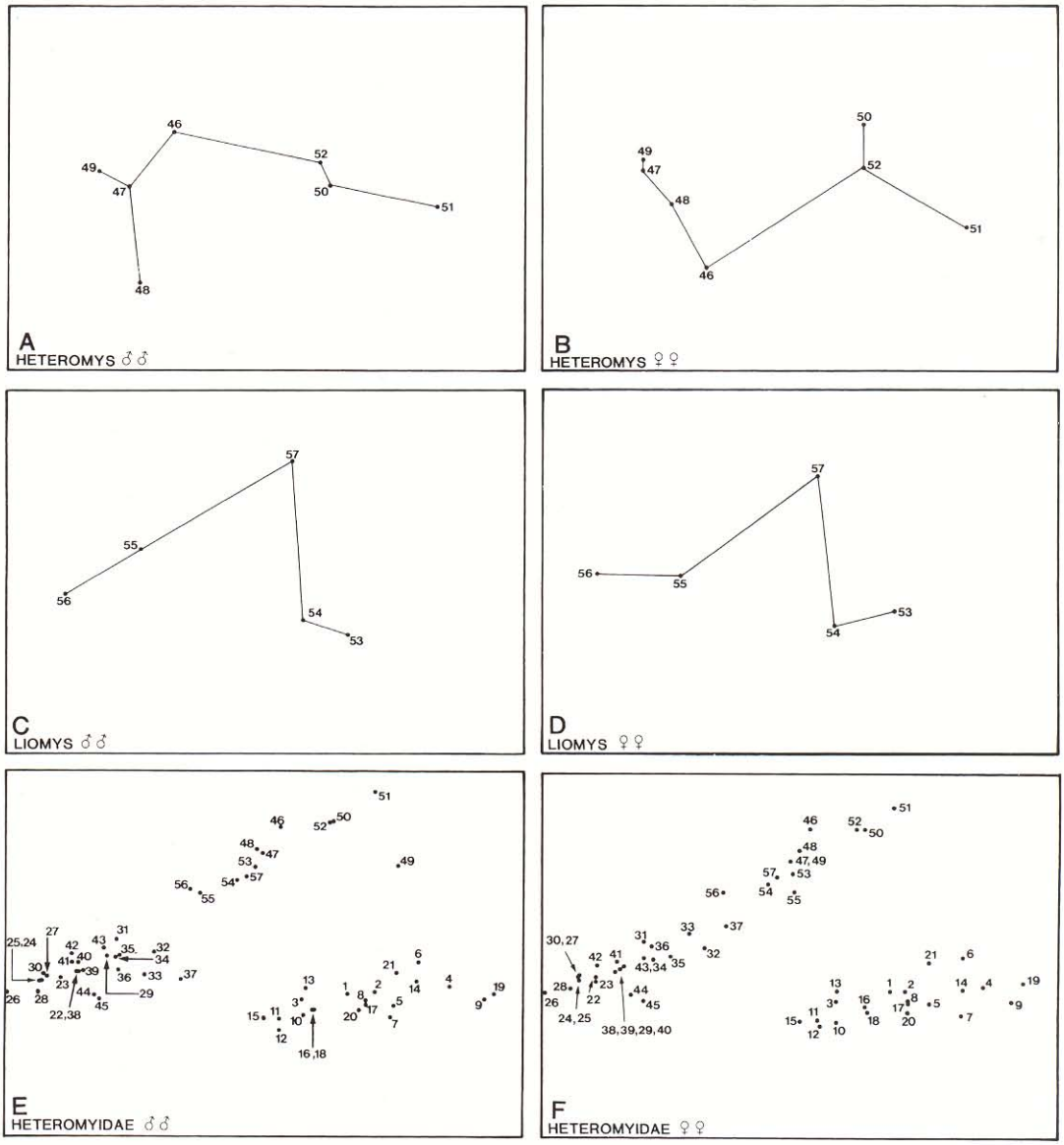


FIG. 7.—Projections of species onto the first two principal component axes of variation in the matrix of correlations for male (A) and female (B) *Heteromys,* male (C) and female (D) *Liomys,* and for 57 species of male (E) and female (F) Heteromyidae. The format is the same as in Fig. 6, except that the shortest simply-connected network for the Heteromyidae plots are listed below to simplify Figs. 7E and 7F. For the Heteromyidae (E and F) the networks are as follows: males, 1-8, 8-17, 8-20, 8-2, 8-7, 7-5, 1-18, 18-10, 10-11, 11-12, 12-15, 10-16, 16-3, 16-13, 2-21, 21-6, 6-14, 14-4, 4-9, 9-19, 13-49, 49-48, 49-47, 49-54, 54-53, 53-57, 47-46, 54-55, 55-56, 56-37, 37-32, 32-33, 33-35, 35-34, 34-29, 34-43, 29-40, 40-39, 39-38, 38-41, 41-42, 39-22, 38-23, 23-27, 27-24, 24-25, 34-31, 31-36, 25-28, 27-30, 28-26, 29-44, 44-45, 46-52, 52-50, and 50-51; females, 1-2, 2-8, 8-17, 8-20, 8-7, 17-5, 1-18, 18-10, 10-12, 12-15, 12-11, 10-3, 3-16, 2-21, 21-6, 6-14, 14-4, 16-13, 4-9, 9-19, 13-53, 53-54, 53-47, 47-49, 49-48, 54-57, 48-46, 54-55, 55-56, 56-37, 46-52, 52-50, 50-51, 37-32, 32-33, 33-35, 35-34, 34-43, 43-36, 36-31, 43-40, 40-39, 39-38, 39-41, 40-29, 39-22, 22-23, 23-27, 27-25, 25-24, 41-42, 27-28, 28-30, 28-26, 29-44, and 44-45.

second component represented 17% of the variation for males and 14% for females. This is about twice the amount of variability represented on principal component II by any of the other genera. Characters with loadings $> \pm 0.50$ on this component were length of body, length of ear, and lacrimal length for both sexes, and length of tail and greatest depth of cranium for males (Table 3). Species 57 (*L. spectabilis*) had the greatest divergence on this component for both sexes (Figs. 7C and 7D).

When the entire family Heteromyidae was examined, there were high loadings on all characters relative to principal component I (Table 3). This component accounted for about 86% of the variation. As in the analyses by genus, this component may be taken to represent overall size in both sexes because it accounts for most of the covariation among characters. For both sexes, species 24 (*P. fasciatus*), 25 (*P. flavescens*), 26 (*P. flavus*), 27 (*P. inornatus*), 28 (*P. longimembris*), and 30 (*C. arenarius*) had the lowest loadings along this component (Figs. 7E and 7F). These are among the smallest heteromyids (Table 2). Highest loadings along component I (Table 3) were for species 4 (*D. deserti*), 9 (*D. ingens*), and 19 (*D. spectabilis*). These are among the largest species (Table 2). Along principal component II, 10% of the variance is explained. The only character with a loading >0.50 was maxillary arch width for both sexes (Table 3). Length of ear, lacrimal length, greatest width of cranium, and nasal width had loadings that approached ± 0.50 for both sexes. This component tends to separate *Dipodomys* from most other taxa for both sexes (Figs. 7E and 7F). In addition, along component II *Heteromys* and *Liomys* are well separated from *Dipodomys, Perognathus,* and *Chaetodipus.* There is some separation of *Microdipodops* (species 44 and 45) from the *Perognathus–Chaetodipus* grouping along principal component II for both males and females.

Discussion

Sexual Dimorphism

Previous studies of sexual dimorphism in *Dipodomys* have included data for *D. agilis* (Best, 1978, 1983*a*), *D. californicus* (Dale, 1939; Dunmire, 1955); *D. compactus* (Baumgardner and Schmidly, 1981; Schmidly and Hendricks, 1976), *D. deserti* (Hall, 1946; Nader, 1978), *D. elator* (Best, 1987; Webster and Jones, 1985), *D. gravipes* (Best, 1978, 1983*b*), *D. merriami* (Hall, 1946; Lidicker, 1960*a*), *D. microps* (Csuti, 1979; Hall and Dale, 1939), *D. ordii* (Baumgardner and Schmidly, 1981; Desha, 1967; Hall, 1946; Kennedy and Schnell, 1978; Schmidly, 1971; Schmidly and Hendricks, 1976; Setzer, 1949), *D. panamintinus* (Hall, 1946), *D. phillipsii* (Genoways and Jones, 1971), and *D. spectabilis* (Nader, 1978). Results presented here generally agree with these earlier studies, but there are differences that should be pointed out. These differences may reflect the effect of sample size, selection of specimens, or the characters examined. Hall (1946) found slight secondary sexual variation in *D. merriami* from Nevada, but Lidicker (1960*a*) observed considerable secondary sexual variation in specimens of *D. merriami*; 17 of 19 characters examined herein show statistically significant differences (14 of which are highly significantly different between sexes). Genoways and Jones (1971) found that males and females of *D. phillipsii* were significantly different in total length and length of tail, but not in other measurements. In the present analyses, five of 19 characters of this species showed sexual dimorphism. Nader (1978) noted that no significant differences existed between sexes of *D. spectabilis,* but the present analyses clearly show it to be among the most sexually dimorphic species of *Dipodomys.* For *D. deserti,* Nader (1978) examined 18 characters and found length of tail, basal length of cranium, greatest length of cranium, breadth of maxillary

arches, least interorbital breadth, greatest breadth of bullae, rostral depth, breadth of exoccipitals, and mandibular length to be significantly larger for males. Herein, 17 of 19 characters were different between sexes.

Best (1983*a*) pointed out that because of the small absolute differences between the means of measurements for male and female *D. agilis,* a large sample probably was necessary to detect the dimorphism. Later, Best (1987) found little difference in the number of sexually dimorphic characters when sample sizes of *D. elator* were reduced to make uniform comparisons among the three populations studied. However, the effect of sample size on the detection of sexually dimorphic characters of *Dipodomys* is considerable. When the number of individuals was reduced to only 20 males and 20 females of each species, the number of sexually dimorphic characters was reduced dramatically. Since the samples used by Best (1987) were 29 males and 20 females, it appears that samples should contain >20 individuals per sex to most accurately determine sexual differences.

The effect of having more than one species in a sample also has been shown to influence the degree of sexual differences that were detected in *Dipodomys.* When Best (1978) evaluated sexual dimorphism in the *heermanni* group of kangaroo rats he found only five of 19 characters exhibited significant secondary sexual dimorphism. This was likely the result of including specimens of both *D. gravipes* and *D. agilis* in the same analyses, which would increase the variance within sexes. The small number of dimorphic characters also could have been due to the relatively small sample examined. When he analyzed *D. gravipes* separately (Best, 1983*b*), there were seven characters that exhibited significant secondary sexual dimorphism, and when he analyzed *D. agilis* separately (Best, 1983*a*), 17 of 19 characters were significantly dimorphic.

Sexual dimorphism also has been examined in *Perognathus.* Hall (1946) did not find significant sexual differences in *P. longimembris,* but noted that males were larger than females for *P. parvus.* Baker (1954) did not detect sexual dimorphism in his examination of *P. flavus.* For *P. flavescens,* Williams (1978) and Reed and Choate (1986) found a few significant differences between sexes, but thought they could be attributed to sampling errors, and Williams and Genoways (1979) found females from one of their geographic groups had significantly greater lengths of interparietals than males, but no other sexual differences were detected. The difference in several characters between sexes of *P. alticola, P. amplus,* and *P. parvus* shown here, coupled with data on other species, indicates a large variation in sexual dimorphism among species in this genus.

Hall (1946) found no significant sexual differences in *C. formosus,* nor did Glass (1947) for *C. hispidus.* No differences were found in this study as well. Differences between sexes were found in *C. artus* and *C. goldmani* in the present study, and by Anderson (1964) who grouped sexes for analyses. Hall (1946) and Hoffmeister and Lee (1967) found males usually averaged larger than females of *C. penicillatus,* but only length of hind foot differed significantly herein. Wilkins and Schmidly (1979) found significant differences in external and cranial dimensions between males and females of *C. intermedius, C. nelsoni,* and *C. penicillatus.* Straney and Patton (1980) found that sexual differences within localities were of about the same magnitude as were differences between localities within races of *C. goldmani.* They considered sexes separately in analyzing geographic trends, and combined sexes to examine relationships between morphologic, environmental, and lineage trends. Weckerly and Best (1985) found varying degrees of differences between sexes of *C. intermedius* in southern New Mexico.

Hall (1941, 1946) reported a lack of significant sexual dimorphism in both species

of *Microdipodops,* and Schitoskey (1968) found one of 14 measurements (zygomatic breadth) differed significantly between sexes of *M. megacephalus.* There were no sexual differences shown in the present analyses.

Sexual differences in *H. gaumeri* were addressed by Engstrom et al. (1987). Using age classes described by Genoways (1973), they compared sexes and found one character differed between sexes in their youngest age class and seven of 14 measurements differed in age class III. However, they concluded that only a minor component of their total variance was attributable to sex. Only *H. australis* and *H. nelsoni* were sexually dimorphic in four or more characters in the present study.

Genoways (1973) determined that males were larger than females in approximately one-half of the 13 measurements tested for *L. adspersus, L. irroratus, L. pictus,* and *L. salvini.* For most of the other means, where no significant differences were found, males averaged larger than females. Only three species of *Liomys* examined herein had dimorphic characteristics, and none to the degree observed by Genoways (1973).

Geographic variation in sexual dimorphism is a factor that could significantly affect the detection of sexual differences in heteromyids. The selection of specimens for analyses of sexual dimorphism appears to be important. Except for *Dipodomys,* which were selected more or less randomly from large data matrices, those animals examined during the present study were measured as encountered, and because of the limited numbers of specimens available for study no attempt was made to insure that specimens were from the same geographic area. Had specimens been selected from one locality for each species, it is likely that a different number of sexually dimorphic traits would have been found among the 57 species.

Schmidly (1971), in his study of *D. ordii,* indicated that sexual dimorphism varied geographically and suggested that the variability may result from genetic and hormonal sex differences or may, to some extent, be due to nongenetic modification of the phenotype caused by local environmental conditions. In his study, females were larger than males in northern Texas, whereas the reverse was true in the southern samples. Baumgardner and Schmidly (1981) noted that sexual differences varied among samples of *D. ordii.* Best (1987) found significant geographic variation in sexual dimorphism across the range of *D. elator* in northcentral Texas.

Geographic variation in sexual dimorphism has been found in *C. intermedius* from three lava fields in New Mexico by Weckerly and Best (1985). They speculated that the varying degree of sexual differences may be related to age of the lava fields or selective pressure of climate, vegetative cover, food, physiology, reproduction, competition, etc. The three samples of *C. penicillatus* examined by Hoffmeister and Lee (1967) and those of *P. flavescens* analyzed by Williams (1978) also exhibited differences in sexual dimorphism among localities. It seems clear that an accurate assessment of sexual dimorphism within a species cannot be achieved without an examination of differences at the population level.

Patterns of Variation

Phenetic analyses have been used to assess relationships among and within species of *Dipodomys* (Baumgardner, 1989; Baumgardner and Schmidly, 1981; Best, 1978, 1983*a,* 1983*b,* 1987; Best and Janecek, 1992; Best and Schnell, 1974; Best et al., 1986; Brownlee, 1973; Genoways and Jones, 1971; Kennedy and Schnell, 1978; Schmidly and Hendricks, 1976; Schnell et al., 1978), *Perognathus* (Williams, 1978; Williams and Genoways, 1979), *Chaetodipus* (Caire, 1976; Straney and Patton, 1980), *Microdipodops* (Hafner, 1978, 1981), *Liomys* (Genoways, 1973), and *Heteromys* (Engstrom et al., 1987; Genoways, 1973; Rogers and Schmidly, 1982). Other than the comparisons of *Liomys* with *Heteromys* (Genoways, 1973), only Hafner (1978) has used phenetic

analyses of morphologic traits to elucidate relationships among genera of heteromyids. Separation of individuals or populations of closely related species of *Dipodomys* (Best, 1978, 1981*a*) and *Microdipodops* (Hafner, 1981) also have been accomplished using phenetic analyses.

Analyses presented in this chapter are the first to investigate morphologic variation among 57 species of Heteromyidae. Analyses of species within the genus *Dipodomys* produced dendrograms that generally grouped taxa on the basis of size. A comparison with the dendrograms in Schnell et al. (1978) indicates several similarities with the present classification. Schnell et al. (1978) grouped sexes and used 41 characters (including all characters examined here, except length of body). The large species, *D. ingens, D. spectabilis,* and *D. deserti* were well separated from the others in their distance phenogram, as well as in the distance phenogram for males presented in this chapter. For females, only *D. ingens* and *D. spectabilis* were well separated, and *D. deserti* was placed into a cluster adjacent to another large species, *D. nelsoni.* Other similarities between this study and Schnell et al. (1978) were the close associations of *D. compactus* with *D. ordii, D. agilis* with *D. heermanni, D. stephensi, D. panamintinus,* and *D. californicus, D. elator* with *D. gravipes, D. insularis* with *D. phillipsii,* and *D. merriami* with *D. nitratoides.* When Schnell et al. (1978) divided their mean measurements by unstandardized principal component I, the phenetic relationships changed considerably. However, their resulting distance phenogram did not have clusters that were any better defined than before the effect of size had been reduced. An examination of that phenogram indicates there is still a tendency for species to group by size.

Grinnell (1921, 1922) grouped *Dipodomys* into species groups that indicated their closest relatives. Burt (1936), Davis (1942), Setzer (1949), and Lidicker (1960*a*) revised these species groupings, and subsequently other authors have referred to them in assessing patterns of variation in karyotypes (Stock, 1974), proteins (Hamilton et al., 1987; Johnson and Selander, 1971), bacula (Best and Schnell, 1974), and skeletal morphology (Schnell et al., 1978). Species in Lidicker's (1960*a*) *heermanni* group are clustered relatively closely in the distance phenograms and the plots of the first two principal components presented here. The occurrence of *D. elator* within the *heermanni* group is interesting since there is a general lack of knowledge relative to its affinities with other *Dipodomys.* In the present analyses, *D. ingens,* considered a member of the *heermanni* group, is morphologically most similar to *D. spectabilis.* Thus, the two largest species have been grouped together; usually near *D. deserti.* The occurrence of *D. ordii* (with *D. compactus*) and *D. microps* somewhat separately from other species, and the presence of *D. merriami, D. nitratoides,* and *D. margaritae* in the same group, likewise, are similar to Lidicker's groupings. The close affinity of *D. insularis* and *D. phillipsii* shown here is not shown in previous groupings, nor is the placement of *D. ingens* with *D. spectabilis,* nor is the placement of *D. nelsoni* in the *heermanni* group. The large and morphologically similar species *D. nelsoni* and *D. spectabilis* were expected to group more closely. Analyses by Baker (1956), Anderson (1972), Matson (1980), and others (see Nader, 1978) separated these species, although Nader (1978) considered them conspecific. The analyses here indicate they are more similar to other species than to each other.

Anderson (1972) used ratio diagrams for comparing morphologic differences among *P. merriami, P. apache,* and *P. flavus,* and Wilson (1973) used discriminant function analyses to compare *P. merriami* and *P. flavus.* Williams (1978) assessed patterns of phenetic variation in *P. flavescens,* and Williams and Genoways (1979) similarly studied *P. fasciatus.* Hafner (1978) and Hafner (1982) used *Perognathus* in their assessments of relationships among the geomyoid rodents. However, the present study is the first to assess morphologic variation for the

eight species of this genus simultaneously. Differences between results of analyses of males and females are in part due to sexual differences within species. However, the primary separation of the species is on the basis of size. The smallest species, *P. flavus,* as well as the largest, *P. parvus,* generally are separated from the others. The morphologically most similar species (*P. amplus* with *P. inornatus* and *P. fasciatus* with *P. flavescens*) group together in the distance phenograms and the principal component plot for males, but are not as clearly aligned on the principal component plot for females. Morphologically, this genus exhibits considerable variation in overall body size, although no species represents a large divergence from the others.

Studies by Hafner (1978) and Hafner and Hafner (1983) included *Chaetodipus* in their assessments of geomyoid phylogenies. The most striking attribute of the analyses of *Chaetodipus* herein was the large difference in body size of *C. hispidus* from the other species; a difference clearly shown in the ratio diagram of Anderson (1972). An examination of bacular characters, such as overall size and configuration of the bacular tip, also shows a similar separation of *C. hispidus* from the other taxa (see Burt, 1960). Within the remaining 13 species, the greatest degrees of consistency in analyses are the close affinities of *C. intermedius* with *C. lineatus* and *C. fallax* with *C. formosus.* The coupling of *C. artus* and *C. goldmani* reflects the similarity studied by Hall and Ogilvie (1960), Anderson (1964), and Patton (1967). Other groupings are more variable, although larger body size generally differentiates *C. baileyi* and *C. californicus* from the other taxa.

Caire (1976) examined phenetic relationships among species of *Chaetodipus,* and concluded that his numerical analyses supported previous species groupings and demonstrated new groupings that were worthy of future consideration. When the results obtained by Caire (1976) are compared with those presented herein, some differences are apparent. In Caire's analysis, *C. hispidus* couples with *C. baileyi,* and *C. formosus, C. californicus, C. pernix, C. artus,* and *C. goldmani* are each well separated from the remaining species. In the analyses presented herein, *C. hispidus* is well separated from the other taxa, and those that remain form two clusters (the clusters differ between sexes). Since the same statistical treatment was used, it is suspected that differences in characters, number of characters, sample sizes, and treatments of sexual differences are responsible for the dissimilarity between the studies. Data on sample size, characters, and sexual differences were not presented by Caire (1976).

Genoways (1973) used *Heteromys* in phenetic comparisons with *Liomys.* Rogers and Schmidly (1982) examined phenetic variation of *Heteromys* in the *desmarestianus* species group, and concluded that this group is represented in northern Middle America by two species, *H. desmarestianus* and *H. goldmani.* Herein, the genus formed two distinct groups in the assessment of patterns of morphologic variation. The larger species, *H. goldmani, H. oresterus,* and *H. nelsoni,* formed a group well separated from the remaining four; a phenetic classification at variance with Rogers and Schmidly (1982).

The only phenetic assessment of relationships among the *Liomys* has been that of Genoways (1973). He found *L. pictus* and *L. spectabilis* were the most similar species pairs; they were most closely associated with *L. irroratus,* and *L. salvini* and *L. adspersus* formed a more distantly related pair of species. In the present analyses, *L. pictus* and *L. salvini* were the most similar species and they grouped separately from *L. adspersus, L. irroratus,* and *L. spectabilis.* The presence of *Heteromys* in Genoways' distance analysis could have affected the placement of the *Liomys* taxa. The inclusion of additional species in phenetic analyses has been shown to affect the relationships resulting from cluster analyses in heteromyids (Best, 1978, 1981*a*). Considering the differences in body size between *L. spectabilis* and *L. pictus* (Genoways, 1971), separation of these spe-

cies was expected in the phenetic analyses herein. Along the second principal component axis, *L. spectabilis* is quite divergent from the other taxa.

Hafner (1978) examined the relationship of *Microdipodops* to *Perognathus, Chaetodipus,* and *Dipodomys,* and found *Microdipodops* to be phenetically most similar to *Perognathus.* Phenetic analyses in this chapter also show a close relationship between *Microdipodops* and the *Perognathus-Chaetodipus* cluster. Most recently, Hafner and Hafner (1983) summarized the evolutionary relationships of heteromyid rodents. Using a variety of data they concluded that extant heteromyids comprise three main lineages, *Chaetodipus-Perognathus, Dipodomys-Microdipodops,* and *Liomys-Heteromys.* Results presented here differ somewhat from their evolutionary scheme. *Dipodomys* is phenetically most similar to *Liomys* and *Heteromys* (including *C. hispidus*), *Perognathus* and *Chaetodipus* are intermixed, and *Microdipodops* shows closest affinities to the *Perognathus-Chaetodipus* cluster. As mentioned previously, the phenetic analyses are heavily biased by size, which likely is not a good indicator of evolutionary relationships. Overall, *Dipodomys* shows more intrageneric variation, for both males and females, than do the four other genera examined.

Pelage and Coloration

Homan and Genoways (1978) analyzed hair structure and its phylogenetic implications among heteromyids. They used both light and scanning electron microscopy and investigated variables such as length and width of hair, imbricate scale pattern, and medullary characteristics. Although the hair of individual species could be characterized with detailed study, they did not believe that hair structure would be of value in evolutionary studies of this group below the generic level. They found that the overhair of heteromyids falls into two morphologic types, that is, hair that is round to oval in outline and hair that has a trough along the dorsal surface. Hair of the first type is found in most perognathines and members of the genera *Dipodomys* and *Microdipodops.* Troughed hairs were found in chaetodipines, *Liomys, Heteromys, P. amplus,* and *P. formosus.*

Odd pelage colors and characteristics have received some attention (e.g., Blair, 1940; Howell, 1923; von Bloeker, 1930), but coloration of desert species has received much attention because of the variability in color among populations occupying habitats with unusually colored substrates (e.g., Benson, 1933; Dice and Blossom, 1937; Sumner, 1921; Sumner and Swarth, 1924). Cloudsley-Thompson (1979) reviewed accounts of the colors of desert animals, including what is known of color variation in heteromyids, and discussed adaptive functions of colors in a wide variety of taxa.

In local areas, such as lava fields or areas with pale-colored substrates, dark or pale-colored populations often are found. Merriam (1890) mentioned *P. flavus fuliginosus* from an Arizona lava field that differed strikingly in its dark coloration from populations in the neighboring desert where the soil was pale in color. Other accounts of unusually colored populations of heteromyids include those of Dice (1929, 1930, 1940), Blossom (1931, 1933), Benson (1932), Bradt (1932), Blair (1943), Baker (1960), Findley (1967), Koschmann (1972), and Elder (1977).

There are many taxonomic descriptions in addition to those cited below that contain information on coloration and pelage characteristics of heteromyids. Osgood (1900) described color and pelage of *Perognathus* and *Chaetodipus.* Color, molt, and pelage descriptions for some *Perognathus, Chaetodipus, Microdipodops,* and *Dipodomys* were presented by Hall (1946). Goldman (1911) provided descriptions of color and molt in *Liomys* and *Heteromys.* Variation in coloration among populations of *P. fasciatus* (Williams and Genoways, 1979), *P. flavescens* (Williams, 1978), and *P. flavus* (Wilson, 1973) have been described. Speth

(1969) described color variation and patterns of molt in *P. parvus*. Color variation in a southern New Mexico population of *C. intermedius* was examined by Elder (1977). Anderson (1964) illustrated and described pelage characters that differentiated *C. artus* from *C. goldmani*. Coloration was a significant factor in Hall's (1941, 1946) discussions of variation in *Microdipodops*. Hafner et al. (1979) separated *M. megacephalus* from *M. pallidus* collected in Penoyer Valley, Nevada, on the basis of three qualitative pelage characters, which closely agreed with identification based upon their 14 mensural characters. Schitoskey (1968) was not able to discern variations in coat color in a Nevada population of *M. megacephalus*. Genoways (1971) used mean reflectance values to demonstrate differences in coloration of *L. spectabilis* and *L. pictus,* and Hooper and Handley (1948) described variation in color of *L. irroratus*.

Grinnell (1922) described variation in coloration and pelage of *Dipodomys* in California, Setzer (1949) examined variation in color of *D. ordii,* and Blair (1949) and Lidicker (1960*a*) assessed variation in color among populations of *D. merriami*. For *D. phillipsii,* Genoways and Jones (1971) described pelage, found color was variable geographically, and noted that color varied to a greater degree among animals from a single locality than did external or cranial measurements. Among their 14 geographic samples, reflectance of red ranged from 5.5 to 13.1 in coefficient of variation. Baker (1960) described specimens of *D. phillipsii* from the Guadiana lava field, Durango, as being darker in dorsal coloration than typical examples of the species. His is the only account that documents darker-colored *Dipodomys* associated with lava fields. Nader (1978) described color variation in *D. spectabilis* and *D. deserti*.

Specimens of *D. agilis* from the northern portion of the range are noticably darker (northern Pacific coast and mountains of Baja California). Paler-colored populations occur southward in Baja California, and populations are very pale in the vicinity of San Francisquito Bay. Darker forms are in areas with darker soils or areas that have a relatively dense cover of vegetation. Pale-colored *Dipodomys* occur in other areas as well (e.g., *D. ordii oklahomae* in Oklahoma and *D. compactus* from Padre Island, Texas, are among the palest-colored *Dipodomys*). Nader (1978) found the palest-colored *D. deserti* in the hottest and driest area within the range of the species (Death Valley, California), and noted that high alkalinity of the soil affects color. However, the original color is restored after molting.

The difference in substrate coloration and degree of isolation required for unusually colored populations to evolve also has resulted in a great deal of morphologic variation, even among geographically close lava fields (Weckerly and Best, 1985; Weckerly et al., 1988). Weckerly and Best (1985) found several morphologic characters that differed statistically among populations from three lava fields in southern New Mexico. Although differences in coloration among their populations were detectable, the degree of morphologic variation was not expected because of the closeness of the populations.

Geographic variation in color was assessed throughout the range of *D. merriami* by Lidicker (1960*a*). He found an extremely broad spectrum of fur color in the dorsal pelage, reflecting variation in both the dusky bases of the bicolored hairs and their reddish tips. In addition to the complex variation in color of the dorsum, he found that *D. merriami* possessed a number of other pelage characters that proved to be useful in examining geographic variation in coloration. Along with a discussion of coloration of *D. merriami,* he included a figure depicting geographic variation in color of the arietiform markings over the species' range.

Huey (1951) pointed out that the darkest race of *D. merriami* in Baja California lives in the relatively cool and humid San Quintin region, whereas directly eastward on the torrid, arid desert east of the Sierra San Pe-

dro Martir, the most pallid race occurs. Hooper and Handley (1948) concluded that pelage coloration in *L. irroratus* may be associated with humidity or, more probably, with color of the substrate. Grinnell (1922) suggested that color intensity in *Dipodomys* was correlated with cloudiness. Lidicker (1960*a*) pointed out that it seems more likely that *Dipodomys* are affected directly by vegetation types and soil colors, which in turn may be related to cloudiness. Color of pelage seems closely related to soil color and moisture.

Bacular Variation

Burt (1936) presented the first comparative data on bacula of the Heteromyidae. He found variation in bacula of adult *Perognathus, Chaetodipus,* and *Dipodomys* was not great within given races and that there was considerable age variation. Bacula of young individuals were smaller with less bulbous basal ends than were those of adults. Burt (1960) later summarized his bacular observations of heteromyids by pointing out that, with the exception of *C. hispidus,* bacula in this family fall into a general pattern. They are simple rods, usually with expanded basal ends, and with tapering shafts that vary in dimensions and amounts of curvature. Burt (1960) included illustrations of many additional heteromyids in his later paper. Kelly (1969) provided data on bacula of *Dipodomys, Perognathus, Chaetodipus, Microdipodops, Heteromys,* and *Liomys,* Hoffmeister (1986) illustrated bacula of *Perognathus* and *Chaetodipus,* and Patterson and Thaeler (1982) assessed patterns of variation in bacula of *Dipodomys, Perognathus,* and *Chaetodipus.*

Additional descriptions of the bacula of *Dipodomys* have been presented (Best, 1981*a*; Blair, 1954; Boulware, 1943; Csuti, 1979; Desha, 1967; Genoways and Jones, 1971; Lackey, 1967; Lidicker, 1960*b*). Best and Schnell (1974) provided data on most species of *Dipodomys* and provided an estimate of relationships within the genus using phenetic analyses of bacular characters. Subsequently, Jannett (1976) provided additional data on *D. compactus* and *D. elator* and pointed out the presence of variation in the tip of bacula and suggested that it would be an informative character in future analyses. Best (1981*a*) studied intraspecific, interspecific, and geographic variation in bacula of Baja California *Dipodomys.*

Following comparison of phenograms for *Dipodomys* bacula, with and without body size considered, Best and Schnell (1974) concluded there was apparently no definite trend in the relationship between bacular size and body size. However, Best (1981*a*) later discovered that if *D. deserti* and *D. nitratoides* were omitted from correlation analyses, there was a significant relationship between body size and bacular length.

Burt (1960) illustrated and described bacula of *Perognathus.* He found that *Perognathus* have a short baculum with a relatively large, bulbous basal end that tapers rapidly into the slender shaft, which turns up at a nearly right angle distally, and terminates in a point.

Burt (1960) also illustrated and described bacula of *C. arenarius, C. baileyi, C. californicus, C. formosus, C. goldmani, C. hispidus, C. intermedius, C. nelsoni, C. penicillatus, C. pernix,* and *C. spinatus.* He described the baculum of *Chaetodipus* (except *C. baileyi* and *C. hispidus*) as relatively longer and more slender than *Perognathus.* The basal portion is slightly bulbous and the distal end is upturned. As viewed from the side, the baculum is roughly sigmoid in outline. In *C. formosus* and *C. baileyi,* the bone is extremely slender, only slightly enlarged at the basal end, the shaft has a gentle curve upward, and the point does not bend abruptly. The baculum of *C. hispidus* differs from others in the genus, as well as in the family Heteromyidae, in having a three-lobed distal end instead of a terminating point. Anderson (1964) provided detailed illustrations of variation in bacula of *C. artus* and *C. goldmani,* and noted that every

baculum studied could be identified to species. When Roth (1976*b*) described *C. dalquesti,* he included illustrations of bacula of *C. arenarius, C. dalquesti,* and *C. penicillatus.*

The baculum of *M. pallidus* was described by Burt (1960) as definitely intermediate between those of *Perognathus* and *Dipodomys.* The large basal part tapers into a shaft that curves moderately upward. Schitoskey (1968) described differences among bacula of *M. megacephalus,* and found no variations in shape of adult specimens.

Burt (1960) described bacula of three species of *Liomys* (*L. irroratus, L. pictus,* and *L. salvini* under the name *L. crispus*) and figured the structure of two (*L. irroratus* and *L. pictus*). Genoways (1973) illustrated and assessed bacular variation in the five recognized species of *Liomys.* He found the bacula of *L. salvini* and *L. adspersus* were similar, as were those of *L. pictus* and *L. spectabilis,* and that the baculum of *L. irroratus* was most similar to *H. desmarestianus* and *H. gaumeri.*

Genoways (1973) described and illustrated the baculum of *H. desmarestianus* and *H. gaumeri.* Rogers and Schmidly (1982) used bacular characteristics to evaluate taxonomic relationships of *H. desmarestianus* and *H. goldmani* to other *Heteromys.* They found considerable variation in bacula and concluded only two species were represented in their samples.

Geographic variation has been shown in bacular characters of heteromyids. Anderson (1964) figured individual and geographic variation in bacula among populations of *C. artus* and *C. goldmani.* Csuti (1979) found geographic variation among samples of bacula from *D. microps* and concluded that bacular characters may be of considerable systematic value. Best (1981*a*) demonstrated significant geographic variation among bacula of the *heermanni* group of kangaroo rats in Baja California (*D. agilis* and *D. gravipes*). Patterson and Thaeler (1982) found no evidence of geographic patterns in bacular lengths of *Dipodomys.* Rogers and Schmidly (1982) elucidated interspecific and geographic variation in bacula of *Heteromys,* and used their findings to reach taxonomic conclusions.

Geographic Variation

Before and after the review of geographic variation by Gould and Johnston (1972), numerous articles have addressed the subject for heteromyids. Many studies of geographic variation in heteromyid rodents that were conducted to assess taxonomic relationships have not been included below because of space limitations and because this chapter deals with morphologic variation (not taxonomic relationships). Under the topics of sexual dimorphism, pelage and coloration, and bacular variation elsewhere in this chapter, comments on geographic variation of those traits have been included.

As the number of specimens from more collecting localities increased near the turn of the century, it became imperative that students of taxonomy evaluate the degree of geographic variation present within species. Once specimens from intermediate localities were shown to have intermediate characters (often between different species), it became clear that geographic variation was an important aspect of examining taxonomic relationships among populations. The early studies and taxonomic reviews of heteromyids by Merriam (1889), Osgood (1900), Goldman (1911), Grinnell (1922), and others, were influenced by examination of geographic variation. Taxa often were named on the basis of a few specimens from an isolated collecting locality. Because of the availability of more specimens from more localities, the investigators that followed have spent even more effort elucidating patterns of geographic variation within or among species (e.g., Best, 1983*a*; Best et al., 1986; Genoways, 1973; Hafner, 1981; Hall, 1941; Hooper and Handley, 1948; Kennedy and Schnell, 1978; Kennedy et al., 1980; Lidicker, 1960*a*; Rogers and Schmidly, 1982; Schmidly, 1971; Setzer, 1949; Williams, 1978).

Within the genus *Dipodomys,* several studies have focused upon geographic variation in morphology within species. The most frequently studied taxon has been *D. ordii* (Anderson, 1972; Baumgardner and Schmidly, 1981; Grisham, 1967; Hall, 1946; Hartman, 1980; Kennedy and Schnell, 1978; Kennedy et al., 1980; Schmidly, 1971; Schmidly and Hendricks, 1976; Setzer, 1949; Shaver, 1973). Other taxa also have been examined, including *D. agilis* (Best, 1978, 1983*a*; Best et al., 1986; Lackey, 1967), *D. californicus* (Dale, 1939), *D. compactus* (Baumgardner and Schmidly, 1981; Shaver, 1973), *D. deserti* (Hall, 1946; Nader, 1978), *D. elator* (Best, 1987), *D. gravipes* (Best, 1978, 1983*b*), *D. merriami* (Best and Janecek, 1992; Hall, 1946; Lidicker, 1960*a*), *D. microps* (Csuti, 1979; Hall, 1946; Hall and Dale, 1939; Lester, 1973), *D. nelsoni* (Nader, 1978), *D. panamintinus* (Hall, 1946), *D. phillipsii* (Genoways and Jones, 1971), *D. spectabilis* (Nader, 1978), and *D. stephensi* (Lackey, 1967). Variation in several species was examined by Grinnell (1922), Villa-R. (1941), Durrant and Setzer (1945), and Huey (1951).

Techniques for studying geographic variation have stressed statistical analyses of mensural data, but analyses of nonmetric characters also have been used. Hartman (1980) examined geographic variation in 18 nonmetric cranial traits for 11 populations of *D. ordii* from Oklahoma, Texas, and New Mexico. He examined frequencies of traits for sex, size, and side dependencies, and found nonmetric traits were clearly of value in studying geographic variation.

Coupling of geographic variation in morphology with other data has allowed a clearer understanding of taxonomic and evolutionary relationships. An example is the separation of *D. heermanni* from *D. californicus,* which was accomplished by use of genetic and morphologic attributes (Patton et al., 1976), and the comparison of results obtained from genetic analyses with those derived from morphologic analyses (Best and Janecek, 1992; Best et al., 1986; Johnson and Selander, 1971; Stock, 1974).

Within *Perognathus,* geographic variation has been examined for relatively few species. Those species that have been examined in detail include *P. flavus* (Baker, 1954; Wilson, 1973), *P. fasciatus* (Williams and Genoways, 1979), and *P. flavescens* (Reed and Choate, 1986; Williams, 1978). Villa-R. (1941) presented information on several species in Baja California and northern Mexico.

Geographic variation in *C. hispidus* was discussed by Glass (1947). Other species of *Chaetodipus* that have been examined are *C. artus* (Anderson, 1964; Hall and Ogilvie, 1960), *C. goldmani* (Anderson, 1964; Hall and Ogilvie, 1960; Patton, 1969), *C. intermedius* (Weckerly and Best, 1985; Weckerly et al., 1988), and *C. penicillatus* (Hoffmeister and Lee, 1967). Villa-R. (1941) presented data for several species of *Chaetodipus.* The study of geographic variation in morphology of *C. penicillatus* by Hoffmeister and Lee (1967) disclosed several significant aspects of intraspecific differentiation. Some seemingly prominent geographic barriers have not been important in differentiation of *C. penicillatus,* whereas others have. They observed some marked morphologic divergence in areas with no obvious geographic barrier, although no large-scale geographic trends were revealed.

Patton (1969) examined geographic variation in *C. goldmani* and ascertained that phenotypic variation (in terms of shifts in direction or magnitude of clines) did not correspond in any significant way to his chromosomal data. He attributed the lack of correspondence to different levels of organization of gross morphology and chromosomes, and pointed out that the expression of the phenotype is more strongly dependent on ecologic factors than on gross chromosomal arrangements. Weckerly and Best (1985) examined morphologic variation among *C. intermedius* from three lava fields in southern New Mexico and found a large amount of variability. Their study has shown that coloration is not the only variable affected by isolation on lava fields. They

found significant geographic variation occurred in 15 of 16 characters.

Geographic variation in morphologic and color traits of *Microdipodops* was examined by Hall (1941, 1946). Hafner (1981) has studied patterns of evolutionary concordance among morphometric, colorimetric, karyologic, electromorphic, and climatic data sets within *M. megacephalus* and *M. pallidus.*

Using univariate and multivariate statistical techniques, the degree of geographic variation within each of the species of *Liomys* was assessed by Genoways (1973). Previously, Hooper and Handley (1948) examined geographic variation in *L. irroratus* and presented taxonomic conclusions.

Rogers and Schmidly (1982) examined geographic variation among *H. desmarestianus* and *H. goldmani,* and their analyses formed the basis for synonomizing *H. longicaudatus, H. lepturus,* and *H. temporalis* with *H. desmarestianus.* Engstrom et al. (1987) evaluated geographic variation in *H. gaumeri.* They found only six of 14 characters were significantly heterogeneous among grouped localities. They concluded that patterns and level of intralocality variation appeared similar to other heteromyines, but geographic variation in *H. gaumeri* was relatively conservative. They postulated that the relative lack of interlocality variance in *H. gaumeri* might be attributable to a restricted geographic distribution, to relative environmental homogeneity on the Yucatan Peninsula, or to a lack of genetic divergence among populations.

Environmental-morphologic Relationships

As eluded to in the previous section, many studies of morphologic variation in heteromyids have examined geographic variation among populations, yet few studies have assessed the relationship of environmental variation with morphologic traits. Roth (1976*a*) quantified and compared morphologic features for *Perognathus, Chaetodipus,* and *Dipodomys* with various degrees of desertification found in Baja California. He found that where there was an increase in openness of habitat to 20–30%, there was a greater development of morphologic specialization of the auditory bullae, hind feet, and tail in the heteromyid population. Further increase in openness (to 80% or more) did not necessarily result in additional specialization. He concluded that desertification was not the source of morphologic adaptations in the heteromyids he studied, but pre-adaptation in a more mesic environment was a significant factor.

Relationships between ecogeographic and morphologic variation in *D. agilis* in Baja California were examined by Best (1981*b*). He analyzed variation in temperature and precipitation and determined those data were correlated with morphologic parameters. His morphologic principal component I (size) was significantly correlated with latitude and longitude for both sexes. The morphologic principal component II of females (nasal width, length of ulna, and length of hind foot) was correlated with July mean temperature and January mean precipitation.

In studies of *D. ordii,* Kennedy and Schnell (1978) and Kennedy et al. (1980) suggested that small body size might be selected for when there is only a limited amount of desirable space available. The reasoning was that small size could reduce the amount of food and space needed by each individual, thereby enhancing survival of small individuals and lowering the probability of extinction in local populations.

For *Perognathus,* Williams (1978) found a strong north-south size cline in *P. flavescens.* Latitude showed 23 significant positive correlations with the morphometric traits; climatic severity index, growing season, and mean July minimum temperature were not significantly correlated with any of the morphometric traits. Mean annual temperature was negatively correlated with body size, indicating that larger animals were in cooler regions. Thus, latitude was more

highly correlated with size than the temperature variables.

Straney and Patton (1980) examined geographic variation in 15 external and cranial characters of *C. goldmani,* and compared their findings to ecogeographic predictor variables including temperature, precipitation, and isophane (a measure of growing season length). They found several morphologic characters to be significantly related to isophane, one to be related to precipitation, and two related to temperature variables.

The morphologic differences between *M. megacephalus* and *M. pallidus* in size and shape of the angular processes, pterygoids, and incisive foramina suggested a means of ecologic separation related to the food resource base (Hafner et al., 1979). These authors reasoned that since these characters are related to, or are direct components of, the masticatory apparatus, it appeared that the functional significance of the differences might be explained by differing food habits between these two species. Hafner (1981) compared results of his assessment of morphologic variation and environmental parameters and found the environment was a good predictor of pelage color patterns, but not morphometric variation in *Microdipodops.*

Geographic variation in size observed in *L. irroratus* by Hooper and Handley (1948) appeared to be correlated with altitude and latitude, and factors associated therewith. Small size was characteristic of low elevations and low latitudes, and largeness was correlated with high altitudes and latitudes.

Since heteromyids vary geographically and there are statistical associations between that variation and some environmental characters, further investigations of these relationships seem warranted. One of many environmental–morphologic relationships of heteromyids yet to be examined in detail is that of the degree of morphologic variation among years. If genetically similar animals such as domesticated livestock can be treated in different ways to get them to grow larger (e.g., a steer in a feedlot will develop larger bones and overall size than one placed onto the open range), then rodents should be expected to differ under varying environmental conditions. Perhaps in favorable years, when food and resources are abundant, developing rodents are larger than those growing up in years with limited resources. This might be difficult to test in wild populations, but laboratory manipulations of resources available to developing heteromyids could help clarify the degree of difference and the factors controlling annual variation in morphologic traits.

Summary

Patterns of morphologic variation were assessed in 57 species of heteromyid rodents using 19 external and cranial measurements for 12,563 adult specimens. Results of this study, coupled with those of previous workers, indicate varying degrees of secondary sexual differences in size among species, and geographic variation in sexual dimorphism of *Chaetodipus* and *Dipodomys.* Phenetic relationships are similar to previous phenetic and phyletic analyses; however, affinities of genera and placement of *C. hispidus* with *Heteromys* and *Liomys* differ from previous findings. Heteromyids exhibit pronounced geographic variation in color attributable to substrate coloration, moisture, or other environmental factors. Bacula are similar among genera, differing primarily in length, diameter, curvature, and size of base, and they vary geographically in some species of *Chaetodipus, Dipodomys,* and *Heteromys.* Geographic variation in morphology is evident across the range of most species, and significant differences are evident over short distances in *Chaetodipus* and *Dipodomys.* Relationships between morphologic and environmental variation indicate a tendency for body size to be associated with latitude and some temperature and precipitation characters.

Acknowledgments

I thank the curators and museum personnel at the following collections for assistance with loans

of specimens and for allowing me to examine specimens in their care: American Museum of Natural History, New York; Arizona State University, Tempe; Brigham Young University, L. L. Bean Museum, Provo; California Academy of Sciences, San Francisco; Carnegie Museum, Pittsburgh; Eastern New Mexico University, Portales; Field Museum of Natural History, Chicago; Harvard University, Museum of Comparative Zoology, Cambridge; Los Angeles County Museum, Los Angeles; Louisiana State University, Baton Rouge; Michigan State University, The Museum, East Lansing; Midwestern State University, Wichita Falls; Oregon State University, Corvallis; San Diego Natural History Museum, San Diego; Texas A&M University, Cooperative Wildlife Collection, College Station; Texas Tech University, The Museum, Lubbock; United States National Museum of Natural History, Washington; University of Arizona, Tucson; University of California, Museum of Vertebrate Zoology, Berkeley; University of California at Los Angeles, Donald R. Dickey Collection, Los Angeles; University of Illinois, Champagne-Urbana; University of Kansas, Museum of Natural History, Lawrence; University of Michigan, Museum of Zoology, Ann Arbor; University of New Mexico, Museum of Southwestern Biology, Albuquerque; University of Oklahoma, Oklahoma Museum of Natural History, Norman; University of Puget Sound, Tacoma; University of Texas, Natural History Laboratory, Austin.

W. R. Barber, P. A. Chappell, and L. L. Janecek assisted with loans at The University of New Mexico, Museum of Southwestern Biology. B. Dennis, H. T. Haagenstad, C. R. Lambert, and R. M. Sullivan assisted in the preparation of the figures. F. H. Best helped verify data, R. L. Garrison assisted in data entry and verification, and T. E. Garrison gathered literature, entered and verified data, and helped with other aspects of the study. D. E. Kidd provided encouragement and assistance throughout the preparation of this chapter. R. C. Calabro, H. H. Genoways, J. C. Hafner, R. M. Lee, and R. M. Sullivan provided helpful suggestions in their reviews of an early draft. I am especially grateful to S. A. Cole who spent many days during the summer of 1985 helping record data from thousands of heteromyids. This is a journal article of the Alabama Agriculture Experiment Station.

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