

Biology of Desert Rodents

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EVOLUTIONARY RELATIONSHIPS OF HETEROMYID RODENTS¹John C. Hafner² and Mark S. Hafner³

ABSTRACT.—The rodent superfamily Geomyoidea is an old, undoubtedly monophyletic lineage having only obscure affinities with other rodent groups. Geomyoid rodents, autochthonous in North America, experienced major evolutionary diversification in the Mio-Pliocene coincident with the development of the Madro-Tertiary Geoflora and the climatic trend toward increasing aridity and coolness. Extant geomyoids are divisible into two groups: (1) the Geomyidae, all members of which are fossorial, and (2) the Heteromyidae, whose members display an adaptive continuum from bipedal, xeric-adapted forms to scansorial, mesic-adapted forms. These moieties, although recognizable on biochemical criteria, become particularly difficult to distinguish when paleontological data are considered. Nevertheless, most lines of evidence indicate that the families Heteromyidae and Geomyidae are distinct, monophyletic lineages.

The extant heteromyids comprise three main lineages (including six genera) that diverged during the Eocene: (1) subfamily Perognathinae (*Chaetodipus* and *Perognathus*); (2) subfamily Dipodomysinae (*Dipodomys* and *Microdipodops*); and (3) subfamily Heteromyinae (*Liomys* and *Heteromys*). Protein differentiation has occurred at heterogeneous rates among these major lineages. Based on available karyotypic data, the main direction of chromosomal evolution in the Heteromyidae appears to be toward increasing chromosome number. Cladistic analysis of morphological characters used in previous studies supports biochemical evidence allying *Microdipodops* with *Dipodomys*. A model is introduced to describe how heterochronic changes in ontogeny may explain the great breadth of morphological diversification within the superfamily. Taxonomic recommendations at the subfamilial, generic, and sub-generic levels are provided.

The most important point to be emphasized is that "Parallelism, parallelism, more parallelism and still more parallelism" is the evolutionary motto of the rodents in general and of the heteromyids in particular. This extends to all parts of the body. It makes the task of determining interrelationships particularly difficult, and renders exceptionally dangerous any postulates as to what the relationships of a given form may really be, if full evidence does not exist to clear the maze of parallel adaptations for us. This shows the insuperable difficulties awaiting anyone who attempts a classification based on a single character or on a group of characters with a common cause.

Albert Elmer Wood (1935:250)

A trio of monographs on the evolutionary biology of heteromyid rodents appeared in the early 1930s and, subsequently, has hall-marked this specialized area of scientific inquiry. Hatt (1932) and Howell (1932) provided definitive accounts of the morphology of the ricochetal forms, and Wood (1935) synthesized the then available data, gleaned from fossil and recent forms, into a coherent summarization. Interestingly, the last comprehensive statement of the evolutionary

relationships within the Heteromyidae was Wood's exhaustive treatment, now aged one-half century. However, during the past 50 years a tremendous volume of literature pertaining to heteromyid evolution has accumulated, justly reflecting the immense interest in these mammals. Some of the questions posed by Wood and the others have been answered to satisfaction, whereas the answers to other queries still elude us and await extrication by future research.

It is the intent of this contribution to present a compendium of the evolution of heteromyid rodents, wherein we attempt to integrate the classic morphological studies of the 1930s with the more recent systematic treatments. As a definitive statement on heteromyid relationships, this effort may appear inchoate in a few years. However, the assimilation of earlier ideas with those of the present, coupled with due introspection, is necessary in any field of science. The study of heteromyid evolution is no exception and

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through this reflection of the present to the past we hope to gain a profitable avenue for further investigations.

The evolution of the Heteromyidae (kangaroo rats, pocket mice, and their allies) is closely associated with that of the Geomyidae (pocket gophers) and, consequently, their taxonomic histories are necessarily intertwined. Together these two families form an internally cohesive superfamily (the Geomyoidea) whose members are united by the presence of externally opening, fur-lined cheek pouches (among other features). Geomyoid rodents underwent major phyletic radiation from the Oligocene to Pliocene of North America, in step with the global trend toward a cooler and drier climate (Flint 1971) and the diversification and migration of geofloras (Axelrod 1950, 1958, 1976). Historic biogeographic considerations have been presented elsewhere (e.g., Wood 1935, Reeder 1956, Genoways 1973, Hafner, J. C., 1981a) and will not be repeated here; for general reviews see Stebbins (1981; coevolution of grasses and herbivores), and Cole and Armentrout (1979; Neogene paleogeography). It is interesting to note, however, that heteromyids and geomyids represent two of the three families of living mammals autochthonous in continental North America (the third being Antilocapridae). As a consequence of the similarities in heteromyid and geomyid biogeographic histories and their intimate phyletic relationships, we have found it illuminating to include relevant geomyid information in this review of the Heteromyidae. Indeed, in order to appreciate fully the history of evolutionary diversification within the Heteromyidae, it is necessary first to view this family within the broader framework of the superfamily Geomyoidea.

REVIEW OF GEOMYOID SYSTEMATICS

The taxonomic history of the Geomyoidea began with the description of the "tucan" or "Indian mole" (probably a pocket gopher, *Thomomys*) by Fernandez in 1651. According to Merriam (1895:201), both Fernandez and, later, Kerr (1792, not seen) believed the tucan to be a large, aberrant species of mole (*Sorex mexicanus* Kerr 1792). *Systema Naturae* (Linnaeus 1758) did not mention geo-

myoids, and it was not until 1848 that Waterhouse recognized the Saccomyina (= modern Geomyoidea) as a distinct group of New World rodents (Waterhouse 1848). In 1872, Gill recognized two closely related families within Waterhouse's Saccomyina, the Geomyidae (= modern Geomyidae) and the Saccomyidae (= modern Heteromyidae). Gill (1872) united these families under the superfamilial nomen, Saccomyoidea. Weber (1904), recognizing that *Sacomys* Cuvier 1823 was a junior synonym of *Heteromys* Desmarest 1817 (see Gray, 1868 for details), first used the superfamily name Geomyoidea.

The phyletic position of the Geomyoidea within the order Rodentia has long been a matter of debate. Coues (1877) considered the geomyoids to be "myomorphs" (*sensu* Brandt, 1855). However, Miller and Gidley (1918) and many recent workers place the geomyoids near, or within, the "sciuriforms" (e.g., Simpson, 1931, 1945). Most recently, Wood (1965:128) suggested that the muroid and geomyoid rodents may have shared a common ancestor within the primitive, protrogomorphous rodent family Sciuridae, and he thus placed the Geomyoidea within the suborder Myomorpha (see also Wood 1955, Wahlert 1978).

Rodents of the family Eomyidae represent a third, wholly extinct group of geomyoid rodents present from late Eocene to Pliocene in Europe and North America. According to Wilson (1949a, 1949b), who first placed the eomyids within the Geomyoidea, the eomyid skull shows many similarities to both primitive heteromyids and cricetids. Wood (1955) concurs with Wilson in recognizing the Eomyidae as a primitive geomyoid group, perhaps ancestral to the Heteromyidae. However, none of the known eomyid forms appears to be directly ancestral to living geomyids or heteromyids (Wahlert 1978).

The phyletic propinquity of geomyids and heteromyids, and the fact that both groups evolved under similar environmental conditions in western North America, may account for the remarkable level of evolutionary parallelism in the two groups as evidenced in the fossil record. Due, in large part, to the confounding effects of parallelism, the taxonomy of extant geomyids has vacillated between a

single family classification (either the Saccomyidae, Geomyidae, or Heteromyidae; Baird 1858, Carus 1868, Gray 1868, Alston 1876, Shotwell 1967, Lindsay 1972) or a classification composed of two families equivalent to the modern Geomyidae and Heteromyidae (Gill 1872, Coues 1877, Merriam 1895, Wood 1931, 1935, Rensberger 1971, 1973). Recently, M. S. Hafner (1982) used biochemical evidence to demonstrate that the extant genera commonly placed in the separate families do indeed represent inclusive, monophyletic lineages, thus supporting the traditional two-family classification.

Pocket Gophers: Family Geomyidae

For almost a century, Merriam's (1895) monograph on the Geomyidae has stood as the definitive statement on systematic relationships among extant members of the family. Merriam's work has been modified to varying degrees by Hooper (1946), Russell (1968), M. S. Hafner (1982), and Honeycutt and Williams (1982). Living geomyids are represented by five genera (six according to Honeycutt and Williams 1982), and 33 nominal species, all of which are fossorial herbivores.

Within early geomyids (= Geomyinae of Shotwell 1967, and Lindsay 1972), there was a Miocene radiation in western North America of forms that ranged from semi-ricochetal to fossorial in habitus as inferred from both cranial and postcranial structure (Rensberger 1971, Munthe 1975). These forms are assigned to the geomyid subfamilies Entoptychinae and Pleurolicinae, which appear to have been early, independent geomyid side-branches not directly ancestral to later geomyids.

Following the radiation and eventual extinction of the Miocene entoptychines and pleurolicines, there was a Pliocene radiation of geomyine pocket gophers in western North America. Most workers agree that all subsequent geomyids had their roots in this Pliocene radiation. Details are very scarce; however Shotwell (1967) and Lindsay (1972) tentatively derive all living pocket gophers directly from the Mio-Pliocene form *Parapliosaccomys*. The geological time ranges of the genera *Thomomys*, *Geomys*, *Zygogeomys*,

and *Pappogeomys* extend from the early Blancan (late Pliocene) to the Recent of both the Great Plains and southwestern United States. *Orthogeomys* (subgenus *Heterogeomys*) is known from the Rancholabrean (late Pleistocene) of Nuevo Leon, Mexico. *Orthogeomys* (subgenera *Orthogeomys* and *Macrogeomys*) are known only from Recent material (Russell 1968).

Kangaroo Rats, Pocket Mice and Their Allies: Family Heteromyidae

The heteromyid rodents constitute a morphologically and ecologically diverse assemblage of geomyids whose fossil history dates back to middle Oligocene of western North America (see review by Wood 1935). Wood arranged the heteromyids into three subfamilies (Perognathinae, Dipodominae, and Heteromyinae) and later recognized a fourth subfamily, the Florentiamyinae, based on the early Miocene genus *Florentiamys* (Wood 1936). More recent, suprageneric systematic treatments of fossil heteromyids include the works of Reeder (1956) and Lindsay (1972).

Living heteromyids are traditionally subdivided into five genera and approximately 66 species. In this paper, we will recommend that a sixth genus, *Chaetodipus*, be recognized. Analyses of suprageneric relationships among extant heteromyids include Kelly's (1969) study of bacular and penile variation, Homan and Genoway's (1978) study of hair structure, and M. S. Hafner's (1982) biochemical analysis of intrafamilial relationships. Results of each of these studies, and others, will be incorporated into the following accounts.

KANGAROO RATS: GENUS *Dipodomys*.—The 24 species of kangaroo rats currently recognized are spread throughout much of western North America from south central Canada to central Mexico. Fossil material referable to *Dipodomys* is known from the Barstovian (late Miocene) to the Recent of western North America. The most recent diagnosis of fossil kangaroo rats is provided by Zakrzewski (1981; see included references).

The phyletic position of *Dipodomys* within the Heteromyidae is an area of controversy that will be addressed in the present study. Morphologically, kangaroo rats are truly bizarre, and they show no obvious affinity to

any other heteromyid genus. Although kangaroo rats show a gross overall resemblance to kangaroo mice (*Microdipodops*), Wood (1935) and J. C. Hafner (1978) attributed shared features such as inflated auditory bullae and elongated hind feet to evolutionary convergence. In contrast, Reeder (1956) interpreted the fossil evidence to suggest a true phyletic link between *Dipodomys* and *Microdipodops*, the same conclusion reached by M. S. Hafner (1982) using biochemical evidence. It is hoped that our reanalysis of Wood's (1935) data, as well as new information presented herein, will clarify this issue.

Relative to other heteromyids, kangaroo rats have received considerable attention from systematic biologists. Studies of interspecific relationships based on morphology include the works of Grinnell (1921, 1922), Wood (1935), Burt (1936), Setzer (1949), Lidicker (1960), Kelly (1969), Best and Schnell (1974), and Schnell et al. (1978). Phylogenies resulting from these analyses are far from concordant (see Schnell et al. 1978). Studies of interspecific relationships in *Dipodomys* based on karyology (Stock 1974) and protein electrophoresis (Johnson and Selander 1971) present still different pictures of kangaroo rat relationships. It is not within the scope of this study to reevaluate *Dipodomys* species relationships; we only wish to call attention to the need for a thorough, comprehensive analysis utilizing a broad spectrum of approaches. In view of the complexity of the situation, we suggest that chromosomal banding studies, DNA hybridization, and protein sequencing analyses may provide new insights to this old problem.

SPINY POCKET MICE: GENUS *Heteromys*.—Spiny pocket mice of the genus *Heteromys* are, by far, the least studied of all heteromyids. To date, the genus has no fossil record. According to Hall (1981), *Heteromys* is represented by 10 Recent species ranging from southern Mexico to northwestern South America. Until very recently, Goldman's (1911) revision of *Heteromys* stood as the most recent taxonomic work focusing on interspecific relationships in the genus. Rogers and Schmidly (1982) have reevaluated interspecific relationships in Hall's (1981) *H. desmarestianus* group (exclusive of *H. gaumeri*) using external, cranial, and bacular charac-

ters and have recognized only two of five species recognized by Hall. Specific results of their analysis will be discussed in a later section of this paper. A comprehensive study of chromosomal and biochemical variation in the genus is now in progress (D. S. Rogers, pers. comm.). *Heteromys* shows close phyletic ties with spiny pocket mice of the genus *Liomys* (Goldman 1911, Wood 1935, M. S. Hafner 1982), and the two genera are placed together in the subfamily Heteromyinae. The relationship of the Heteromyinae to other heteromyid subfamilies remains obscure.

SPINY POCKET MICE: GENUS *Liomys*.—Five extant species of *Liomys* are currently recognized, ranging from northern Mexico to Panama. The fossil record of the genus extends back to late Pliocene of Kansas (Hibbard 1941). Goldman's (1911) revision of *Liomys* has been substantially updated by Genoways (1973), who subducted 6 of 11 species recognized prior to his analysis. As discussed previously, *Liomys* shows its closest phyletic affinity to *Heteromys*, and the placement of these genera into the subfamily Heteromyinae has never been seriously contested.

KANGAROO MICE: GENUS *Microdipodops*.—There are but two living species of kangaroo mice (*M. megacephalus* and *M. pallidus*), both forms restricted to the arid Great Basin region of western North America. Fragmentary fossil material (referred to *M. megacephalus*) is known from late Pleistocene of Nevada (Miller 1979). The genus was described by Merriam (1891) and subsequently revised by Hall (1941) and J. C. Hafner (1981a). D. J. Hafner et al. (1979) affirmed the specific status of the two living forms using morphological, chromosomal, and biochemical evidence.

The genus *Microdipodops* is certainly the most problematic heteromyid in terms of our understanding of its phylogenetic affinities within the family. Wood (1935:107–117) discussed at length the morphology of *Microdipodops* relative to *Dipodomys* and *Perognathus* (subgenus *Perognathus*). Although he pointed out a close morphological resemblance between *Microdipodops* and *Perognathus* (see also J. C. Hafner 1976, 1978), Wood remained equivocal as to its phyletic placement (see Wood 1935:78). Both Reeder

(1956) and Lindsay (1972) derived *Microdipodops* and *Dipodomys* from the Mio-Pliocene form *Cupidinimus* and, thus, suggest dipodomysine affinities for kangaroo mice. In contrast, J. C. Hafner (1976, 1978) derived *Microdipodops* from perognathine stock while recognizing the possibility that kangaroo mice may represent an independent heteromyid lineage with no close relatives in the extant fauna. M. S. Hafner (1982) assessed the phylogenetic affinities of *Microdipodops* using electrophoretic and immunological evidence and concluded that kangaroo mice are genetically somewhat closer to kangaroo rats than to other living heteromyids. In this study we will reexamine the phyletic position of *Microdipodops* relative to other heteromyids and introduce new evidence relevant to the issue.

POCKET MICE: GENUS *Perognathus*.— The genus *Perognathus*, as defined prior to this study, includes 25 nominal species spanning much of western North America from southern Canada to central Mexico. The genus exhibits an unusually long and complete fossil record extending from Lower Miocene of western North America (Reeder 1956, Lindsay 1972).

In traditional treatments dating from Merriam (1889), *Perognathus* is subdivided into two subgenera, *Perognathus* and *Chaetodipus*. For reasons detailed beyond, we recommend that *Chaetodipus* be elevated to full generic status and, thus, reduce the number of extant *Perognathus* species to a total of nine.

Species groups within the genus *Perognathus* (*sensu lato*) are not clearly delineated using the evidence available at present. Studies of interspecific relationships based on morphology include works by Merriam (1889), Osgood (1900), Wood (1935), and Caire (1976). Systematic treatments based on karyology include studies by Patton (1967a, 1967b) and Williams (1978). Protein variation in the genus (with emphasis on *Chaetodipus*) has been analyzed by Patton et al. (1981). It appears that a complete elucidation of interspecific relationships within *Perognathus* and *Chaetodipus* must await future studies involving finer considerations of chromosomal evolution (banding studies) and molecular change (DNA hybridization; protein sequencing).

COMPARATIVE ANALYSIS OF THE MALE REPRODUCTIVE SYSTEM

A large body of data concerning morphology of the glans penis, baculum, spermatozoa, and accessory glands of the male reproductive system in heteromyids is now available and may be brought to bear on the issue of phyletic relationships within the family. Much of the evidence presented here is previously unpublished; in particular, we wish to call attention to the work of Kelly (1969), which is a particularly thorough analysis of penile and bacular variation in heteromyids. Figure 1 illustrates representative phalli, bacula, and spermatozoa from eight geomyoid taxa. In the interest of brevity, we have omitted detailed descriptions of the various structures in individual species; for this, we refer the reader to the original literature.

Glans Penis

The glans penis has been shown to be a valuable tool in systematic studies of rodents (Hooper 1961, 1962, and included references, Hershkovitz 1966, Lidicker 1968, and others) but the glans penis of heteromyids has received little attention. Noteworthy exceptions include Kelly's (1969) study of penile variation in *Dipodomys*, Genoways' (1973) study of the glans penis in *Heteromys* and *Liomys*, and J. C. Hafner's (1976) analysis of penile variation in *Dipodomys*, *Perognathus*, and *Microdipodops*. Following is a synthesis of the results of these studies, emphasizing salient differences in penile morphology among heteromyids.

Kelly (1969) and Genoways (1973) reported that the glans penes of *Heteromys* and *Liomys* (Fig. 1 C, D) are similar in overall structure and share several characteristics unique among heteromyids. These features (spineless phalli; glans long relative to bacular length; unique urethral lappet morphology) may be viewed as shared-derived characters supporting the union of these genera into the subfamily Heteromyinae. Outgroup comparison with *Thomomys* (Kelly 1969) supports the derived nature of penile characters used to define the Heteromyinae.

Based on outgroup comparison with geomyids, the male phalli of *Dipodomys*, *Micro-*

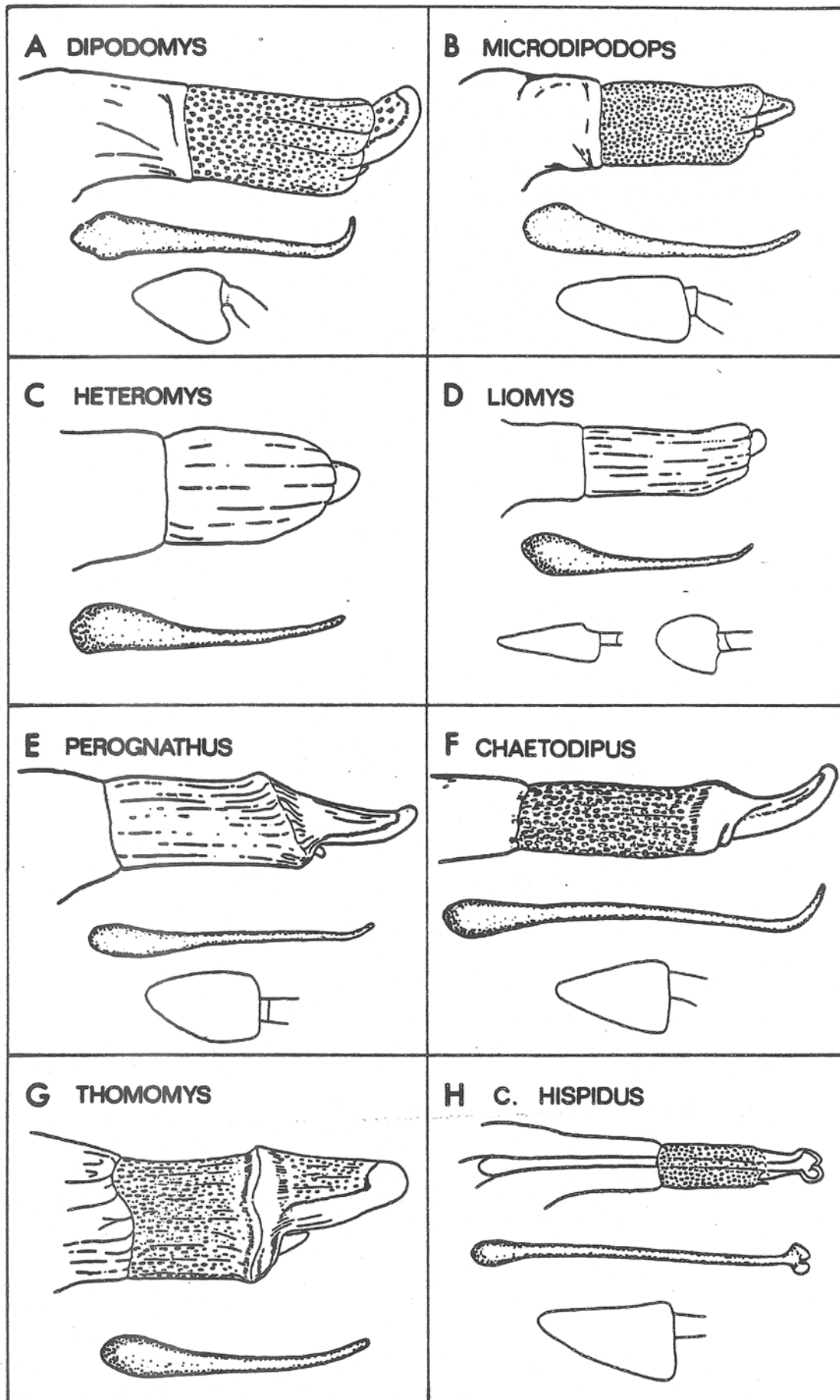


Fig. 1. Representative phalli, bacula, and spermatozoa from seven heteromyid and one geomyid taxa. Phalli and bacula are shown in lateral view. To facilitate comparison, all illustrations are drawn to different scales. Sperm from *Liomys salvini* (right) and *Liomys pictus* (left) are illustrated. Sperm from *Heteromys* and *Thomomys* are as yet undescribed. (Illustrations modified from Kelly, 1969, Genoways, 1973, and J. C. Hafner, 1976).

dipodops, and pocket mice of the subgenus *Perognathus* (Fig. 1 A, B, E) have retained a broad spectrum of primitive geomyoid characters. The phallus of *Thomomys* (Fig. 1 G) most closely resembles that of perognathine pocket mice (Kelly 1969), and in this and other respects (see beyond) members of the subgenus *Perognathus* appear to be extremely conservative morphologically.

The glans penis of *Microdipodops* is similar in most respects to that of *Dipodomys* (Kelly 1969). Importantly, several phallic characters shared between *Microdipodops* and *Dipodomys* (including morphology of urethral lappets and external spines) are unique within the Geomyoidea and, hence, are of phylogenetic significance. Those features used by J. C. Hafner (1976) to suggest a close relationship between *Microdipodops* and members of the subgenus *Perognathus* (cylindrical, nonelongated phallus; dorsal groove) are now known to be present in the geomyid genus *Thomomys* (Kelly 1969) and are thus regarded as shared-primitive characters. The sharply upturned distal portion of the phallus in *Dipodomys* (Fig. 1 A) clearly distinguishes kangaroo rats from all other heteromyid genera.

The male phallus in pocket mice of the subgenus *Chaetodipus* (Fig. 1 F) is unique among all geomyids examined thus far (Kelly 1969, J. C. Hafner 1976). The chaetodipine penis is long and slender, lacks urethral lappets, and the rim of the terminal crater forms a ventlike urethral opening. The structure of the chaetodipine phallus is, doubtlessly, derived within the Heteromyidae. The terminal portion of the phallus in *Perognathus* (*Chaetodipus*) *hispidus* (Fig. 1 H) is markedly different from that of other chaetodipine species in possessing a distinctly ornate tip.

Os Baculum

Bacular variation in heteromyids has received considerable attention, including studies by Burt (1936, 1960), Schitoskey (1968), Kelly (1969), Genoways (1973), Best and Schnell (1974), and J. C. Hafner (1976). Because of considerable intrageneric variation in bacular morphology, the use of this structure in delineating higher-level heteromyid relationships is very limited.

A combination of three bacular features (bulbous base, stout midregion, sharply upturned distal end) clearly distinguishes *Dipodomys* species from other heteromyids (Fig. 1 A). The bacula of *Microdipodops*, *Heteromys*, *Liomys*, *Thomomys*, *Geomys*, and *Pappogeomys* also have bulbous bases, and this feature appears to be primitive for the Geomyoidea. The bacula of certain pocket mice of the subgenus *Chaetodipus* (Fig. 1 F) have moderately to sharply upturned distal ends (Anderson 1964), a feature which appears to have been derived independently in *Dipodomys* and *Chaetodipus*.

Pocket mice of the subgenus *Chaetodipus* are clearly distinguished from members of the subgenus *Perognathus* using bacular morphology (Burt 1936, J. C. Hafner 1976). The baculum in chaetodipine pocket mice is long relative to body length such that the soft tissue of the penis terminates approximately midway along the length of the baculum. In perognathine pocket mice, the baculum is much shorter and soft tissue extends approximately two-thirds of the length of the baculum. The baculum of *Perognathus* (*Chaetodipus*) *hispidus* (Fig. 1 H) possesses an ornate, trifold tip seen nowhere else in the Geomyoidea.

Spermatozoan Morphology

Genoways (1973) presented a rather detailed study of the spermatozoa of *Liomys* and provided a brief statement as to the relative shape of the sperm head in *Perognathus pernix* (*Heteromys* was not examined). J. C. Hafner (1976) analyzed gross sperm morphology in *Dipodomys*, *Microdipodops*, and additional species of *Perognathus*. The head and neck region (minus the acrosomal tip) of representative heteromyid spermatozoa are illustrated in Figure 1.

The spermatozoa of *Microdipodops* (Fig. 1 B) are characteristically large, with especially long heads. The head is roughly triangular in shape, with rounded vertices. The sperm tail is of medium length relative to other heteromyid species. Species of the subgenus *Perognathus* (Fig. 1 E) possess spermatozoa similar in general morphology to those of *Microdipodops*, except that the head is smaller and the tail shorter. These similarities do

not indicate a close phyletic relationship between *Microdipodops* and *Perognathus* (subgenus *Perognathus*), inasmuch as the sperm of certain species of *Liomys* also share these features (Genoways 1973).

The spermatozoa of chaetodipine pocket mice are easily distinguished from those of all other heteromyids (Fig. 1 F, H). Here, the sperm head resembles a somewhat elongated isosceles triangle with acute (unrounded) vertices. The sperm of *Perognathus* (*Chaetodipus*) *hispidus* is peculiar in some respects because the tail is very long and the neck region is not discernible.

In *Dipodomys*, the spermatozoan head approximates an equilateral triangle (Fig. 1 A) and this feature alone distinguishes kangaroo rat sperm from that of other heteromyids; the apex of the sperm head is rather acute and the tail long.

Accessory Glands of the Male Reproductive Tract

With the exception of Gunther's (1960) description of the male reproductive tract in *Thomomys*, no studies of geomyoid reproductive tract morphology have appeared prior to this analysis. The descriptions below are

taken from M. S. Hafner (1979). The male accessory reproductive gland complements of 11 geomyoid genera are listed in Table 1. *Microtus* is included in Table 1 to represent the most common muroid (outgroup) condition, i.e., all gland complements present (Arata 1964).

Loss of glandular complements appears to be much more widespread among geomyid than among heteromyid taxa. Patterns in loss or retention of gland complements agree in general with patterns seen in muroid rodents (Arata 1964); for example, it is not uncommon to find the preputial glands absent in taxa representing either group of rodents (geomyoids or muroids), whereas the bulbo-urethral glands are present thus far in all muroid and geomyoid taxa examined.

By far the most striking changes in the male reproductive tract of geomyoid rodents involve changes in the morphology of the vesicular glands (seminal vesicles). In the large majority of geomyoids (and in rodents in general), the vesicular glands are elongate, hook- or cane-shaped, translucent structures. In contrast, most specimens examined thus far of the genus *Thomomys* (subgenus *Megascapheus*) have tubular, translucent vesiculars (J. L. Patton, pers. comm.), and all specimens

TABLE 1. Male accessory reproductive gland complements in 14 geomyoid taxa (+ indicates gland complement present). *Microtus* is representative of the typical muroid condition (Arata, 1964). Terminology as per Arata (1964).

Taxa examined	Gland complements ¹							
	v ²	vmp	vlp	ap	dp	a	bu	p
<i>Thomomys bottae</i>	3		+	+	+		+	
<i>Thomomys umbrinus</i>	3		+	+	+		+	
<i>Geomys bursarius</i>	1		+	+	+	+	+	+ ³
<i>Zygoeomys trichopus</i>	1		+		+	+	+	
<i>O. (Orthogeomys) grandis</i>	1		+	+			+	
<i>O. (Macrogeomys) heterodus</i>	1		+	+	+	+	+	
<i>Pappogeomys gymnurus</i>	1		+	+	+	+	+	
<i>Heteromys desmarestianus</i>	1		+			+	+	
<i>Liomys pictus</i>	1	+	+	+	+	+	+	
<i>Perognathus spinatus</i>	2	+	+	+	+	+	+	
<i>Perognathus parvus</i>	1	+	+	+	+	+	+	+
<i>Microdipodops megacephalus</i>	1		+	+	+	+	+	+
<i>Dipodomys ordii</i>	1	+	+	+	+	+	+	
<i>Dipodomys merriami</i>	1	+	+	+	+	+	+	
<i>Microtus</i> sp.	1	+	+	+	+	+	+	+

¹v = vesicular; vmp = ventromedial prostate; vlp = ventrolateral prostate; ap = anterior prostate; dp = dorsal prostate; a = ampullary; bu = bulbo-urethral; p = preputial.

²Numbers refer to shape of vesicular gland complement: (1) elongate; (2) round; and (3) short, tubular.

³The presence or absence of preputial glands in *Geomys* was difficult to ascertain due to the presence of large amounts of connective tissue and fat in the preputial region.

examined belonging to the subgenus *Chaetodipus* of the genus *Perognathus* have round, smooth, yellow- to gray-colored vesicular glands (pinkish and granular in appearance in fresh specimens). The morphologies of the respective vesicular glands in *Thomomys* and *Chaetodipus* are unique among those described thus far for rodents. This unusual vesicular morphology in the subgenus *Chaetodipus* is particularly striking in that all specimens examined belonging to the subgenus *Perognathus* have more typical rodent vesicular glands. Typical *Perognathus* and *Chaetodipus* male reproductive tracts are contrasted in Figure 2.

Among the heteromyid genera examined (Table 1), *Heteromys* shows an unusually high level of evolutionary loss of glandular complements (4 of 8 glands are absent). In contrast, all glandular complements are present in *Perognathus parvus* (subgenus *Perognathus*). In *Heteromys* and *Microdipodops*, the absence of ventromedial prostates is certainly a derived condition; however, it would be dangerous to link these two genera phylogenetically based solely on the absence of a single gland complement, especially when loss of ventromedial prostates is seen in the outgroup (Geomyidae). Similarly, the presence of preputial glands in *Perognathus parvus* and *Microdipodops* should not be used to infer a special phylogenetic relationship; the genera have merely retained a gland complement normally present in nongeomyoid rodents.

A conservative assessment of the data reviewed above leads to five conclusions:

1. *Liomys* and *Heteromys* show close phylogenetic relatedness based primarily on morphology of the glans penis.
2. *Dipodomys* and *Microdipodops* are also suggested to be phylogenetically allied, again based largely on morphology of the glans penis.
3. Pocket mice of the subgenus *Chaetodipus* show only remote morphological similarities to species of the subgenus *Perognathus*. All aspects of the male reproductive system support this conclusion.
4. Within *Chaetodipus*, *P. (Chaetodipus) hispidus* is unique with respect to mor-

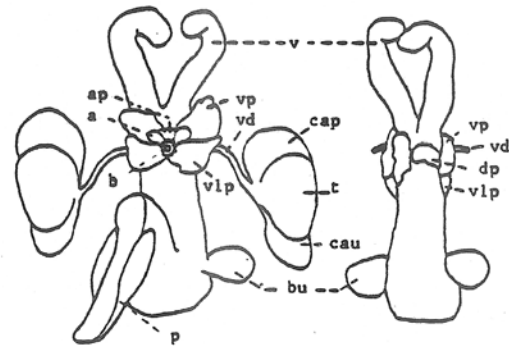
phology of the glans penis, baculum, and spermatozoa.

5. Species of the pocket mouse subgenus *Perognathus* show extreme morphological conservatism with respect to the male reproductive system.

BIOCHEMICAL VARIATION

Analyses of intrapopulation protein variation in *Microdipodops* (D. J. Hafner et al. 1979) and *Perognathus*, subgenus *Chaetodipus* (Patton et al. 1981), have revealed levels of genetic polymorphism and heterozygosity approximately equivalent to averages summarized for 46 species of mammals by Nevo (1978). In contrast, the average values of polymorphism and heterozygosity measured in populations of *Dipodomys* (Johnson and

PEROGNATHUS



CHAETODIPUS

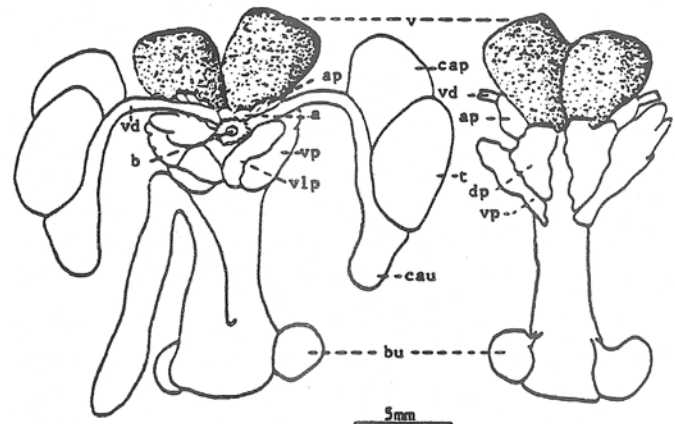


Fig. 2. Ventral (left) and dorsal (right) views of the male reproductive tracts of *Perognathus (Perognathus) longimembris* and *P. (Chaetodipus) spinatus*. The urinary bladder (b) has been excised to reveal underlying accessory gland complements. Abbreviations as per Table 1 with following additions: caput epididymis (cap); cauda epididymis (cau); testis (t); vas deferens (vd).

Selander 1971, Patton et al. 1976) are only half as large as those measured in most mammalian populations. Johnson and Selander (1971) suggest that a combination of phylogenetic and ecological factors may explain depressed levels of intrapopulation genetic variation in kangaroo rats relative to other mammals. Indeed, future genetic analyses of kangaroo rat populations may find a causal link between ecological amplitude (niche width) and genetic variation, but a clear connection was not evident in Johnson and Selander's (1971) study.

Interpopulation genetic differentiation in *Dipodomys* and *Perognathus* (*Chaetodipus*) has been shown to be approximately commensurate with values measured between populations of other rodents, and mammals in general (Johnson and Selander 1971, Csuti 1979, Patton et al. 1981). Genetic studies at the intra- and interpopulation level are currently in progress for the genera *Liomys* and *Heteromys* (D. S. Rogers, pers. comm.).

Estimates of interspecific protein differentiation within the three heteromyid genera thus far examined (*Microdipodops*, *Dipodomys*, and *Perognathus*, subgenus *Chaetodipus*) reveal two divergent patterns. First, *Microdipodops megacephalus* and *M. pallidus*, which are sibling species on morphological criteria (D. J. Hafner et al. 1979), are genetically differentiated at the appropriate "sibling species level" as defined by Zimmerman and Nejtek (1977) based on data from 10 species of mammals. Similarly, genetic distances measured between morphologically well-differentiated species of *Dipodomys* (Johnson and Selander 1971) are approximately equivalent to those measured between well-differentiated species in other mammalian taxa (Zimmerman and Nejtek 1977). In *Perognathus*, on the other hand, Sarich (1975), M. S. Hafner (1979, 1982), and Patton et al. (1981) have shown that the genetic distance measured between perognathine and chaetodipine pocket mice is extremely large, in fact larger than that measured between *Liomys* and *Heteromys*. Clearly, the rate of exomorphologic change between *Perognathus* and *Chaetodipus* has lagged far behind that of biochemical change. Moreover, all indications from comparative rate tests suggest that protein evolu-

tion has proceeded at the same rate within the perognathine and heteromyine lineages. Thus, due to extreme exomorphological conservatism, *Perognathus* and *Chaetodipus* are, in a sense, "cryptic genera."

Studies of albumin (M. S. Hafner 1982) and transferrin (Sarich 1975) immunology in heteromyids show *Microdipodops* to be extremely conservative with respect to rate of protein change through time. In immunological comparisons with nonheteromyid outgroups, *Microdipodops* shows consistently lower levels of protein change relative to other heteromyids. According to Sarich (pers. comm.), the high degree of protein conservatism seen in *Microdipodops* is unique among taxa thus far examined immunologically belonging to several different mammalian orders. At present, we have no explanation, or even hypotheses, to account for extreme protein conservatism in *Microdipodops*.

KARYOTYPIC EVOLUTION

Chromosomal Variation

Heteromyid and geomyid rodents have attracted a great deal of attention from evolutionary biologists and systematists. Interest in these rodents stems, among other reasons, from the great degree of chromosomal variation across the group. Whereas karyotypic information has been applied commonly to questions at the species level, such information has not been used adequately in assessing evolutionary relationships at higher levels. Further, the fusion paradigm of karyotypic reorganization has been invoked to the near exclusion of other possible mechanisms that alter diploid number (e.g., Thaeler 1968, Davis et al. 1971, Genoways 1973, Selander et al. 1974, Stock 1974, Williams and Genoways 1975, Williams 1978). The Robertsonian fusion model (Robertson 1916), whereby the karyotype is reduced in diploid number through the joining of uniarmed chromosomes to form biarmed elements, has reigned as the predominant view in interpretations of geomyoid chromosomal evolution despite there being no convincing argument to support its occurrence. In geomyoid studies, empiricism has lagged well behind theoretical considerations; and other hypoth-

eses, alternative to the fusion paradigm, have not been seriously considered (see also Imai and Crozier 1980).

Diploid numbers are now known for representatives of all genera and subgenera within the Geomyoidea (Heteromyidae: *Dipodomys*, Cross 1931, Matthey 1952, 1956, Csuti 1971, Dingman et al. 1971, Fashing 1973, Stock 1974; *Microdipodops* D. J. Hafner et al. 1979, J. C. Hafner 1981a; *Chaetodipus*, Patton 1967a, 1969, 1970; *Perognathus*, Patton 1967b, Williams 1978; *Liomys*, Genoways 1973; *Heteromys*, Genoways 1973, A. L. Gardner, pers. comm., D. S. Rogers, pers. comm., M. S. Hafner and J. C. Hafner, unpubl. data; Geomyidae: *Geomys*, Davis et al. 1971, Baker et al. 1973, Selander et al. 1974, Williams and Genoways 1975, Hart 1978, Honeycutt and Schmidly 1979; *Pappogeomys*, Laguarda-Figueras et al. 1971, Berry and Baker 1972, Hart and Patterson 1974, Smolen et al. 1980, Honeycutt and Williams 1982; *Thomomys*, Thaeler 1968, 1972, 1973, 1974a, 1974b, 1976, 1977, 1980, Thaeler and Hinesley 1979; *Thomomys*, subgenus *Megascapheus*, Patton and Dingman 1968, 1970, Patton et al. 1972, Patton 1973, 1980, Patton and Yang 1977, Patton and Feder 1978, J. C. Hafner et al. 1983; *Orthogeomys*, M. S. Hafner 1979, M. S. Hafner and J. C. Hafner, unpubl. data; *Zygogeomys*, M. S. Hafner, 1979, M. S. Hafner and J. C. Hafner, unpubl. data).

Figure 3 summarizes the chromosomal variability for geomyoid species. If Robertsonian chromosomal events (fusion and/or fissions) were chiefly responsible for effecting diploid number change in the six major groups of the Geomyidae, the dots representing karyotypes within a species and species within the major groupings would be expected to be aligned in vertical patterns. It can be seen (Fig. 3A) that this does not appear to be the general case. In the Heteromyidae (Fig. 3B), a similar situation exists. Within the major heteromyid groups, karyotypes are not, for the most part, aligned in vertical arrays. Lacking G- and C-banding information for most groups in the Geomyoidea, it is premature to speculate on the specific mechanisms, or actual mechanics, of chromosomal rearrangement. Moreover, even banding data will not allow us to assess directionality of change, vis-a-vis the fusion/fission controversy.

Directionality in Chromosomal Evolution

Geomyoid karyotypic data do warrant a close evaluation of directionality of chromosome number change within the superfamily, irrespective of the mechanism(s) that may be involved in the change (J. C. Hafner 1981b). The Geomyoidea, with its high degree of diploid number variation and doubtless monophyletic origin, is an appropriate group in which to examine polarity in diploid number change. Are high numbers primitive with a general reductional trend, or are low numbers primitive with an increasing trend? If no general trend is discernible, we must consider the possibility that both trends operate, but in separate geomyoid lineages or at different times in the history of a single lineage.

In this analysis we have considered 12 major taxonomic groups (genera and subgenera listed above). Note that we include both subgenera within the genus *Thomomys* (*Thomomys* and *Megascapheus*, sensu Thaeler 1980) as well as the subgenera *Chaetodipus* and *Perognathus* of the genus *Perognathus*. A histogram plot of species numbers versus diploid numbers (including intraspecific chromosomal variation) reveals that the distribution of geomyoid karyotypes is rather trimodal and seems to exhibit a damped oscillatory pattern (Fig. 4). Therefore, the array of diploid numbers can be trisected into chromosomal subgroups or character states: low chromosome numbers ($2n = 34-50$), medium numbers (about 60), and high diploid numbers (68-88).

Invoking the criterion of character state distribution, we first attempt to assign polarity by using in-group analysis. According to the criterion of in-group analysis, the character state that occurs most frequently within the group under study (the common state) is considered to be the primitive state (Stevens 1980:335-37, Criterion 1A). The low chromosome number character state contains 47 karyotypes, the medium state 44 karyotypes, and the high number state has 27 karyotypes (Fig. 4). Although the evidence may not be strong, the criterion of in-group analysis would lead to the conclusion that lower chromosome numbers ($2n = 34-64$) are primitive and higher numbers ($2n > 64$) are derived, which is contradictory to earlier

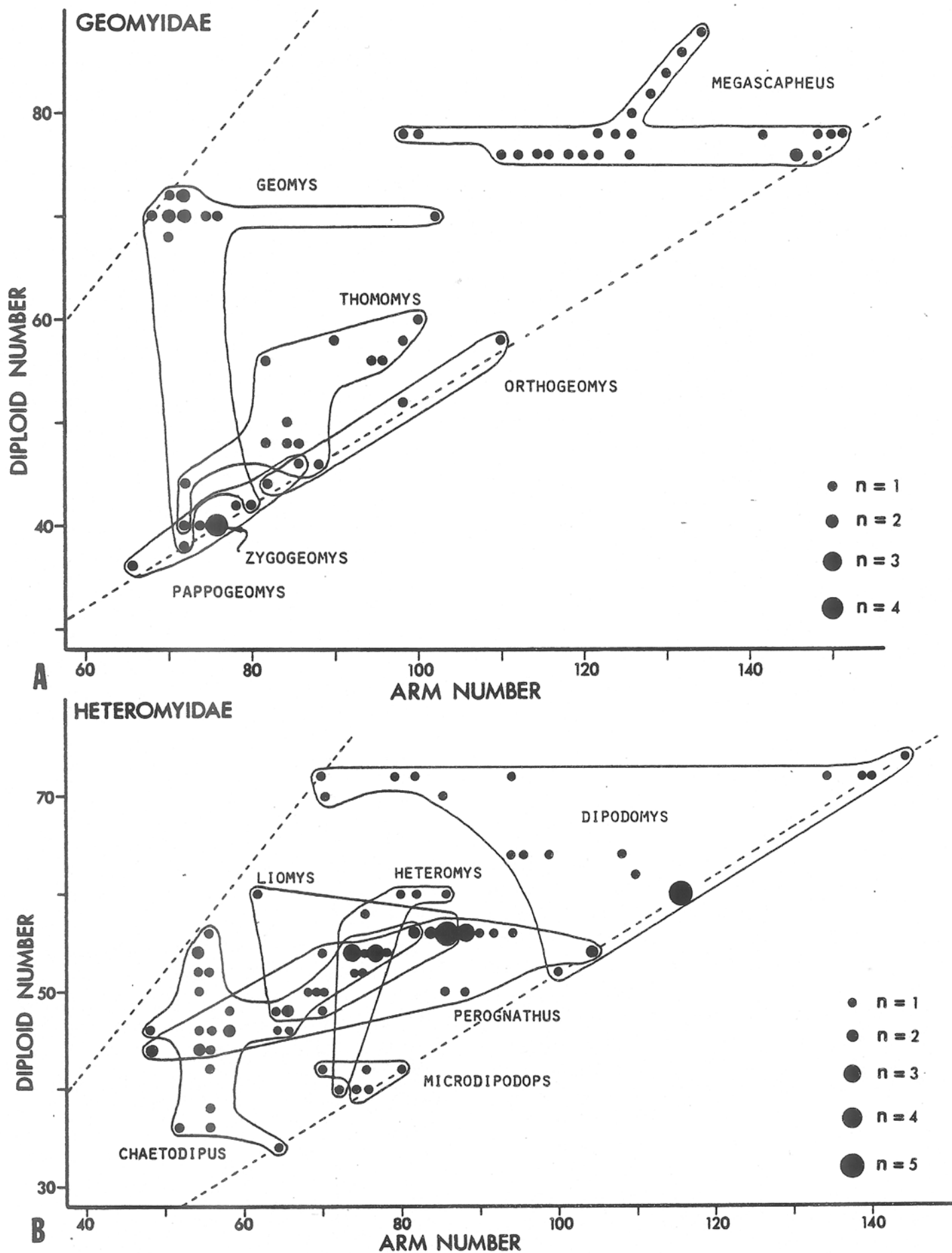


Fig. 3. Chromosomal variation in the Geomyoidea: A, Geomyidae; B, Heteromyidae. See text for data sources. Dashed lines represent the karyotype bounds; n = number of karyotypes. Odd diploid numbers have been omitted for clarity.

published opinions.

To view this in-group analysis at a higher taxonomic level, we next examine the number of major geomyoid groups versus diploid numbers (Fig. 5). Again, the criterion would maintain that the most common character state across the major groupings is primitive. The low chromosome number character state contains 10 of the 12 major geomyoid taxa. In comparison, the medium character state contains 8 of the major taxa and the high chromosome number state contains only three major taxa (*Dipodomys*, *Geomys*, and *Megascapheus*; Fig. 4). The conclusion to be drawn from this refined in-group treatment, once again, is that the lower diploid numbers are primitive and the higher character state derived.

Such evolutionary polarity, assigned by in-group analysis must be confirmed using other criteria. We therefore must consider out-group analysis (see Stevens 1980:337-340, Criterion 1B). Following the out-group method, the character state that is shared with the out-group is taken to be primitive. It has been suggested by some workers that the murids stand as a distant sister group to the Geomyoidea. The range of diploid numbers in the Muridae (Fig. 6A) is almost entirely with-

in the low diploid number character state defined earlier; the mode for the Muridae is $2n = 48$. Selecting another out-group for comparison, the Cricetidae, again we see that the vast majority of cricetid karyotypes fall into the low chromosome number character state (mode: $2n = 48$; Fig. 6B). Further, out-group comparison with the Sciuridae (Fig. 6C; mode: $2n = 38$) and the Aplodontidae ($2n = 46$; Matthey 1973), two families commonly believed to represent primitive rodents, again corroborates the earlier assigned polarity. Thus, all out-group comparisons indicate that the low character state is primitive.

One other criterion that can be used to determine the polarity of character states is that of correlation among character states (Stevens 1980:345-348, Criterion 5). This argument is based on the assumption that primitive character states frequently occur together. As Stevens (1980) aptly noted, the criterion of correlation should be used in combination with other criteria (e.g., in-group and out-group analyses) as has been done here.

One morphological character whose character state polarity is reasonably well supported is that of sulcation in the upper incisors. It seems that grooved upper incisors is

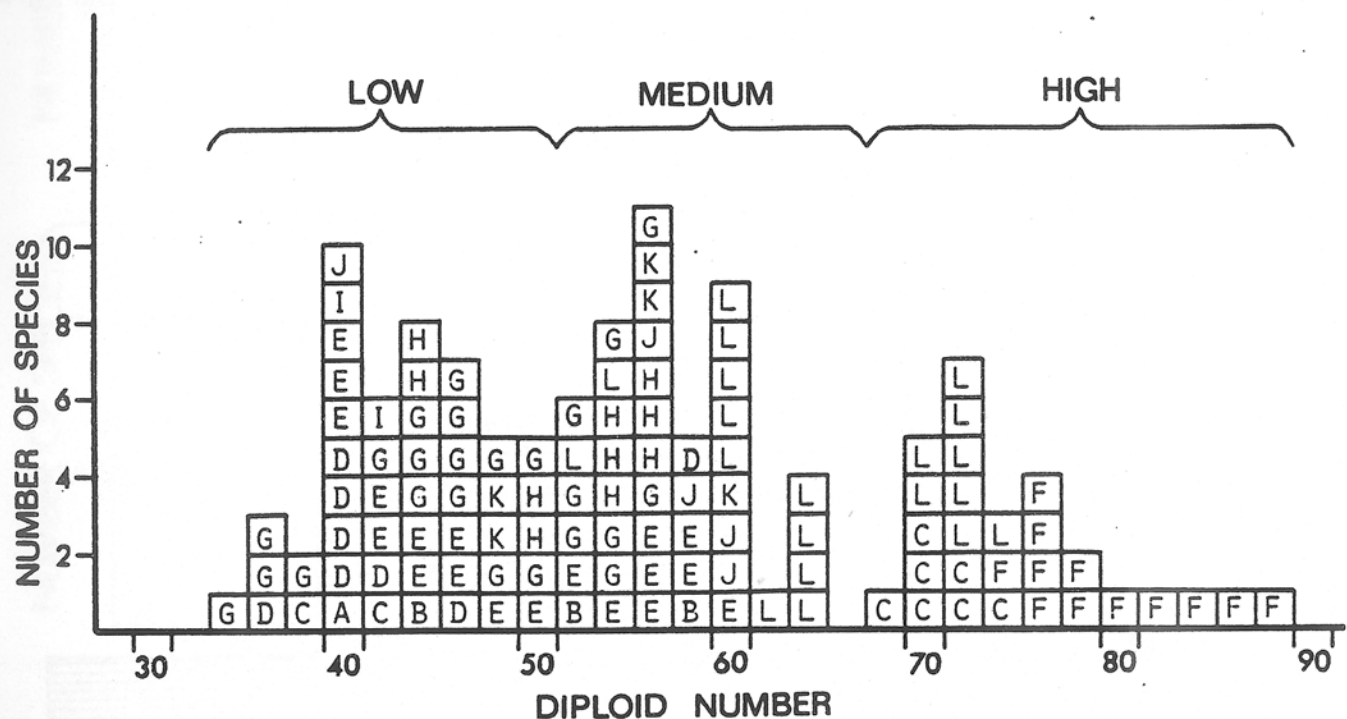


Fig. 4. Frequency distribution of the chromosome numbers in the Geomyoidea. The distribution is trimodal and skewed to the right. Odd diploid numbers have been omitted for clarity. GEOMYIDAE: A, *Zygoeomys*; B, *Orthogeomys*; C, *Geomys*; D, *Pappogeomys*; E, *Thomomys*; F, *Megascapheus*. HETEROMYIDAE: G, *Chaetodipus*; H, *Petrognathus*; I, *Microdipodops*; J, *Heteromys*; K, *Liomys*; L, *Dipodomys*.

plesiomorphic for groups within the Geomyoidea, with loss of a sulcus being the derived state (see Merriam 1895, Wood 1935, Russell 1968). Within the Geomyidae, only one extant group totally lacks sulci in the upper incisors. This is the smooth-toothed pocket gophers, which include *Thomomys* and *Megascapheus*. Interestingly, pocket gophers of the subgenus *Megascapheus* have the highest diploid numbers in the superfamily (Fig. 4), and *Megascapheus* is a major taxon that is entirely restricted to the high diploid number character state. Although it cannot be demonstrated that this instance of character state correlation is not due to chance alone, it is nevertheless in accord with the aforementioned polarity and the general trend for increase in chromosome number.

Within the Heteromyidae, kangaroo rats (*Dipodomys*) display a surfeit of derived morphological characters. Kangaroo rats are generally large in body size, have large eyes, long hind feet, expanded auditory bullae, a middorsal sebaceous gland, a long tail, and elaborate pelage markings; doubtless, kangaroo rats are the most morphologically derived members of the Heteromyidae (see beyond). Correlated highly with the derived nature of these characters is the high diploid

numbers of *Dipodomys*. Kangaroo rats are distributed chromosomally in the medium and high diploid number character states and exhibit the highest diploid number for the Heteromyidae. This correlation criterion again supports our initially assigned polarity. We shall argue beyond that *Microdipodops*, which exhibits relatively low diploid numbers ($2n = 40,42$), is much less derived morphologically than is *Dipodomys*.

Further evidence that can be used to support this mode of directionality comes from recent information on *Thomomys bottae* pocket gophers in Colorado (J. C. Hafner et al. 1980, J. C. Hafner et al. 1983). Throughout its extensive range, *T. bottae* is known to have, almost without exception, 76 chromosomes. However, a chromosomal race of *T. bottae* recently discovered in Colorado had 88 chromosomes (the second highest known for the Mammalia); yet allozymically it is nearly identical with the parental $2n = 76$ form. Clearly, this anomalous race, characterized by a diploid number of 88, is derived from the common $2n = 76$ form. Had the 88 chromosomal race been primitive, one would have expected its level of genic divergence to be equal to or greater than levels of major protein differentiation seen within the $2n =$

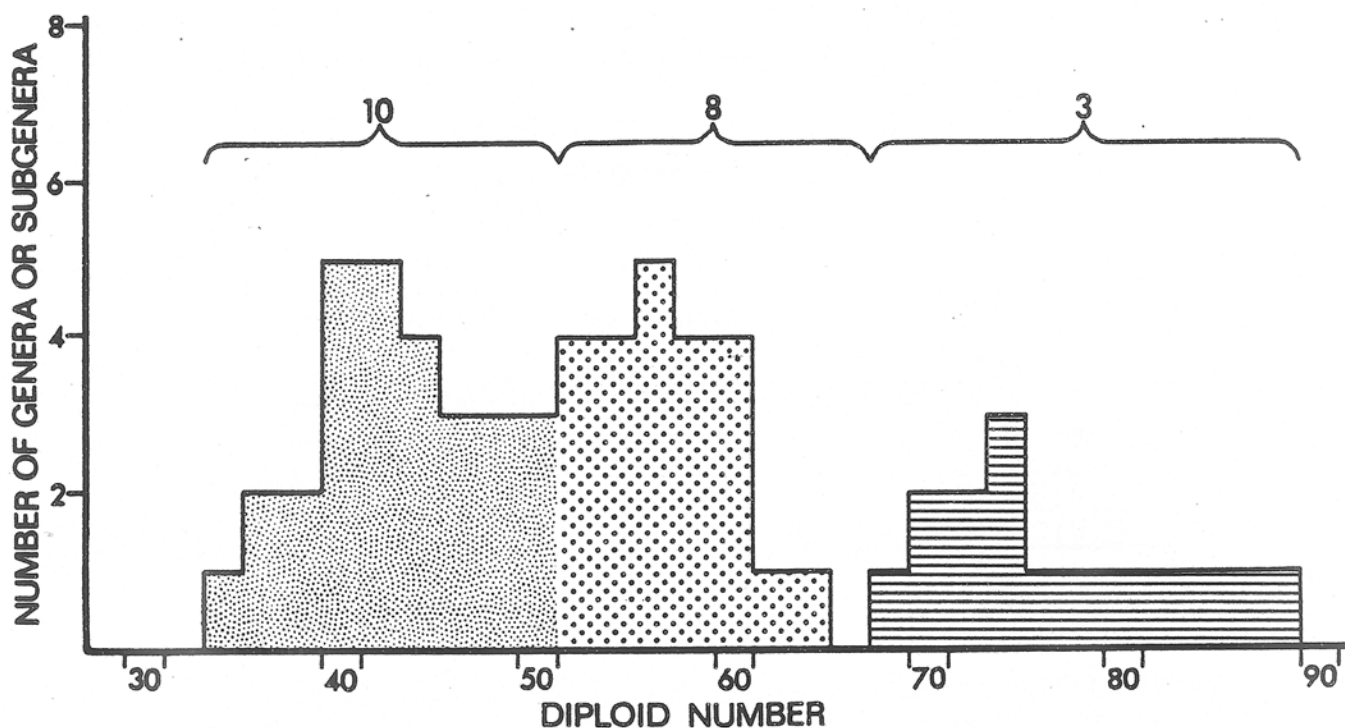


Fig. 5. Number of genera or subgenera versus diploid number. Numbers above brackets indicate number of major taxa represented in the three chromosomal character states.

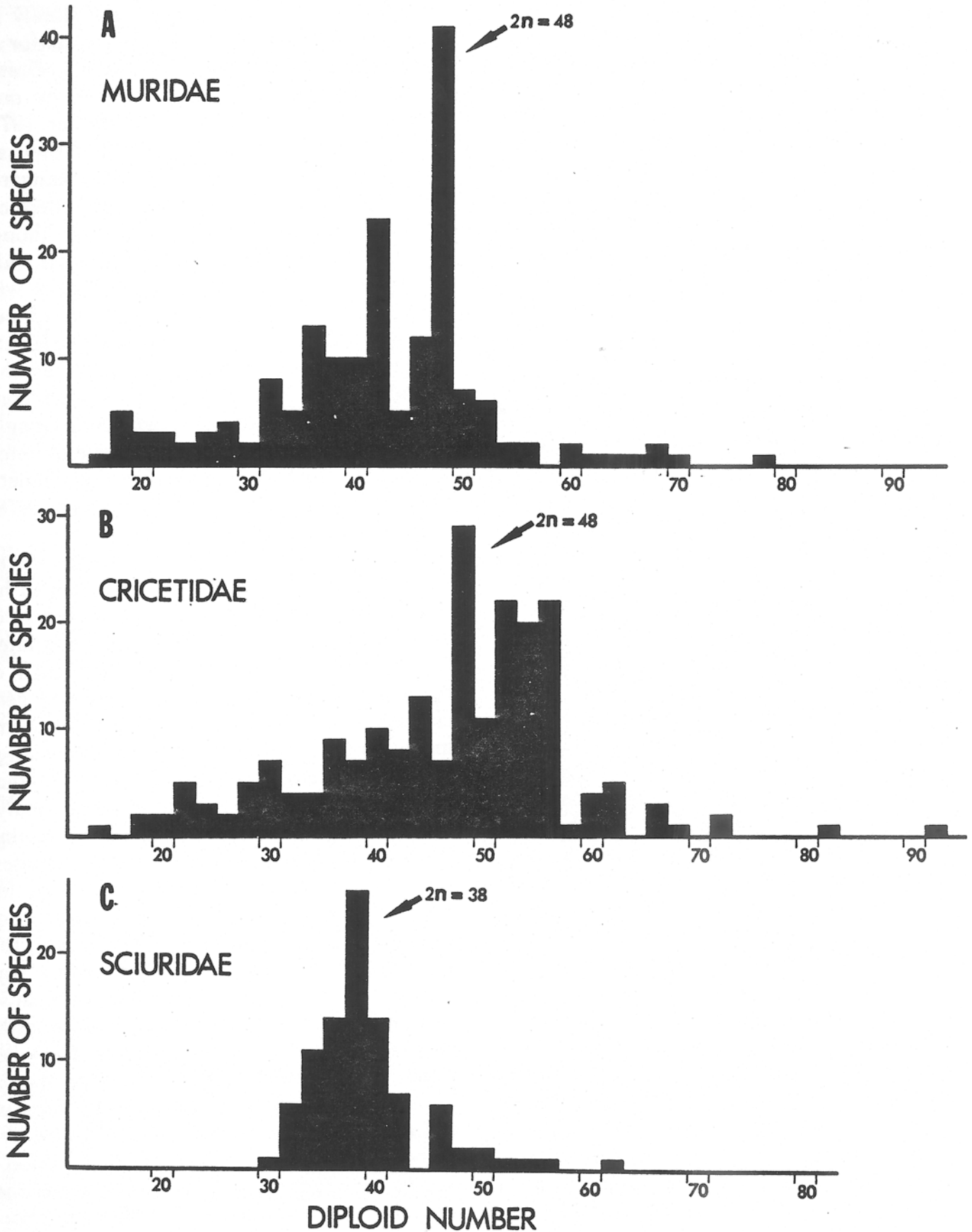


Fig. 6. Frequency distributions of diploid numbers for out-group comparisons: A, Muridae; B, Cricetidae; C, Sciuridae. Data are taken from Hsu and Benirschke (1967-1977) and Matthey (1973). Modal numbers are indicated in the figures.

76 form; this is not the case (see Patton and Yang 1977, J. C. Hafner et al. 1983). Importantly, this study represents the only thoroughly documented (chromosomal, allozymic, morphologic) demonstration of chromosomal directionality in the Geomyoidea.

In view of the foregoing, it seems that there is certainly ample justification for an alternative viewpoint with respect to the direction of chromosomal number change in the Geomyoidea. Several statements in the literature claiming high diploid numbers to be primitive for particular heteromyid groups and for the entire Geomyoidea (e.g., Williams 1978:605) are without support. We fully realize that reductional trends may indeed have occurred in specific geomyoid lineages; however, arguments used to support the diploid number reductional trend are weak and commonly utilize general biogeographical and ecological explanations (e.g., Williams and Genoways 1975). As pointed out by numerous authors, such reasoning is fraught with problems of circularity and is inadmissible in the assignment of polarity to character states. In contrast, in-group and out-group analyses and correlation among character states support an alternative view that low diploid numbers seem to be primitive for the Geomyoidea, and the overall direction of karyotypic change has been that of increase in chromosome number. We shall not speculate on the mechanism of increased numbers at this time, but will mention that fission may be involved, as well as other mechanisms such as chromosome duplication and addition of euchromatin or heterochromatin to centromeric fragments. A full discussion of karyotypic interconversions within the Geomyoidea must await the time when more karyotypes have been banded and we have a more firm understanding of the complexities of chromosomal evolution.

MORPHOLOGICAL EVOLUTION

Cladistic Analyses of Heteromyid Relationships

A prominent issue in the study of heteromyid relationships is the question of the subfamilial affinity of kangaroo mice. Since Mer-

riam's (1891) description of *Microdipodops* there has been much controversy as to whether kangaroo mice are most closely related to kangaroo rats or pocket mice (for review see J. C. Hafner 1978, M. S. Hafner 1982). Kangaroo mice are phenetically most similar to pocket mice (J. C. Hafner 1978), yet biochemical data indicate that they are somewhat more closely related to kangaroo rats (M. S. Hafner 1982). One might therefore hypothesize that *Microdipodops*, although being a cladistically old group, is patristically primitive and the similarities it shares with pocket mice are actually symplesiomorphous. Thus, it is necessary to perform a cladistic study in which shared-derived characters (hypothesized on the basis of out-group comparisons) are used to unite taxa. Accordingly, herein we evaluate this central issue in heteromyid phylogeny by analyzing the phenetic data of Wood (1935) and J. C. Hafner (1978), using cladistic procedures.

WOOD (1935) REVISITED.— Fifty-three characters were used by Wood (1935) in his treatment of the evolutionary relationships of kangaroo mice. Wood (1935:108) tabulated the character-state distribution for each of these characters across the heteromyid genera and concluded that kangaroo mice were most closely related to pocket mice. It is these tabulated data (Wood 1935:108) that are available for the present cladistic analysis; we have made no effort to reexamine Wood's characters and, for present purposes, accept his selection of characters and his interpretations concerning character homologies. In our analysis of Wood's data, the Heterominae (*Liomys* and *Heteromys*) was chosen for out-group comparison because most authors agree that it is an evolutionarily independent lineage quite removed from *Perognathus*, *Microdipodops*, and *Dipodomys*. Consequently, characters shared with *Liomys* and *Heteromys* (see Wood 1935:108) are hypothesized to be primitive. Ten of Wood's original characters were omitted from the analysis (all three genera shared seven characters with the out-group and three other characters were ambiguous), reducing the total number to 43 characters (Table 2).

The three possible phylogenetic hypotheses, showing the apportionment of the 43 morphological characters, are presented in

TABLE 2. Characters used in our reanalysis of Wood (1935). Ten of the 53 characters listed by Wood (1935:108) have been omitted in the reanalysis (see text).

Character number	Wood's (1935) ordering	Description of feature
1	1	Locomotion ricochetal
2	5	Protoloph of P ⁴ unites between hypocone and metacone.
3	7	Upper molars do not surround central lakes
4	8	Playa lake in metaloph of P ⁴ absent
5	9	Check teeth hypsodont
6	10	Occlusal pattern not elongated with crown
7	11	Teeth unrooted or form roots late in life
8	13	Bases of upper molars in orbit
9	14	Zygomatic process of Mx. expanded
10	15	End of palate not behind M ³
11	16	Pits in basioccipital absent
12	17	One pair of pterygoid fossae
13	18	Pterygoid fossae reach endocranium
14	19	Masseter separated from IOF by crest
15	20	Orbit overhung by frontal
16	21	Ethmoid foramen absent
17	22	Incipient postorbital process
18	23	Temporal fossa not distinct
19	24	Alisphenoid canal anterodorsad
20	25	Bulla extends anterad of glenoid
21	27	Squamosal perforated by bulla
22	28	Lacrymal expanded not free of Mx.
23	29	Parietal between squamosal and mastoid
24	31	Paroccipital process not latero-caudad
25	33	Knob for pulp cavity at lower edge of ascending ramus
26	34	Pit by M ₃ , no foramen on condyloid
27	35	Cervical vertebrae fused in part
28	36	No median ventral foramen in caudals
29	37	Notch in transverse process of caudals gently curved
30	38	Tail tufted
31	39	Scapula prolonged posteriorly
32	40	End of acromion not expanded
33	41	Short supinator crest
34	42	Deltoid crest ends steeply
35	43	Articulation of trapezium and scapholunar
36	44	Triangular obturator foramen
39	47	Process of pubis at front of obturator foramen
40	49	Cnemial crest ends at gentle slope
41	50	External and internal malleoli do not reach same level
42	51	No astragalo-cuboid contact
43	53	Metatarsal IV not the longest

Figure 7A–C. Six derived characters unite *Perognathus* with *Microdipodops* (Fig. 7A), nine characters unite *Perognathus* with *Dipodomys* (Fig. 7B), and the *Microdipodops*-*Dipodomys* association is supported by 12 synapomorphies (Fig. 7C). Hence, the tree topology in Figure 7C is most parsimonious and contradicts the conclusion proffered by Wood (1935). It is interesting to note that the murinelike *Perognathus* is lacking an autapomorphic descriptor; we view this to be a problem not in the analysis or with the taxon, per se, but in the nature and breadth of the characters analyzed.

It is possible that the association of *Microdipodops* with *Dipodomys* (Fig. 7C) is incorrect because the analysis does not recognize possible parallelisms associated with the ricochetal mode of locomotion; the apomorphies used to unite the two taxa may be independently derived characters. To evaluate this possibility, we remove all those features in the analysis that are shared with the distantly related bipedal form, *Jaculus* (Fig. 7D–F; see Wood 1935:107–109). It can be seen in this refined analysis, controlling for ricochetal habitus characters (Fig. 7D–F), that there is still stronger support for the *Microdipodops*-*Dipodomys* phylogenetic hypothesis (Fig. 7F) than the other two possibilities. However, problems exist. If the presumed synapomorphic characters uniting kangaroo mice and kangaroo rats are to be believed, then the others must be misleading. As Wood (1935) himself observed, however, parallelism is the evolutionary motto of heteromyids.

REANALYSIS OF HAFNER (1978).— In an attempt to resolve the *Microdipodops* controversy, J. C. Hafner (1978) compared the two kangaroo mouse species with three species of kangaroo rats and four species of pocket mice (two species each of the subgenera *Perognathus* and *Chaetodipus*), using phenetic clustering and ordination procedures. Hafner (1978) concluded that *Microdipodops* is most closely related, phenetically, to pocket mice and adduced a broad spectrum of phenetic characters with assumed overall genotypic representation. Here we reanalyze Hafner's (1978) data hypothesizing shared-derived characters, using out-group comparison with *Liomys* and *Heteromys* (het-

eromyine data from Genoways 1973). A total of 17 characters was available for cladistic analysis (Table 3) after paring down Hafner's (1978:363-364) data matrix of 40 characters (quantitative characters were omitted from our analysis as well as those characters with indeterminable character-state polarity). Throughout our analysis, we have accepted as a working hypothesis that *Perognathus* and *Chaetodipus* form a clade relative to the other lineages; this assumption is supported by biochemical evidence (e.g., Sarich 1975, M. S. Hafner 1982).

Figure 8 shows the three phylogenetic hypotheses with the 17 characters (Table 3) apportioned among them. The results of this analysis, in accord with our above treatment of Wood's (1935) data, suggest that the most parsimonious phylogenetic hypothesis is that which links *Microdipodops* and *Dipodomys* as a clade independent of the *Perognathus-Chaetodipus* clade (Fig. 8C). However, the analysis is less than robust; the *Perognathus-Chaetodipus* clade lacks an autapomorphic character, and the characters that define the *Microdipodops-Dipodomys* association (Fig. 8C) are dubious (fully haired soles of hind

TABLE 3. Seventeen characters used in the reanalysis of Hafner (1978). Quantitative characters (J. C. Hafner 1978:363-364) and characters whose character-state polarity was indeterminable were omitted in our analysis.

Character number (Hafner 1978)	Description of feature
3	Lacrimal joined
4	Molars nonrooted
7	Morphology of Y chromosome metacentric
9	Urethral lappets absent
12	Sharply upturned morphology of baculum tip
13	Harsh pelage characteristics
15	Middorsal gland present
16	Soles of hind feet (naked, a; fully haired, b)
17	Crested tail present
18	Flank stripes present
21	Locomotion: partially bipedal to fully bipedal
31	White side stripes on tail present
33	Molar wear patterns: enamel limited to anterior and posterior plates
34	Tail greater diameter in middle than at base or tip
35	Absence of median ventral foramina in caudal vertebrae
36	Astragalus-cuboid articulation present
40	White ring at base of tail present

REANALYSIS OF WOOD (1935)

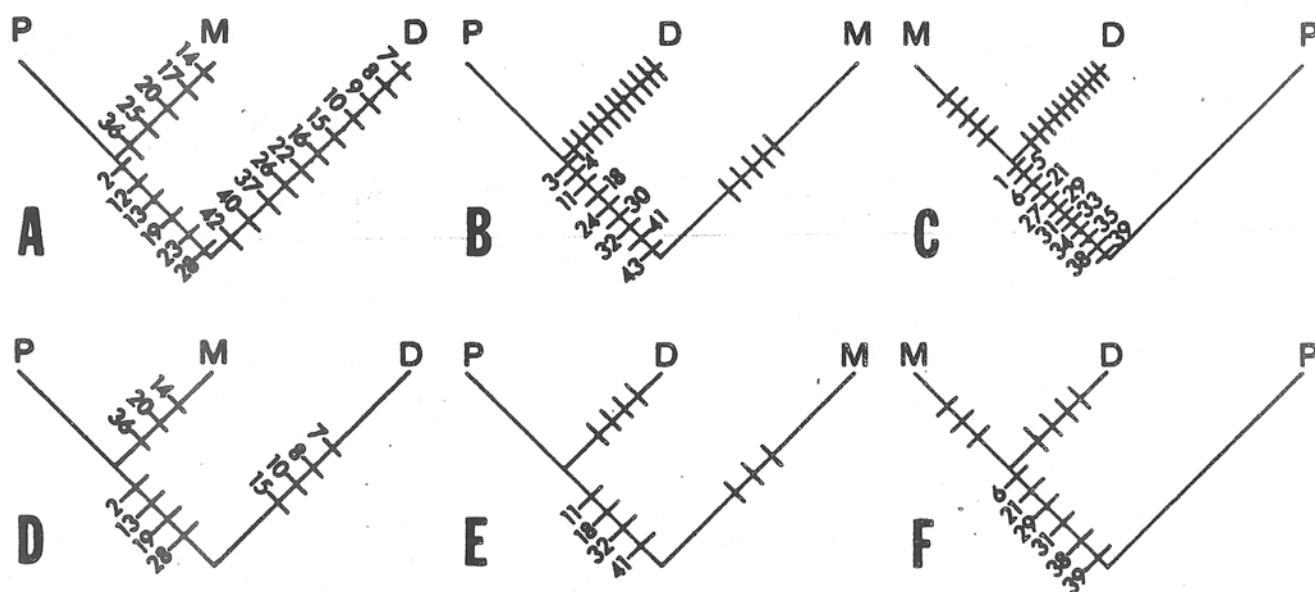


Fig. 7. Cladistic analysis of morphological data presented by Wood (1935) for *Perognathus* (P), *Microdipodops* (M), and *Dipodomys* (D). In A, B, and C, 43 of Wood's original 53 characters (see Table 2) are apportioned on the three possible trees, omitting those characters shared with *Liomyx* and *Heteromyx*. In D, E, and F, those characters shared with the ricochet form *Jaculus* (Dipodidae) are also omitted to remove features that are functionally related to bipedality. Note the high number of autapomorphies on the *Dipodomys* branch and the conspicuous absence of autapomorphies on the *Perognathus* branch.

eromyine data from Genoways 1973). A total of 17 characters was available for cladistic analysis (Table 3) after paring down Hafner's (1978:363-364) data matrix of 40 characters (quantitative characters were omitted from our analysis as well as those characters with indeterminable character-state polarity). Throughout our analysis, we have accepted as a working hypothesis that *Perognathus* and *Chaetodipus* form a clade relative to the other lineages; this assumption is supported by biochemical evidence (e.g., Sarich 1975, M. S. Hafner 1982).

Figure 8 shows the three phylogenetic hypotheses with the 17 characters (Table 3) apportioned among them. The results of this analysis, in accord with our above treatment of Wood's (1935) data, suggest that the most parsimonious phylogenetic hypothesis is that which links *Microdipodops* and *Dipodomys* as a clade independent of the *Perognathus-Chaetodipus* clade (Fig. 8C). However, the analysis is less than robust; the *Perognathus-Chaetodipus* clade lacks an autapomorphic character, and the characters that define the *Microdipodops-Dipodomys* association (Fig. 8C) are dubious (fully haired soles of hind

TABLE 3. Seventeen characters used in the reanalysis of Hafner (1978). Quantitative characters (J. C. Hafner 1978:363-364) and characters whose character-state polarity was indeterminable were omitted in our analysis.

Character number (Hafner 1978)	Description of feature
3	Lacrimal joined
4	Molars nonrooted
7	Morphology of Y chromosome metacentric
9	Urethral lappets absent
12	Sharply upturned morphology of baculum tip
13	Harsh pelage characteristics
15	Middorsal gland present
16	Soles of hind feet (naked, a; fully haired, b)
17	Crested tail present
18	Flank stripes present
21	Locomotion: partially bipedal to fully bipedal
31	White side stripes on tail present
33	Molar wear patterns: enamel limited to anterior and posterior plates
34	Tail greater diameter in middle than at base or tip
35	Absence of median ventral foramina in caudal vertebrae
36	Astragalus-cuboid articulation present
40	White ring at base of tail present

REANALYSIS OF WOOD (1935)

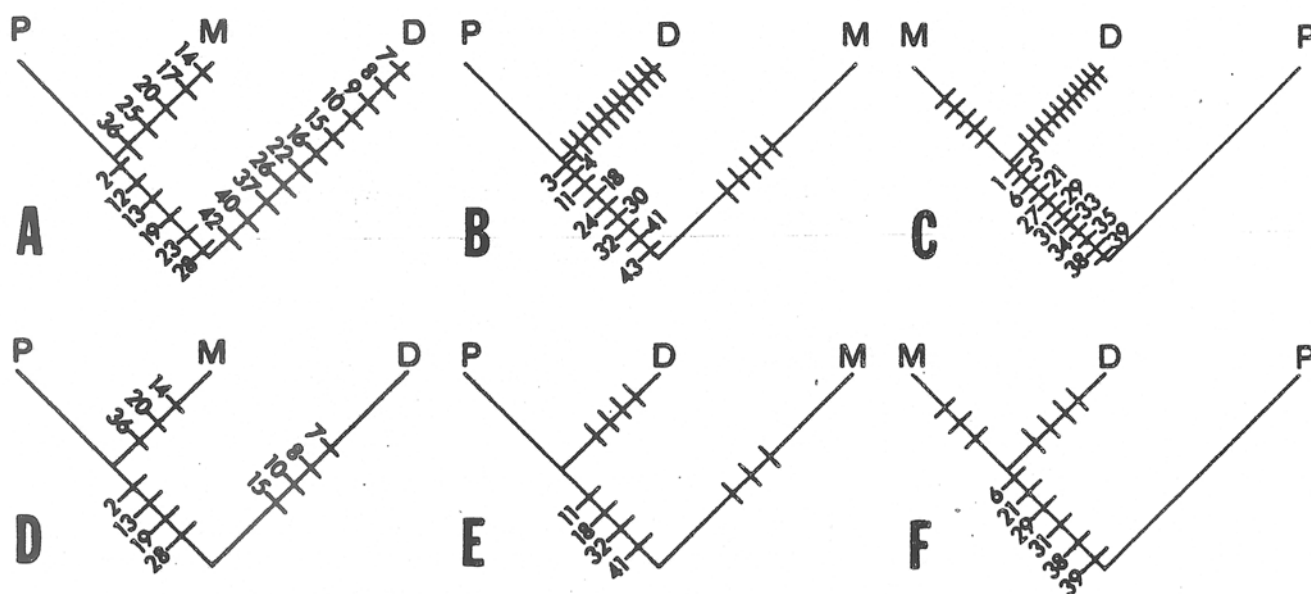


Fig. 7. Cladistic analysis of morphological data presented by Wood (1935) for *Perognathus* (P), *Microdipodops* (M), and *Dipodomys* (D). In A, B, and C, 43 of Wood's original 53 characters (see Table 2) are apportioned on the three possible trees, omitting those characters shared with *Liomys* and *Heteromys*. In D, E, and F, those characters shared with the ricochet form *Jaculus* (Dipodidae) are also omitted to remove features that are functionally related to bipedality. Note the high number of autapomorphies on the *Dipodomys* branch and the conspicuous absence of autapomorphies on the *Perognathus* branch.

feet and ricochet mode of locomotion).

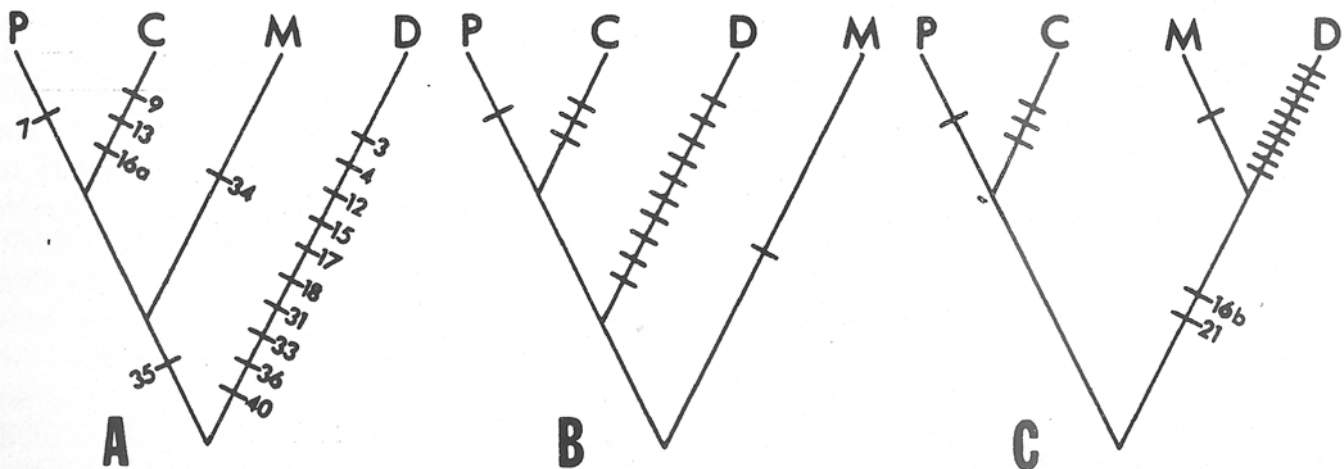
CONCLUSIONS ABOUT THE *Microdipodops* CONTROVERSY.—The above cladistic analyses of the data of Wood (1935) and J. C. Hafner (1978) are necessary exercises, yet the results are not unequivocal and provide us with only a preliminary insight to the problems of ascertaining phylogenetic relationships within the Heteromyidae using morphological characters. Both reanalyses demonstrate modest support for the recognition of the *Microdipodops-Dipodomys* clade; thus, they are in agreement with biochemical evidence. However, the treatments are inchoate and there is a need for a detailed phylogenetic analysis wherein character homologies and character-state transformations are determined. As noted by many workers (e.g., Hennig 1966), the crux of any analysis and its attending arguments relies on the characters under study.

Several other points emerge from the above analyses. Importantly, these cladistic treatments tabulate quantitatively the tremendous amount of parallelism in the heteromyids. That the morphology of these rodents is rife with parallelisms is documented convincingly in Figure 7A-C. The analyses also provide a comparative measure of the degree of morphological divergence among the heteromyid genera. In accord with intuition, these results document that *Dipodomys* is the most derived genus in terms of morphology (highest number of autapomorphic features;

Figs. 7 and 8), the pocket mice are the least derived, and *Microdipodops* exhibits an intermediate number of derived features.

Evolution of Geomyoid Morphotypes: An Hypothesis

The diversity of morphological forms, or morphotypes, within the superfamily Geomyoidea eclipses that seen within any other mammalian group of comparable size. The evolution of forms as structurally divergent as kangaroo rats, pocket mice, and pocket gophers is commonly believed to be the result of orthoselection; i.e., directional selection acting on ancestral species favoring certain adaptations which are accentuated in descendant species. The origin of each structural novelty is thus explained in terms of its present day functional advantage to the animal. Although it cannot be denied that a conspicuous morphological feature present in a living animal may, and probably does, have an adaptive function today, we agree with Gould and Vrba (1982:13) that "current utility carries no automatic implication about historical origin." As Lewin (1982:1212) points out, "it is folly to infer without caution the historical genesis of a feature from its current utility." Accordingly, we herein introduce a causal hypothesis, devoid of functional explanations, to account for the evolutionary origin of morphological diver-



sification within the Geomyoidea. This hypothesis is expanded and supportive evidence is detailed elsewhere (J. C. Hafner and M. S. Hafner, in manuscript).

Several years ago we observed that the conspicuous morphological features of adult kangaroo rats and kangaroo mice, most notably the large head and eyes, enlarged brain, long hind feet, and delicate, weakly fused skeleton, were traits commonly seen in the juvenile state of other animals. Further examination revealed that kangaroo rats and kangaroo mice possess many of the classical features characteristic of paedomorphic forms. This initial observation, coupled with the subsequent discovery that neonatal pocket gophers look remarkably like mature pocket mice, prompted further investigation culminating in our hypothesis that geomyoid morphological transformations through phylogeny may be the result of evolutionary epigenetics (for recent reviews see Gould 1977, Alberch et al. 1979, Alberch 1980, Løvtrup 1981a, 1981b, Rachootin and Thomson 1981). In other words, regulatory changes in ontogeny may have affected the timing of gene action and rates of morphogenesis and growth and thus have led to morphological phyletic evolution in this group.

Most authors would agree that pocket mice, including *Perognathus*, *Liomys*, and *Heteromys*, exhibit a generalized body plan and probably represent a good approximation of the ancestral geomyoid morphotype (e.g., Eisenberg 1981:90). Our hypothesis suggests that perturbations in developmental "control parameters" in ancestral (pocket-mouse-like) geomyoids, including changes in the time of onset of growth, cessation of development, and rate of growth, could deform the ancestral ontogenetic pathway and effect phylogenetic transmutations in morphology leading to such diverse forms as kangaroo mice, kangaroo rats, and pocket gophers.

According to our hypothesis, paedomorphosis in kangaroo mice and kangaroo rats may have originated via different kinds of developmental perturbations. Both morphology and general life history of kangaroo mice suggest that they are progenetic descendants of pocket-mouse-like ancestors. Progenesis is the process whereby ontogeny is truncated

and maturation is accelerated. Gould (1977) argues that the key to understanding the immediate significance of shifts in developmental timing (heterochrony) lies in the theory of r and K selection (life history strategies). Gould (1977:293) predicts that progenesis will be associated with r -strategists, and, indeed, early kangaroo mouse evolution is postulated to have occurred in an obvious r -selected environment (ephemeral sand-dune habitats in the Great Basin Desert; J. C. Hafner 1978); kangaroo mice possess many of the classical attributes of an r -strategist. It appears that in kangaroo mice there has been progenetic truncation by precocious maturation and that this early maturation is the principal object of selection. That is, there has been a "redirection of selection" (Gould 1977) away from morphology, per se, and toward precocious maturation as a life history strategy; juvenilization may have been entirely incidental.

Both morphology and general life history of kangaroo rats lead us to suggest that paedomorphosis in this group is the result of neoteny. Neoteny is fundamentally different from progenesis and involves retardation in growth rate resulting in juvenilization of the adult animal. According to Gould's (1977) hypothesis, neoteny is a common occurrence and may result from direct selection for juvenile features and/or larger body size in environmental regimes that are more K -selected. Indeed, kangaroo rats are all medium to large heteromyids possessing many of the classical features associated with the neotenic syndrome (e.g., long life span, slow development, small litters, enlarged brain; J. C. Hafner and M. S. Hafner, in manuscript). The early evolution of kangaroo rats appears to have been confined to grasslands (Reeder 1956), and several living forms inhabit fairly stable, nondesert environments; those that are strictly desert-dwelling forms tend to buffer an otherwise unstable environment by subsisting on a fairly stable resource (leaves) and/or utilizing large stores of hoarded food during periods of food scarcity.

Lastly, we suggest that pocket gophers may be hypermorphic descendants of a pocket-mouse-like ancestor. Hypermorphosis is a process wherein heterochronic perturbation in ontogeny has led to a length-

ened growth period producing a "peramorphic" (as opposed to paedomorphic; Alberch et al. 1979) organism. The marked similarities between neonatal pocket gophers and adult pocket mice suggest that reproductive maturation in pocket gophers has been retarded relative to exomorphological maturation, allowing for extreme development of somatic features prior to reproduction. Adult pocket gophers possess many of the classical features characteristic of late mammalian ontogeny, most notably a rugose, heavily ossified skeleton that results from prolongation of somatic growth late in life.

In summary, we suggest that many, perhaps most, of the flamboyant morphological modifications seen in heteromyids and geomyids may have *originated* as incidental by-products of heterochronic shifts in ontogeny. Instead of acting separately on each morphological feature (e.g., large head, long legs, delicate skeleton, etc.), natural selection may have acted at the developmental level favoring the new life history strategy associated with a progenetic, neotenic, or hypermorphic animal. The paedomorphic traits invariably associated with these developmental changes (peramorphic traits in the case of hypermorphism) may have been "tolerated" by natural selection initially and subsequently modified (adapted) for functional purposes. On the other hand, certain novel traits may provide little or no functional improvement over the ancestral condition, but are maintained (as long as they are not deleterious) because they are developmentally mandated.

TAXONOMIC COMMENTS ON THE HETEROMYIDAE ALLEN AND CHAPMAN 1893

The following is an up-to-date statement on the taxonomy of the Recent Heteromyidae, necessarily reflecting the views and biases of the authors. We use as our point of departure Hall (1981) and included references. In the interest of brevity, those heteromyid species recognized by Hall (1981) are not listed, except where we feel taxonomic comments are warranted. For species groupings within each genus we again refer the reader to Hall (1981), but we hasten to add that species groupings within *Dipodomys*, *Heteromys*, *Perognathus*, and *Chaetodipus* are

suspect and in need of thorough reevaluation. Finally, we provide a synonymy for *Chaetodipus*, which we herein evaluate to full generic rank. Our views on supraspecific relationships within the family are summarized in Figure 9.

Subfamily Dipodomysinae Coues 1875

GENUS *Dipodomys* GRAY 1841.—Hall (1981) recognizes 22 species of kangaroo rats, partitioned into six species groups following Setzer (1949; see Schnell et al. 1978, for discussion of interspecific taxonomy in the genus). Best (1978) has used morphologic criteria to suggest that three species recognized by Hall, *D. antiquarius* Huey 1962, *D. paralius* Huey 1951, and *D. penisularis* (Merriam 1907), are conspecific with *D. agilis* Gambel 1848. Biochemical (Johnson and Selander 1971) and morphological (Schmidly and Hendricks 1976) evidence has been used to suggest that *D. compactus* True 1899 (not recognized by Hall 1981) warrants full specific status. Similarly, Patton et al. (1976) have used biochemical evidence to document *specific status for D. californicus* Merriam 1890.

GENUS *Microdipodops* MERRIAM 1891.—Herein, kangaroo mice are placed provisionally in the subfamily Dipodomysinae, based largely on biochemical evidence (M. S. Hafner 1982) and comparative analysis of the male reproductive system (this study). We regard the many morphological similarities between *Microdipodops* and *Perognathus* (Wood 1935, J. C. Hafner 1978) to be shared primitive features. Nevertheless, more detailed analyses at the molecular level are needed to confirm or refute the placement of *Microdipodops* within the Dipodomysinae. Two species of *Microdipodops* are recognized by Hall (1981). Hall's suggestion (1981:560) that *M. megacephalus leucotis* may warrant specific status is not supported by chromosomal or protein evidence (J. C. Hafner 1981a).

Subfamily Heteromyinae Coues 1875

GENUS *Heteromys* DESMAREST 1817.—Hall (1981) recognizes 10 species of *Heteromys* partitioned into two subgenera, *Heteromys* and *Xylomys*. *Heteromys nigricaudatus*

Goodwin 1956 (recognized by Hall 1981) was synonymized under *H. lepturus* Merriam 1902 by Goodwin (1969). Rogers and Schmidly (1982) have analyzed phenetic relationships in Hall's (1981) *desmarestianus* group (exclusive of *H. gaumeri*) and have synonymized *H. longicaudatus* Gray 1868, *H. temporalis* Goldman 1911, and *H. lepturus* under *H. desmarestianus* Gray 1868.

GENUS *Liomys* MERRIAM 1902.— We have reviewed a large body of evidence supporting the phyletic affinity of *Liomys* and *Heteromys*. Hall (1981) follows Genoways (1973) in recognizing five species in the genus *Liomys*. Future biochemical and chromosomal banding studies may serve to identify species groups within the genus.

Subfamily Perognathinae Coues 1875

GENUS *Perognathus* WIED-NEUWIED 1839.— Our elevation of *Chaetodipus* to full generic rank (see beyond) results in the inclusion of only "silky pocket mice" (formerly referred to the subgenus *Perognathus*) within the genus *Perognathus*. Hall (1981) recognizes 10 species of silky pocket mice, includ-

ing the problematic species *P. formosus* Merriam 1889 (see Osgood 1900). Patton et al. (1981) have shown that *P. formosus* is clearly referable to *Chaetodipus*, thus reducing the number of Recent taxa of *Perognathus* to nine.

GENUS *Chaetodipus* MERRIAM 1889.— *Chaetodipus* is here elevated to full generic status. Following is a synonymy and a rediagnosis of the taxon.

Genus *Chaetodipus* Merriam, new status

Chaetodipus Merriam, 1889, N. Amer. Fauna 1:5 (25 October). Type-species: *Perognathus spinatus* Merriam, original designation. Subgenus elevated to generic level.

DIAGNOSIS.— Size medium to large (total length 152–230; Hall 1981). Pelage generally harsh, often with spiny bristles on rump. In those species lacking harsh pelage and rump spines, tail crested distally and longer than head and body. Hair flattened in cross section with distinct trough having well-developed ridges on dorsal surface (Homan and Genoways 1978). Soles of hind feet naked. Interparietal width equal to or greater than interorbital width. Auditory bullae not

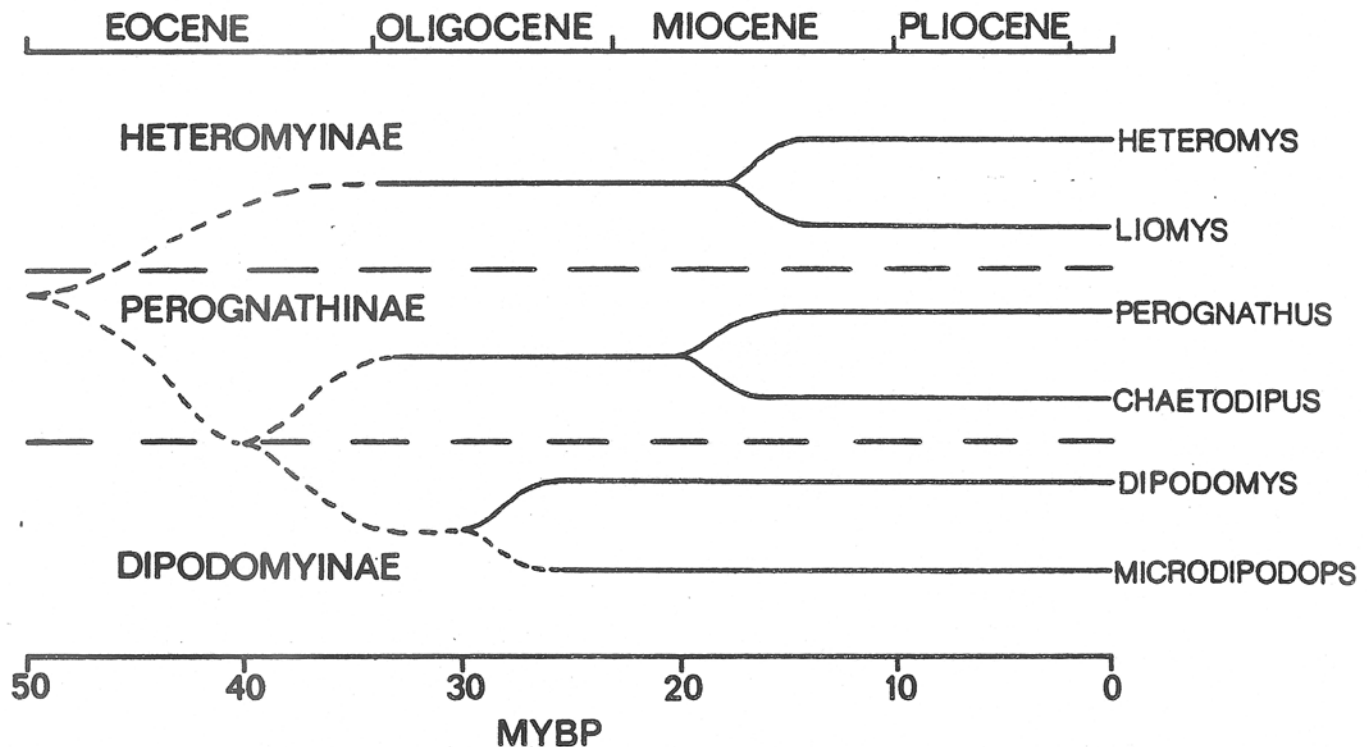


Fig. 9. Phylogeny of the extant Heteromyidae indicating subfamilial groupings. Dashed lines in the dendrogram indicate probable relationships and signal areas where further investigation is needed. The time scale is approximate and is based on fossil evidence (Wood 1935, Lindsay 1972) and immunological and allozymic time calculations (Sarich 1975, M. S. Hafner 1979, 1982).

markedly inflated as in *Perognathus*. Male phallus long and slender, lacking urethral lappets; rim of terminal crater forms ventlike urethral opening. Baculum long relative to body length (Burt, 1936), having a narrow proximal end and sharply upturned distal end (the baculum of *C. hispidus* is unique in possessing an ornate, trifid tip). Head of spermatozoa resembling elongated isosceles triangle with acute, unrounded vertices. Vesicular glands round or bulb shaped, yellow to gray in color (pinkish in fresh specimens).

INCLUDED TAXA.—*Chaetodipus anthonyi*, *C. arenarius*, *C. artus*, *C. baileyi*, *C. californicus*, *C. dalquesti*, *C. fallax*, *C. formosus*, *C. goldmani*, *C. hispidus*, *C. intermedius*, *C. lineatus*, *C. nelsoni*, *C. penicillatus*, *C. pernix*, *C. spinatus*. *Chaetodipus anthonyi* Osgood 1900 is most likely an island race of *C. fallax* Merriam 1889 (J. L. Patton, pers. comm.). The specific status of *C. lineatus* Dalquest 1951 is dubious (Patton et al. 1981), and further study is necessary to confirm the validity of *C. dalquesti* Roth 1976, which has a karyotype identical to *C. arenarius* Merriam 1894 (J. C. Hafner and M. S. Hafner, unpubl. ms.). According to Patton et al. (1981), no strongly delineated species groupings are apparent within *Chaetodipus*. However, *C. hispidus* is biochemically divergent from other members of the group.

COMMENTS.—Extreme evolutionary conservatism in exomorphology in the genera *Perognathus* and *Chaetodipus* belies their long history of evolutionary independence as documented by fossil (Wood 1935) and biochemical evidence (Sarich 1975, Patton et al. 1981, M. S. Hafner 1982). M. S. Hafner (1982) has shown that the genetic distance between *Perognathus* and *Chaetodipus* exceeds that measured between *Liomys* and *Heteromys* and approaches that measured between *Dipodomys* and *Microdipodops*. Taxonomic consistency within the Heteromyidae demands that the high degree of chromosomal, anatomical, and biochemical differentiation between *Perognathus* and *Chaetodipus* be recognized at the generic level.

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