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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 157

Phylogenetic Relationships in Neotomine-Peromyscine Rodents (Muroidea) and a Reappraisal of the Dichotomy within New World Cricetinae

by
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INTRODUCTION

Living rodents are believed to be as abundant individually and in variety as all other mammals put together. . . Their relationships are involved in an intricate web of convergence, divergence, parallelism, and other taxonomic pitfalls. Their great numbers, their marked mutability and variability, their spread over almost every conceivable environment, their remarkable adaptability, the shortness of their generations, their usual great fertility with overpopulation and severe mortality. . . give them the possibility of exceptionally rapid evolution and of phyletic connections remarkably difficult to retrace.

George Gaylord Simpson (1945:197)

Although Simpson's comments were intended to encapsulate the myriad of obstacles to comprehending phylogenetic relationships within the Order Rodentia as a whole, the accuracy of his purview is most acutely felt by those who have studied the ubiquitous "rats and mice" that constitute the suborder Myomorpha. This single suborder accounts for fully thirty percent of all living species of mammals. Furthermore, a substantial majority of myomorph rodents, over one thousand species or one-quarter of Recent Mammalia, are encompassed by one superfamily, the Muroidea (Arata, 1967; Table 1). Muroids are world-wide in distribution, and in terms of the overall number of species and the diversity of habitats occupied, constitute the most successful radiation of contemporary rodents.

While a consensus exists regarding what species properly belong to the Muroidea, there is less comprehension and agreement concerning the suprageneric relationships within the superfamily. Their sheer prodigy in numbers, coupled with apparently rampant parallelism, have rendered

TABLE 1

NUMBER OF LIVING SPECIES OF MUROIDEA
IN RELATION TO TOTAL NUMBER OF MAMMALIA
(adapted from Anderson and Jones, 1967).

Taxa	Number of Recent Species
Mammalia	4060
Rodentia	1687
Sciuromorpha	263
Hystricomorpha	184
Myomorpha	1240
Muroidea	1045

phylogenetic inferences most difficult. In grappling with just one complex of muroids, a notable student of the Order, Sir John Ellerman, lamented (1941:328) that "... the task of arranging these [in this instance New World Cricetinae] in any natural order is almost impossible." While I do not agree that achieving this objective is anywhere near impossible, it is most certainly a challenging and formidable task. My study focuses on one such problematic group of muroid rodents, the neotomine-peromyscines, a New World assemblage of approximately 111 species arranged in 12 genera, and illuminates the kinds of problems that must be met and dealt with in order to gain further insight to muroid phylogeny.

Background of the Problem

The following brief review of previous classifications of Muroidea emphasizes the taxonomic treatment accorded the neotomine-peromyscines and their hypothesized closest relatives, South American cricetines. I have selected only seven classificatory schemes. There are others, but these seven are most important in an historical sense and collectively exhibit the major variations in the taxonomic arrangements of the Muroidea. Most standard reference works, such as Anderson and Jones (1967) and Hall and Kelson (1959), follow Simpson's (1945) classification of Muroidea; the contribution of Chaline, Mein and Petter (1977) is too recent for me to judge the extent of its acceptance and impact.

The neotomine-peromyscines were not always recognized as a distinct phyletic unit separable from other New World cricetines. Thomas (1896) arranged most species currently placed in Muroidea under an all-encompassing family Muridae and separated them into twelve subfamilies (Table 2A). His concept of the Sigmodontinae was considerably broader than that generally employed today (which includes only the forty genera of South American muroids), for it included not only the South American cricetines and most neotomine-peromyscines but also Old World hamsters and the Malagasy forms. Thomas did segregate the Sigmodontinae into Palearctic, African *(Mystromys),* Mascarene and American categories; all New World cricetines were contained in the last. Interestingly, Thomas maintained Merriam's (1894) subfamily Neotominae (then including the genera *Neotoma, Hodomys* and *Xenomys*), suggesting that he viewed the differentiation of the wood rats from those genera he listed as American sigmodontines at the same level as the separation of the Microtinae.

Tullberg's (1899) detailed treatise on the anatomy and classification of rodents removed Old World cricetines, which he placed in the Cricetidae, from New World forms, which he segregated as the Hesperomyidae (Table 2B). Thus, Tullberg's Cricetidae was much restricted in content compared to the family as defined by Simpson (1945), which includes the above taxa as well as nesomyines, microtines and gerbillines. The latter three were considered separate families by Tullberg.

TABLE 2

PREVIOUS CLASSIFICATORY ARRANGEMENTS OF MUROIDEA.

A. Thomas, 1896
- Muridae
  - Hydromyinae
  - Rhynchomyinae
  - Phloeomyinae
  - Gerbillinae
  - Otomyinae
  - Dendromurinae
  - Murinae
  - Lophiomyinae
  - Sigmodontinae (= N-Ps, SACs, OWCs and Nesomyines)
  - Neotominae
  - Microtinae
  - Myospalacinae
- Spalacidae
  - Rhizomyinae
  - Spalacinae

B. Tullberg, 1899
- Muriformes
  - Spalacidae
  - Nesomyidae
  - Cricetidae (= OWCs)
  - Lophiomyidae
  - Arvicolidae (= Microtidae)
  - Hesperomyidae (= N-Ps and SACs)
  - Muridae
    - Murini
    - Phloeomyini
    - Otomyini
  - Gerbillidae

C. Miller and Gidley, 1918
- Muroidae
  - Muscardinidae
  - Cricetidae
    - Cricetinae (= N-Ps, SACs, OWCs and Nesomyines)
    - Gerbillinae
    - Microtinae
    - Lophiomyinae
  - Platacanthomyidae
  - Rhizomyidae
  - Spalacidae
    - Myospalacinae
    - Spalacinae
  - Muridae
    - Dendromyinae
    - Murinae
    - Phloeomyinae
    - Hydromyinae

D. Ellerman, 1940
- Muroidea
  - Muscardinidae
  - Lophiomyidae
  - Spalacidae
  - Rhizomyidae
  - Muridae
    - Deomyinae
    - Murinae
    - Rhynchomyinae
    - Hydromyinae
    - Dendromyinae
    - Otomyinae
    - Cricetinae (= N-Ps, SACs, and OWCs)
    - Gerbillinae
    - Myospalacinae
    - Microtinae

E. Simpson, 1945
- Muroidea
  - Cricetidae
    - Cricetinae
      - Hesperomyini (= N-Ps and SACs)
      - Cricetini (= OWCs)
      - Myospalacini
    - Nesomyinae
    - Lophiomyinae
    - Microtinae
    - Gerbillinae
  - Spalacidae

F. Chaline *et al.*, 1977
- Muroidea
  - Cricetidae
    - Hesperomyinae (= N-Ps and SACs)
    - Cricetinae (= OWCs)
    - Spalacinae
    - Myospalacinae
    - Lophiomyinae
    - Platacanthomyinae
  - Nesomyidae
  - Rhizomyidae
  - Gerbillidae

N-Ps = neotomine-peromyscines; SACs = South American cricetines; OWCs = Old World cricetines

TABLE 2
(Continued)

Rhizomyidae	Arvicolidae
Muridae	Dendromuridae
Murinae	Cricetomyidae
Dendromurinae	Muridae
Otomyinae	Murinae
Phloeomyinae	Hydromyinae
Rhynchomyinae	
Hydromyinae	

N-Ps = neotomine-peromyscines; SACs = South American cricetines; OWCs = Old World cricetines

The classification set forth by Miller and Gidley (1918) presaged that adopted by Simpson (1945) in assigning most genera of muroids to the Cricetidae or Muridae (Table 2C). The few remaining species, seemingly highly specialized fossorial types, were allocated to other families (Spalacidae, Rhizomyidae). The Cricetinae, as delimited by Miller and Gidley, was basically equivalent to the Sigmodontinae of Thomas (1896); that is, it contained Old World cricetines, neotomine-peromyscines, South American cricetines and nesomyines of Madagascar.

Like Thomas (1896), Ellerman (1940, 1941) favored a comprehensive definition of the family Muridae, acknowledging ten subfamilies that embraced most species of Muroidea (Table 2D). South American cricetines and neotomine-peromyscines, together with the Old World cricetines, composed his subfamily Cricetinae, and this basic composition of the subfamily persists today.

Simpson's (1945) influential classification reestablished the Cricetidae/Muridae schism within Muroidea (Table 2E). The Cricetinae of Simpson corresponds closely in content to the subfamily as envisioned by Ellerman, except that Simpson included the mole-rats *Myospalax* at the tribal level. Furthermore, he nomenclatorially reinforced the notion of a fundamental separation between Old and New World cricetines by placing them in the Cricetini and Hesperomyini, respectively. However, like the authors of previous classifications, Simpson did not indicate an awareness of any significant divergence within New World cricetines.

The recent contribution of Chaline *et al.* (1977) represents an attempt to integrate our rapidly growing knowledge of fossil muroids into a cohesive classificatory system. I have listed only the pertinent groups of living muroids for the purpose of this comparative review (Table 2F). In general, they recognized the same fundamental groups of muroids as in earlier works but treat most at the rank of family. And, like Simpson, Chaline *et al.* separated the Old and New World cricetines, in this case at the subfamilial level (Cricetinae and Hesperomyinae).

Despite the number of formal classifications that have been advocated for the Muroidea, a few major themes recur.

1. While the same assemblages of muroids are agreed upon, the classifications differ in the nomenclatorial rank — that is, tribe, subfamily or family — at which those assemblages are defined. In part, the application of different taxonomic ranks reflects the prevailing taxonomic philosophy of the time. Perhaps an inevitable consequence of further intensive study of the Muroidea will be to recognize the major phyletic units as families and to express the emergent, finer details of relationships within those assemblages as tribes and subfamilies. In this sense, the classification proposed by Chaline *et al.* (1977) may anticipate a future trend.

2) Most subgroups of Muroidea, those containing the vast majority of species, are placed in one family, the Muridae (e.g. Thomas, 1896; and Ellerman, 1940), or in two families, Muridae and Cricetidae (e.g. Miller and Gidley, 1918, and Simpson, 1945). The remaining forms are placed in satellite families (Spalacidae, Rhizomyidae, etc.) with relatively few species. The tendency has been to isolate the highly modified fossorial forms as outliers, which probably grossly distorts the cladistic relationships of the forms involved. In this regard, Chaline *et al.* (1977) depart from earlier arrangements in placing both Myospalacinae and Spalacinae as subfamilies of Cricetidae.

3) Neotomine-peromyscines and South American cricetines have always been classified together, usually in the subfamily Cricetinae, with no suggestion of a basic dichotomy within New World cricetines. Some rodent specialists have asserted a fundamental separation of New World cricetines from Old World cricetines or hamsters (such as the classification of Tullberg, 1899; Simpson, 1945; and Chaline *et al.*, 1977), but others (namely, Miller and Gidley, 1918; and Ellerman, 1940) have combined then into a single taxon without formal subdivisions.

The first suggestion of a dichotomy within New World cricetines was expressed by Rinker (1954). Summarizing the results of his comparative myological study of four New World genera, he observed that (1954:118):

> Rather, it seems to indicate that there were first two lines of descent from that common stock [*i.e.* New World Cricetinae], one line characterized by, among other characters, relationships of these muscles as exemplified by the *Sigmodon-Oryzomys* complex; the other line characterized by the relationships of the corresponding muscles as seen in the *Neotoma-Peromyscus* complex. Adaptive differentiation within each of these secondary lines may then have given rise to the genera as we see them at present.

The *"Sigmodon-Oryzomys"* and *"Neotoma-Peromyscus"* complexes were adumbrations of the South American cricetines, or sigmodontines, and the neotomine-peromyscines, or peromyscines, of later authors.

Beginning in 1958, Hooper published a series of papers surveying the morphology of the male phallus in rodents, culminating with the 1964 overview of muroid taxonomy by Hooper and Musser. The impact of this latter paper upon our thinking about muroid relationships was truly revolutionary in two primary aspects. Firstly, they hypothesized a hierarchical scheme of relationships, one expressing the relative recency of common

ancestry of the major groups of Muroidea (Fig. 1). Previous classificatory arrangements usually had merely listed these groups under one or two families with little or no indication of their recency of common ancestry or degree of affinity. It is certainly true that the unification of forms into a classificatory scheme partially conveys the systematist's best estimate of propinquity. Still, the graphic portrayal of cladistic relationships among Muroidea offered by Hooper and Musser was inherently more explicit and conducive to testing than earlier efforts. Secondly, they gave substantial credence, built upon a much broader data base, to Rinker's suspicion of divergence within New World Cricetinae. They recognized this dichotomy as the simple penis, predominantly North American, neotomine-peromyscines and the complex penis, largely South American, assemblage of cricetines. Moreover, their diagram of relationships clearly implied that they considered the degree of differentiation of the neotomine-peromyscines and South American cricetines as great as that marking other muroid divisions, such as the Microtinae, Gerbillinae, and Murinae, currently treated as subfamilies.

Subsequent studies based on male accessory reproductive glands (Arata, 1964), ectoparasites and their host associations (Wenzel and Tipton, 1966), zoogeography (Hershkovitz, 1966b) and gastric morphology (Carleton, 1973) have purported to validate, to a greater or lesser degree, Hooper and Musser's postulated dichotomy. The validity of the dichotomy has also been affirmed or assumed in paleontological studies (Baskin, 1978; Hibbard, 1968; Jacobs, 1977; Patterson and Pascual, 1972) and in investigations of Latin American faunal interchange (Hershkovitz, 1966b, 1972; Marshall, 1979; Savage, 1973). The division within New World Cricetinae has been solidified by some by recognizing either the tribes Sigmodontini and Peromyscini (Hershkovitz, 1966b, 1972) or the subfamilies Sigmodontinae and Peromyscinae (Reig, 1977). However, I shall continue to view this division as an hypothesis as originally proposed and subsequently informally refer to the two groups as "South American cricetines" and "neotomine-peromyscines".

The South American cricetines, as their name implies, are distributed primarily throughout South America and consist of some 40 genera representing about 180 species (Fig. 2). Their total distribution is somewhat misleading in that just a few genera occur in Central America, and only two species of two genera, *Sigmodon* and *Oryzomys,* reach the northern limits shown in Figure 2. For further review of systematic relationships and ecological and zoogeographic affinities within this diverse complex, see Hershkovitz (1962, 1972).

The neotomine-peromyscines consist of fewer genera, only twelve, but still number an impressive 111 species. Yet in some respects, the amount of morphological variation encompassed by these twelve genera exceeds that collectively observed among the 40 genera of South American cricetines. The center of distribution and abundance of neotomine-peromyscines lies in Mexico, and only two genera, *Tylomys* and *Reithrodontomys,* penetrate the northern margin of South America (Fig. 3).

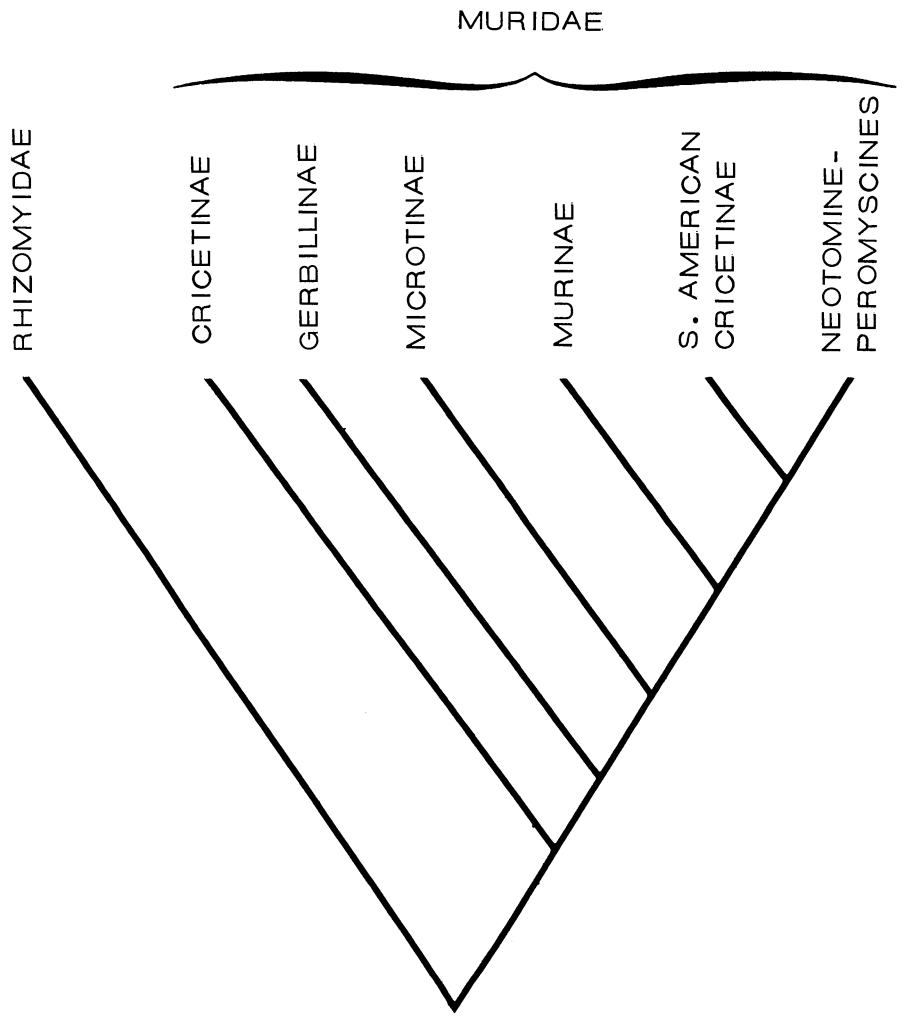

Fig. 1. Hierarchical arrangement of major groups of Muroidea (modified from Hooper and Musser, 1964a).

Objectives of the Study

Two observations stimulated my interest in exploring the phylogenetic relationships among neotomine-peromyscines.

First, there is a striking disparity in size and morphological diversity embraced by the various genera of neotomine-peromyscines. One-half of the species are contained in the one genus *Peromyscus* (Table 3). *Neotoma* and *Reithrodontomys* are moderately speciose, but eight of the nine remaining genera are represented only by one or two species each. Hall and Kelson (1959) list seven species for *Tylomys,* but this figure is almost certainly

Fig. 2. Collective distribution of South American cricetines.

inflated because the genus has not been revised recently. Also, the morphological diversity revealed in previous anatomical studies has not been equally and consistently applied in delimiting the genera. For example, the range of variation in morphology of the male phallus in *Neotoma* and *Peromyscus* (Hooper, 1960; Hooper and Musser, 1964b) surpasses that observed among all genera of South American cricetines examined (Hooper and Musser, 1964a). And one only need consider the uniformity in male accessory glands exhibited by such muroid groups as microtines and

South America cricetines (Arata, 1964) to appreciate the remarkable variety of accessory glands substantiated just for the subgenera of *Peromyscus* (Linzey and Layne, 1969). Also, past studies emphasized single character or organ-system surveys, such as male accessory glands (Arata, 1964), spermatozoan morphology (Linzey and Layne, 1974), and gastric anatomy (Carleton, 1973). Predictably, the results of these investigations corroborate some of Hooper and Musser's ideas, dispute others, or proffer no resolution whatever. Therefore, I was interested in determining the

Fig. 3. Collective distribution of neotomine-peromyscines.

pattern of differentiation among neotomine-peromyscines as revealed by simultaneously analyzing many characters from an array of organ systems, weighting all characters equally, and performing this analysis for many species. In part, this objective logically relates to the next.

TABLE 3

THE TWELVE GENERA OF NEOTOMINE-PEROMYSCINES AND THEIR NUMBER OF CONSTITUENT SPECIES.

Peromyscini	Neotomini
Nelsonia (1)	*Tylomys* (7)
Baiomys (2)	*Otolylomys* (1)
Scotinomys (2)	*Xenomys* (1)
Onychomys (2)	*Neotoma* (19)
Ochrotomys (1)	
Neotomodon (1)	
Reithrodontomys (19)	
Peromyscus (55)	

Second, I was intrigued by the polarity of relationships portrayed by Hooper and Musser's dendrogram of neotomine-peromyscine affinities based primarily on the anatomy of the glans penis (Fig. 4). Clearly, their tree conveys two major lines of descent, sometimes termed the Neotomini and Peromyscini, one leading to *Neotoma* and the other to *Reithrodontomys* and *Peromyscus*. Could I corroborate the essence of their phylogeny, again by broadly sampling the phenotype for many characters, especially ones for which I was reasonably confident of discerning ancestral and derived states. Such broad-scale studies, using numerical phylogenetic methods such as character compatability and Wagner tree analysis, have been attempted in other vertebrate classes (Osteichthyes — Lundberg, 1972 and Cichocki, 1976; Amphibia — Kluge and Farris, 1969; Reptilia — Kluge, 1976; and Aves — Payne and Risley, 1976 and Strauch, 1978), but not in Mammalia.

A third problem emerged soon after I began the study. Initially, I accepted the neotomine-peromyscines as a monophyletic assemblage as given by Hooper and Musser (1964). This assumption proved suspect based on my preliminary survey of characters, especially morphology of the glans penis. As a result, I have evaluated more closely the notion of a fundamental dichotomy in New World Cricetinae, that is, the neotomine-peromyscines and South American cricetines, and reexamined the data from which this schism was originally inferred.

In summary, the three primary purposes of my investigation are:

1) to evaluate the size and equivalence of the currently defined genera of neotomine-peromyscines;

2) to study the cladistic relationships among neotomine-peromyscines, particularly with reference to the phylogeny proposed by Hooper and Musser (1964);

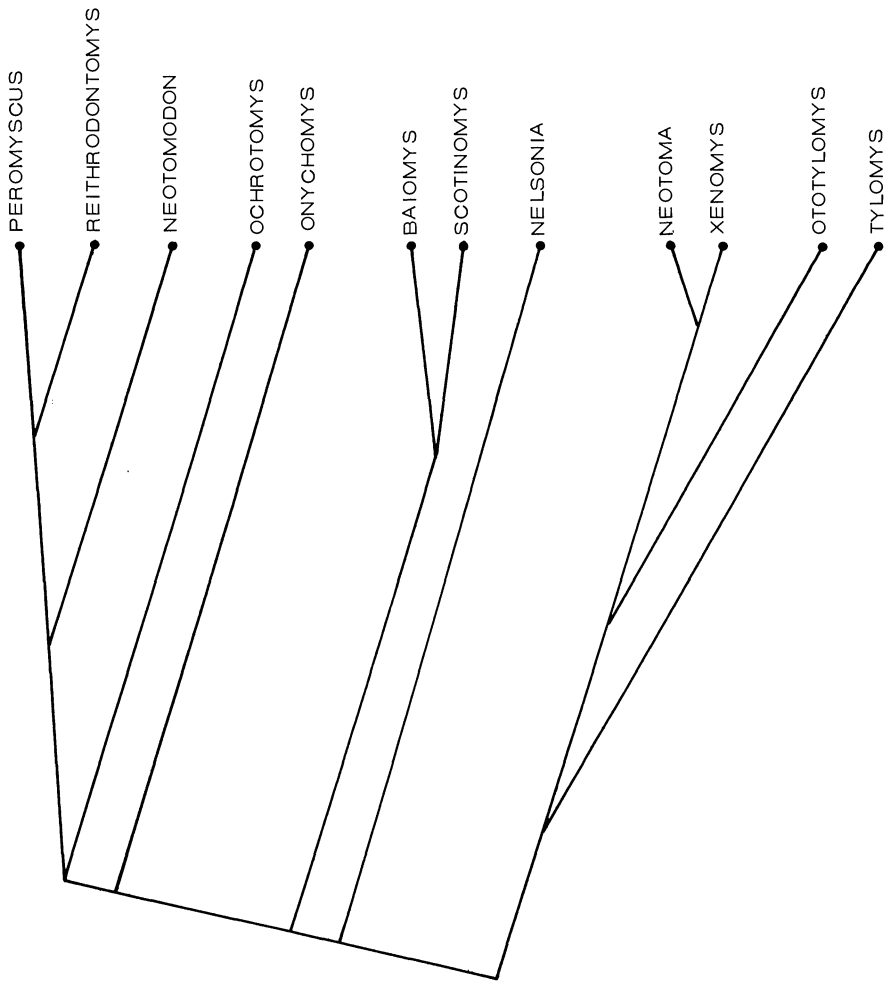

Fig. 4. Relationships of neotomine-peromyscines as proposed by Hooper and Musser (1964b).

3) to assess the relationships of neotomine-peromyscines to South American cricetines.

One might argue that the logical order of my three objectives is reversed. Perhaps the third issue deserves resolution first, and the monophyletic nature of neotomine-peromyscines should be "proven" in some sense before one even starts examining phyletic relationships within the group. The choice of enumeration faithfully recapitulates my stages of interest and awareness of the problems. Moreover, I would contend that incontrovertible establishment of monophyly for one's study collection, although a laudable ultimate goal, is not always an immediately practical one, especially in large taxa in which the current level of understanding of phylogenetic affinity is so poor. The Muroidea supremely exemplifies just that situation. Thus, to inaugurate any phylogenetic study, one must per-

force accept, at some level, the higher order classification which currently obtains, in this instance, the higher-level, phylogenetic hypothesis set forth by Hooper and Musser (1964). As indicated above, their hypothesis, as it pertains to the schism between neotomine-peromyscines and South American cricetines, is firmly entrenched and formally recognized in recent mammalian literature.

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Many people have contributed to this study and improved its final form and content. I thank the members of my committee, Philip Myers, Arnold G. Kluge, John B. Burch and John A. Dorr, for their thoughtful reading of the manuscript and helpful suggestions. The conception and development of my thesis topic have been influenced and shaped by others who have served in function, if not officially, as committee members in the past. Among those, David J. Klingener, Guy G. Musser, Douglas M. Lay, the late Claude W. Hibbard, and Emmet T. Hooper deserve special mention.

My graduate matriculation, interrupted by a technical sabbatical, spanned two generations of graduate students and afforded me an interesting juxtaposition of ideas and approaches to systematic biology. Interaction with students of both the old order (Tim Lawlor, Al Lackey and Dave Huckaby) and the current one (Rob Voss, Ken Creighton and Steve Dobson) benefitted me greatly. Somehow, Richard W. Redding has managed to equal my longevity and provided a source of friendly continuity. I particularly enjoyed the many discussions concerning problems of muroid taxonomy, details of rodent anatomy and rat miscellanea held with R. S. Voss.

Numerous individuals lent their time and technical expertise in rounding out various aspects of the dissertation. Scott Moody gave advice and assistance on operating some of the numerical programs. The ink drawings were excellently rendered by Kathy Simpson, and the figures were prepared by Rob Voss, Richard Redding and Al Sutton. Rob Voss drew Figure 21 and kindly allowed me to reproduce it here. Gloria Lake deciphered my hand-written rough draft and transcribed it into typed copy, and Peggy Lubahn overcame the plethora of scientific names and anatomical terms in typing a flawless final copy. Thousands of computer cards were key-punched by Sandy Bowne, and Eli Rockwell graciously accomodated an urgent plea for some last-minute typing. Projection slides were prepared by David Bay, wildman of the biosciences lab, who manages to combine a frenetic work-pace with his usual high quality product and last-minute punctuality. I appreciate their conscientious efforts on my behalf.

I gratefully acknowledge the curators who made available for loan specimens in their care: Dr. D. G. Huckaby, California State University at Long Beach; Dr. R. Baker, The Museum, Michigan State University;

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MATERIALS AND METHODS

Selection of Species' Samples

Implementation of any phylogenetic study, particularly one directed at resolving higher-level evolutionary relationships (beta taxonomy, *sensu* Mayr, 1969), poses methodological problems concerning what species to include, what unit (individual specimen, single population sample, array of population samples from geographic variants) to employ in characterizing the morphology of the species, and what characters and organ systems to survey as a basis for estimating relationships.

In deciding exactly what species to treat, I was greatly aided by previous workers' attention to the alpha systematics of most genera, or at least significant portions of the larger genera, of neotomine-peromyscines (Table 4). The delimitation of species, documentation of ranges, and identification of major subdivisions within genera are perhaps better known for neotomine-peromyscines than for any other group of muroid rodents of comparable size, with the possible exception of the Microtinae. As a result of the intensive study focused upon neotomine-peromyscines, the peripheral or problematic status of certain species has already been recognized and solidified nomenclatorially by allocation to specific tribes, subgenera and species-groups. This advanced state of the art proved important because it has allowed me to select species that represent a wide range of diversity within the neotomine-peromyscines assemblage or species that typify particular taxonomic units. For example, I chose only *P. maniculatus* as a representative of the six species comprising the *maniculatus* species-group, subgenus *Peromyscus*. In the case of larger taxa whose internal affinities were poorly understood, such as the subgenus *Neotoma* and *mexicanus* species-group, subgenus *Peromyscus,* I was less typological and included several species. Consequently, my basic collection of neotomine-peromyscines totals 49 of the 111 recognized species (Table 4). These 49 species represent all 12 genera and all subgenera but one, the monotypic *Teanopus phenax* of the genus *Neotoma.* I lacked fluid examples of *Xenomys nelsoni* and had only one specimen consisting of a skin, skull and skeleton. However, I felt a reasonable estimate of its relationships could be obtained based on attributes of its skull and skeleton, together with already-published information on the anatomy of its phallus (Hooper, 1960). In the speciose genus *Peromyscus,* I obtained examples of all subgenera and all

seven species-groups of the nominate subgenus (Table 4). I believe this set of 49 species fairly brackets the range of phenetic, if not evolutionary, divergence within the neotomine-peromyscines.

The common demonimator of my study is a population sample of a nominal species, termed operational taxonomic units (OTUs) by Sneath and Sokal (1973) or evolutionary units (EUs) *sensu* Estabrook (1972). I observed differences, defined character states, and weighed the nature of variation based on the morphology of specimens comprising these samples of the species. I did not include samples of all 111 species of neotomine-peromyscines, in part for the reason of redundancy as mentioned above. A more pragmatic factor influencing my choice of species involved the availability of adequate series. This was exacerbated by the fact that I desired not only suitable series of skins and skulls (20–30 adult animals), but also skeletal and fluid-preserved specimens, all from one local population or at least nearby localities. My success in achieving geographic congruence of the three sets of preparations varied. Generally, adequate series of skins and skulls could be accumulated. Geographic homogeneity of the sample was less often maintained in the case of skeletons and fluid-preserved specimens, a situation that underscores the relative recency of standardly saving such preparations. In such instances, I at least tried to draw my samples from the same subspecies.

I cannot judge the extent to which my single population sample is a "reliable" or "typical" example of the entire species. Consequently, I had to be somewhat typological at the species level and have assumed that my single population is representative of the species' morphology as a whole. In making this assumption, I have adopted the exemplar method as propounded by Sneath and Sokal (1973:183–4).

In view of my results, I think this approach is wholly vindicated because the degree of evolutionary separation between the species' samples is generally so great. That is to say, the distance, phenetic or patristic (*sensu* Farris, 1967), between *Peromyscus (Isthmomys) pirrensis* and *P. (Peromyscus) leucopus* would not be appreciably altered if I had selected a sample of *P. leucopus castaneus* instead of *P. leucopus noveboracensis*. In fact, Moss (1968) reached a similar conclusion in a more rigorous, systematic testing of exemplar substitutions and their effect upon higher-level groupings in strictly phenetic methods of numerical taxonomy. I do believe that the selection of species samples becomes most important in resolving the finer branching patterns of one's phylogeny; for example, a more refined elucidation of the cladistic relations of the many species in the subgenus *Peromyscus*. However, I am expressly not interested in such detailed resolution and have refrained from drawing phylogenetic inferences at those levels. Rather, my study is aimed at delineating major phyletic lines, explicitly those currently recognized at the taxonomic rank of subgenus and higher.

The 49 species of neotomine-peromyscines are listed below, together with the number of specimens examined and their localities. Abbreviations of the species, which appear in the tables and figures, are enclosed in

TABLE 4

CURRENT CLASSIFICATION OF NEOTOMINE-PEROMYSCINES AND MAJOR GENERIC REVISIONS OR SYNOPSES.

Peromyscini	
Baiomys	Packard, 1960
taylori *	
musculus *	
Ochrotomys	Packard, 1969
nuttalli *	
Onychomys	Hollister, 1914
leucogaster *	
torridus *	
Scotinomys	Hooper, 1972
teguina *	
xerampelinus *	
Reithrodontomys	Howell, 1914;
(Reithrodontomys)	Hooper, 1952
megalotis group	
humulis *	
burti	
montanus *	
megalotis *	
raviventris	
sumichrasti *	
chrysopsis	
fulvescens group	
fulvescens *	
hirsutus	
(Aporodon)	
mexicanus group	
gracilis	
spectabilis	
darienensis	
mexicanus *	
brevirostris	
paradoxus	
tenuirostris group	
microdon	
tenuirostris	
rodriguezi	
creper *	
Neotomodon	
alstoni *	
Nelsonia	Hooper, 1954
neotomodon *	
Peromyscus	Osgood, 1909; Hooper, 1968
(Peromyscus)	
maniculatus group	
polionotus	
maniculatus *	
sejugis	
slevini	

* = species included in this study

TABLE 4
(Continued)

sitkensis
melanotis
leucopus group
leucopus *
gossypinus
crinitus group
crinitus *
pseudocrinitus
boylii group
pectoralis
boylii *
attwateri
stephani
simulus
madrensis
polius
ochraventer *
aztecus
spicilegus *
winkelmanni
truei group
truei *
bullatus
difficilis *
melanophrys group
melanophrys *
mekisturus
perfulvus
mexicanus group
stirtoni
yucatanicus *
mexicanus *
zarhynchus
grandis
guatemalensis *
megalops *
melanurus
species group, *incertae sedis: mayensis*
(Haplomylomys)
eremicus *
merriami
caniceps
guardia
interparietalis
eva
dickeyi
pembertoni
californicus *
(Osgoodomys)
banderanus *

* = species included in this study

TABLE 4
(Continued)

(Habromys)	
simulatus	
lophurus *	
lepturus *	
chinanteco	
(Podomys)	
floridanus *	
(Megadontomys)	
thomasi *	
(Isthmomys)	
flavidus *	
pirrensis *	
subgenus, *incertae sedis: hooperi*	
Neotomini	
Tylomys	
bullaris	
fulviventer	
gymnurus	
nudicaudus *	
panamensis	
watsoni	
tumbalensis	
Ototylomys	Lawlor, 1969
phyllotis *	
Xenomys	
nelsoni *	
Neotoma	Goldman, 1910; Burt and Barkalow, 1942
(Neotoma)	
floridana group	
floridana *	
angustipalata	
micropus	
albigula group	
albigula *	
nelsoni	
palatina	
varia	
goldmani	
lepida group	
lepida *	
bryanti	
anthonyi	
martinensis	
bunkeri	
stephensi	
mexicana group	
mexicana *	
fuscipes group	
fuscipes *	
(Teonoma)	

* = species included in this study

TABLE 4
(Continued)

cinerea *	
(Hodomys)	
alleni *	
(Teanopus)	
phenax	

* = species included in this study

parentheses following the specific appellation. Unless otherwise indicated, all specimens are housed in the University of Michigan Museum of Zoology; some were borrowed from the United States National Museum of Natural History (USNM), The Museum, Michigan State University (MSU), and California State University at Long Beach (CSULB). In addition to the twelve genera of neotomine-peromyscines, I included examples of South American cricetines, Old World cricetines, microtines and gerbillines. My selection of species from these muroid groups was dictated partially by availability. Nonetheless, each was included with an intent to represent the spectrum of morphological diversity within those taxa as revealed by other investigators, notably Hooper and Hart (1962) and Hooper and Musser (1964a). These additional species proved necessary in order to evaluate the differentiation of neotomine-peromyscines with respect to other assemblages of Muroidea, especially South American cricetines, and to provide outgroup comparisons for determining character polarities. One might argue that examples of Murinae would be at least as, if not more, appropriate as an outgroup based upon their hypothesized cladistic relationship to neotomine-peromyscines and South American cricetines (see Figure 1). In view of our meager comprehension of affinities within that subfamily, the multitude of subdivisions that have been recognized by various authors, and the resultant subjectivity in choosing any one species or even several, I declined to do so. Thus my basic study collection of 75 species conforms closely to Simpson's (1945) concept of the family Cricetidae.

Neotomine-Peromyscines

1. *Baiomys taylori* (BAI)
   Skin and skull.—ARIZONA, *Cochise Co.:* 5-9 mi W Hereford, 16.
   Skeleton.—ARIZONA, *Cochise Co.:* 5-9 mi W Hereford, 12.
   Fluid.—TEXAS, *Harris Co.:* vicinity Houston, 10.
2. *B. musculus* (BAI)
   Skin and skull.—MEXICO, *Oaxaca:* Sola de la Vega, 24; Mihuatlan, 9.
   Skeleton.—MEXICO, *Oaxaca:* Sola de la Vega, 2; Ejutla, 3; Miahuatlan, 2; Nejapa, 2; Tehuantepec, 2.
   Fluid.—MEXICO, *Oaxaca:* 2 mi N Etla, 4.

3. *Ochrotomys nuttalli* (OCHRO)
   Skin and skull.—NORTH CAROLINA, *Mecklenburg Co.:* Davidson, 3; Charlotte, 2; *Wake Co.:* Raleigh, 8; *Madison Co.:* Marshall, 10.
   Skeleton.—ALABAMA, *Lee Co.:* Auburn, 1; FLORIDA, *Alachua Co.:* Gracies Crossing, 1.
   Fluid.—FLORIDA, *Alachua Co.:* 8 mi NW Gainesville, 2; NORTH CAROLINA, *Wake Co.:* Raleigh, 3.
4. *Onychomys leucogaster* (ONYCH)
   Skin and skull.—NEBRASKA, *Cherry Co.:* Hackberry Lake, 3; *Hooker Co.:* Kelso, 2; *Grant Co.:* Hyannis, 2; *Custer Co.:* 1-2 mi NW Gavin, 6; *Lincoln Co.:* 6 mi NE Dickens, 1; *Sheridan Co.:* 4 mi N Antioch, 4; 16 mi NE Alliance, 3; *Garden Co.:* 10 mi S Antioch, 5.
   Skeleton.—NEBRASKA, *Cherry Co.:* Hackberry Lake, 3; NORTH DAKOTA, *Richland Co.:* 6 mi S Fairmont, 1; OKLAHOMA, *Woods Co.:* Waynoka, 4.
   Fluid.—ARIZONA, *Cochise Co.:* Fort Huachuca, 5; NEBRASKA, *Cherry Co.:* Hackberry Lake, 3.
5. *O. torridus* (ONYCH)
   Skin and skull.—TEXAS, *Jeff Davis Co.:* Fort Davis, 5; 15-16 mi N Fort Davis, 6; *Presidio Co.:* 1 mi NE Marfa, 4; *Brewster Co.:* Del Nortes, 3.
   Skeleton.—TEXAS, *Jeff Davis Co.:* Fort Davis, 2; Limpia Canyon, 1; *Presidio Co.:* 10 mi NE Marfa, 2.
   Fluid.—ARIZONA, *Cochise Co.:* Fort Huachuca, 5.
6. *Scotinomys teguina* (SCOT)
   Skin and skull.—COSTA RICA, *Cartago:* Volcan Irazu, 2875-2940 m, 27.
   Skeleton.—COSTA RICA, *Cartago:* Volcan Irazu, 8; *Puntarenas:* Monte Verde, 3.
   Fluid.—COSTA RICA, *Cartago:* Volcan Irazu, 5.
7. *S. xerampelinus* (SCOT)
   Skin and skull.—COSTA RICA, *Cartago:* Volcan Turrialba, 2590 m, 18.
   Skeleton.—COSTA RICA, *Cartago:* Volcan Turrialba, 2590 m, 15.
   Fluid.—COSTA RICA, *Cartago:* Volcan Turrialba, 5.
8. *Reithrodontomys creper* (R)
   Skin and skull.—COSTA RICA, *Cartago:* Cerro de la Muerte, 2730-3335 m, 27.
   Skeleton.—COSTA RICA, *Cartago:* Cerro de la Muerte, 7; Volcan Irazu, 4.
   Fluid.—COSTA RICA, *Cartago:* Cerro de la Muerte, 5.
9. *R. mexicanus* (R)
   Skin and skull.—MEXICO, *Chiapas:* Prusia, 1200 m, 9; Bochil, 1320 m, 2; Pueblo Nuevo, 1; 5 mi N Pueblo Nuevo, 3; GUATE-

MALA, *Huehuetenango:* Barillas, 4; Hda. El Injerto, 2; *Alta Verapaz:* Finca Concepcion, 2.
Skeleton.—GUATEMALA, *Huehuetenango:* Barillas, 10.
Fluid.—COSTA RICA, *Cartago:* 1 mi SW Paraiso, 3; GUATEMALA, *Huehuetenango:* Barillas, 6.

10. *R. fulvescens* (R)
Skin and skull.—MEXICO, *Jalisco:* 7 mi W Ameca, 4000 ft, 30.
Skeleton.—MEXICO, *Jalisco:* 7 mi W Ameca, 2; 2 mi N Resolana, 1; 2 mi W San Andreas, 1; *Tamaulipas:* Jaumave, 2; Acuna, 3.
Fluid.—ARIZONA, *Cochise Co.:* Fort Huachuca, 3; MEXICO, *Guerrero:* 0.5 km W Acahuizotla, 3.

11. *R. megalotis* (R)
Skin and skull.—TEXAS, *Jeff Davis Co.:* Ft. Davis, 8; Limpia Canyon, 5; *Presidio Co.:* 10 mi NE Marfa, 3; *Brewster Co.:* Chisos Mts., 2.
Skeleton.—TEXAS, *Jeff Davis Co.:* Fort Davis, 3; Mt. Locke, 2; 10 mi NE Marfa, 3.
Fluid.—ARIZONA, *Cochise Co.:* Fort Huachuca, 4.

12. *R. sumichrasti* (R)
Skin and skull.—COSTA RICA, *Cartago:* Volcan Irazu, 2860–3300 m, 26.
Skeleton.—COSTA RICA, *Cartago:* Volcan Irazu, 15.
Fluid.—COSTA RICA, *Cartago:* Volcan Irazu, 5.

13. *R. montanus* (R)
Skin and skull.—TEXAS, *Bailey Co.:* 9 mi SW Muleshoe, 10; *Briscoe Co.:* 22 mi E Tulia, 8.
Skeleton.—OKLAHOMA, *Rogers Co.:* Garnett, 1; TEXAS, *Jeff Davis Co.:* Fort Davis, 1.
Fluid.—ARIZONA, *Cochise Co.:* Fort Huachuca, 2; NEBRASKA, *Cherry Co.:* Hackberry Lake, 3.

14. *R. humulis* (R)
Skin and skull.—VIRGINIA, *Smyth Co.:* 0.5 mi E Konnarock, 3; *Washington Co.:* Konnarock, 12; *Montgomery Co.:* 0.5 mi W Blacksburg, 12.
Skeleton.—ALABAMA, *Lee Co.:* Auburn, 3; TEXAS, *Jeff Davis Co.:* 7 mi S la Belle, 1; VIRGINIA, *Montgomery Co.:* Blacksburg, 2.
Fluid.—FLORIDA, *Alachua Co.:* 10 mi NW Gainesville, 2; SOUTH CAROLINA, *Aiken Co.:* Savannah River Plant, 2.

15. *Neotomodon alstoni* (NEOT)
Skin and skull.—MEXICO, *Morelos:* Mexico City–Acapulco Hwy., 10,000 ft, 26.
Skeleton.—MEXICO, *Morelos:* Mexico City–Acapulco Hwy., 10,000 ft, 7.
Fluid.—MEXICO, *Morelos:* Mexico City–Acapulco Hwy., 5.

16. *Nelsonia neotomodon* (NELS)
Skin and skull.—MEXICO, *Aguascalientes:* Sierra Fria, 8200 ft, 1; *Durango:* Cerro Huehuento, 8500 ft, 1; 1.5 mi W San Luis, 3, 5 (MSU); 28 mi S Vicente Guerrero, 1 (MSU); *Zacatecas:* Sierra Madre, 8500 ft, 4 (USNM).
Skeleton.—MEXICO, *Aguascalientes:* Sierra Fria, 1; *Durango:* 1.5 mi W San Luis, 3, 5 (MSU).
Fluid.—MEXICO, *Durango:* 1.5 mi W San Luis, 2 (MSU).

17. *Peromyscus crinitus* (Pc)
Skin and skull.—CALIFORNIA, *Inyo Co.:* Saline Valley, 15; Inyo Mts., 6; Panamint Mts., 3; Owens Valley, 8.
Skeleton.—CALIFORNIA, *Riverside Co.:* San Jacinto Mts., 1.
Fluid.—CALIFORNIA, *San Bernardino Co.:* Cottonwood Springs, 5.

18. *P. leucopus* (P)
Skin and skull.—OHIO, *Ottawa Co.:* S. Bass Island, 23.
Skeleton.—OHIO, *Ottawa Co.:* S. Bass Island, 16.
Fluid.—MICHIGAN, *Washtenaw Co.:* Ann Arbor, 10.

19. *P. maniculatus* (P)
Skin and skull.—IOWA, *Winneshiek Co.:* Decorah, 17; *Winnebago Co.:* 1 mi N, 3 mi W Forest City, 10; *Hancock Co.:* 1 mi S Forest City, 2.
Skeleton.—IOWA, *Winnebago Co.:* 1 mi N, 3 mi W Forest City, 10; *Hancock Co.:* 1 mi S Forest City, 13.
Fluid.—MICHIGAN, *Washtenaw Co.:* vicinity Ann Arbor, 5.

20. *P. boylii* (P)
Skin and skull.—MEXICO, *Guerrero:* Omilteme, 18; 8.6 mi WSW Chilpancingo, 5; 20 mi N Chilpancingo, 5.
Skeleton.—MEXICO, *Guerrero:* Omilteme, 5; *Michoacan:* 6.4 mi WSW Dos Aguas, 4.
Fluid.—MEXICO, *Guerrero:* 0.5 mi W Acahuizotla, 5.

21. *P. ochraventer* (P)
Skin and skull.—MEXICO, *Tamaulipas:* Rancho del Cielo, 11; Gomez Farias, 6; 3 mi W El Carrizo, 6.
Skeleton.—MEXICO, *Tamaulipas:* Rancho del Cielo, 11; Gomez Farias, 7.
Fluid.—MEXICO, *Tamaulipas:* Rancho del Cielo, 5.

22. *P. spicilegus* (P)
Skin and skull.—MEXICO, *Michoacan:* 5–7 mi S Uruapan, 13; Rancho Reparto, 9; 6.4–7.5 mi E Dos Aguas, 15.
Skeleton.—MEXICO, *Michoacan:* 7 mi S Uruapan, 3; Uruapan, 2; 7.5 mi E Dos Aguas, 10.
Fluid.—MEXICO, *Michoacan:* 7.5 mi E Dos Aguas, 6.

23. *P. truei* (P)
Skin and skull.—NEW MEXICO, *Valencia Co.:* Canyon Lobo Ranger Station, 5; 4 mi W McCarty's, 5; 8 mi SE Grants, 6; Shuman's Ranch, 4; 1.5 mi SW San Mateo, 2; 4 mi WSW Cebolleta, 6.
Skeleton.—CALIFORNIA, *Napa Co.:* 7 mi E Napa, 4; COLORADO, *Las Animas Co.:* Mesa de Maya, 3; NEW MEXICO, *Otero Co.:* 2 mi N Tularosa, 1.
Fluid.—NEW MEXICO, *Lincoln Co.:* Carrizozo, 2; *Valencia Co.:* 1.5 mi SW San Mateo, 1.

24. *P. difficilis* (P)
Skin and skull.—MEXICO, *Veracruz:* Acultzingo, 24; 1.5 mi S Perote, 6.
Skeleton.—MEXICO, *Hidalgo:* Zimapan, 1; *Nuevo Leon:* 20 mi N Galeana, 1; *Veracruz:* 1.5 mi S Perote, 6.
Fluid.—MEXICO, *Aguascalientes:* Sierra Fria, 5.

25. *P. melanophrys* (P)
Skin and skull.—MEXICO, *Oaxaca:* 85 km WNW Tehuantepec, Nejapa, 16; 10 mi W Tehuantepec, 8.
Skeleton.—MEXICO, *Oaxaca:* Sola de la Vega, 1; Nejapa, 1; 10 mi W Tehuantepec, 7; 7 mi NNE Oaxaca City, 1.
Fluid.—MEXICO, *Oaxaca:* 7 mi NNE Oaxaca City, 1; *Zacatecas:* 3 mi WNW Soldena, 1.

26. *P. mexicanus* (P)
Skin and skull.—GUATEMALA, *Huehuetenango:* Rio El Injerto, 10; *Esquintla:* Volcan de Agua, 20.
Skeleton.—GUATEMALA, *Huehuetenango:* Rio El Injerto, 8; *Esquintla:* Volcan de Agua, 6.
Fluid.—GUATEMALA, *Esquintla:* Volcan de Agua, 7.

27. *P. guatemalensis* (P)
Skin and skull.—GUATEMALA, *Huehuetenango:* Hda. El Injerto, 30.
Skeleton.—GUATEMALA, *Huehuetenango:* Hda. El Injerto, 30.
Fluid.—GUATEMALA, *Huehuetenango:* Hda. El Injerto, 5.

28. *P. megalops* (P)
Skin and skull.—MEXICO, *Guerrero:* Omilteme, 13; 1 mi W Omilteme, 4; 20 mi N Chilpancingo, 26.
Skeleton.—MEXICO, *Guerrero:* Omilteme, 13; 20 mi N Chilpancingo, 5.
Fluid.—MEXICO, *Guerrero:* 20 mi N Chilpancingo, 5.

29. *P. furvus* (P)
Skin and skull.—MEXICO, *Veracruz:* 1 mi W Xico, 15; 2 mi SE Huayacoctla, 3; 5 mi S Jalapa, 2.
Skeleton.—MEXICO, *Veracruz:* 1 mi W Xico, 13; 2 mi SE Huayacoctla, 3; *Puebla:* 2.5 mi SW Huauchinango, 5.
Fluid.—MEXICO, *Puebla:* 5.7–7.3 mi SW Huauchinango, 4.

30. *P. yucatanicus* (P)
Skin and skull.—MEXICO, *Campeche:* 7 km W Escarcega, 28.
Skeleton.—MEXICO, *Campeche:* 7 km W Escarcega, 28.
Fluid.—MEXICO, *Yucatan:* near Chichen Itza, 7.

31. *P. (Haplomylomys) eremicus* (H)
Skin and skull.—ARIZONA, *Pima Co.:* 38 mi S Tuscon, 7; 30 mi NE Sells, 21.
Skeleton.—ARIZONA, *Pima Co.:* 10 mi S Tuscon, 2; TEXAS, *Brewster Co.:* Rio Grande, 4; *Jeff Davis Co.:* 15 mi N Fort Davis, 4.
Fluid.—ARIZONA, *Cochise Co.:* Fort Huachuca, 2; TEXAS, *Brewster Co.:* 5.

32. *P. (Haplomylomys) californicus* (H)
Skin and skull.—CALIFORNIA, *Santa Cruz Co.:* Corralitos, 5; *Alameda Co.:* Strawberry Canyon, 12; *Santa Clara Co.:* 2 mi SW Saratoga, 7.
Skeleton.—CALIFORNIA, *Alameda Co.:* Strawberry Canyon, 1; *Santa Cruz Co.:* Corralitos, 6.
Fluid.—CALIFORNIA, *Alameda Co.:* Strawberry Canyon, 3.

33. *P. (Osgoodomys) banderanus* (OSGOOD)
Skin and skull.—MEXICO, *Jalisco:* 4 mi NE Autlan, 3000 ft, 6; 1 mi N San Gabriel, 4000 ft, 4; Chamela Bay, 5; 6 km E Chamela, 1; 3 mi E Navidad, 4; Tenacatita Bay, 5.
Skeleton.—MEXICO, *Jalisco:* Chamela Bay, 5; 6 km E Chamela, 1; *Michoacan:* Apatzingan, 1; *Nayarit:* 3 mi SE Sayulita, 1.
Fluid.—MEXICO, *Nayarit:* 3 mi SE Sayulita, 4.

34. *P. (Habromys) lepturus* (HAB)
Skin and skull.—MEXICO, *Oaxaca:* 11-13 mi NE Llano de las Flores, 29.
Skeleton.—MEXICO, *Oaxaca:* 12 mi N Ixtlan de Juarez, 1; 13 mi NE Llano de las Flores, 2.
Fluid.—MEXICO, *Oaxaca:* 13 mi NE Llano de las Flores, 5.

35. *P. (Habromys) lophurus* (HAB)
Skin and skull.—GUATEMALA, *Huehuetenango:* 4 km NW Santa Eulalia, 12.
Skeleton.—GUATEMALA, *Huehuetenango:* 4 km NW Santa Eulalia, 12.
Fluid.—GUATEMALA, *Huehuetenango:* 4 km NW Santa Eulalia, 5.

36. *P. (Podomys) floridanus* (POD)
Skin and skull.—FLORIDA, *Citrus Co.:* 6 mi W Inverness, 8 (USNM); *Osceola Co.:* Kissimmee River, 18 (USNM).
Skeleton.—FLORIDA, *Marion Co.:* Ocala Forest, 1 (USNM); *Sarasota Co.:* Englewood, 1 (USNM); St. Augustine's Beach, 2; Anastasia Island, 4.
Fluid.—FLORIDA, *Alachua Co.:* 15 mi SW Otter Creek, 2; 6 mi W Gainesville, 2.

37. *P. (Megadontomys) thomasi* (MEGADON)
Skin and skull.—MEXICO, *Guerrero:* 20 mi N Chilpancingo, near Puerto Chico, 24.
Skeleton.—MEXICO, *Guerrero:* 20 mi N Chilpancingo, near Puerto Chico, 23.
Fluid.—MEXICO, *Guerrero:* 20 mi N Chilpancingo, near Puerto Chico, 5.

38. *P. (Isthmomys) flavidus* (ISTH)
Skin and skull.—PANAMA, *Los Santos:* Cerro Hoya, 7 (USNM).
Skeleton.—PANAMA, *Los Santos:* Cerro Hoya, 2 (USNM).

39. *P. (Isthmomys) pirrensis* (ISTH)
Skin and skull.—PANAMA, *Darien:* Cerro Mali, 4700 ft, 20 (USNM).
Skeleton.—PANAMA, *Darien:* Cerro Mali, 4700 ft, 5 (USNM); Cerro Nique, 2 (MSU).
Fluid.—PANAMA, *Darien:* Cerro Mali, 5 (USNM).

40. *Neotoma (Neotoma) albigula* (Na)
Skin and skull.—NEW MEXICO, *Valencia Co.:* 1.5 mi S Grants, 7; 4 mi W McCarty's, 3; 8–9 mi SE Grants, 12; Shuman's Ranch, 4.
Skeleton.—NEW MEXICO, *Dona Ana Co.:* Kenzin, 1; *Lincoln Co.:* 6 mi NW Capitan, 1; 4 mi W Carrizozo, 1; 5 mi W Oscuro, 4; *Otero Co.:* 3 mi NE Tularosa, 2; *Valencia Co.:* 8 mi SE Grants, 2.
Fluid.—UTAH, *Grand Co.:* Castle Valley, 4.

41. *N. (Neotoma) floridana* (Nf)
Skin and skull.—OKLAHOMA, *Tulsa Co.:* Garnett, 6; *Osage Co.:* Okesa, 10; *Adair Co.:* 5 mi S Kansas, 4; *Payne Co.:* Stillwater, 3.
Skeleton.—OKLAHOMA, *Rogers Co.:* Garnett, 1; *Osage Co.:* Okesa, 5; *Adair Co.:* 5 mi S Kansas-Oklahoma line, 6.
Fluid.—KANSAS, *Douglas Co.:* 2 mi W Lawrence, 2.

42. *N. (Neotoma) mexicana* (Nm)
Skin and skull.—NEW MEXICO, *Lincoln Co.:* 4 mi NW Lincoln, 4; *Otero Co.:* 2.5 mi N Cloudcraft, 1; Highrolls, 2; 0.5 mi W Highrolls, 3; *Valencia Co.:* 8 mi SE Paxton, 10; 17 mi SW Grants, 3; 8–9 mi SE Grants, 3; Point of Malpais, 7; 1.5 mi SW San Mateo, 2; 4 mi WSW Cebolleta, 4.
Skeleton.—NEW MEXICO, *Lincoln Co.:* 5 mi W Oscuro, 1; *Valencia Co.:* 8 mi SE Grants, 3; Point of Malpais, 1; 4 mi WSW Cebolleta, 1; TEXAS, *Jeff Davis Co.:* Fort Davis, 3; 2 mi W Fort Davis, 2; Limpia Canyon, 3; 1 mi N Mt. Lawrence, 1.
Fluid.—COLORADO, *Montrose Co.:* 4 mi SE Uravan, 2; NEW MEXICO, *Otero Co.:* Highrolls, 1.

43. *N. (Neotoma) fuscipes* (Nfus)
Skin and skull.—CALIFORNIA, *San Diego Co.:* La Jolla, 1; 1 mi S Escondido, 3; *Santa Barbara Co.:* 2 mi SW Buellton, 5; *Los Angeles*

Co.: Los Angeles, 9; Punete Hills, 4; Westwood, 2.
Skeleton.—CALIFORNIA, *Alameda Co.:* Berkeley, 2; *San Diego Co.:* La Jolla, 1; Bonsall, 1; *San Luis Obispo Co.:* Munro, 2.
Fluid.—CALIFORNIA, *Alameda Co.:* San Francisco, 2; *Los Angeles Co.:* Los Angeles, 1; *Riverside Co.:* Cleveland National Forest, 2 (CSULB).

44. *N. (Neotoma) lepida* (Nl)
Skin and skull.—MEXICO, *Baja California Sur:* Turtle Bay, 2; Santa Maria Bay, 7; Magdalena Bay, 5; Santa Margarita Island, 12.
Skeleton.—MEXICO, *Baja California Sur:* Turtle Bay, 2; Santa Maria Bay, 7; Magdalena Bay, 5; Santa Margarita Island, 12.
Fluid.—CALIFORNIA, *Los Angeles Co.:* San Antonio, 2; 10 mi E Palmdale, 2; *Imperial Co.:* 1 mi E Mountain Spring, 1 (CSULB); *Riverside Co.:* 1 (CSULB); *San Diego Co.:* 5.5 mi NW Banner, 1 (CSULB).

45. *N. (Teonoma) cinera* (TEON)
Skin and skull.—MONTANA, *Cascade Co.:* 11 mi NE Great Falls, 9; *Golden Valley Co.:* Big Snowy Mtn., 3; *Hill Co.:* Bearpaw Mtns., 1; *Sweetgrass Co.:* Sweetgrass Creek Canyon, 4.
Skeleton.—MONTANA, *Cascade Co.:* 11 mi NE Great Falls, 1; *Golden Valley Co.:* Big Snowy Mtn., 2; *Sweetgrass Co.:* Sweetgrass Creek Canyon, 1; OREGON, *Tillamook Co.:* Dolph, 3; WYOMING, *Sweetwater Co.:* 6 mi S Point of Rocks, 4.
Fluid.—MONTANA, *Carbon Co.:* 4 mi WSW Red Lodge, 3.

46. *N. (Hodomys) alleni* (HOD)
Skin and skull.—MEXICO, *Guerrero:* Chilpancingo, 14.
Skeleton.—MEXICO, *Colima:* 13 mi SE Manzanillo, 2; *Jalisco:* Chamela Bay, 2; 4 mi NE Autlan, 1; *Guerrero:* S side Acapulco Bay, 1.
Fluid.—MEXICO, *Colima:* 13 mi SE Manzanillo, 2.

47. *Xenomys nelsoni* (XEN)
Skin and skull.—MEXICO, *Jalisco:* Chamela Bay, 1.
Skeleton.—MEXICO, *Jalisco:* Chamela Bay, 1.

48. *Ototylomys phyllotis* (OTOTYL)
Skin and skull.—MEXICO, *Campeche:* 3 km W Escarcega, 4; *Quintana Roo:* Esmeralda, 10; *Yucatan:* 1 km W Chichen Itza, 1.
Skeleton.—MEXICO, *Campeche:* 3 km W Escarcega, 2; 7.5 km W Escarcega, 5 (MSU); EL SALVADOR, *San Miguel:* Volcan San Miguel, 1; NICARAGUA, *Chinandega:* San Antonio, 1.
Fluid.—MEXICO, *Campeche:* vicinity Escarcega, 7.

49. *Tylomys nudicaudus* (TYL)
Skin and skull.—MEXICO, *Chiapas:* Soconusco, 1; *Oaxaca:* 5 mi E Rio Grande, 15 (MSU).

Skeleton.—MEXICO, *Chiapas:* Soconusco, 1; *Oaxaca:* 5 mi E Rio Grande, 3 (MSU); 10 mi S Valle Nacional, 2 (MSU).
Fluid.—MEXICO, *Chiapas:* 1 mi S Tuxtla Gutierrez, 1; *Oaxaca:* 5 mi E Rio Grande, 4 (MSU).

South American Cricetines

50. *Akodon cursor* (AKO)
Skin and skull.—PARAGUAY, *Itapua:* 3.5 km E San Rafael, 14; 8 km N San Rafael, 3.
Skeleton.—PARAGUAY, *Itapua:* 3.5 km E San Rafael, 13.
Fluid.—PARAGUAY, *Itapua:* vicinity of San Rafael, 5.

51. *Oxymycterus delator* (OXYMYC)
Skin and skull.—PARAGUAY, *Canendiyu:* 6.3 km N Curuguaty, 10.
Skeleton.—PARAGUAY, *Canendiyu:* 13.3 km N Curuguaty, 8.
Fluid.—PARAGUAY, *Canendiyu:* 13.3 km N Curuguaty, 4.

52. *Scapteromys tumidus* (SCAP)
Skin and skull.—PARAGUAY, *Cordillera:* 1.6 km S Tobati, 3; ARGENTINA, *Buenos Aires:* Punta Lara, 3.
Skeleton.—PARAGUAY, *Cordillera:* 1.6 km S Tobati, 3.
Fluid.—PARAGUAY, *Cordillera:* 1.6 km S Tobati, 1.

53. *Sigmodon hispidus* (SIGMO)
Skin and skull.—MEXICO, *Chiapas:* Bochil, 6; Prusia, 15.
Skeleton.—MEXICO, *Veracruz:* 2 km SSW Tenochtitlan, 3; Vicente, 2.
Fluid.—MEXICO, *Campeche:* 6 km S Champoton, 6.

54. *Holochilus brasiliensis* (HOLO)
Skin and skull.—PARAGUAY, *Presidente Hayes:* 15.5 km NNW Chaco-i, 13.
Skeleton.—PARAGUAY, *Presidente Hayes:* 15.5 km NNW Chaco-i, 13.
Fluid.—PARAGUAY, *Chaco:* 15 km WNW Fortin Madrejon, 5.

55. *Calomys callosus* (CAL)
Skin and skull.—PARAGUAY, *Chaco:* 50 km WNW Fortin Madrejon, 25.
Skeleton.—PARAGUAY, *Chaco:* vicinity Fortin Madrejon, 11.
Fluid.—PARAGUAY, *Chaco:* 50 km WNW Fortin Madrejon, 5.

56. *Graomys griseoflavus* (GRA)
Skin and skull.—PARAGUAY, *Chaco:* 28.8 km W Fortin Madrejon, 4; 50 km WNW Fortin Madrejon, 6.
Skeleton.—PARAGUAY, *Chaco:* 50 km WNW Fortin Madrejon, 2.
Fluid.—PARAGUAY, *Chaco:* 50 km WNW Fortin Madrejon, 5.

57. *Nectomys squamipes* (NECT)
Skin and skull.—PARAGUAY, *Canendiyu:* 13.3 km N Curuguaty, 4; *Paraguari:* 17 km SW Pirebebuy, 7.
Skeleton.—PARAGUAY, *Canendiyu:* 13.3 km N Curuguaty, 4.
Fluid.—PARAGUAY, *Canendiyu:* 13.3 km N Curuguaty, 2.

58. *Oryzomys capito* (ORYZ)
Skin and skull.—PARAGUAY, *Amambay:* 28 km SW Pedro Juan Caballero, 6; 4 km SW Cerro Cora, 2; *Canendiyu:* 13.3 km N Curuguaty, 2.
Skeleton.—PARAGUAY, *Canendiyu:* 13.3 km N Curuguaty, 2.
Fluid.—PARAGUAY, *Amambay:* 28 km SW Pedro Juan Caballero, 4.

59. *Oryzomys fulvescens* (ORYZ)
Skin and skull.—MEXICO, *Chiapas:* Cintalapa, 4; Bochil, 11.
Skeleton.—MEXICO, *Chiapas:* Cintalapa, 6; Bochil, 3.
Fluid.—COSTA RICA, *Cartago:* 3 mi SE Turrialba, 4.

60. *Oryzomys palustris* (ORYZ)
Skin and skull.—MEXICO, *Veracruz:* Tierra Blanca, 21.
Skeleton.—MEXICO, *Veracruz:* 2 km SSW Tenochtitlan, 6.
Fluid.—GEORGIA, *McIntosh Co.:* Sapello Island, 5.

61. *Thomasomys aureus* (THOM)
Skin and skull.—ECUADOR, *Pichincha:* Mt. Pichincha, 1; *Napo:* 6.9 km W Papallacta, 1.
Fluid.—ECUADOR, *Pichincha:* Mt. Pichincha, 1; *Napo:* 6.9 km W Papallacta, 1.

62. *Nyctomys sumichrasti* (NYCT)
Skin and skull.—PANAMA, *Bocas del Toro:* Caya Agua, 5 (USNM); *Chiriqui:* Cerro Punta, 1 (USNM).
Skeleton.—COSTA RICA, *Guanacaste:* 0.5 mi E Finca Jimenez, 1; GUATEMALA, *Huehuetenango:* Hda. El Injerto, 1; MEXICO, *Oaxaca:* Santa Cruz Bay, 1; PANAMA, *Bocas del Toro:* Caya Agua, 1 (USNM); *Chiriqui:* Cerro Punta, 1 (USNM); 10 km W El Aguacate, 2 (MSU).
Fluid.—GUATEMALA, *Solola:* Panajachel, 4; PANAMA, *Bocas del Toro:* Caya Agua, 1 (USNM).

Old World Cricetines

63. *Mesocricetus auratus*
Skin and skull.—ISRAEL, 2; lab stock, 6.
Skeleton.—ISRAEL, 2; lab stock, 6.
Fluid.—Lab stock, 2.

64. *Cricetulus migratorius*

Skin and skull.—IRAN, *Kerman:* Kerman, 2; *Fars:* Maylan, 2.
Skeleton.—IRAN, *Kerman:* Kerman, 2.
Fluid.—IRAN, *Khorassan:* 50 km E Mashad, 2.

Microtinae

65. *Ondatra zibethicus*
Skin and skull.—MICHIGAN, *Washtenaw Co.:* vicinity Ann Arbor, 10.
Skeleton.—MICHIGAN, *Washtenaw Co.:* vicinity Ann Arbor, 8.
Fluid.—MICHIGAN, *Washtenaw Co.:* Ann Arbor, 2.

66. *Clethrionomys gapperi*
Skin and skull.—MICHIGAN, *Schoolcraft Co.:* Cusino Wildlife Station, 8.
Skeleton.—MICHIGAN, *Schoolcraft Co.:* Cusino Wildlife Station, 12.
Fluid.—MICHIGAN, *Keewenaw Co.:* 2.

67. *Dicrostonyx groenlandicus* (DICR)
Skin and skull.—CANADA, *Northwest Territories:* Beverly Lake Region, 11.
Skeleton.—CANADA, *Northwest Territories:* Beverly Lake Region, 11.
Fluid.—CANADA, *Manitoba:* Churchill, 1.

68. *Lemmus sibiricus*
Skin and skull.—ALASKA, *Barter Island, 20.*
Skeleton.—ALASKA, Barter Island, 6.
Fluid.—ALASKA, Point Barrow, 2.

69. *Synaptomys cooperi* (SYN)
Skin and skull.—MICHIGAN, *Washtenaw Co.:* vicinity Ann Arbor, 15.
Skeleton.—MICHIGAN, *Livingston Co.:* E.S. George Reserve, 3; *Washtenaw Co.:* Ann Arbor, 2.
Fluid.—MICHIGAN, *Iron Co.:* 2, *Schoolcraft Co.:* 1.

70. *Microtus pennsylvanicus*
Skin and skull.—MICHIGAN, *Washtenaw Co.:* Ann Arbor, 20.
Skeleton.—MICHIGAN, *Washtanaw Co.:* Ann Arbor, 12.
Fluid.—MICHIGAN, *Washtenaw Co.:* Ann Arbor, 5.

Gerbillinae

71. *Gerbillus cheesmani*
Skin and skull.—PAKISTAN, *Baluchistan:* Nushki, 15.
Skeleton.—PAKISTAN, *Baluchistan:* Nushki, 15.
Fluid.—PAKISTAN, *Baluchistan:* Nushki, 5.

72. *Meriones shawi*
Skin and skull.—EGYPT, *Matruh:* Bahig, Burg El Arab, 15.
Skeleton.—EGYPT, *Matruh:* Bahig, Burg El Arab, 15.
Fluid.—EGYPT, *Matruh:* Bahig, Burg El Arab, 4.

73. *Pachyuromys duprasi*
Skin and skull.—EGYPT, *Beheira:* Kom Hamada, 13.
Skeleton.—EGYPT, *Beheira:* Kom Hamada, 12.
Fluid.—EGYPT, *Beheira:* Kom Hamada, 3.

74. *Psammomys obesus*
Skin and skull.—MOROCCO, Goulimine, 8.
Skeleton.—MOROCCO, Goulimine, 8.
Fluid.—MOROCCO, 27 km S Goulimine, 2.

75. *Tatera indica*
Skin and skull.—INDIA, *Maharashtra:* Thana, Bhiwandi Taluka, 12.
Skeleton.—INDIA, *Maharashtra:* Thana, Bhiwandi Taluka, 12.
Fluid.—INDIA, *Maharashtra:* Thana, Bhiwandi Taluka, 3.

Character Description and Numerical Methods

As stated above, a primary design of this study is to broadly sample the phenotype to represent a variety of character complexes, ones presumably subject to an array of selective pressures. In a group such as the Muroidea, wherein parallelism and convergence appear commonplace, this approach is clearly warranted if not demanded. Thus, I believe that a diversity and abundance of information are preferred in elucidating phylogenetic affinities of the organisms under study. Fortunately, there is an incredible richness of information that can be retrieved from a rodent's anatomy. I have endeavoured to include in my basic data set the traditional characters upon which much of muroid taxonomy rests, namely cranial and dental traits, as well as data from non-traditional organ systems heretofore not employed extensively in resolving problems of muroid relationships. In doing so, my study substantially extends the anatomical surveys of previous investigators and explores other sets of characters.

Although a systematist may strive to represent the morphology of the organisms under study in an unbiased manner, the mere act of utilizing certain specimen preparations and ignoring others, for whatever reasons, imposes partiality upon one's conclusions. I have limited my comparisons of the species to their cranial anatomy and associated dentition, postcranial skeleton, alimentary canal, morphology of the male phallus and accessory reproductive glands, and a few external features.

The characters used as a basis for estimating relationships of the species are coded as nominal, or discrete, variables. In most instances, they express either the presence/absence or degree of development of anatomical

structures. Some variables are meristic (numbers of ribs and vertebrae) and a few are qualitative states extrapolated from the ratios of continuous variables (relative size of the third molar or auditory bullae). In defining character states, I tried to stress what I perceived as gross or major differences and avoid the proliferation of many, huge multistate characters. Such an approach unavoidably masks finer points of dissimilarity. The definition of nominal variables reduces to the identification of characters that appear to vary little within OTUs but greatly between them. The 75 species samples enumerated above served as my ultimate base for interpreting such within- and between-OTU variations. I devoted considerable effort to searching out, defining and encoding, and frequently discarding characters from a variety of organ systems. A preliminary data set consisting of 103 variables was accumulated, but I eliminated some and combined others in arriving at the definitive list of 79 characters given below (see SURVEY OF CHARACTERS).

I cannot judge the equivalence of the characters in terms of the magnitude of differences as conveyed by the character state assignments. That is to say, one does not know whether a difference of one nominal unit in development of the vesicular glands corresponds to, or somehow reflects the same amount of genetic change as, a unit difference in distribution of gastric glandular epithelium. Therefore, one is initially constrained to treat all characters equally. Later, I employed an *a posteriori* weighting strategem in which characters are weighted inversely to the amount of homoplasy they exhibit in the first tree generated (Farris, 1969).

Most examination of specimens was aided by a Wild binocular dissecting-scope (60x–500x magnification). Fluid specimens consisted of whole animals preserved in ten percent buffered formalin and stored in 70 percent buffered ethanol. Male reproductive tracts were removed intact and stored separately. I attempted to limit my comparisons of phalli and accessory glands to males judged to be completely fertile, as indicated by maximal descent and size of the testis and full distention of the accessory glands. In the case of species with small sample sizes, I had to contend with the material at hand. To observe the various processes of the glans penis, especially structures situated within the crater of complex glans, I found it more informative to use the formalin-fixed material rather than cleared and stained preparations. The latter kind of preparation (see Hooper, 1958, or Lawlor, 1971, for procedure) of course proved necessary to view and measure the baculum, cartilaginous tip and lateral bacular digits. The actual number of prepared glandes utilized in the study greatly exceeds that listed above, for I have reexamined the majority of specimens contained in the University of Michigan Museum of Zoology, which served as the basis of the reports of Hooper (1958, 1959, 1960, 1962), Hooper and Hart (1962) and Hooper and Musser (1964a, b).

The following dimensions were measured in order to calculate certain ratios and thereby more precisely define differences in proportion.

1) Total length of lower molar row. — from the anterior face of the anteroconid to the posterior edge of the third molar.
2) Length of lower third molar. — from the edge of the anterior cingulum to the posterior border of the tooth.
3) Length of auditory bulla. — from the posterior border of the tympanic bulla (near the jugular foramen) to the flexure at the base of the bony eustachian tube.
4) Depth of auditory bulla. — from the ventralmost contour of the typpanic bulla to the top of the ascending arm of the tympanic bone, above the external auditory meatus. The skull was mounted on a glass slide and measured from a lateral view for this dimension.
5) Total length of skull. — from the tip of the nasal bones to the posterior projection of the supraoccipital.
6) Length of tibia. — from the proximal articular surface to the tip of the lateral malleolus.
7) Length of tibial-fibular fusion. — from the angle formed by the fusion of the fibula and tibia to the tip of the lateral malleolus of the tibia.
8) Length of the glans penis. — from the point of attachment of the prepuce to the apex of the cartilaginous tip.
9) Width of the glans penis. — The greatest width of the body of the glans.
10) Length of baculum. — length of the osseous portion; that is, excluding the cartilaginous tip.
11) Width of baculum. — across the apices of the bacular base.
12) Length of cartilaginous tip. — from the distal end of the osseous baculum to the apex of the cartilaginous tip.
13) Depth of crater. — from the floor of the crater to the crater rim; measured at the midfrontal plane.

All measurements were recorded to the nearest 0.1 mm with a craniometer (Anderson, 1968). Sample means were used to compute ratios. In formulating nominal variables based on these ratios, I visually inspected histograms and sought to define characters that embraced distinct modes and spanned approximately equal intervals.

In order to discern patterns of taxonomic structure, I analyzed the 79 characters with the species samples as cases by principal component and cluster analyses and a shortest connection (Prim) network. Principal components were computed from a correlation matrix, and loadings of the characters on the principal components were expressed by correlation coefficients (Morrison, 1967). Amalgamation of samples was accomplished by the unweighted pair-group method using arithmetic averages; charac-

ters were standardized to have a mean of zero and standard deviation of one. I employed both a Manhattan distance metric and the simple matching coefficient as resemblance coefficients in the clustering analyses (see Sneath and Sokal, 1973, for further discussion). A shortest connection network unites samples such that the sum of character differences over all OTUs is minimal (Prim, 1957). Unlike the phylogenetic methods mentioned below, hypothetical intermediates are not calculated in the construction of a shortest connection network; the species' samples themselves serve as the nodes of the network. The resemblance coefficient employed in the shortest connection network is the absolute sum of the character differences between any pair of specimens, termed the Manhattan or city-block metric. The principal component and clustering analyses are available through the Michigan Interactive Data Analysis System formulated by the University of Michigan Statistical Research Laboratory. The program for computation of the Prim network was written by James S. Farris.

I used three multivariate methods expressly intended to provide an estimate of the cladistic history of the organisms under study. These are the Wagner Tree program, Character Compatability analysis and the Weighted Invariant Step Strategy (WISS). Only a brief characterization of each method is given here. I refer the reader who desires further exposition of the underlying theory and methodology of these alternative approaches to phylogenetic inference to the attendant references.

Kluge and Farris (1969) developed the Wagner Tree program as a numerical formalization of the Wagner ground plan analysis, an informal elaboration of principles useful in phylogenetic inference (Wagner, 1961). Implementation of the Wagner Tree analysis requires designation of ancestral and derived states for each character and the specification of a hypothetical common ancestor to be included with the real specimens. Hypothetical intermediates (HTUs) are generated to minimize the total length of the tree; thus, the Wagner Tree program seeks that tree which minimizes the total number of character state transformations over all characters, the "most parsimonious tree", as the most reasonable estimate of cladistic and patristic history (also see Farris, 1970; Lundberg, 1972). In doing so, the analysis permits instances of character reversals and parallelism. A measure of the amount of homoplasy in the resultant tree is reflected by the index of consistency, c; c = R divided by L, where R is the size of the original data set (*i.e.,* the total number of evolutionary changes predicted by the sum of the individual character state trees) and L is the length of the tree (*i.e.,* the observed total number of character state transformations in the calculated tree). The Wagner Tree version used herein was programmed by J. S. Farris in 1978.

The method of character compatability (Estabrook, 1972; Estabrook *et al.,* 1976) makes operational Le Quesne's (1969, 1972) concept of the uniquely derived character. As defined by Le Quesne (1969:201), a uniquely derived character is one ". . . that has evolved only in one direc-

tion on a single occasion . . ." during the evolutionary history of the group of organisms under study. Such characters would divulge a more reliable estimate of the group's phylogenetic history than ones suspected of undergoing parallelism, convergence, or reversal. The problem is to differentiate *a priori* the goodness of the characters. Two characters are said to be compatible if they both postulate at least one unambiguous estimate of relationships of the organisms involved; incompatible characters predict different phylogenies. Character compatability analysis, then, searches for that tree based on the largest number of mutually compatible characters as the best reconstruction of the group's phylogeny, and disregards those believed to exhibit homoplasy. Generally, the maximal set, or clique, of mutually compatible characters is substantially smaller than the total number of variables in the data set, and there may be more than one clique of maximal size generated. As in the Wagner Tree analysis, character polarities must be designated and hypothetical intermediates may be constructed. The program I employed was written by G.F. Estabrook and K.L. Fiala. For additional discussion and applications of the method of character compatability, see Estabrook *et al.* (1977) and Strauch (1978).

The Weighted Invariant Step Stragety (WISS), developed by Farris *et al.* (1970), quantifies some of the principles of phylogenetic inference propounded by Hennig (1966). Again, primitive and derived attributes of characters are defined and hypothetical taxonomic units are generated in tree construction. Monophyletic groups are recognized on the basis of sharing the greatest number of derived states (synapomorphies) and progressively amalgamated. The algorithm admits instances of parallelism or convergence but not character reversals on the computed tree. J.S. Farris wrote the fortran program for implementing the WISS analysis.

SURVEY OF CHARACTERS

The crux of my analyses and arguments relies upon the 79 qualitative characters enumerated below, which represent a distillation from a larger set of 103 variables. After preliminary character analyses and initial trials using both phenetic and phylogenetic numerical methods, I condensed or eliminated some traits for reasons of obvious redundancy of information, strong correlations between characters, ambiguous or difficult character-state recognition, or lack of cladistic significance for the focal group under study, the neotomine-peromyscines. In the review of characters, I shall note which ones represent combinations or refinements of those defined earlier.

The following accounts of characters are ordered under the general headings of Dentition, Cranium, Post-Cranial Skeleton, Alimentary Canal, Phallus, Male Accessory Reproductive Glands, and Miscellaneous External Features. Each character is indexed by a number that serves to identify it in the various tables. Character states are indicated by whole numbers in parentheses, the inferred ancestral (plesiomorphic) condition

being (0) and derived (apormorphic) states consisting of positive whole numbers. Character-state transformations generally follow the logical numeric order, except in instances of furcating character-state trees; in such cases, the immediately ancestral state is indicated next to the character-state description (also, see Table 8). The majority of characters are two- or three-state variables but a few contain five to seven character expressions. I have not attempted to portray every character or character-state difference for each species, especially because many features have been described and illustrated previously by other authors. Where appropriate, descriptive paragraphs are included to expand or clarify the nature of character variation and problems of homology, and to offer my rationale for determining character polarities.

Dentition

Character 1: Index of Dental Complexity.

(0) Complex; score 0–6.
(1) Moderately complex; score 7–13.
(2) Simple; score 14–20.

This index is a compilation of eight different dental features which I originally had recorded as eight separate "characters". These features are (terminology follows Reig, 1977): the anteroloph-parastyle, protostyle, mesoloph-mesostyle, and enteroloph-enterostyle of the upper first molar; and the anterolophid-metastylid, prostylid, mesolophid-mesostylid, and ectolophid-ectostylid of the lower first molar. I employed a simplified coding system modified from that used by Hooper (1957) in his analysis of dental variation in *Peromyscus* and encoded four states of development of each loph(id) and associted style(id), except the protostyle(id) which I simply noted as present/absent. The state of a given species was the modal value recorded for specimens of the representative population. Hence, a total of 28 character states was recognized for the eight dental traits, and I tallied those 28 states for each species to obtain the index of complexity.

My reasons for doing this were two-fold. First, as noted by Hooper (1957), there is a marked tendency for co-occurrence of the various lophs(ids) and styles(ids), both on a single tooth or between teeth of the upper and lower molar rows. A rank-order correlation analysis verified these strong associations. Consistently high intercorrelations were obtained for most pairwise comparisons involving the anteroloph-parastyle, mesoloph-mesostyle, anterolophid-metastylid, mesolophid-mesostylid and ectolophid-ectostylid (Table 5). Those accessory features that usually were not significantly correlated, such as the protostyle(id) and enteroloph-enterostyle, occurred as regular dental elements in very few taxa; for example, the enteroloph-enterostyle was present (and just weakly developed) only in *Nyctomys* and *Ototylomys*. Second, although the formation of the accessory styles(ids) and lophs(ids) is generally stable

within a population, substantial geographic variation has been demonstrated within a single species (Bader, 1959; Hooper, 1957; Lawlor, 1971; Wolfe and Layne, 1968). Thus one might expect the occurrence of these traits to be evolutionarily labile, and they should not be accorded exceptional weight. In my analyses, this suspicion was vindicated as low consistency and compatability indices were obtained for these characters, whether entered as a single index of complexity or as eight separate characters.

I have accepted the prevalent opinion that the complex (or pentalophodont) condition is ancestral and gave rise to the simple (or tetralophodont) state by loss of the various accessory crests, primarily the mesoloph(id)-mesostyle(id) (Stehlin and Schaub, 1951; Hershkovitz, 1962, 1967; Reig, 1977). Indeed, Hershkovitz (1962:82) cites this trend as a "basic principle in cricetine evolution". However, one should note that eumyine and cricetodontine rodents from the Oligocene already exhibit considerable variation both within and between species with regard to the occurrence of such ridges and tubercles (Clark *et al.*, 1964; Alker, 1967; Mein and Freudenthal, 1971). Therefore, the potential for variable patterns of fixation, loss, and reacquisition of such structures in descendent populations seems great.

Character 2: Bifurcation of Anterocone.

(0) Single, undivided cusp.
(1) Weak anteromedian flexus with marginal definition of anterolabial and anterolingual conules.
(2) Deep anteromedian flexus; separation of anterolingual and anterolabial conules into distinct cusps as large as the primary (paracone, metacone etc.) cusps.

The anterocone phyletically appears after loss of the fourth premolar, which transpired some time prior to the Oligocene, and develops as a distinct cusp from the anterior cingulum. Consequently, I coded a single cone as primitive and viewed division of the anterocone into distinct conules as derived states. I also recorded development of the anteroconid of the lower first molar, but discarded this character since it corresponded closely to configuration of the anterocone.

Character 3: Cusp Arrangement.

(0) Primary cusps opposite in position.
(1) Primary cusps intermediate.
(2) Primary cusps alternate.

I selected the degree of opposition of primary cusps (protoconid-metaconid and hypoconid-entoconid) on the lower first molar as the basis for scoring this character. Some readers may detect a discrepancy in my description of the molars of *Neotoma* as "alternate", while Hooper (1954:10) characterized the "... sections ... located opposite each other". I agree that the prismatic sections are aligned oppositely; however, examination

TABLE 5

SPEARMAN'S RANK-ORDER CORRELATION COEFFICIENTS (Rho) FOR DENTAL LOPHS(IDS) AND STYLES(IDS).

	Protostyle	Mesoloph-mesostyle	Enteroloph-enterostyle	Anterolophid-metastylid	Protostylid	Mesolophid-mesostylid	Ectolophid-ectostylid
Anteroloph-parastyle	.19	.94 **	.19	.35 **	.19	.90 **	.60 **
Protostyle		.18	.49 **	.06	.03	.24	.04
Mesoloph-mesostyle			.18	.27 *	.18	.90 **	.67 **
Enteroloph-enterostyle				.25 *	.03	.24	.09
Anterolophid-metastylid					.06	.39 **	.03
Protostylid						.08	.04
Mesolophid-mesostylid							.64 **

* = P ≤ .05; ** = P ≤ .01

of the unworn crowns of young woodrats led me to conclude that those particular "sections" homologous to the four major cusps are actually positioned alternately.

Based solely on my collection of species, designation of the "alternate" or "opposite" cusp position as primitive is ambiguous. However, the high incidence of muroids that have developed transverse connections of the molar cusps of one kind or another (see, for example, Hershkovitz, 1967) suggests that cusps were primitively aligned opposite one another. Furthermore, trends toward alternation have been described for North American eumyine rodents during the Oligocene and Miocene (Clark *et al.*, 1964; Lindsay, 1972; Wood, 1937).

Character 4: Molar Topography.

(0) Bunodont, molars relatively low-crowned.
(1) Planar, molars moderately high-crowned with cusps flattened and even in height.
(2) Hypsodont, rooted.
(3) Hypsodont, evergrowing or rooted only in old adults.

The derivation of high-crowned molars from an ancestral bunodont condition is well documented for many lines of Muroidea. Hershkovitz (1967) discusses and illustrates various evolutionary trends in molar modification.

Character 5: Cusp Arrangement (Shape) of Lower Third Molar.

(0) Hypoconid and entoconid opposite or nearly so; posterior cingulum well-developed; M3 essentially a replicate of M2; wears to "8-shape".
(1) Entoconid reduced and shifted anteriorly relative to the hypoconid; wears to "S-shape".
(2) Entoconid and hypoconid greatly reduced; wears to "C-shape".
(3) Hypoconid and entoconid absent; M3 cylindriform; derived from state (1).
(4) Hypoconid and entoconid greatly reduced but remain opposite (murid through center of tooth); derived from state (1).

Reduction of complexity of the third molars is a well-established phyletic trend among muroid rodents in general (Hershkovitz, 1967; Misonne, 1969).

Character 6: Relative Size of Lower Third Molar.

(0) Greater than 30% of length of molar row.
(1) 29 to 24% of length of molar row.
(2) Less than 23% of length of molar row.

This ratio variable was derived by dividing the mean length of the lower third molar by the mean total length of all three cheek teeth and plotting a histogram to code character states (Fig. 5). Predictably, there is a strong association between this variable and character 5; I recorded it only for samples of neotomine-peromyscines.

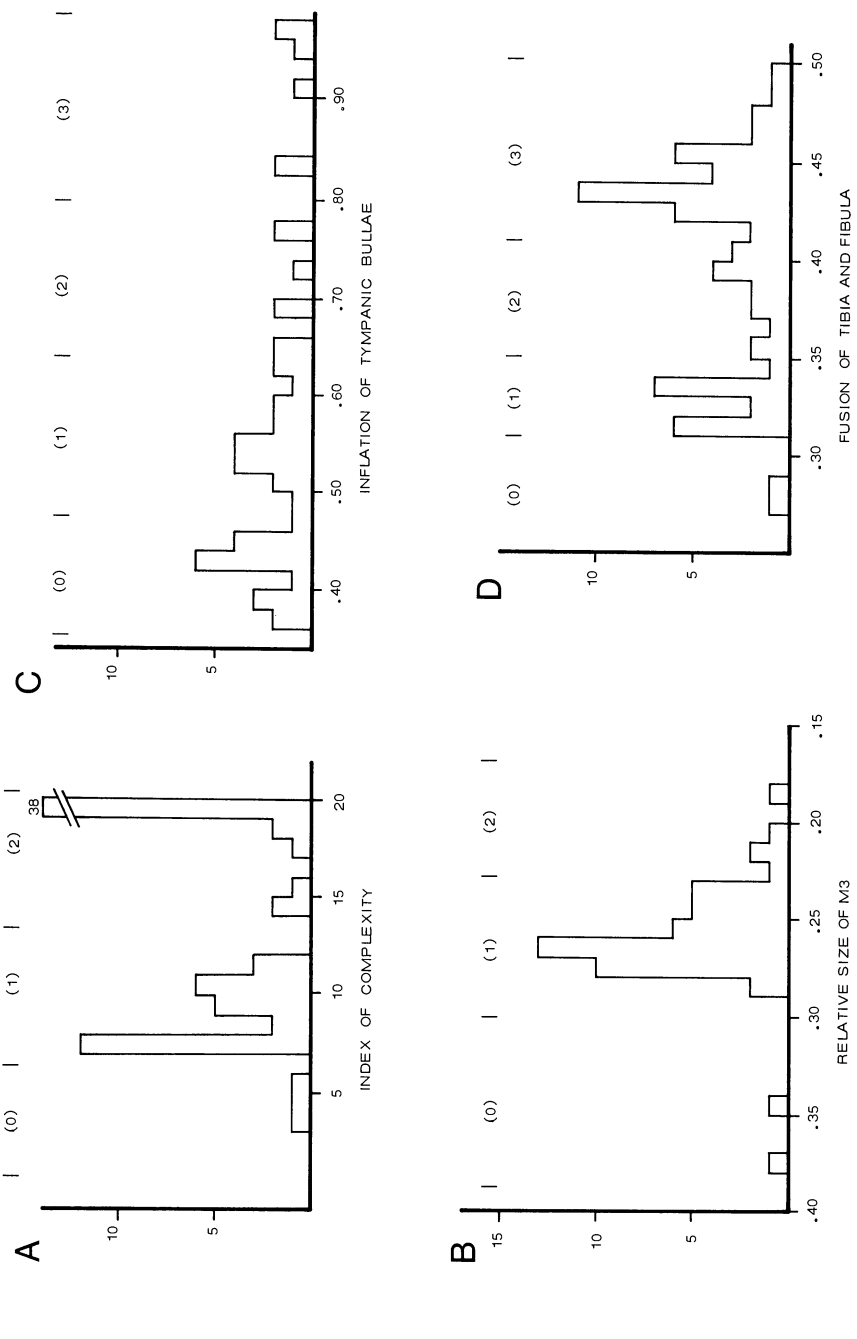


Fig. 5. Frequency histograms used to compute Character Nos. 1, 6, 33, and 42.

Hershkovitz (1967) and Misonne (1969) view reduction in size of the lower M3 as a progressive feature, and Misonne *(op. cit.),* at least, considers the M3 to have equalled the M2 in the ancestral state. Certainly, such trends of reduction can be documented in the fossil record (for example, Carleton and Eshelman, 1979). Although I recognized them as plesiomorphic, it is possible that large third molars, which slightly exceed the second molars in length, are derived from a subequal condition.

Character 7: Grooves on Upper Incisors.

(0) Absent.
(1) Present, deep and located medially.
(2) Present, shallow and located laterally, derived from state (0).

Based on the rarity of this character among outgroups and its rarity within neotomine-peromyscines (present only in species of *Reithrodontomys*), I have treated grooved incisors as derived.

Character 8: Lingual Root of Upper First Molar.

(0) Single, large root.
(1) Intermediate.
(2) Two roots.
(3) Rootless, evergrowing, derived from state (0).

The occurrence of accessory roots is another character whose polarity is difficult to determine on the basis of distributional patterns among outgroups and within the focal study group. Only a few neotomine-peromyscines (e.g. *Scotinomys,* some forms of *Reithrodontomys, Tylomys* and *Ototylomys*) possess supernumerary roots; the majority display three-rooted upper molars and two-rooted lower ones (Fig. 6). Yet additional roots are common among Gerbillinae, South American cricetines and Old World cricetines (Fig. 6). Because multiplication of accessory roots has been suggested for a limited number of fossil lineages (*Sigmodon*—Eshelman, 1975; Martin, 1974; *Bensonomys*—Baskin, 1978; European Cricetinae—Freudenthal, 1967; and several murids—Jacobs, 1978), I have recognized three roots as ancestral for upper molars and two roots for lower ones.

The impossibility of identifying roots in Microtinae, which possess rootless, evergrowing cheek teeth, presented another problem. However, primitive voles from the Pliocene, such as *Ophiomys, Ogmodontomys, Microtoscoptes,* and *Cosmomys,* do have three roots on the superior molars and two on the inferior molars (Hibbard, 1959; Hibbard and Zakrzewski, 1967; Zakrzewski, 1967). On this basis, I arranged the rootless condition as arising by coalescence from the three-rooted (upper molars) and two-rooted (lower molars) states.

Character 9: Labial Root of Upper First Molar.

(0) Absent.
(1) Present, small, set medially.
(2) Present, large, set laterally.
(3) Rootless, evergrowing; derived from state (0).

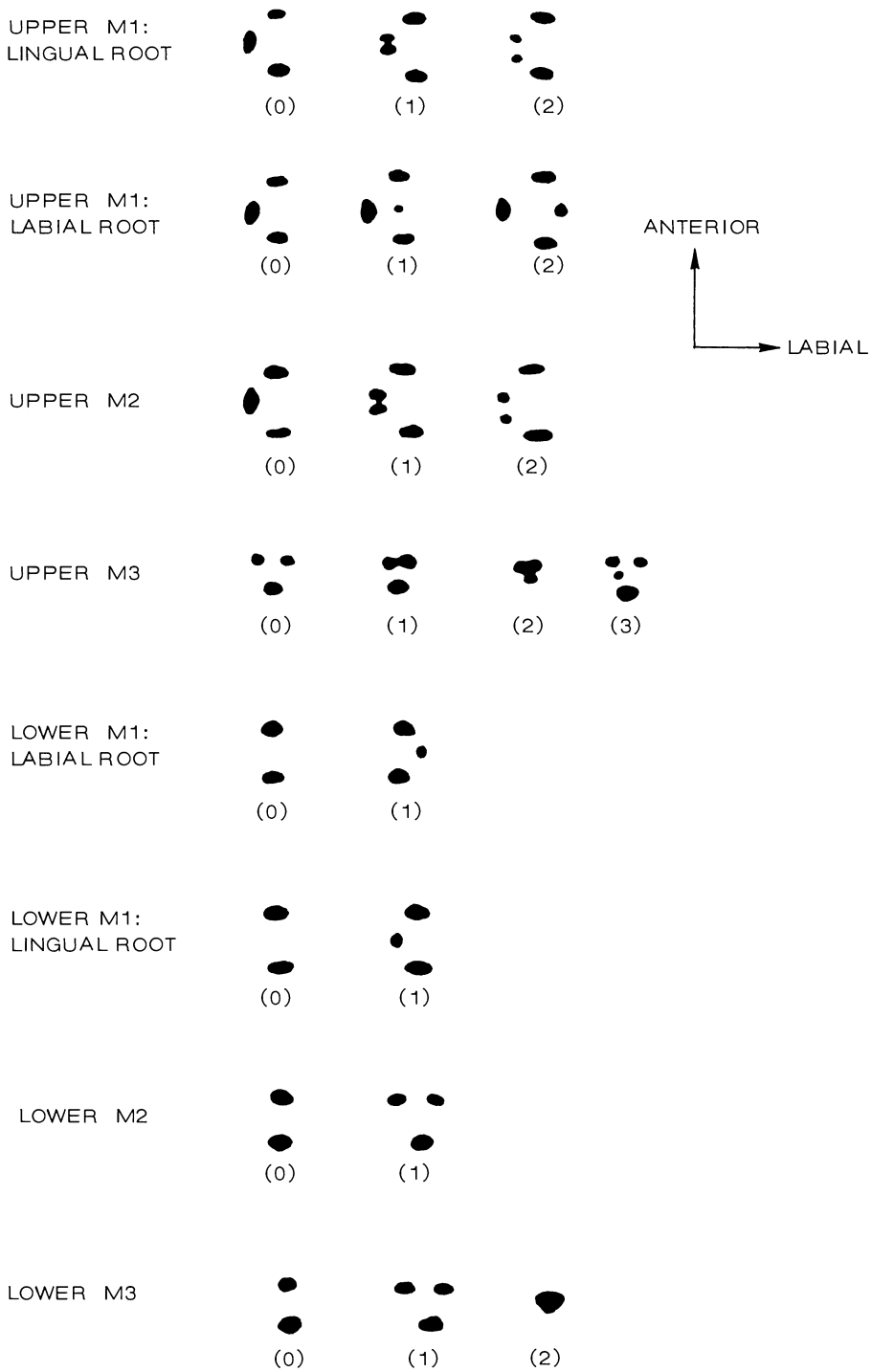


Fig. 6. Alveolar patterns of upper and lower cheek teeth. Numbers in parentheses correspond to character states recognized for each molar (see Character Nos. 8–15).

Character 10: Lingual Root of Upper Second Molar.
(0) Single, large root.
(1) Intermediate.
(2) Two roots.
(3) Rootless, evergrowing; derived from state (0).

Character 11: Upper Third Molar.
(0) Three roots.
(1) Two roots.
(2) One root.
(3) Four roots; derived from state (0).
(4) Rootless, evergrowing; derived from state (0).

Character 12: Lingual Root of Lower First Molar.
(0) Absent.
(1) Present.
(2) Rootless, evergrowing; derived from state (0).

Character 13: Labial Root of Lower First Molar.
(0) Absent.
(1) Present.
(2) Rootless, evergrowing; derived from state (0).

Character 14: Lower Second Molar.
(0) Two roots.
(1) Three roots.
(2) Rootless, evergrowing; derived from state (0).

Character 15: Lower Third Molar.
(0) Two roots.
(1) Three roots.
(2) One root; derived from state (0).
(3) Rootless, evergrowing; derived from state (0).

Cranium

Character 16: Stapedial and Sphenofrontal Foramina (Carotid Circulation).
(0) Both foramina present, groove present on squamosal.
(1) Stapedial foramen present, sphenofrontal foramen absent, but groove present on squamosal.
(2) Stapedial foramen present, sphenofrontal foramen absent, no groove on squamosal.
(3) Both foramina absent (or stapedial foramen closed to a minute pinhole), no groove on squamosal.

Initially, I had tabulated the occurrence of these foramina as different characters (here and in succeeding sections, I have followed Hill, 1935, for terminology regarding cranial foramina). Upon further study, it became apparent that the association of these foramina assumed a consistent pattern that in fact reflects complex changes in the carotid circulation to the orbit and brain (Guthrie, 1963; Klingener, 1968; Bugge, 1970,

1971a, b). Accordingly, I recoded these foramina to correspond to the underlying changes in the cartoid circulatory supply.

Disappearance of the sphenofrontal and stapedial foramina describes capture of the orbital circulation by the internal carotid artery. In the plesiomorphic state, the stapedial artery (arterial names follow Klingener, 1968) divides inside the tympanic bulla forming the opthalmic and internal maxillary arteries; these exit to the orbit via the sphenofrontal foramen and sphenoidal fissure respectively (Fig. 7). The passage of the opthalmic artery imparts a faint groove, which is generally evident on cleaned skulls, upon the inner surface of the squamosal bone. Usually, the absence of the sphenofrontal foramen denotes a lack of the squamosal groove (but see below). In this condition, the opthalmic artery unites with the internal maxillary as it emerges from the sphenoidal fissure; the stapedial foramen remains quite large. In the most derived state, the stapedial and sphenofrontal foramina are absent, and the opthalmic and internal maxillary arteries arise from the internal carotid and emerge from the sphenoidal fissure. The stapedial foramen may persist as a tiny pinhole because the stapedial artery maintains a small supply to the otic capsule. This summary perhaps oversimplifies the complexity of modifications involving the cephalic arterial supply. For further information, the reader should consult the excellent studies of Bugge (1970, 1971a, b). My order of character transformation observes that author's determination of polarity.

In *Neotoma fuscipes* and *N. cinerea,* I observed a condition tentatively coded as an annectent grade. A sphenofrontal foramen is lacking, at least in the normal position at the junction of the frontal, orbitosphenoid and alisphenoid bones. Nevertheless, a distinct groove crosses the squamosal but merges with the sphenoidal fissure (Fig. 7). A strut of bone separates the exit of the groove as a foramen distinct from the sphenoidal fissure in some specimens, but in others no division from the sphenoidal fissure is apparent. Guthrie (1963) reported the sphenofrontal foramen absent in *Neotoma* and questioned Hill's (1935) assertion that it was present in that genus; Hill's lone representative of *Neotoma* was *N. fuscipes.* Interestingly, a few specimens of *Nelsonia neotomodon* lacked a sphenofrontal foramen in the typical position, but possessed the supplementary foramen inside the sphenoidal fissure, and the squamosal groove passed to that small foramen.

Character 17: Foramen Ovale.

(0) Present.
(1) Absent.

The foramen ovale is universally present in species of neotomine-peromyscines. I cannot determine if absence results from coalescence with the masticatory foramen or complete disappearance.

Character 18: Postglenoid Foramen.

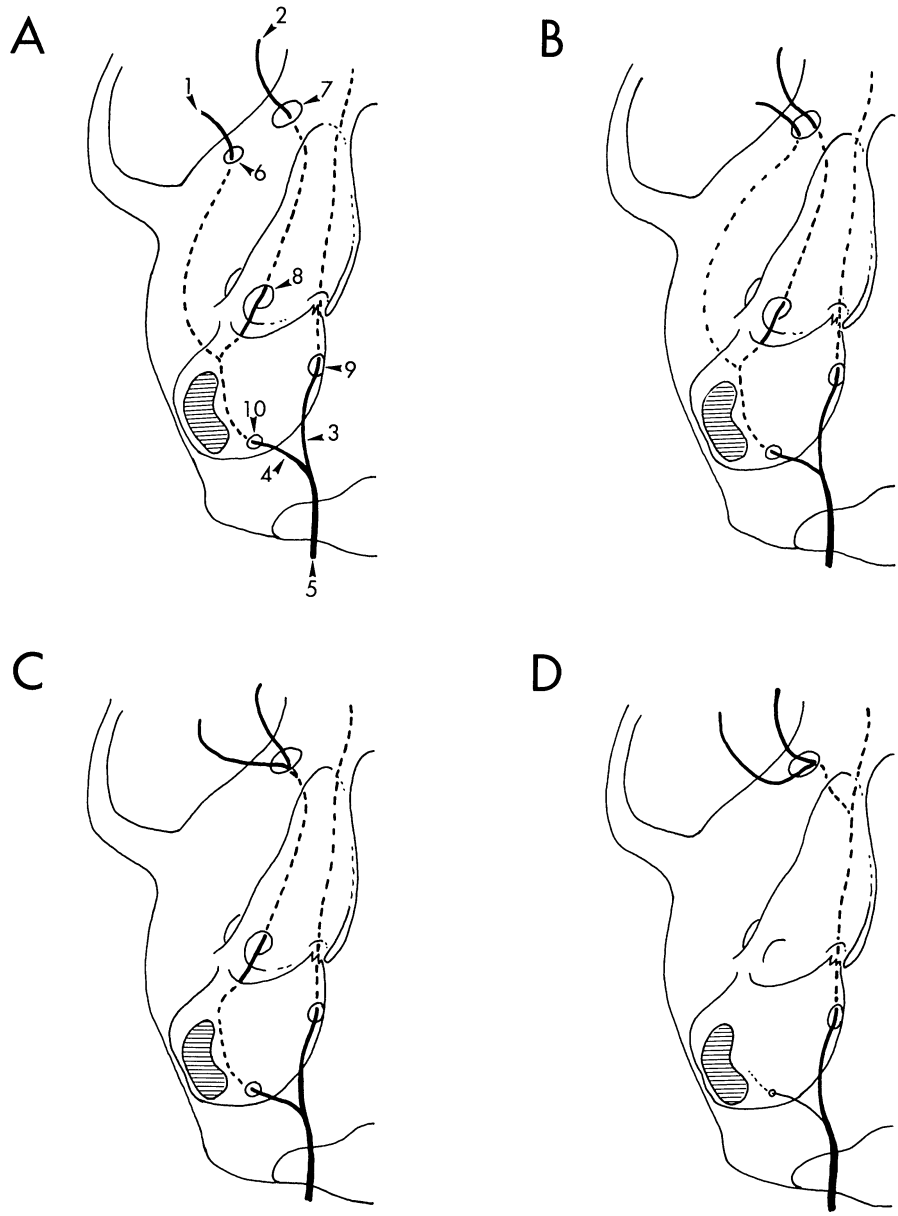


Fig. 7. Schematic diagrams of carotid circulatory patterns (ventral aspect) illustrating transitional states (letters A–D) defined for Character No. 16. Anatomical features indicated are: 1) opthalmic artery; 2) internal maxillary artery; 3) internal carotid artery; 4) stapedial artery; 5) common carotid artery; 6) sphenofrontal foramen; 7) sphenoidal fissure; 8) alisphenoid canal; 9) internal carotid canal; 10) stapedial foramen.

(0) Absent.
(1) Present, small.
(2) Present, large.

Character 19: Subsquamosal Foramen.
(0) Absent.
(1) Present, small.
(2) Present, large.

The postglenoid and subsquamosal foramina (perhaps more appropriately termed fenestra, because they have not been shown to transmit nerves or vessels in muroid rodents—Hill, 1935) appear as excavations of the squamosal bone superior to the auditory bullae and separated from each other by a thin strut of bone, the hamular process of the squamosal. The postglenoid foramen may be continuous with a narrow fissure anterior to the bullae. In most species, both foramina are patent, but this is not always true, especially for samples of *Neotoma.*

Here is another instance where my sequence of character transformation contradicts a strict application of outgroup criteria. Both foramina are present in most representatives of the Gerbillinae, Microtinae, Old World cricetines and South American cricetines I examined; furthermore, this is the wisespread condition among neotomine-peromyscines. Still, the sporadic occurrence of a completely ossified squamosal among some South American cricetines, African and Indo-Australian murids (Davis, 1965; Tate, 1951) persuaded me to consider these foramina as apomophic. Perforation of the squamosal bones probably has evolved independently in several lines of muroids.

Character 20: Sphenopalatine Vacuities.
(0) Absent, sphenopalatine area wholly ossified.
(1) Present, narrow slit at the juncture of the basisphenoid and prephenoid.
(2) Present, elongate vacuities extending over one-half the length of the presphenoid bone.

Formation of spaces in the bony walls of the mesopterygoid fossa is another character that may have a history of frequent parallelism (Fig. 8).

Character 21: Posterolateral Palatal Pits.
(0) Absent, or one or two small foramina.
(1) Multiple foramina recessed in fossa.

At first, I recognized an intermediate grade for forms having just a few foramina, not recessed within a pit, located just posterior and medial to the third molars. Because this trait proved so variable within samples, ranging from none to several foramina, I later combined it with state (0). I concur with Hershkovitz (1962) that an uncomplicated postpalatal region represents the primitive stage.

Character 22: Palatine Foramina.
(0) Pair of round foramina at junction of the maxillary and

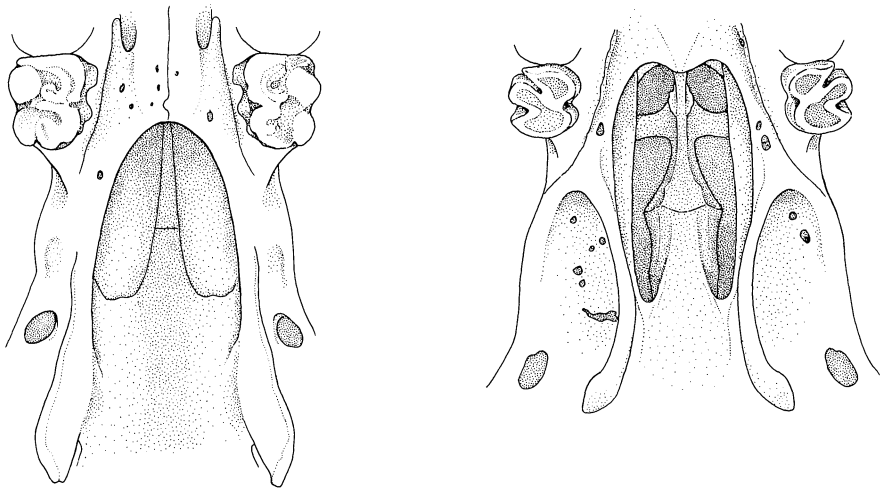


Fig. 8. Ventral view of mesopterygoid fossa showing absence (left, *Tylomys nudicaudus,* UMMZ 122586) and presence (right, *Neotoma lepida,* UMMZ 80964) of sphenopalatine vacuities (see Character No. 20).

palatine bones, or occasionally a pair of larger foramina accompanied by one or two minute ones.

(1) Pair of oblong foramina, substantially penetrating both the maxillary and palatine bones.

(2) Pair of larger foramina and many tiny foramina perforating hard palate; derived from state (0).

A single pair of palatine foramina is the cosmopolitan state within my study collection. Multiple foramina occur in those species with a constricted, narrow palate, notably the Microtinae (Fig. 9). In this condition, identification of a pair of foramina homologous to the palatine foramina of state (0) is sometimes difficult.

Character 23: Lateral Pterygoid Fossa.

(0) Flat, even with bony palate.

(1) Recessed slightly above level of bony palate.

(2) Deeply excavated above level of bony palate.

The lateral pterygoid fossae mark the origin of the internal pterygoid muscles, which are typically better developed in species having more high-crowned molars (Kesner, 1977; Rinker, 1954). Accordingly, more cavernous fossa are treated as derived states.

Character 24: Supraorbital Shape and Temporal Ridges.

(0) Sides smooth and concave or parallel-sided; "hourglass" shape as viewed dorsally; temporal ridges absent.

(1) Distinct shelf projecting over the posterior aspect of the orbit; temporal ridges absent.

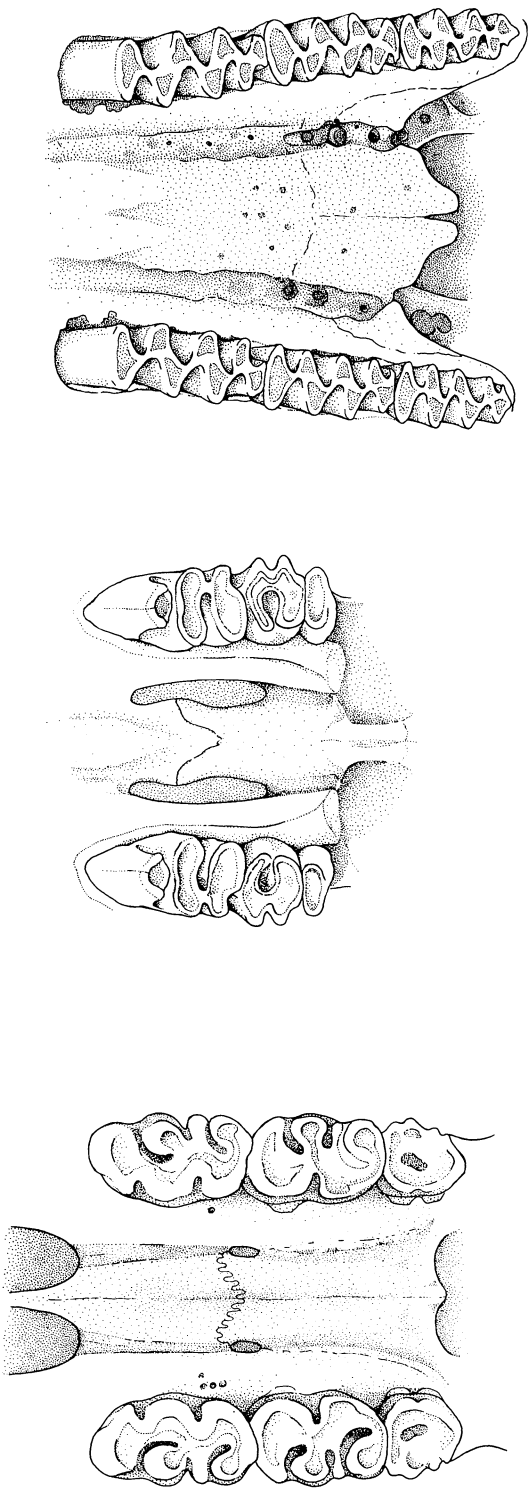


Fig. 9. Variation in posterior palatine foramina (see Character No. 22); left, *Peromyscus thomasi* (UMMZ 122882); middle, *Gerbillus cheesmani* (UMMZ 117671); and right, *Dicrostonyx groenlandicus* (UMMZ 109262).

(2) Shelf with weakly raised ridge; temporal ridges poorly developed and extending over part of parietal.
(3) Strong ridge or "bead"; temporal ridges pronounced, extending from frontal-parietal suture to the lambdoidal ridge.

This character is a combination of two formerly coded separately; however, the development of temporal ridges was found to correspond almost precisely to supraorbital shape.

A skull with a smooth interorbital region, devoid of a shelf or ridge, is common among neotomine-peromyscines and frequently observed within South American cricetines, Old World cricetines and microtines. Therefore, this condition is considered plesiomorphic. This arrangement also agrees with Hershkovitz's (1962:57) interpretation of supraorbital variation in neotropical cricetines.

Character 25: Zygomatic Spine (Depth of Zygomatic Notch).
(0) Absent or barely described.
(1) Moderate notch.
(2) Deep recess, zygomatic plate extending past root of incisor.

The degree of pronouncement of the zygomatic spine generally correlates with the width of the zygomatic plate (except in Microtinae) and depth of the zygomatic notch. I coded the lack of a zygomatic spine as primitive because its absence is the widespread condition within the neotomine-peromyscines and throughout other subgroups of Muroidea as well.

Character 26: Postorbital Process.
(0) Absent.
(1) Present.

The presence of a postorbital process, actually more like a crest, is clearly a derived trait limited to the Microtinae and probably correlated with the evolution of prismatic, evergrowing molars and concomitant masticatory accomodations (Kesner, 1977; Repenning, 1968).

Character 27: Lacrymal Projection.
(0) Lacrymal bone scarcely evident dorsally.
(1) Lacrymal bears a shelf projecting into preorbital region.

Since a lacrymal projection appears in a limited number of species (*Graomys* and all Gerbillinae), it is viewed as derived.

Character 28: Angular Process of the Dentary.
(0) Directed posteriorly in the same plane as the ascending ramus.
(1) Directed laterally away from the plane of the ascending ramus.

The state coded as primitive occurs throughout the neotomine-peromyscines and South American cricetines; a deflected angular process is char-

acteristic of the Gerbillinae and Microtinae (Fig. 10). At least for the Microtinae, my determination of polarity accords with that of Kesner (1977).

Character 29: Hyoid Apparatus.

(0) Entoglossal process a small knob; basihyal arched; thyrohyal long, greater than or equal to the length of the basihyal.

(1) Entoglossal process absent; basihyal straight; thyroyal short, less than length of basihyal.

(2) Entoglossal process long and attentuate; basihyal arched; thyrohyal long, greater than length of the basihyal; derived from state (0).

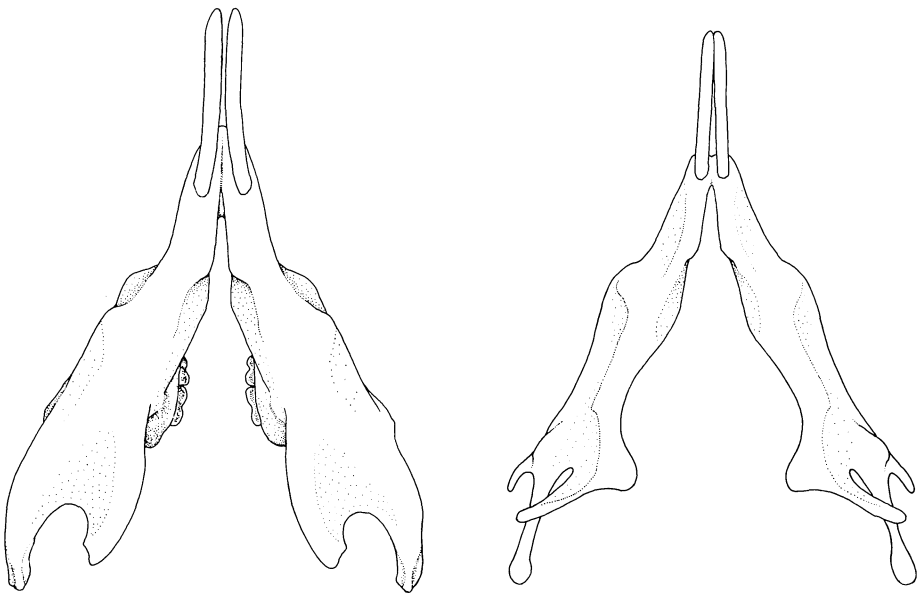


Fig. 10. Ventral view of lower jaws illustrating posteriorly directed angular processes (left, *Peromyscus thomasi,* UMMZ 112882) and deflected angular process (right, *Gerbillus cheesmani,* UMMZ 117671) (see Character No. 28).

The presence/absence of the entoglossal process, shape of the basihyal, and relative size of the thyrohyals were defined preliminarily as three characters. All three are clearly interrelated and seem to reflect a basic change in conformation of the hyoid apparatus (Fig. 11).

My observations of the hyoid complex of *Baiomys* differ from that reported by Sprague (1941), who examined only one specimen of *B. taylori.* He concluded that the entoglossal process was absent in the genus, but examination of several specimens of both *B. taylori* and *B. musculus* demonstrated the presence of a small entoglossal process on the basihyal.

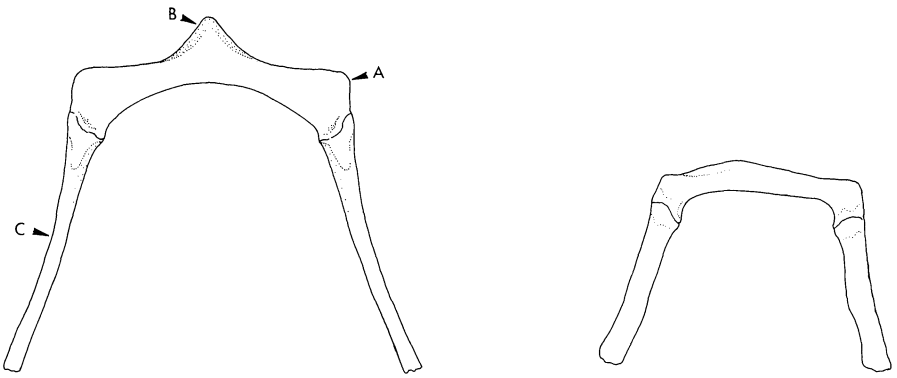


Fig. 11. Ventral view of the hyoid bones of *Neotoma fuscipes* (left, UMMZ 117549) and *Sigmodon hispidus* (right, UMMZ 76764) (see Character No. 29). Anatomical features indicated are: A) basihyal bone; B) entoglossal process; C) thyrohyal bone.

In this regard, the hyoid of *Baiomys* more closely resembles that of other neotomine-peromyscines, particularly *Onychomys, Reithrodontomys* and *Scotinomys,* instead of that seen in South American cricetines, which have a straight basihyal lacking an entoglossal process.

The primitive condition is displayed by most neotomine-peromyscines, Microtinae, some Gerbillinae, and *Cricetulus* of the Asiatic Cricetinae. Furthermore, this hyoid plan is associated with muscular arrangements (principally involving the stylohyal cartilage and attachment of the hyoid apparatus to the basicranium) interpreted as primitive (Kesner, 1977; Klingener, 1964, 1968; Rinker, 1954; Sprague, 1941, 1942). Character state (2) resembles the ancestral condition except for the longer, distinctive entoglossal process, which occurs in just a few samples.

Character 30: Configuration of Malleus.

(0) Perpendicular.

(1) Parallel.

Two fundamental kinds of mallei are found within the Muridae *sensu latu* (Cockerell, Miller and Printz, 1914; Wassif, 1948, 1957). Oaks (1967) termed these "perpendicular" and "parallel" in reference to the general orientation of the manubrium in relation to the frontal plane of the skull. In the "parallel" type, the manubrium approximately forms a right angle with the head, a broad lamina extends anteriorly from the junction of the head and manubrium, and the orbicular apophysis is present and generally well-developed (Fig. 12). In contrast, the manubrium of a "perpendicular" malleus extends vertically from the head, the lamina is narrow, and an orbicular apophysis is absent. Some forms, especially examples of Palaearctic Cricetinae, appear intermediate; however, across the entire order Rodentia departure from these morphological schemes is remarkably rare, and their mallei can readily be identified as one or the other kind.

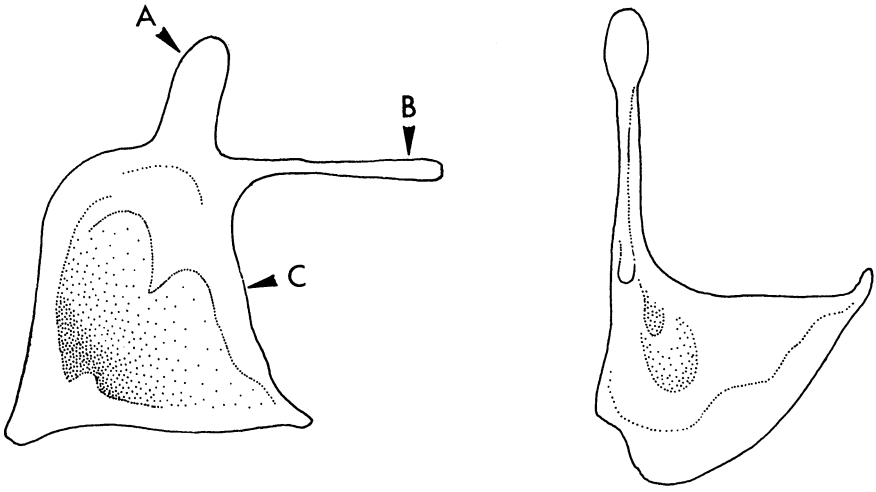


Fig. 12. Left mallei of *Neotoma lepida* (left, UMMZ 80964) and *Dicrostonyx groenlandicus* (right, UMMZ 109263) (see Character No. 30). Anatomical features indicated are: A) orbicular apophysis; B) manubrium; C) lamina.

In view of the distribution of perpendicular and parallel mallei among Rodentia, the designation of the parallel types as apomorphic appears, at first glance, unequivocal (Table 6), and I have coded it in this manner. Yet the parallel malleus found in many Muroidea disturbingly resembles that described for Chiroptera and Insectivora (Doran, 1878; Cockerell *et al.*, 1914; Wassif, 1948, 1957). In fact, Cockerell *et al.* (op cit.) considered the parallel configuration as primitive and postulated a nearness of common ancestry for the Rodentia and Insectivora largely for this reason. It seems peculiar that some species of Myomorpha would retain the plesiomorphous condition, particularly when the perpendicular malleus is apparently ubiquitous for the Sciuromorpha and Hystricomorpha. Resolution of the question of primitiveness for this character really bears on the larger question of the origin of the Rodentia, the answer to which remains elusive (see McKenna, 1975).

For purposes of my study, I have relied, albeit with reservations, upon the outgroup distributional pattern within the Rodentia in deciding the transformation sequence of this character. The decision is unimportant with regard to my central study group, the neotomine-peromyscines, because all display the parallel malleus. The choice of primitiveness obviously bears critically on the cladistic relationships of neotomine-peromyscines to gerbillines, microtines and South American cricetines. Whatever the ultimate answer, the configuration of the malleus presents an interesting case of some combination of parallelism and reversal, not only within rodents but among other mammalian orders as well.

TABLE 6

OCCURRENCE OF PERPENDICULAR AND PARALLEL MALLEI WITHIN RODENTIA.

Taxa	Perpendicular	Parallel
Sciuromorpha	+	–
Hystricomorpha	+	–
Myomorpha		
Gliroidea	+	–
Geomyoidea	+	–
Dipodoidea		
Dipodidae	+	–
Zapodidae	–	+
Muroidea		
Rhizomyidae	+	–
Spalacidae	+	–
Muridae	–	+
Cricetidae		
Gerbillinae	+	–
Microtinae	+	–
Cricetinae		
Old World Cricetines	+ (most)	+ (some)
Neotomine-Peromyscines	–	+
South American Cricetines	–	+

Character 31: Accessory Tympanum.

(0) Absent, anterior and posterior lamina complete.
(1) Present, small, only anterior lamina eroded.
(2) Present, large.

Character 32: Mastoid Bullae.

(0) Small, unmodified.
(1) Moderately inflated.
(2) Large, greatly inflated.

I have employed a simplistic characterization of mastoid inflation because all neotomine-peromyscines possess relatively unmodified mastoid chambers. Detailing the compartmentalization that occurs in the mastoid bullae of some forms, notably the Gerbillinae (see Lay, 1972), would not contribute phylogenetic resolution to the neotomine-peromyscines. Thus, I simply coded those bullae as "greatly inflated".

Character 33: Inflation of Tympanic Bullae.

(0) Less than 48%.
(1) 49–61%.
(2) 62–80%.
(3) Greater than 80%.

I calculated this ratio variable from the length times depth of the auditory bulla and divided by the mean total length of skull (Fig. 5). My

polarity assumes an orthodirectional increase in bullar volume as advanced. This assumption seems reasonable in view of the many groups of rodents that exhibit hypertrophy of the tympanic bullae. This character was coded only for species of neotomine-peromyscines.

Character 34: Development of Tentorium Cerebellum.

(0) Present as a crest of low relief.
(1) Present as a small, thin flange.
(2) Present as a large, broad lamina.

The tentorium cerebellum arises from the medial surface of the petromastoid bone and partially extends between lobes of the cerebrum and cerebellum. I recorded a broad flange as derived because it was restricted to the Gerbillinae and Microtinae; most species displayed a low crest. Perhaps the expression of this character correlates with relative size of the auditory bullae.

Post-Cranial Skeleton

Character 35: Entepicondylar Foramen.

(0) Present.
(1) Absent.

An entepicondylar foramen, located above the medial epicondyle of the humerous, occurs sporadically throughout my study group (Fig. 13). It may be absent in whole groups currently considered monophyletic, *e.g.* microtines and South American cricetines, or present, *e.g.* gerbillines (except *Tatera indica*). Within the neotomine-peromyscines, the foramen is typically present. Given this distribution, determination of the ancestral state is enigmatic. However, the foramen was a feature of archaic mammals (Landry, 1958), and Wood (1962) reported its presence in those paramyid rodents for which humeri were recovered. The absence of an entepicondylar foramen in *Ochrotomys,* once treated as a subgenus of *Peromyscus,* has been considered derived (Manville, 1961; Rinker, 1960). Although this evidence does not bear critically on the question of the state of the foramen in the immediate common ancestor of the neotomine-peromyscines, it lends some credence to the polarity adopted.

Character 36: Numbers of Thoracic and Lumbar Vertebrae.

(0) 13 thoracic and 6 lumbar vertebrae.
(1) 14 thoracic and 6 lumbar vertebrae.
(2) 15 thoracic and 6 lumbar vertebrae.
(3) 13 thoracic and 7 lumbar vertebrae; derived from state (0).
(4) 12 thoracic and 7 lumbar vertebrae; derived from state (0).

This coding scheme represents a consolidation of three characters, the number of thoracics (12, 13, 14, or 15), the number of lumbars (6 or 7), and the number of dorsals (19, 20, or 21). In preliminary trials, I included the number of dorsals (admitting the obvious redundancy since dorsals

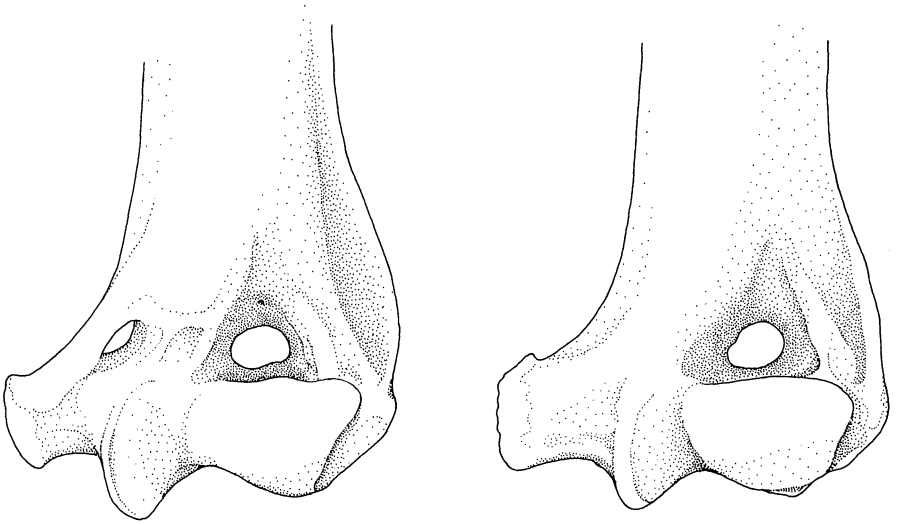


Fig. 13. Distal portion of left humeri demonstrating presence (left, *Neotoma floridana,* UMMZ 87636) and absence (right, *Neotoma alleni,* UMMZ 103191) of entepicondylar foramen (see Character No. 35).

equal the thoracics and lumbars combined) because they could remain stable in absolute numbers even though the number of thoracics or lumbars changed. I finally accepted the character-state tree given above as the most realistic sequence. Even so, the potential for convergence to a particular thoracolumbar formula from different antecedents seems likely. Although Wood (1962) speculated that the ancestral rodent condition was 12 thoracics and 7 lumbars, I selected 13 and 6 as the plesimorphic state for the species listed here. That thoraco-lumbar ratio is found in most neotomine-peromyscines, all microtines and Old World cricetines (species reported here and others in University of Michigan, Museum of Zoology), and many South American cricetines. Consequently, the character-state tree chosen admits an evolutionary reversal within Rodentia to 12 thoracics and 7 lumbars. Only *Peromyscus (Habromys) lophurus* and *lepturus* have 13 thoracic and 7 lumbar vertebrae. I favored derivation of that morphology from character state (0) because all other species of *Peromyscus* examined here have the ancestral condition.

Character 37: Number of Caudal Vertebrae.

(0) Less than 25.
(1) 26–31.
(2) 32–36.
(3) Greater than 36.

This variable is based on modal numbers of caudal vertebrae. Surprisingly, the distribution of caudal vertebral counts displays a strong modal-

ity in species with adequate sample sizes (also see Thorington, 1966). The mode usually equals the mean when the latter is rounded off, and the range seldom exceeds five vertebrae and is usually three or four.

I cannot reliably infer polarity for this character. It was employed only in phenetic exercises and tabulated solely for neotomine-peromyscines.

Character 38: Spine on Second Thoracic Vertebra.

(0) Present.
(1) Absent.

A pronounced neural spine, dwarfing those on adjacent vertebrae, occurs on the second thoracic vertebra of all species except representatives of Microtinae (Fig. 14). This process is uniformly lacking on all other skeletons of microtines contained in the University of Michigan Museum of Zoology, suggesting its absence is derived.

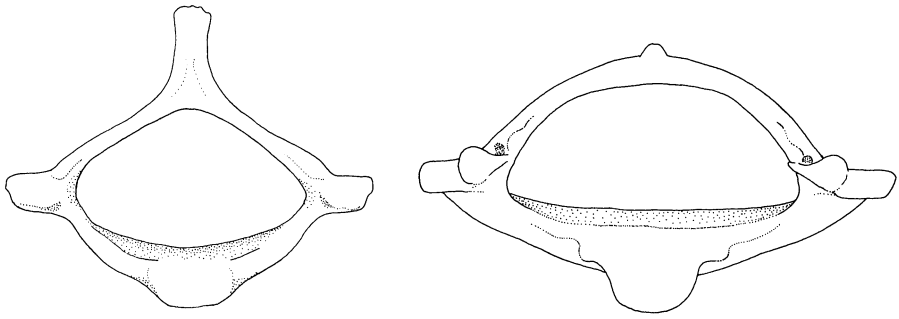


Fig. 14. Frontal aspect of second thoracic vertebrae, one having pronounced neural spine (*Peromyscus boylii,* UMMZ 109530) and the other lacking this process (*Lemmus sibiricus,* UMMZ 123714) (see Character No. 38).

Character 39: Articulation of First Rib.

(0) Rib articulates with transverse process of first thoracic only.
(1) Rib contacts transverse processes of both the first thoracic and seventh cervical vertebrae.

The tuberculum of the first rib is braced by the transverse process of the seventh cervical as well as its normal articulation with the first thoracic in most species comprising my study (Fig. 15). I believe this arrangement is a real anatomical feature and not some artifact of the skeletal cleaning process. This is suggested by the usual presence of a demifacet on the posterior aspect of the transverse process of the seventh cervical for reception of the tuberculum of the rib. Moreover, the tuberculum is typically broad and rounded in forms in which it contacts both vertebrae; whereas, it is narrow in species which lack this additional articulation. In some species, the transverse processes of the sixth and even the fifth cervical appear to function as buttresses applied against the transverse process of the seventh. I have not recognized degrees of articulation since they did not

bear on relationships of the neotomine-peromyscines, which usually exhibit only light contact. I consider the dual articulation as secondarily achieved, even though it is the more widespread situation.

Character 40: Position of Trochlear Process of Calcaneum.

(0) Level with posterior articular facet; trochlear process broad and shelf-like.

(1) Intermediate; gap between proximal edge of trochlear process and posterior articular facet; process shorter and less shelf-like.

(2) Large gap between trochlear process and posterior articular facet; process a small tubercle near distal end of calcaneum.

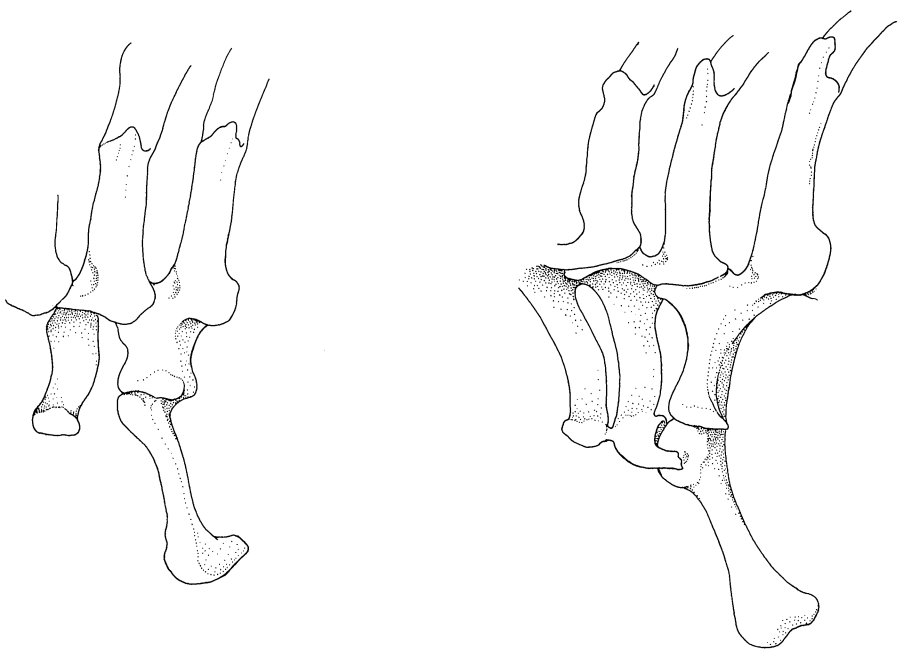


Fig. 15. Dorsal view of seventh cervical and first thoracic vertebrae, demonstrating articular arrangements of the first rib (see Character No. 39): left, *Peromyscus thomasi,* UMMZ 114226; right, *Peromyscus pirrensis,* USNM 338274.

The size and position of the trochlear process of the calcaneum differs greatly among rodents as a whole, but may remain remarkably uniform within a particular taxonomic group (Stains, 1959). The differences can best be appreciated by viewing the orientation of the trochlear process with respect to the posterior articular facet and the sustentaculum astraguli (Fig. 16). My polarity recognizes the most proximal position of the process as primitive because it is the common plan found within neotomine-peromyscines; in addition, that position is typical within Sciuromorpha (Stains, 1959).

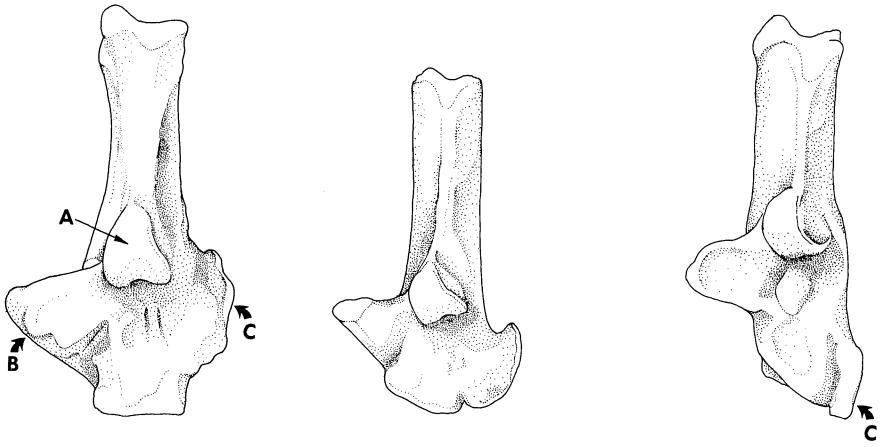


Fig. 16. Left calcanea of *Neotoma cinerea* (left, UMMZ 95890), *Holochilus brasiliensis* (middle, UMMZ 126074) and *Tatera indica* (right, UMMZ 119052). The following anatomical traits are indicated (see Character No. 40): A) posterior articular facet; B) sustentaculum astraguli; C) trochlear process.

Character 41: Third Scapular Fossa.

(0) Absent.
(1) Present.

In addition to the supraspinous and infraspinous fossae, the scapulae of Gerbillinae studied possess a third fossa along the axillary border (Fig. 17), presumably for attachment of the teres major muscle.

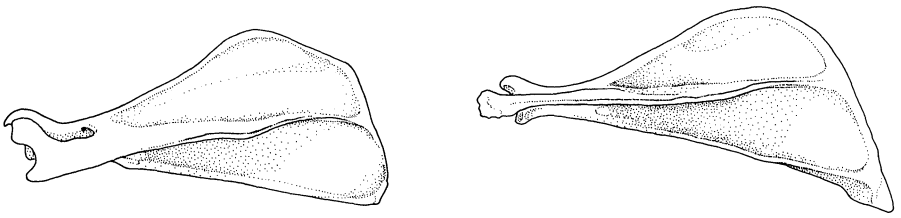


Fig. 17. Left scapulae of *Peromyscus boylii* (left, UMMZ 109530) and *Gerbillus cheesmani* (right, UMMZ 117670) illustrating development of third scapular fossa (see Character No. 41).

Character 42: Fusion of the Tibia-Fibula.

(0) Less than 30%.
(1) 31–36%.
(2) 37–41%.
(3) Greater than 42%.

This character was obtained by dividing the length of fusion of the tibia and fibula by the total length of the tibia and forming character states (Figs. 5, 18).

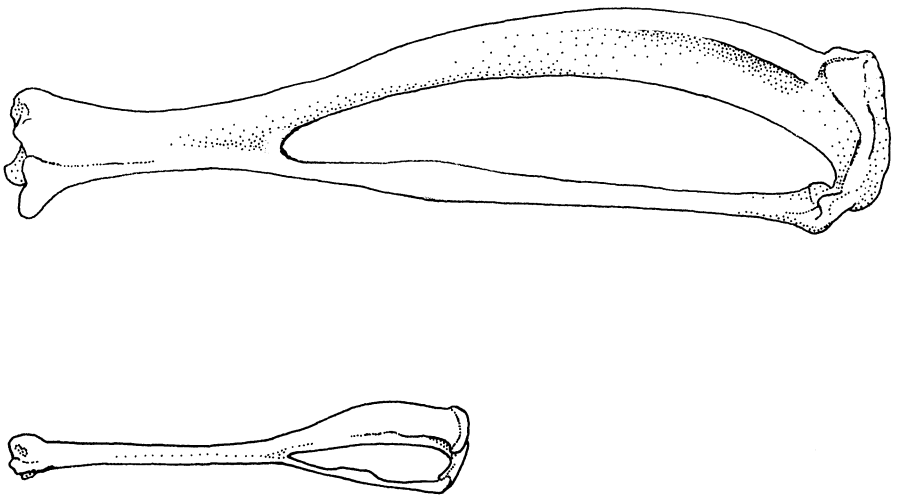


Fig. 18. Differences in degree of fusion of the tibia and fibula (Character No. 42) as seen in *Tylomys nudicaudus* (top, UMMZ 117328) and *Reithrodontomys creper* (bottom, UMMZ 123361).

There is little doubt that more extensive fusion of the fibula to the tibia is a progressive feature within Rodentia. Alston (1876), in fact, employed this trait as an important criterion in his classificatory arrangement of rodents. Hooper (1954) has drawn attention to substantial differences in degree of tibia-fibular fusion between species of *Neotoma* and *Peromyscus,* among others.

Alimentary Canal

Character 43: Internal Cheek Pouches.

(0) Absent (or poorly developed).
(1) Present.

Large, capacious cheek pouches with muscular pouch retractors are found only in the Palaearctic hamsters among the species examined. Rinker (1963) reported cheek pouches in some *Peromyscus,* but those pouches are relatively minuscule evaginations of the oral mucosa and lack retractors. Klingener (1964) argued that the diversity of muscular arrangements that function as pouch retractors among rodents supports the notion of independent acquisition of pouches. My polarity follows his argument.

Character 44: Anterior Longitudinal Ridge.

(0) Complete, high relief; generally separating inflexi labii superioris.
(1) Complete, low relief; inflexi labii superioris generally in contact.
(2) Absent; inflexi labii superioris in broad contact.

The character-state sequence presented agrees with those trends noted by Quay (1954) for the Microtinae.

Character 45: Transverse Palatal Ridges.

(0) Three complete and four incomplete palatal ridges.
(1) Three complete and five to nine incomplete palatal ridges.
(2) Two complete and five incomplete palatal ridges; derived from state (0).
(3) Two complete and four incomplete palatal ridges; derived from state (0).

The transverse palatal rugae are distributed from the diastemal palate approximately to the termination of the hard palate. Typically, those ridges anterior to the first molars are complete; whereas the ones situated between the cheek teeth are incomplete, forming pairs of ridges separated by a median trough. In his study of Microtinae, Quay (1954) noted a reduction in the number of diastemal ridges. I concur with his observations concerning the diastemal region, but further note that the total number of palatal folds is usually constant. The most common modification involves a shift from three complete–four incomplete to two complete–five incomplete. The number of diastemal ridges apparently is diminished by one, but the number of interdental ridges is augmented by same. The many incomplete palatal folds of *Tylomys* and *Ototylomys* are much lower in relief compared to the interdental folds of other forms. Considerable diversity exists in the size and shape of the various palatal rugae, which generally appear constant within species and even genera. My character-state tree conveys only gross differences in number rather than attempting to describe the finer embellishments of shape and size.

I have assumed that the three complete–four incomplete condition found in Old World cricetines and many neotomine-peromyscines represents the ancestral state; all variants are derived independently from that state.

Character 46: Distribution of Gastric Glandular Epithelium.

(0) Hemiglandular.
(1) Intermediate grade I.
(2) Intermediate grade II.
(3) Discoglandular.
(4) Hemipouched.
(5) Fully pouched.

For this and the following two characters, the reader is referred to Carleton (1973) for explanation of terminology, illustration of principal gastric variation, and exposition of criteria for determining polarities. The evolutionary sequences recognized agree with those proposed by other authors (Bensley, 1902; Dearden, 1969; Vorontsov, 1962, 1967).

Character 47: Development of Incisura Angularis.

(0) Shallow, stomach unilocular.

(1) Intermediate.
(2) Deep, stomach bilocular.

Character 48: Sulcus on Greater Curvature of Stomach.
(0) Absent.
(1) Present.

Character 49: Gall Bladder.
(0) Present.
(1) Absent.

A distinct, saccular gall bladder, generally nestled between the cystic lobes of the liver, occurs in most species examined and is treated as the ancestral state.

Character 50: Coils of the Large Intestine.
(0) None, one, or two.
(1) Three or four.
(2) Five or six.
(3) Seven or more.

The first segment of the large intestine, near its junction with the small intestine and caecum, is convoluted upon itself to form a tapered series of coils in many species. Vorontsov (1962) collectively termed these coils the "spire" of the large intestine. The number of coils constituting this spire appears to be a permanent feature of the large intestine, not a transient state reflecting intestinal motility at the time of preservation. The state coded as primitive is widespread among neotomine-peromyscines, South American cricetines, gerbillines and Old World cricetines; augmentation of the number of coils forming the spire is treated as progressive. The development of this character appears correlated with complexity of the caecum; the largest spires are found in microtine species (Vorontsov, 1962, 1967).

Character 51: Complexity of the Caecum.
(0) Moderately long, simple internally.
(1) Short, simple sac.
(2) Long, elaborate infoldings; derived from state (0).

The designation of the ancestral state is somewhat arbitrary and depends upon one's viewpoint concerning the trophic niche of ancestral muroids, which has been interpreted as herbivorous or, alternatively, omnivorous. In view of the wide variety of foods consumed by species of Muroidea (see Landry, 1970, and Carleton, 1973, for review), I prefer the latter. The interpretation of the diminutive, saccular caecum as secondarily derived seems less open to debate and is probably associated with insectivory (Vorontsov, 1962).

Phallus

The polarity suggested for certain characters of the male phallus departs radically from that conventionally recognized. These departures

concern traits that characterize the "simple" and "complex" glandes penis (Fig. 19) and question the notion that the simple type evolved from the complex by reduction and loss of parts (see Hooper and Hart, 1962; Hooper and Musser, 1964a; Hershkovitz, 1966a). Justification for this viewpoint and an overview of the structure and evolution of the glans penis within muroids are deferred to a following section. Regardless of whether the simple or complex type is ancestral, the question has little import for the immediate purpose of evaluating phylogenetic affinities

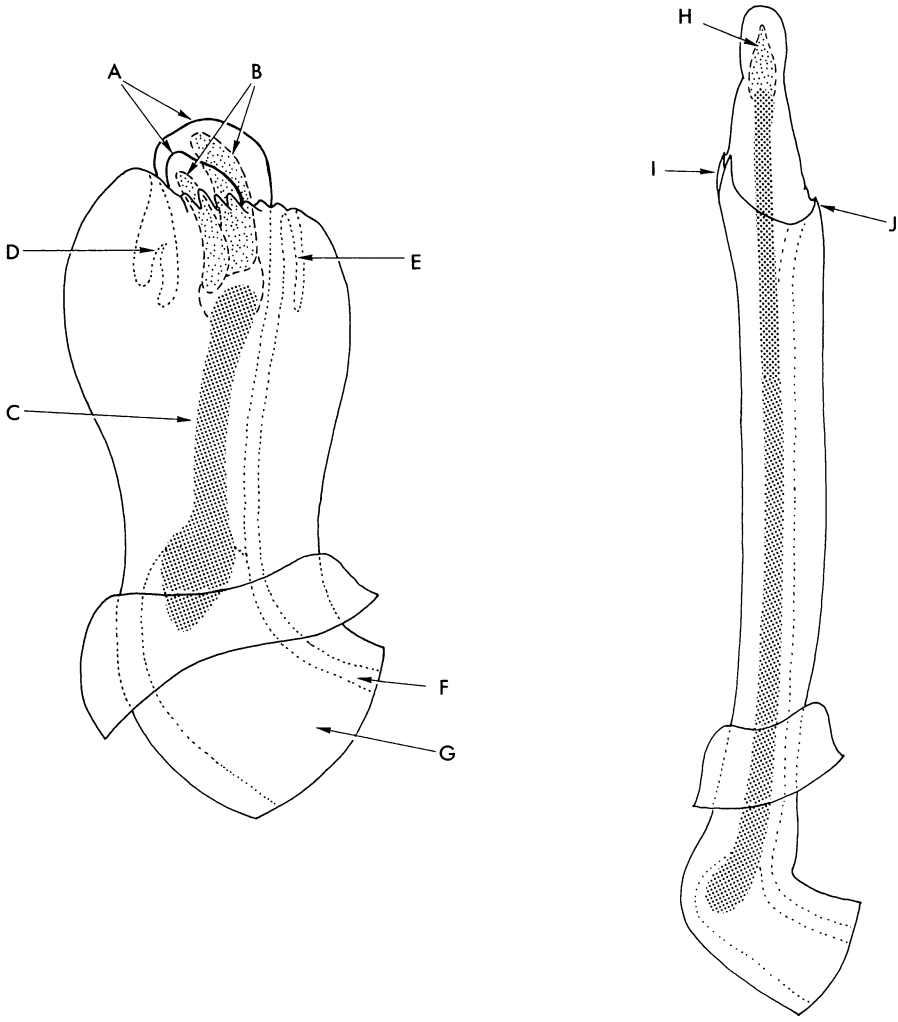


Fig. 19. Schematic diagrams of complex (left) and simple (right) glandes penis as seen from lateral view. Anatomical features indicated are: A) medial and lateral bacular mounds; B) medial and lateral bacular digits; C) osseus portion of baculum; D) dorsal papilla; E) urethral flap; F) urethra; G) corpus cavernosum penis; H) cartilaginous tip; I) dorsal lappets; J) ventral lappet. (Diagram of complex penis adapted from Hooper and Hart, 1962: Fig. 1).

within neotomine-peromyscines. Most traits so affected by my unconventional coding (*e.g.* lateral bacular mounds, urethral processes etc.) occur infrequently among neotomine-peromyscines, and for those that do, such as urethral processes and dorsal papillae in *Xenomys nelsoni* and *Neotoma (Hodomys) alleni,* I shall argue that such traits arose independently of similar structures in South American cricetines.

Character 52: Distribution of Spines on Body of Glans.
(0) Entire spinous investiture of body.
(1) One-half to three-quarters of body spiny.
(2) Less than one-half of body spiny.
(3) Body wholly denude of spines.

A glans with a nearly complete covering of spines is cosmopolitan among muroids (see Hooper and Hart, 1962; Hooper and Musser, 1964; Lidicker, 1968). Absence or reduction of spines is primarily limited to a few species of *Peromyscus, Neotoma* and *Reithrodontomys* (Hooper, 1958, 1959, 1960; Hooper and Musser, 1964b) and here treated as derived states.

Character 53: Occurrence of Spines on Internal Crater Wall.
(0) Absent.
(1) Present.

The derived condition is found only in the glandes of *Nelsonia* and *Xenomys* (Hooper, 1960).

Character 54: Corrugation of Body Surface.
(0) Absent.
(1) Present.

Pronounced furrowing of the body of the glans is clearly an autapomorphic condition characterizing the phallus of *Peromysus (Megadontomys) thomasi* (Hooper, 1958; Hooper and Musser, 1964b).

Character 55: Position of Urinary Meatus.
(0) Terminal or nearly so.
(1) Subterminal.

Rationale for adopting this polarity is treated in another section.

Character 56: Dorsal Lappets.
(0) Absent.
(1) Present.

Character 57: Ventral Lappet.
(0) Absent.
(1) Present.

Dorsal and ventral lappets are flap-like projections from the body of the glans either onto the soft tissue of the protrusible tip or at the ventral lip of the urinary meatus, respectively, and occur in species of the subgenera *Peromyscus* and *Haplomylomys* (Carleton, 1977; Hooper, 1958; Hooper and

Musser, 1964b; Lawlor, 1971). Typically, epidermal spines of the glans body extend onto these lappets. Although Hooper (1958) and Hooper and Musser (1964b) described these processes, they offered no opinion regarding their evolutionary sequence. Subsequently, Lawlor (1971), studying interrelationships of species of *Peromyscus (Haplomylomys),* suggested that dorsal and ventral lappets are acquired features, a viewpoint I endorse.

Character 58: Urethral Process.

(0) Absent.
(1) Present.

Justification for choosing this evolutionary direction for this and the following two characters is provided below.

Character 59: Dorsal Papilla.

(0) Absent.
(1) Present.

Character 60: Lateral Bacular Mounds.

(0) Absent.
(1) Present, weakly defined.
(2) Present, strongly defined, free of crater walls.
(3) Present, strongly defined, buried in tissue adherent to crater walls.

Character 61: Crater Hood.

(0) Absent.
(1) Present.

In some species of *Neotoma,* a soft, pliant fold of tissue completely envelopes the distal baculum and cartilaginous tip. Hooper (1960) referred to this structure in *N. albigula* as a "hood", and I have applied this terminology to those forms in which tissue of the body of the glans wholly encloses, and hides from the external view, the free portion of the baculum and its cartilaginous tip. Folds of tissue of similar appearance are observed for the phalli of *Ototylomys phyllotis* and *Peromyscus (Megadontomys) thomasi,* and although I have regarded them as crater hoods, I am not entirely confident that they are homologous to the structures found in *Neotoma.*

Character 62: Ventral Shield.

(0) Absent.
(1) Present.

The ventral shield consists of a fold of soft tissue that projects between the ventral wall of the crater and the urethral process (see Hooper and Hart, 1962; Fig. 1). Among muroid species with a complex penis, the ventral shield is present in species of microtines and Old World cricetines, but not others (Hooper, 1962; Hooper and Musser, 1964a); in view of its restricted occurrence, the shield is considered derived.

Character 63: Length Divided by Width of Glans Penis.

(0) 1-3 : 1.

(1) 4–6 : 1.
(2) 7–9 : 1.
(3) Greater than 10 : 1.

For characters 63–67, I have attempted to convey differences in size and proportion of the glans penis, which I believe exhibit as definite phylogenetic trends as the other traits enumerated above, in a more objective, quantified manner than simple verbal descriptions, such as longer than wide, etc. Accordingly, measurements were recorded from the phalli of each specimen and compounded into ratio variables from which nominal characters were coded (Fig. 20).

A glans that is almost as wide as long is ubiquitous among microtines, gerbillines, South American and Old World cricetines, and is found even

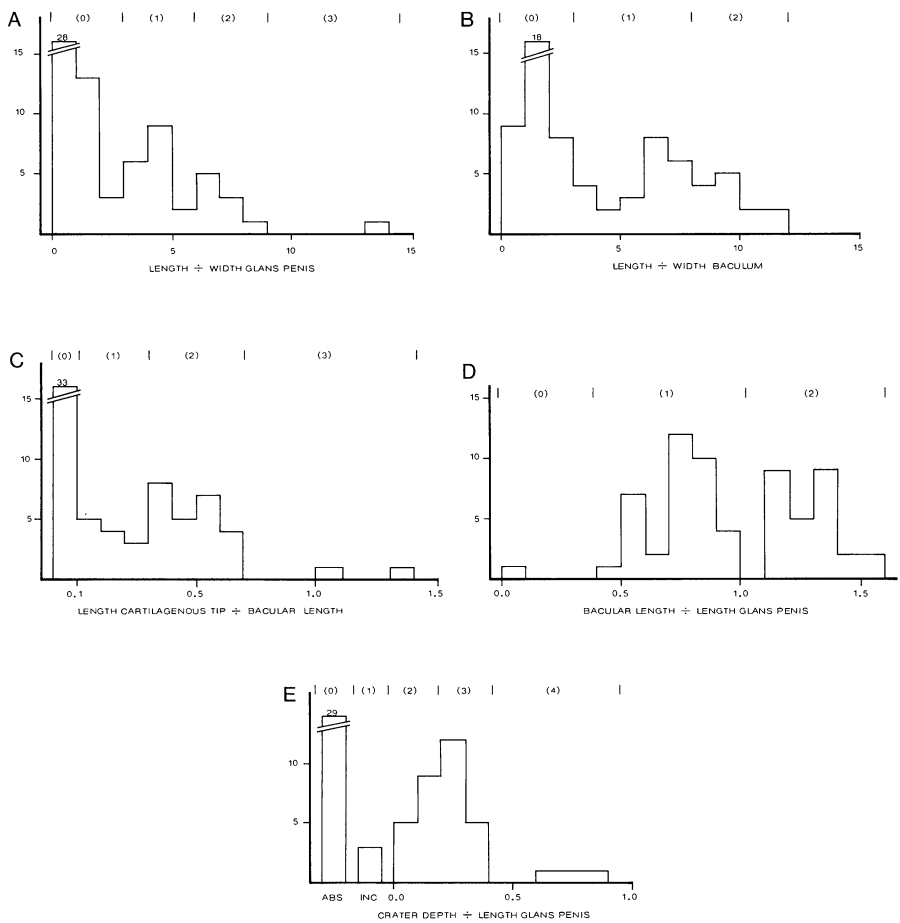


Fig. 20. Frequency histograms used to compute proportional characters of the glans penis (see Characters Nos. 63–67).

in some neotomine-peromyscines, for example *Baiomys, Scotinomys* and some *Neotoma.* A long, narrow glans penis is regarded as apomorphic.

Character 64: Length Divided by Width of Baculum.
(0) 1–4 : 1.
(1) 5–8 : 1.
(2) 9–12 : 1.

The same trend argued above for the shape of the glans penis is assumed for modifications of the baculum.

Character 65: Length of Cartilaginous Tip Divided by Bacular Length.
(0) Less than 0.09 : 1.
(1) 0.1–0.3 : 1.
(2) 0.4–0.6 : 1.
(3) Greater than 0.8 : 1.

Character 66: Bacular Length Divided by Length of Glans Penis.
(0) 0.4–1.0 : 1.
(1) Less than 0.3 : 1.
(2) 1.2–1.6 : 1; derived from state (0).

In most specimens measured, the length of the baculum is less than or subequal to the length of the glans. This state is therefore viewed as primitive and elongation of the baculum relative to the glans is advanced. One species, *Neotoma fuscipes,* possesses an atypically short baculum that is also regarded as evolving from the ancestral condition.

Character 67: Depth of Crater Divided by Length of Glans Penis.
(0) Crater absent.
(1) "Incipient" crater.
(2) 0.1–0.2 : 1.
(3) 0.3–0.4 : 1.
(4) Greater than 0.5 : 1.

Rationale for determining this character's polarity is deferred to a following section.

Male Accessory Reproductive Glands

The complement of male accessory reproductive glands displayed by muroid rodents is remarkably complex and diverse, a combination of properties making this array of glands attractive for a phylogenetic study. On the other hand, because one is dealing with organs of soft anatomy that can vary extraordinarily according to reproductive status of the animal, this diversity is sometimes difficult to interpret and to represent as qualitative character states. Furthermore, some of these glands, such as the anterior mass of ramifying tubules observed in some species of *Neotoma,* diverge so markedly from the common morphological plan that questions of homology assume great importance. I do not believe that errors in homology would seriously affect phenetic distances between spe-

cies, but such misinterpretations could substantially alter cladistic patterns. The male accessory glands are in urgent need of fine histological, histochemical and embryological studies to settle issues of homology, perhaps more so than any other suite of characters treated herein, with the possible exception of the glans penis.

Implementation of my study, however, necessitates identification of the glands and the tentative adoption of operational homologies. In general, evidence for homology was based on position of the glands and entrance of their ducts into the urethra, texture, and conformation. Fortunately, my decisions concerning glandular identifications have been aided immensely by broad-scale, anatomical surveys conducted by other authors (Arata, 1964; Linzey and Layne, 1969; Voss and Linzey, 1980). I have elected a conservative tact in delineating character states of these glands, emphasizing presence/absence alternatives or unquestionably gross differences in proportion. Regretfully, this approach disregards finer alterations in size and proportion, which do occur but are subjective to codify. The nomenclature employed for these glands adheres to that used by Linzey and Layne (1969).

I accept the following assortment of male accessory glands as exemplifying the plesiomorphic condition: one pair of preputials; two pairs (medial and lateral) of ventral prostates; and one pair each of anterior prostates, dorsal prostates, bulbo-urethrals, ampullaries, and vesiculars (Fig. 21). Deviations from this complement represent derived states. Comparative evidence suggests that this aggregate of glands constitutes the ancestral muroid morphology. One pair each of anterior, dorsal and ventral prostates, bulbo-urethrals, and vesiculars occur in dipodoid rodents (Wrigley, 1972; Kowalska-Dyrcz, 1973), the probable sister group of Muroidea. Although preputials and ampullaries are apparently lacking in Dipodoidea, Voss and Linzey (1980) pointed out that the widespread occurrence of these two glands in various groups of muroids argues for their early acquisition during muroid evolution. A single pair of preputials has been reported for some murines, most microtines and South American cricetines, and some neotomine-peromyscines (Arata, 1964; Brown, 1972; Carleton *et al.*, 1975; Jackson, 1938; Kowalska-Dyrcz and Pawlowska-Indyk, 1969; Voss and Linzey, 1980). Although my limited dissections of gerbillines failed to reveal preputials, they have been noted for certain species of *Tatera* (Allanson, 1933). Similarly, ampullaries are found within the same muroid assemblages. Additional comments on polarities of accessory glands are considered under the appropriate character.

Character 68: Preputials.

(0) One pair present.
(1) Two pairs, or more, present.
(2) Absent (or not visible macroscopically); derived from state (0).

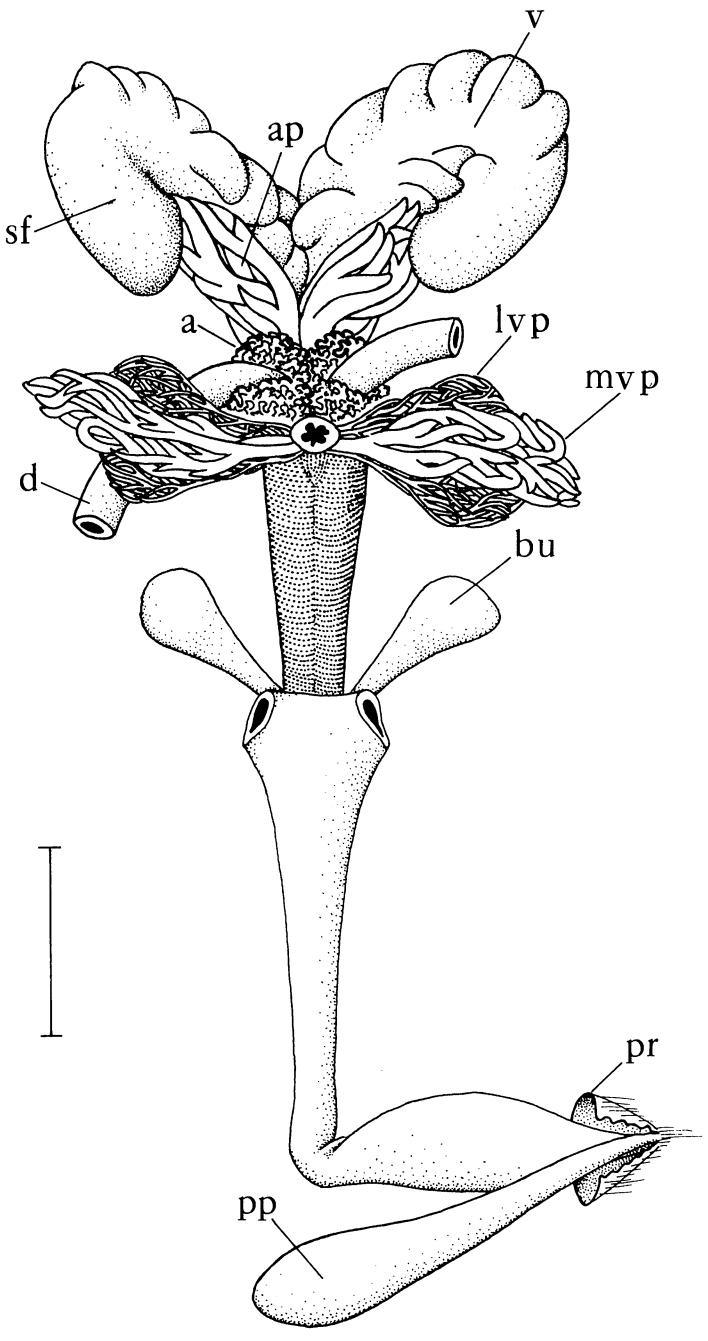


Fig. 21. Ventral view of male reproductive tract of *Nectomys squamipes* (RSV 178) illustrating proposed ancestral complement of accessory glands. Anatomical abbreviations include: a, ampullary gland; bu, bulbourethral gland; d, deferent duct; lvp, lateral ventral prostate; mvp, medial ventral prostate; pp. preputial gland; pr, prepuce; sf, subterminal flexure of vesicular gland; v, vesicular gland. Scale equals 10 mm (from Voss and Linzey, 1980: Fig. 1).

The single specimen of *Nyctomys* examined by Arata (1964) lacks preputials; however, my samples clearly possess two pairs, which corresponds to the observations of Voss and Linzey (1980). Two pairs, treated as derived from a single-pair state, also occur in some South American cricetines (Voss and Linzey, *op. cit.*). I qualified character state (2) to read "or not visible macroscopically" because Linzey and Layne (1969) discovered minute preputials in some *Peromyscus* only through examination of histological preparations; these glands were not visible upon gross dissection.

Character 69: Medial Ventral Prostates.

(0) Present, "normal".
(1) Absent.
(2) Present, "elaborate"; derived from state (0).

The modifier "elaborate" refers to the finely-branched mass of tubules comprising the ventral prostatic tissue found only in *Peromyscus (Habromys) lepturus* (Linzey and Layne, 1969). *Peromyscus lophurus,* another species of the subgenus *Habromys,* essentially matches *lepturus* in morphology of the accessory glands.

Character 70: Lateral Ventral Prostates.

(0) Present.
(1) Absent.

The case for the primitiveness of two pairs of ventral prostates is uncertain. The uncertainty involves that pair designated as lateral prostates. They occur as distinct glands, separable from the medial pair, in most microtines and South American cricetines, some neotomine-peromyscines, and at least some of the limited number of murines examined thus far (Arata, 1964; Voss and Linzey, 1980). In light of their broad distribution among muroids, I elected their presence as plesiomorphic. Yet, lateral ventral prostates are clearly lacking in many neotomine-peromyscines, *e.g. Neotoma, Tylomys* and *Ototylomys,* or are only indistinctly defined in the gerbillines I studied and in *Ochrotomys.* Therefore, one must admit the possibility that a single ventral pair, the median one, existed in ancestral muroids, and that the poorly-defined lateral ventral prostates observed in certain forms constitute an intermediate stage leading to entirely separate pairs of ventral prostates.

Character 71: Dorsal Prostates.

(0) Present.
(1) Absent.
(2) Present, "elaborate"; derived from state (0).

To describe the prostatic tissue of *Neotoma* as only "elaborate" grossly understates their intricate, dendritic nature and wholly unique appearance. But, in so identifying "elaborate" dorsal prostates in certain species of *Neotoma,* I depart from Arata (1964), who considered these glands anterior prostates and suggested that dorsal prostates were absent. I here treat

them as dorsal prostates because I believe there are really two sets of glands, partially entangled and intertwined, in a huge, fan-shaped mass of tissue on the cephalic border of the urethra. In addition to the large tubules, which Arata called anterior prostates, my dissections have consistently revealed a second pair of glands, ventral to and closely adnate with the larger set of tubules. Because of their usually whitish texture, tubules of smaller diameter, and the apparent entrance of their ducts near the ductus deferens, I believe the smaller pair of glands are anterior prostates. This second set of glands was consistently demonstrable in specimens of *Neotoma albigula, floridana, mexicana* and *lepida* as well as other *Neotoma* available to me but not included in the study (*micropus, goldmani,* and *stephensi*). I am less confident of their existence in specimens of *N. cinerea* and *fuscipes,* none of which seemed in a completely fertile condition, but have reservedly coded them as so. The example of *Neotoma (Hodomys) alleni* has typical anterior and dorsal prostates and otherwise conforms closely to the proposed ancestral accessory glandular complement. Consequently, I have termed the mass of larger tubules "elaborate" dorsal prostates. The obvious uncertainty of these identifications underscores the need for ontogenetic and histological evidence to resolve the problems of homology of the accessory glands.

Character 72: Anterior Prostates.

(0) Present.
(1) Absent.
(2) Present, "elaborate"; derived from state (0).

"Elaborate" in the case of anterior prostates refers to the unique condition of these glands observed in specimens of *Nyctomys* (see Arata, 1964: Fig. 5). I have followed Arata in naming them anterior prostates; however, Voss and Linzey (1980) suggest they may be considered, with equal plausibility, highly modified dorsal prostates. *Nyctomys* is another candidate for histological and embryological investigation of its accessory gland complement.

Character 73: Bulbo-Urethrals.

(0) Present, "normal" in size.
(1) Present, large.
(2) Present, huge.

In the "normal" state, the bulbo-urethals are wedged between and partly obscured by the bulbocavernosus and ischiocavernosus muscles. Only two species of *Peromyscus* exhibit large bulbo-urethrals, and only those observed in specimens of *Tylomys* are mammoth in comparison to other species.

Character 74: Ampullaries.

(0) Present.
(1) Absent.

(2) Present, elaborate and filamentous; derived from state (0).
(3) Present, elaborate and coiled; derived from state (0).

In the majority of specimens, ampullary glands surround the base of the deferent ducts, tightly invested by a membrane which imparts a compact, coiled appearance. In a few forms, namely *Baiomys, Scotinomys* and perhaps *Neotoma (Hodomys) alleni,* some ampullary tubules are isolated from the central mass, which may not wholly enclose the bases of the deferent ducts; I did not view this modification as sufficiently different to recognize another character state. The ampullary glands of *Peromyscus (Podomys) floridanus* are large but retain the tightly coiled configuration (Linzey and Layne, 1969); this condition, treated as derived, was also noted in specimens of *Neotomodon alstoni.* Another variant of ampullary glandular morphology consists of proliferation of the tubules but without a tight, membranous vesture, thereby presenting a loose, filamentous rather than a compact, coiled appearance.

Character 75: Vesiculars.
(0) Present, shaped like a cane or inverted "J".
(1) Present, straight or weakly J-shaped.
(2) Present, small and straight.
(3) Present, minute diverticula.
(4) Absent.
(5) Present, cranial border elaborate; derived from state (0).
(6) Present, long and intestiniform, flaccid; derived from state (0).

The shape of the vesiculars resembles a cane, or the letter "J" inverted, in most neotomine-peromyscines, and in all South American cricetines, microtines and Old World cricetines surveyed here (Fig. 21). Apparently, this is the typical conformation of the vesiculars in other muroid species as well (Arata, 1964; Voss and Linzey, 1980). Deviations from this state occur either as reductions in size of the vesiculars, resulting in their absence in some specimens (character states 1–4), or as increases in size or complexity with the resultant loss of the characteristic J-shape. The intricately dissected, fan-shaped configuration of the vesiculars in *Peromyscus (Isthmomys) pirrensis* and *flavidus* is clearly derived from the ancestral condition. Certain specimens retain vestiges of a fundamental J-shape; furthermore, Linzey and Layne (1969) report that the vesiculars in immature tracts are less lobulated and more J-shaped. The vesicular glands in specimens of *Tylomys* exceed in relative length those of any other species examined. The long glands lack any suggestion of a subterminal flexure.

Character 76: Ampullae of Ductus Deferens.
(0) Absent.
(1) Present.

Large, conspicuous ampullae were noted near the base of the deferent ducts only in *Tylomys* and *Ototylomys.*

Miscellaneous External Features

Character 77: Number and Position of Plantar Pads.

(0) Six plantar pads; first through fourth interdigitals close together, first and fourth opposite one another; thenar and hypothenar pads situated closely behind the interdigitals.

(1) Second through fourth interdigitals arranged closely, but first set farther back on heel, not opposite the fourth; thenar and hypothenar also displaced posteriorly and strongly alternate.

(2) Second and third interdigitals close together; first and fourth situated more posteriorly and slightly alternate; thenar and hypothenar as in state (1).

(3) Interdigitals arranged as in state (2); hypothenar pad absent; thenar pad present or absent; total plantar pads four or five.

(4) Interdigitals arranged as in state (2); hypothenar pad greatly reduced or, more often, absent; total plantar pads usually five; derived from state (1).

(5) Interdigital pads arranged as in state (1); both thenar and hypothenar pads absent; only four plantar pads; derived from state (4).

The character-state tree given above also reflects changes in the shape of the hindfoot and relative lengths of digits. That in the ancestral is relatively short and broad, the fifth digit only slightly shorter than digits two, three and four. The hindfoot described by character state (2) is proportionately longer and narrower; digits two through four substantially exceed the first and fifth in length.

Character-state (1) is more frequently observed within neotomine-peromyscines. However, my choice of the primitive state acknowledges the hypothesis that ancestral New World cricetids were sylvan and arboreal or scansorial (see Hershkovitz, 1962, 1972). Such a short, broad hindfoot with closely approximated plantar pads occurs in *Tylomys* and *Ototylomys* among neotomine-peromyscines, in the arboreal oryzomyines of the genus *Oecomys,* and in members of the thomasomyine group (Hershkovitz, 1960, 1972). Descriptive terms for the plantar pads are found in Brown and Yalden (1973).

Character 78: Fur Coverage of Plantar Surface.

(0) Plantar surface naked or only lightly furred on heel.

(1) Plantar surface densely furred to thenar pad.

(2) Plantar surface densely furred to first interdigital pad.

(3) Plantar surface entirely fur-covered or nearly so.

An essentially naked plantar surface was selected as the plesiomorphic condition on the basis of its more widespread occurrence within my collection of specimens.

Character 79: Number of Mammary Glands.

(0) Eight or ten; generally arranged as two pair inguinal, one pair axillary and one pair pectoral.
(1) Six; one pair axillary and two pair inguinal.
(2) Four; two pair inguinal.

The cosmopolitan state in neotomine-peromyscines is three pairs of mammary glands. Nevertheless, a count of eight mammae is more common among my outgroups, and I have recognized that number as ancestral. Moreover, eight is the modal number detected in a much broader survey of mammary glands in rodents (Arvy, 1974).

Table 7 contains character-state values of the 79 characters for all 75 species. In addition, the characters are summarized according to the topology of their character-state trees (Table 8).

RESULTS

Phenetic Analyses of Neotomine-Peromyscines

Principal component analyses were applied to the basic data matrix of Table 7. Because I lacked fluid examples of *Peromyscus (Isthmomys) flavidus* and *Xenomys nelsoni,* most analyses were performed with 47 of the 49 neotomine-peromyscine samples; in order to include those samples, the principal component analyses were performed on reduced sets of variables. Also, only 60 characters were used in the phenetic studies of neotomine-peromyscines; the additional characters scored lacked variability when the other muroid groups were excluded. My presentation of the results of principal component analysis first treats all neotomine-peromyscines and then selected subsets of species corresponding to currently recognized taxonomic categories.

The dispersion of samples along the first three principal components discloses three major aggregations (Fig. 22). *Tylomys* and *Ototylomys* are consistently associated and generally set far apart from other neotomine-peromyscines. Species' samples of *Neotoma* represent another persistent cluster; *Neotoma lepida* and *N. (Holomys) alleni* are the most distinctive outliers of this complex of forms. The remaining species, with the exception of *Nelsonia,* comprise a loose assemblage corresponding to the tribe Peromyscini. Within that tribe, examples of the subgenera *Haplomylomys, Peromyscus, Habromys* and *Podomys* of *Peromyscus* form a tight cluster. The other subgenera of *Peromyscus (Megadontomys, Isthmomys* and *Osgoodomys*) are as distinctive as some other currently defined genera (*e.g. Reithrodontomys, Ochrotomys* and *Neotomodon*). The monotypic *Nelsonia neotomodon,* presently placed in Peromyscini, is not clearly aligned with any of the three clusters; its position is approximately equidistant to the OTUs representing *Neotoma* and those of Peromyscini. Principal components one through three account for only 51.4 percent of the variation among samples (Table 9). Even the first ten components extracted summarized only 82 percent of

TABLE 7

BASIC DATA MATRIX OF 75 SPECIES OF MUROIDEA DESCRIBED BY 79 CHARACTERS.

	Character Number															
	1		2		3		4		5		6		7			
Taxa	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	6789
Neotomine-Peromyscines																
Baiomys taylori	21202	20000	00000	30222	00000	00001	20001	00011	01002	00000	10000	00000	00001	02001	00001	0212
Baiomys musculus	21202	10000	00000	30222	00000	00001	20001	01011	01002	00000	10000	00000	00001	02001	00001	0212
Ochrotomys nuttalli	10202	10000	00000	00222	00000	00001	20101	01010	03000	11010	00001	00100	00001	00000	00011	0111
Onychomys leucogaster	20205	20000	10000	00222	00000	00001	20000	00011	03003	51000	10000	00000	00010	00001	01014	0521
Onychomys torridus	20205	20000	20000	00222	00000	00001	20000	00011	03003	51000	10000	00000	00010	00001	01014	0521
Scotinomys teguina	21202	10202	00000	30222	00000	00001	20001	01011	03002	00000	10000	00000	00000	03001	00000	0202
Scotinomys xerampelinus	21202	10202	00000	30222	00000	00001	20001	01011	03002	00000	10000	00000	00000	02001	00000	0201
Reithrodontomys																
(Aporodon)																
creper	11102	11000	00000	00222	00000	00001	20000	03010	03012	31000	01001	00000	00110	20200	00000	0101
mexicanus	11102	11000	00000	00222	00000	00001	20000	03010	03012	31000	01001	00000	00110	20200	00000	0101
(Reithrodontomys)																
fulvescens	20202	11000	00000	00222	00000	00001	20000	02010	03012	21000	01001	00000	00110	20200	00000	0111
megalotis	20203	21020	10000	00222	00000	00001	20001	01010	02012	21000	01001	00000	00120	20200	00000	0111
sumichrasti	20203	11010	20000	00222	00000	00001	20001	02010	03012	21000	01001	00000	00110	20200	00000	0111
montanus	20203	21020	10100	00222	00000	00001	20001	01010	03012	11000	01001	00000	00110	20200	00000	0111
humulis	21203	11000	00000	00222	00000	00001	20001	01010	03012	11000	11001	00000	00110	20200	00000	0211
Neotomodon alstoni	20212	10000	20000	00222	00001	00001	20200	01000	03002	32000	00000	00000	00110	00201	00033	0111
Nelsonia neotomodon	20222	10000	00000	00221	00000	00001	20200	02000	03000	32002	21101	00000	00002	04201	00000	0112
Peromyscus																
(Peromyscus)																
crinitus	20202	10000	10000	00222	00000	00001	20100	02010	03000	32000	00001	11000	00110	20200	00000	0102
leucopus	11202	10000	00000	00222	00000	00001	20100	01010	03000	32000	00001	11000	00111	20200	00000	0111
maniculatus	21202	10000	00000	00222	00000	00001	20000	01010	03000	32000	00001	11000	00111	20200	00000	0111
boylii	11202	10000	00000	00222	00000	00001	20100	02010	03000	32000	00001	11000	00220	20200	00000	0111
ochraventer	11202	10000	00000	00222	00000	00001	20100	02010	03000	32000	00001	10000	00110	20200	00000	0101

TABLE 7

(Continued)

Taxa	Character Number 1 12345	1 67890	2 12345	2 67890	3 12345	3 67890	4 12345	4 67890	5 12345	5 67890	6 12345	6 67890	7 12345	7 67890	12345	6789
Peromyscus																
spicilegus	11202	10000	00000	00222	00000	00001	20000	02010	03000	32000	00001	00000	00120	20200	00000	0111
truei	11202	10000	00000	00222	00000	00001	20200	02010	03000	32000	00001	11000	00110	20200	00000	0101
difficilis	11202	10000	10000	00222	00000	00001	20200	03010	03000	32000	00001	00000	00220	20200	00000	0101
melanophrys	21202	10000	00000	00222	00010	00001	20200	03000	03000	32000	00001	10000	00220	20200	00000	0101
mexicanus	11202	10000	00000	00221	00010	00001	20100	02000	03000	52000	00001	10000	00220	20200	00000	0102
guatemalensis	10202	10000	10000	00221	00010	00001	20100	02000	03000	52000	00001	10000	00220	20200	00000	0102
megalops	11202	10000	00000	00221	00020	00001	20100	02000	03000	52000	00001	11000	00220	20200	00000	0102
furvus	11202	10000	00000	00222	00000	00001	20100	02000	03000	32000	00001	00000	00220	20200	00000	0111
yucatanicus	11202	10000	00000	00222	00010	00001	20100	02000	01000	32000	00001	10000	00220	20200	00000	0112
(Haplomylomys)																
eremicus	20202	10000	00000	00222	00000	00001	20200	02000	03000	32000	00001	00000	00000	20000	00000	0102
californicus	20202	10000	00000	00222	00000	00001	20200	02000	03000	32000	00001	00000	00110	20000	00000	0102
(Osgoodomys)																
banderanus	10202	10000	00000	30220	00020	00001	20100	02010	02000	32000	00000	00000	00120	00001	01124	0102
(Habromys)																
lepturus	10202	10000	00000	00221	00000	00001	20100	32010	03000	32000	03000	00000	00110	20221	00003	0101
lophurus	11202	10000	00000	00222	00000	00001	20200	33010	03000	32001	03000	00000	00220	20221	00003	0101
(Podomys)																
floridanus	20202	10000	00000	00222	00010	00001	20200	01000	03000	32000	02000	00000	00220	20200	00132	0411
(Megadontomys)																
thomasi	11202	10010	00000	00221	00020	00001	20100	03000	01010	32001	20011	00100	10010	21200	00000	0101
(Isthmomys)																
flavidus	11202	10000	00000	00201	00020	00001	20001	03010	030--	-----	00000	00000	00010	21201	00005	-102
pirrensis	11202	10000	00000	00211	00020	00001	20001	03010	02010	42000	00000	00000	00010	20201	00005	0102

TABLE 7

(Continued)

Taxa	Character Number 1 12345	1 67890	2 12345	2 67890	3 12345	3 67890	4 12345	4 67890	5 12345	5 67890	6 12345	6 67890	7 12345	7 67890	12345	6789
Neotoma																
(Neotoma)																
albigula	20221	10000	00000	30012	00101	00001	20300	01000	01000	32001	20001	00100	10102	03201	20024	0002
floridana	20221	10000	10000	30122	00111	00001	20300	01000	01000	32001	20001	00100	10002	03201	20024	0002
mexicana	20221	10000	00000	30222	00111	00001	20300	02000	01000	32001	20001	00100	10002	03001	20024	0002
fuscipes	20221	10000	00000	10222	00101	00001	20300	02000	01000	32001	21001	00100	10003	14001	20024	0002
lepida	20221	10000	10000	30222	00111	00001	20300	01000	01010	32000	22001	00000	10311	03201	20024	0002
(Teonoma)																
cinerea	20221	10000	00000	10011	00101	00001	20300	01000	01000	32001	22001	00100	10003	04001	20024	0012
(Hodomys)																
alleni	20222	10201	30000	30110	00111	00021	20101	02000	01000	22001	20001	00110	00001	02001	00000	0002
Xenomys nelsoni	20222	10000	00000	30221	00111	00021	20311	1-000	01---	-----	-0101	00110	00001	02---	-----	----
Ototylomys phyllotis	12000	00002	30000	30011	00030	00021	20200	22000	01011	00010	20001	00000	10001	03001	01004	1002
Tylomys nudicaudus	12000	00002	30000	30000	00030	00021	20100	12000	00011	00010	20000	00100	00001	01001	00206	1002
South American Cricetines																
Akodon cursor	11202	-0000	00000	00221	00001	00011	20-01	0-011	03013	00010	00001	00112	00002	03000	00000	0200
Oxymycterus delator	11202	-0000	10000	00221	00000	000-1	20-01	0-011	01010	50000	10001	00112	00002	03100	00000	0200
Scapteromys tumidus	11202	-0020	00111	01222	00101	000-1	20-01	0-011	0-012	30000	00001	00110	00001	03000	00000	0200
Sigmodon hispidus	20212	-0020	01111	30222	00121	00011	20-01	0-011	01012	00001	00001	00112	00002	03100	00000	0200
Holochilus brasiliensis	20212	-0020	01111	30212	00011	00011	20-01	4-011	01022	00010	00001	00112	00002	03000	00000	0300
Calomys callosus	21202	-0020	00111	01222	00011	000-1	20-01	0-011	01012	00000	00001	00112	00002	03000	00000	0210
Graomys griseoflavus	20202	-0020	01111	00222	00011	01011	20-01	0-011	0-012	00000	00001	00112	00002	03100	00000	0100
Nectomys squamipes	10102	-0020	01100	31200	10031	00011	20-01	4-011	0-012	00010	00001	00112	00002	03000	00000	0300
Oryzomys capito	00102	-0000	00000	21221	10011	000-1	20-01	4-011	0-011	00010	00001	00112	00002	03000	00000	0200
Oryzomys fulvescens	11102	-0000	10000	21222	10001	00011	20-01	4-011	02012	00010	00001	00112	00002	03200	00000	0200

TABLE 7

(Continued)

Taxa	Character Number 1 12345	1 67890	2 12345	2 67890	3 12345	3 67890	4 12345	4 67890	5 12345	5 67890	6 12345	6 67890	7 12345	7 67890	12345	6789
South American Cricetines																
Oryzomys palustris	10102	-0020	00100	31221	10021	00011	20-01	4-011	01012	00010	10001	00112	00002	03000	00000	0200
Thomasomys aureus	01202	-0020	00100	30220	00000	000-1	20-0-	--011	0-01-	21001	20001	00112	00002	03100	00000	0001
Nyctomys sumichrasti	01100	-0010	00000	30001	00030	00001	20-00	0-000	00012	00011	20001	00111	00001	02100	00000	0002
Old World Cricetines																
Mesocricetus auratus	21100	-0202	00000	01222	00100	00020	10-01	0-010	01100	02100	00001	00112	01002	02201	00000	0000
Cricetulus migratorius	21200	-0202	00000	00202	00000	00100	20-00	0-010	02110	02110	00001	00112	01002	02200	00000	0110
Microtinae																
Ondatra zibethicus	2-23-	-0333	52223	21222	22200	10100	00-21	0-111	02022	32003	20001	00112	01002	02000	00000	0301
Clethrionomys gapperi	2-23-	-0333	52223	21222	22100	10100	10-21	0-111	03002	22001	00001	00112	01002	02000	00000	0210
Dicrostonyx groenlandicus	2-23-	-0333	52223	21222	22200	10100	00-21	0-111	03002	32002	00000	00101	01001	02000	00000	0330
Lemmus sibiricus	2-23-	-0333	52223	30222	22200	10100	01-11	0-111	02012	00003	20001	00112	01002	02000	00000	0230
Synaptomys cooperi	2-23-	-2333	52223	30222	22200	10100	01-21	0-111	02012	00003	20001	00112	01001	02000	00000	0211
Microtus pennsylvanicus	2-23-	-0333	52223	21222	22200	10100	01-21	0-111	03022	32001	20001	00112	01002	02000	00000	0200
Gerbillinae																
Gerbillus cheesmani	20014	-1000	20002	21222	01232	01110	22-20	4-012	13022	00000	00001	00113	00002	03200	00000	0530
Meriones shawi	20024	-1000	21000	21222	01232	01110	12-20	4-002	12022	00000	01001	00113	00002	02200	00000	0510
Pachyuromys duprasi	20004	-1020	21102	21222	01212	01110	22-20	4-002	13023	00000	00001	00113	00002	02200	00000	0500
Psammomys obesus	20024	-0000	20002	21222	01212	01100	02-20	4-002	12022	00000	20001	00113	00002	02200	00000	0400
Tatera indica	20014	-1020	11100	21222	01232	01100	01-21	4-002	12022	00000	00001	00113	01002	03200	00000	0300

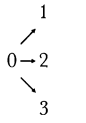
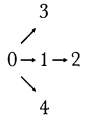
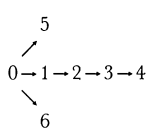
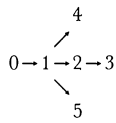
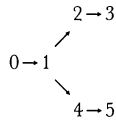
TABLE 8

CHARACTER STATE TREES AND CORRESPONDING ADDITIVE BINARY RECODING SCHEMES.

	Original Tree	Binary Version
1.	0→1	same
	Characters: 17, 21, 26-8, 30, 35, 38-9, 41, 43, 48-9, 53-9, 61-2, 70, 76 = 24.	
2.	0→1→2	(0) (1) (2) 0 1 1 0 0 1
	Characters: 1-3, 6, 18-20, 23, 25, 31-2, 34, 40, 44, 47, 64, 73, 79 = 18.	
3.	0→1→2→3	(0) (1) (2) (3) 0 1 1 1 0 0 1 1 0 0 0 1
	Characters: 4, 16, 24, 33, 42, 50, 52, 60, 63, 65, 78 = 11.	
4.	0→1→2→3→4	(0) (1) (2) (3) (4) 0 1 1 1 1 0 0 1 1 1 0 0 0 1 1 0 0 0 0 1
	Character: 67.	
5.	0→1→2→3→4→5	(0) (1) (2) (3) (4) (5) 0 1 1 1 1 1 0 0 1 1 1 1 0 0 0 1 1 1 0 0 0 0 1 1 0 0 0 0 0 1
	Character: 46.	
6.	1 ↗ 0 ↘ 2	(0) (1) (2) 0 1 0 0 0 1
	Characters: 7, 12-14, 22, 29, 51, 66, 68-9, 71-2 = 12.	
7.	1→2 ↗ 0 ↘ 3	(0) (1) (2) (3) 0 1 1 0 0 0 1 0 0 0 0 1
	Characters: 8-10.	

TABLE 8

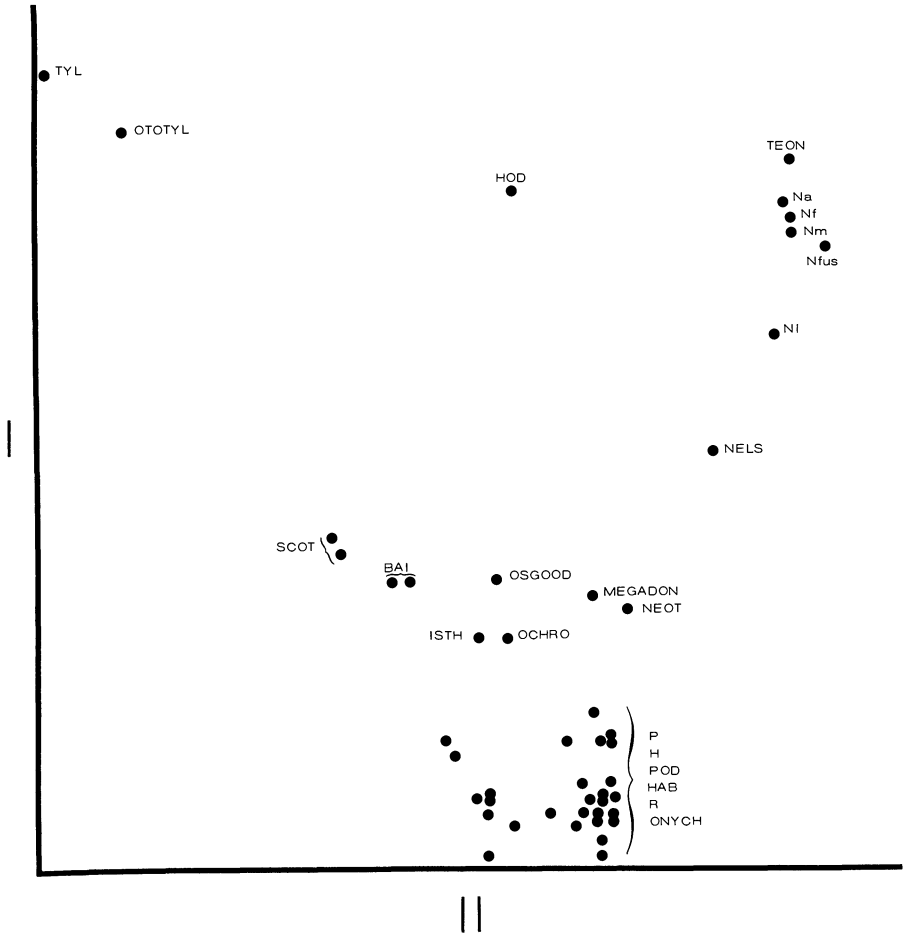
(Continued)

Original Tree	Binary Version
8. 	(0) (1) (2) (3) 0 1 0 0 0 0 1 0 0 0 0 1
Characters: 15, 45, 74.	
9. 	(0) (1) (2) (3) (4) 0 1 1 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 1
Characters: 11, 36.	
10. 	(0) (1) (2) (3) (4) (5) (6) 0 1 1 1 1 0 0 0 0 1 1 1 0 0 0 0 0 1 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1
Character: 75.	
11. 	(0) (1) (2) (3) (4) (5) 0 1 1 1 1 1 0 0 1 1 0 0 0 0 0 1 0 0 0 0 0 0 1 0 0 0 0 0 0 1
Character: 5.	
12. 	(0) (1) (2) (3) (4) (5) 0 1 1 1 1 1 0 0 1 1 0 0 0 0 0 1 0 0 0 0 0 0 1 1 0 0 0 0 0 1
Character: 77.	

the total variance. These figures correspond favorably to results reported by other investigators (for instance, Schnell, 1970) who have performed principal component analyses on large suites of qualitative variables, and contrast with the usually great amount of variation condensed on the first few major axes for a morphometric data set. This reflects the generally lower level of correlation among discrete variables. To reveal the varia-

tion encompassed by all components extracted, the species were clustered based on their scores for principal components one through ten (Fig. 23) rather than represented in a series of two-way scatter diagrams.

Restricting my analyses to samples representing the Peromyscini (excluding *Nelsonia*) reduced the number of characters that vary to 52 (Table 10). The results suggest that examples of *Onychomys, Baiomys* and *Scotinomys* are the most strongly differentiated of the 37 OTUs (Fig. 24). Of the three genera, *Baiomys* and *Scotinomys* are phenetically closest. Again, the distances of the other subgenera of *Peromyscus,* except *Hapolmylomys,* to the nominate subgenus are usually great and match, or even exceed, the separation of genera such as *Ochrotomys* and *Reithrodontomys.* In this instance, the subgenera *Habromys* and *Podomys* are further removed from *Peromyscus, sensu strictu,* than indicated in the previous principal components exercise. This relationship is additionally corroborated in a trial involving only the



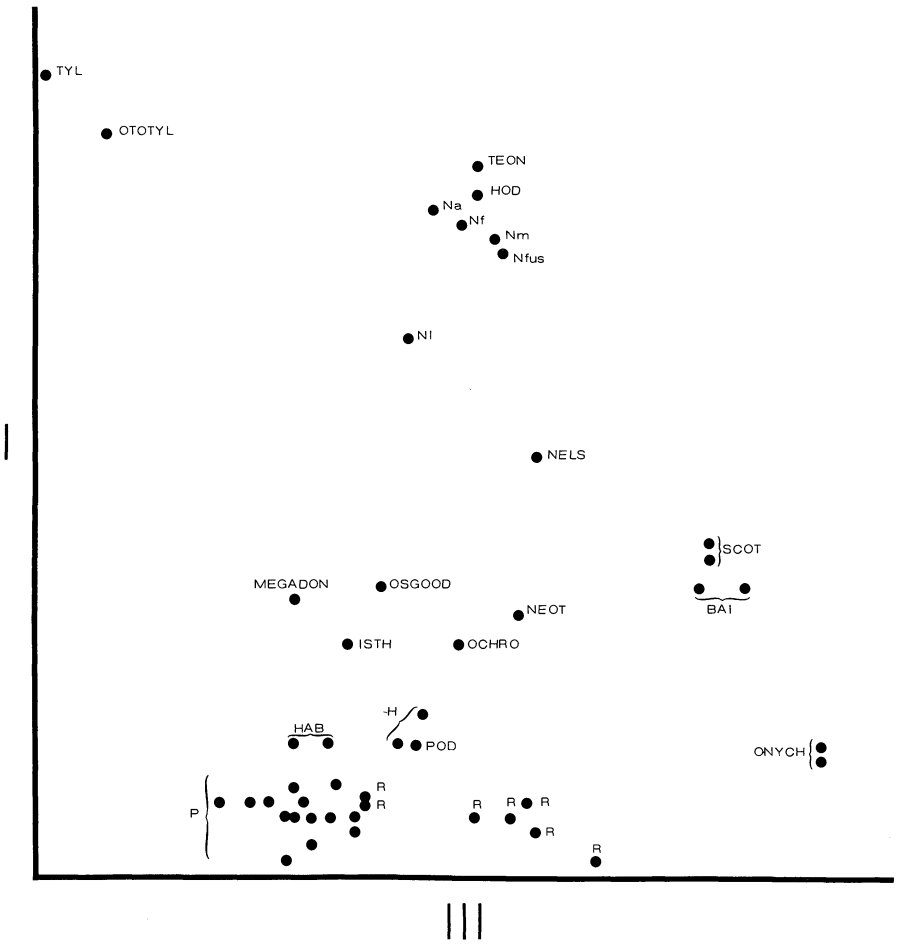


Fig. 22. Scatter plot of principal component I versus II and I versus III using 47 species of neotomine-peromyscines as described by 60 characters (see Table 9). Abbreviations of taxa for this and subsequent figures given in MATERIALS AND METHODS.

genera *Peromyscus, Ochrotomys, Reithrodontomys* and *Neotomodon* (cases = 31; characters = 48)(Table 11). The divergence of species of *Reithrodontomys* is also noteworthy in this plot (Fig. 25).

I included the sample of *Nelsonia* in the principal component analysis of *Neotomini* (N = 11). The number of variables equalled only 31 with the addition of *Xenomys nelsoni.* Nonetheless, the taxonomic structure revealed was well defined and unambiguous. Examples of *Tylomys* and *Ototylomys* are separated by a large hiatus from those of *Neotoma, Xenomys* and *Nelsonia* (Fig. 26). Members of the subgenera *Neotoma* and *Teonoma* comprise one cluster of points, but *Neotoma (Hodomys) alleni* is significantly removed from that aggregation to the same degree as *Xenomys nelsoni.* The sample of

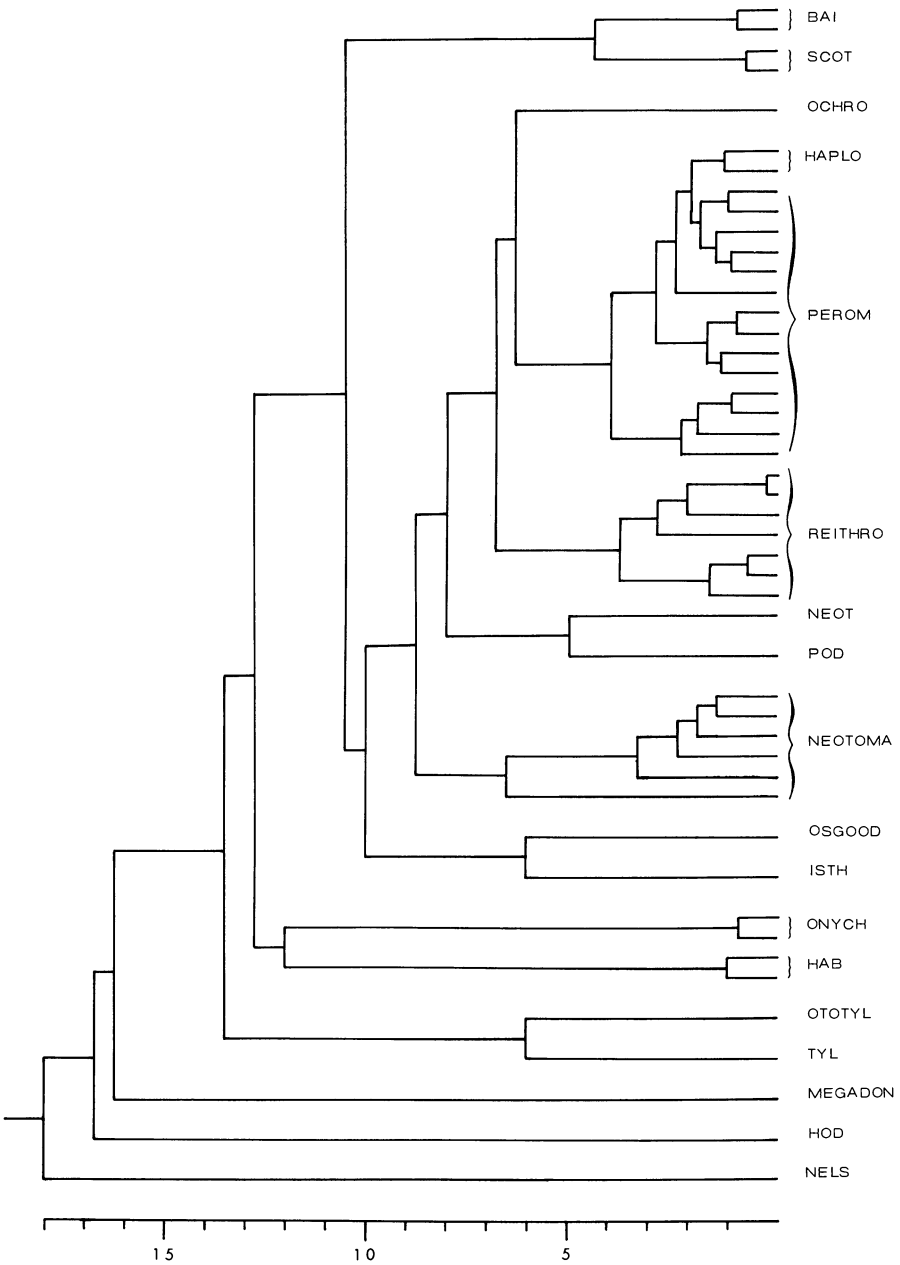


Fig. 23. Cluster analysis (unweighted, pair-group method using arithmetic averages) of 47 neotomine-peromyscines based on principal components one through ten. Coefficient of cophenetic correlation = 0.93.

TABLE 9

RESULTS OF PRINCIPAL COMPONENT ANALYSIS OF 47 NEOTOMINE-PEROMYSCINES, AND CORRELATIONS OF CHARACTERS WITH FIRST THREE COMPONENTS EXTRACTED (see Fig. 22).

	Component		
	I	II	III
Eigenvalue	14.8	8.5	7.0
Cumulative % variation explained	25.2	39.5	51.4
Character Number			
Dentition			
1	.25	.20	.69
2	-.05	-.57	-.45
3	-.37	.64	.44
4	.73	.59	.15
5	-.62	-.07	.59
6	-.40	.17	.71
7	-.33	-.15	.14
8	.23	.28	.33
9	-.15	-.06	.11
10	.47	-.69	-.04
11	.38	.45	-.06
13	-.14	-.06	.15
Cranium			
16	.77	-.22	.19
18	-.75	.18	.26
19	-.65	.38	.32
20	-.42	.27	.37
23	.73	.55	.10
24	.42	-.35	-.53
25	.70	.55	.13
29	.56	-.56	-.34
33	.55	.60	-.29
Post-cranial Skeleton			
35	.01	-.39	.50
36	.13	-.25	-.32
37	.11	-.24	-.68
39	-.83	-.25	.09
40	.01	-.41	.76
42	-.81	.10	-.01
Alimentary Canal			
44	.06	-.38	-.17
45	.16	-.53	.64
46	-.31	.56	-.18
47	-.15	.80	.39
49	.40	-.57	-.34
50	.56	.48	.08
51	.72	-.06	.42

For $P \leq .05$, $r = .29$; for $P \leq .01$, $r = .37$

TABLE 9
(Continued)

Character Number	I	II	III
Phallus			
52	.00	.22	.00
53	.11	.15	.10
54	.03	.04	.11
55	.07	.45	-.38
56	-.44	.18	-.45
57	-.30	.13	-.28
58	.73	.23	-.05
59	.28	-.04	.05
61	.72	.39	-.07
63	-.49	.30	-.45
64	-.70	.14	-.37
65	.77	.41	.06
66	-.75	.15	-.46
67	.84	.19	.24
Accessory Reproductive Glands			
68	-.52	.36	-.40
69	-.09	.04	-.14
70	.73	-.10	.37
71	.66	.61	.09
72	.11	-.36	.20
73	.28	-.42	.30
74	.42	.43	.21
75	.66	-.03	.02
76	.48	-.66	-.44
Miscellaneous External Features			
77	-.43	-.26	.58
78	-.29	-.07	.53
79	.63	.02	.00

For $P \leq .05$, $r = .29$; for $P \leq .01$, $r = .37$

Nelsonia associates with those of *Neotoma (Neotoma)* and *N. (Teonoma)* on principal components one and two but sets far apart from them on the third component (Fig. 26). Unlike the results disclosed in the above analyses, the first three principal components accounted for 71.6 percent of the variation among Neotomini (Table 12).

In the shortest-connection network, and hereafter, I have restricted my comparisons of the genera *Baiomys, Scotinomys* and *Onychomys* to their type species (*B. taylori, S. teguina* and *O. leucogaster,* respectively) to avoid congestion in the various graphs. No loss of information was incurred by these eliminations. The sibling species-pairs of these genera always clustered near one another, whether in a phenetic or phylogenetic analysis.

Construction of a Prim network allows inspection of graphically connected clusters of species. Although character states are ordered, no indication of character polarities is required or implied. *Tylomys* and *Ototylo-*

TABLE 10

RESULTS OF PRINCIPAL COMPONENT ANALYSIS OF PEROMYSCINI, AND CORRELATIONS OF CHARACTERS WITH FIRST THREE COMPONENTS EXTRACTED (see Fig. 24).

	Component		
	I	II	III
Eigenvalue	11.1	6.0	5.6
Cumulative % variation explained	21.3	32.8	43.7
Character Number			
Dentition			
1	.57	.20	-.31
2	-.12	-.63	.10
3	.08	.09	.30
4	.05	.42	.16
5	.43	.62	-.33
6	.49	.41	-.37
7	.01	.04	-.78
8	.56	-.44	.14
9	.03	.01	-.42
10	.56	-.44	.14
11	.19	.63	-.29
13	.05	.08	-.45
Cranium			
16	.72	-.37	.34
19	-.02	.06	-.20
20	.18	-.01	-.59
24	-.24	-.06	.57
25	.05	.42	.16
33	-.54	.15	.46
Post-cranial Skeleton			
35	.63	-.32	-.30
36	-.14	.14	.27
39	.04	-.29	-.32
40	.90	-.04	.10
42	-.44	.39	-.29
Alimentary Canal			
44	.00	-.08	-.51
45	.73	.25	-.48
46	-.54	.48	.23
47	-.86	.24	.33
49	.07	-.07	-.02
50	-.13	-.08	.30
51	.81	-.12	.07
Phallus			
52	-.14	.25	-.08
54	-.06	-.20	.21
55	-.66	-.31	-.54
56	-.56	-.21	.05
57	-.35	-.16	-.02

For $P \leq .05$, $r = .32$; for $P \leq .01$, $r = .42$

TABLE 10
(Continued)

Character Number	I	II	III
58	.01	-.20	.14
61	-.06	-.20	.21
63	-.76	.11	.01
64	-.68	.31	.12
65	.11	-.19	.05
66	-.84	-.16	-.30
67	.73	-.54	.24
Accessory Reproductive Glands			
68	-.76	.03	-.24
69	-.14	.14	.27
70	.70	.22	.49
72	.38	.60	.21
73	-.01	.31	.43
74	.15	.68	.38
75	.31	.63	.49
Miscellaneous External Features			
77	.58	.52	.05
78	.36	.52	-.37
79	.25	-.39	.43

For $P \leq .05$, $r = .32$; for $P \leq .01$, $r = .42$

TABLE 11
RESULTS OF PRINCIPAL COMPONENT ANALYSIS
OF *PEROMYSCUS* AND RELATED GENERA, AND CORRELATIONS
OF CHARACTERS WITH FIRST THREE COMPONENTS EXTRACTED
(see Fig. 25).

	Component		
	I	II	III
Eigenvalue	8.5	6.7	5.7
Cumulative % variation explained	17.8	31.8	43.7
Character Number			
Dentition			
1	-.45	.12	.35
2	.14	-.40	-.51
3	.25	.04	.03
4	.12	.30	.40
5	-.77	.24	.09
6	-.58	.19	.09
7	-.84	.16	.09
9	-.51	.36	-.24
13	-.48	.16	.07

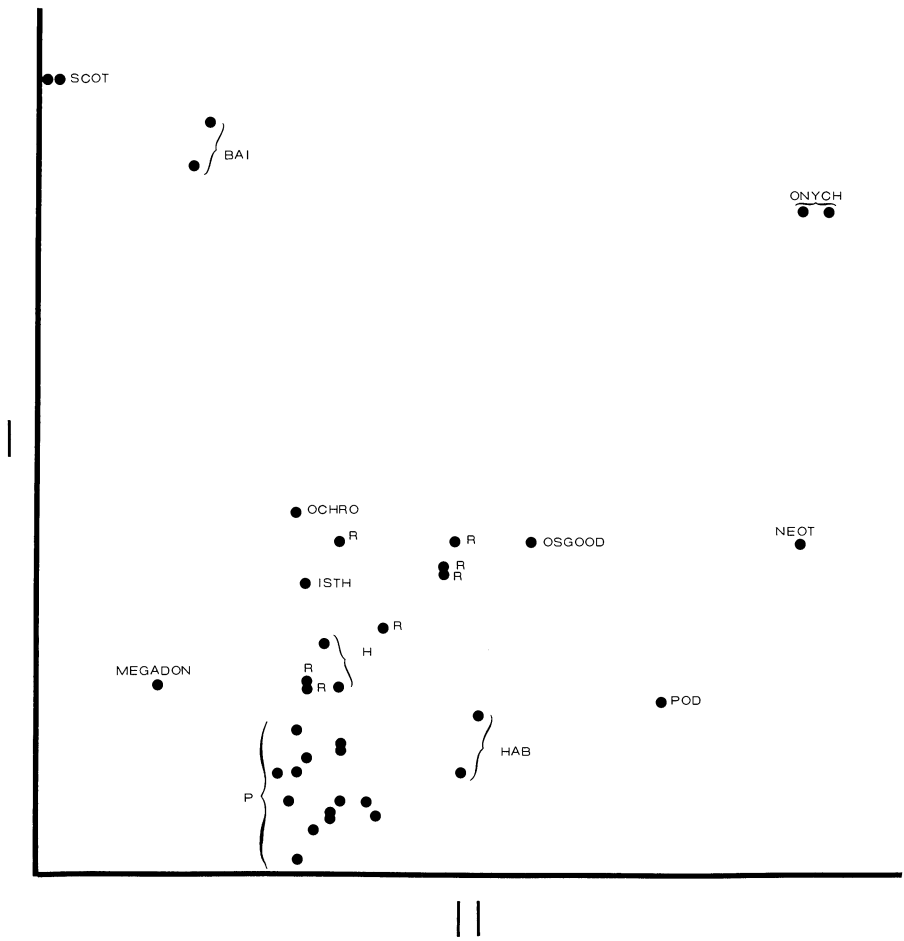
For $P \leq .05$, $r = .36$; for $P \leq .01$, $r = .45$

TABLE 11
(Continued)

Character Number	I	II	III
Cranium			
16	.40	.40	.23
19	-.16	-.28	.20
20	-.57	-.40	.21
24	.54	.36	-.43
25	.12	.30	.40
33	.60	-.10	.18
Post-cranial skeleton			
35	-.63	.41	.02
36	.24	.14	.18
39	-.19	-.54	.07
42	-.17	-.45	.54
Alimentary Canal			
44	-.64	.45	-.34
45	-.76	.25	.24
46	.70	-.33	-.22
47	.85	-.23	-.12
49	-.11	.18	.08
50	.17	.37	-.50
51	-.19	.39	-.57
Phallus			
52	-.15	.27	.31
54	.06	.44	-.78
55	-.51	-.60	-.42
56	.28	-.73	-.18
57	.13	-.49	-.10
58	-.04	.44	-.51
61	.06	.44	-.78
63	.26	-.53	.23
64	.36	-.25	.03
65	-.07	-.11	.02
66	-.24	-.53	-.42
67	.16	.52	-.70
Accessory Reproductive Glands			
68	-.19	-.26	-.20
69	.24	.14	.18
70	.48	.57	.32
72	.40	.40	.23
73	.39	.40	.35
74	.32	.52	.55
75	.50	.64	.32
Miscellaneous External Features			
77	.03	.19	.25
78	-.48	.04	.29
79	.47	-.07	-.09

For $P \leq .05$, $r = .36$; for $P \leq .01$, $r = .45$

mys, separated from *Ochrotomys* by a wide gap, are clearly the most isolated forms on the network (Fig. 27). As in the principal component analyses, *Baiomys* and *Scotinomys* are closely associated and also link with *Ochrotomys.* The remaining samples comprise two aggregations, a smaller one consisting of examples of *Neotoma* and a larger, more diffuse one composed of *Peromyscus* and allied genera. *Neotoma (Hodomys) alleni* is a distant outlier to other species of *Neotoma,* certainly much farther removed than the other subgenus *Teonoma. Nelsonia* connects to samples of *Neotoma* but is equally distant from *Peromyscus (Haplomylomys).* Species of *Peromyscus (Peromyscus)* and *P. (Haplomylomys)* form the nucleus of the second aggregation with the remaining subgenera and genera positioned as distinct offshoots from them (Fig. 27). Of these satellite OTUs, the seven species of *Reithrodontomys* are most closely joined to members of the subgenus *Peromyscus.* The subgenera *Isthmomys* and *Megadontomys* form one line, the subgenera *Osgoodomys* and *Habromys* another, and *Peromyscus (Podomys)* and *Neotomodon* a



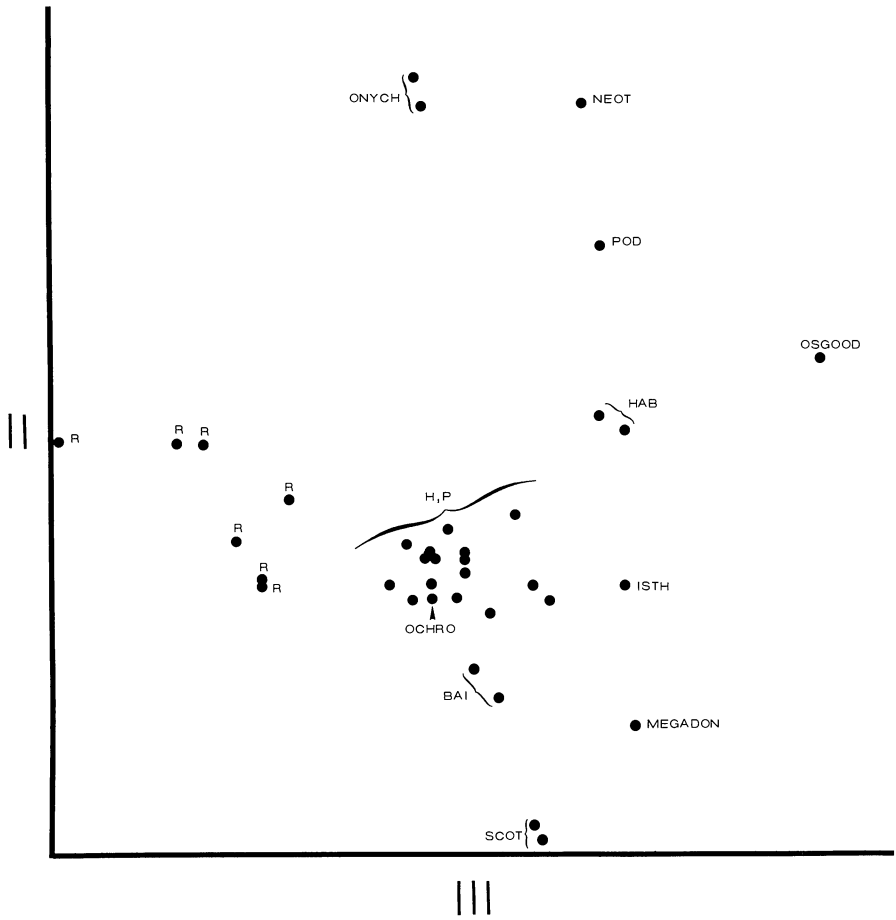


Fig. 24. Scatter plot of principal component I versus II and II versus III using 37 species of Peromyscini as described by 52 characters (see Table 10).

third branch from different species representing the subgenus *Peromyscus*. The example of *Onychomys* is linked, albeit at a great distance, to that of *Neotomodon*.

Based on the results disclosed in the phenetic analyses, the following points of summary deserve mention.

1) *Tylomys* and *Ototylomys* are the most distinctive forms of neotomine-peromyscines surveyed here. Although placed in the Neotomini, they appear at least as far removed from other species in the tribe as from species of Peromyscini.

2) *Baiomys* and *Scotinomys* are another generic pair that are consistently associated. Their phenetic affinities lie nearer other members of *Peromyscini*.

3) Representatives of two of three subgenera of *Neotoma* (*Teonoma* and

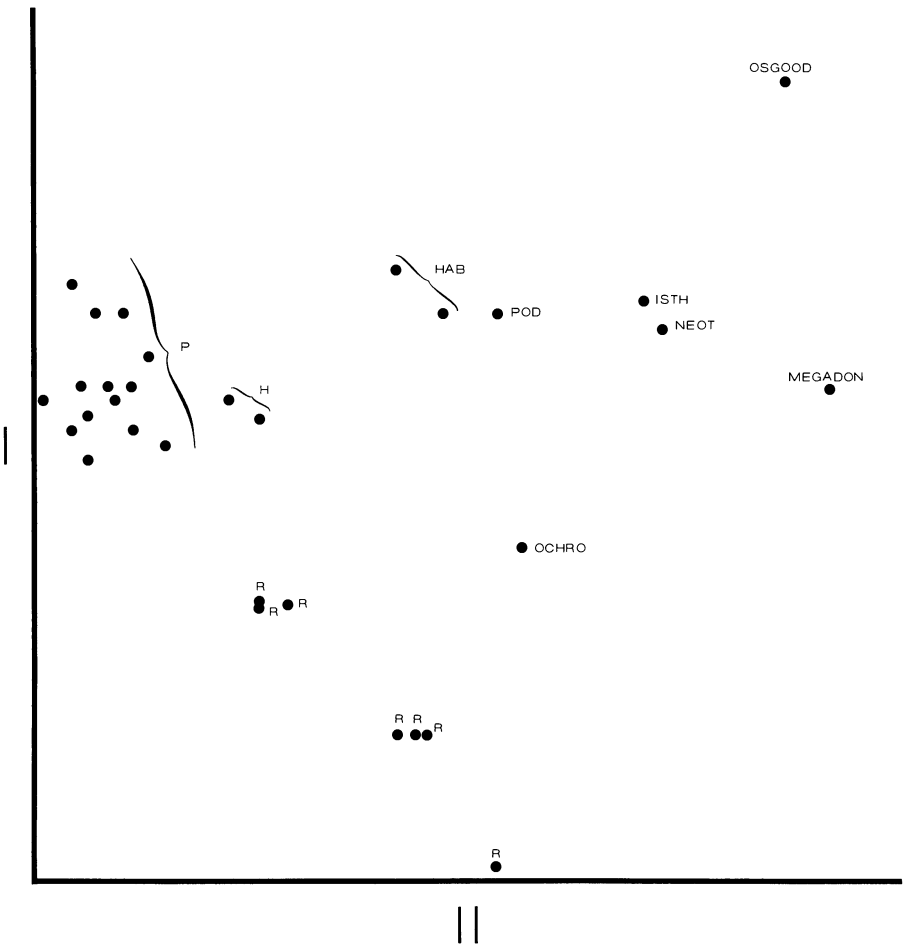


Fig. 25. Scatter plot of principal component I versus II using 31 species of *Peromyscus* and related genera as described by 48 characters (see Table 11).

Neotoma) comprise another regular cluster. *Neotoma lepida* diverges most strongly from this aggregation, even more so than *N. (Teonoma) cinerea.* The third subgenus, *Hodomys,* is as differentiated from its supposed congenors as *Xenomys* and *Nelsonia.*

4) The relationships of *Nelsonia* remain enigmatic. Currently placed in the *Peromyscini,* the genus is approximately equally removed from species of *Neotoma* and *Peromyscus.*

5) *Peromyscus, Ochrotomys, Neotomodon, Onychomys* and *Reithrodontomys* constitute a poorly-defined assemblage. Within this group, species of the subgenera *Peromyscus* and *Haplomylomys* are most similar. *Reithrodontomys* displays affinities with the subgenus *Peromyscus.* The remaining five subgenera of *Peromyscus* differ as much from the nominate subgenus as do *Ochrotomys* and *Neotomodon. Onychomys* is perhaps the most isolated of the

TABLE 12

RESULTS OF PRINCIPAL COMPONENT ANALYSIS OF NEOTOMINI AND *NELSONIA*, AND CORRELATIONS OF CHARACTERS WITH FIRST THREE COMPONENTS EXTRACTED (see Fig. 26).

	Component		
	I	II	III
Eigenvalue	12.4	6.0	3.8
Cumulative % variation explained	40.2	59.5	71.6
Character Number			
Dentition			
1	.95	.27	.09
2	-.95	-.27	-.09
3	.95	.27	.09
4	.95	.27	.09
5	.62	.71	-.29
8	-.09	.62	.22
11	-.97	-.04	-.01
13	-.85	.11	.15
Cranium			
16	-.43	.25	.68
18	.59	.27	-.27
19	.77	.07	-.21
20	.66	-.47	.23
23	.69	.25	.66
24	-.93	-.04	.08
25	.69	.25	.66
29	-.79	.56	-.02
34	.05	.68	-.13
Post-cranial Skeleton			
35	-.03	.97	.07
36	-.80	.02	-.19
42	.48	.02	-.80
Phallus			
52	.47	-.40	-.15
53	.19	.49	-.76
54	.71	.09	-.05
58	.11	.33	.58
59	-.03	.97	.45
61	.33	-.71	.45
63	.23	-.24	.27
64	.19	-.21	.18
65	.62	-.45	-.03
66	.29	-.22	.02
67	.69	-.51	-.37

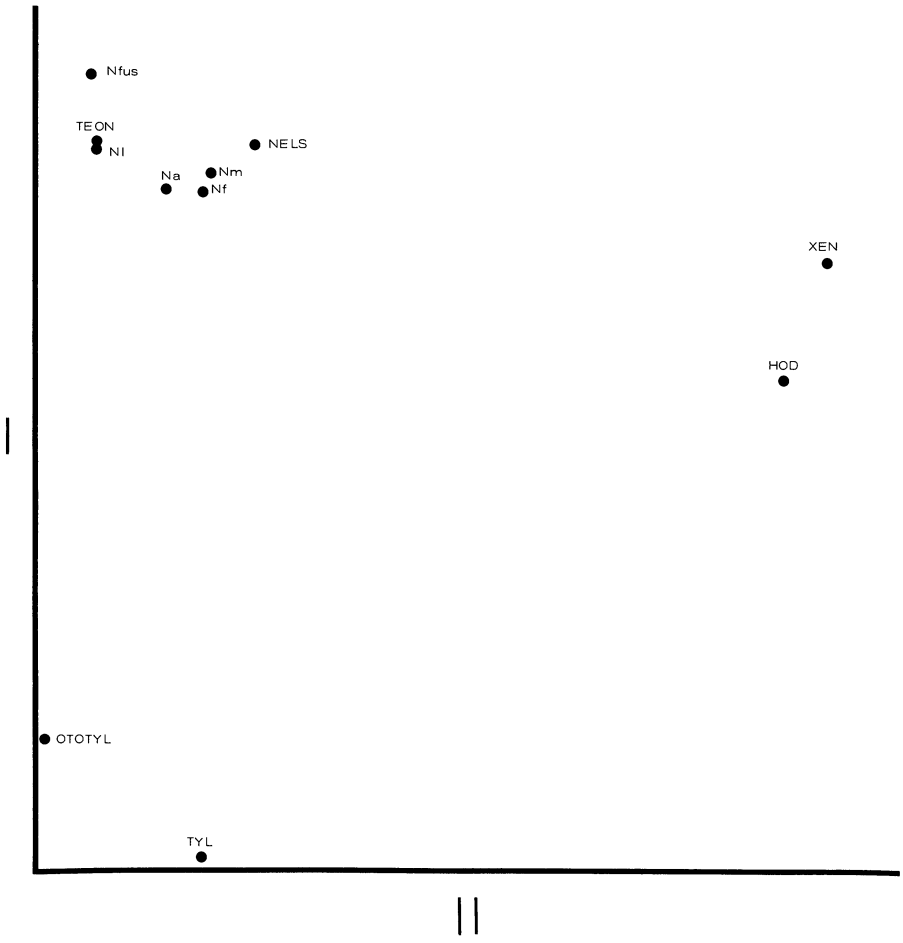
For $P \leq .05$, $r = .60$; for $P \leq .01$, $r = .73$

five genera; a clear indication of its affinities within this complex is wanting.

6) The major aggregations of species are not defined by any one set of characters (e.g., cranial, dental, or reproductive). This is suggested by the fact that no one complex of characters is loaded exclusively on a particular principal component (see Tables 9–12).

Phylogenetic Analyses of Neotomine-Peromyscines

All characters used in the phylogenetic analyses conform to a 0–1 scale, obtained by converting the original variables into binary factors according to the method of additive binary coding (Farris *et al.*, 1970). The procedure exactly preserves the topology of the original character-state trees (see Table 8). As a result of applying additive binary coding, my original set of 59 cladistic characters expanded to 121 two-state transformations.



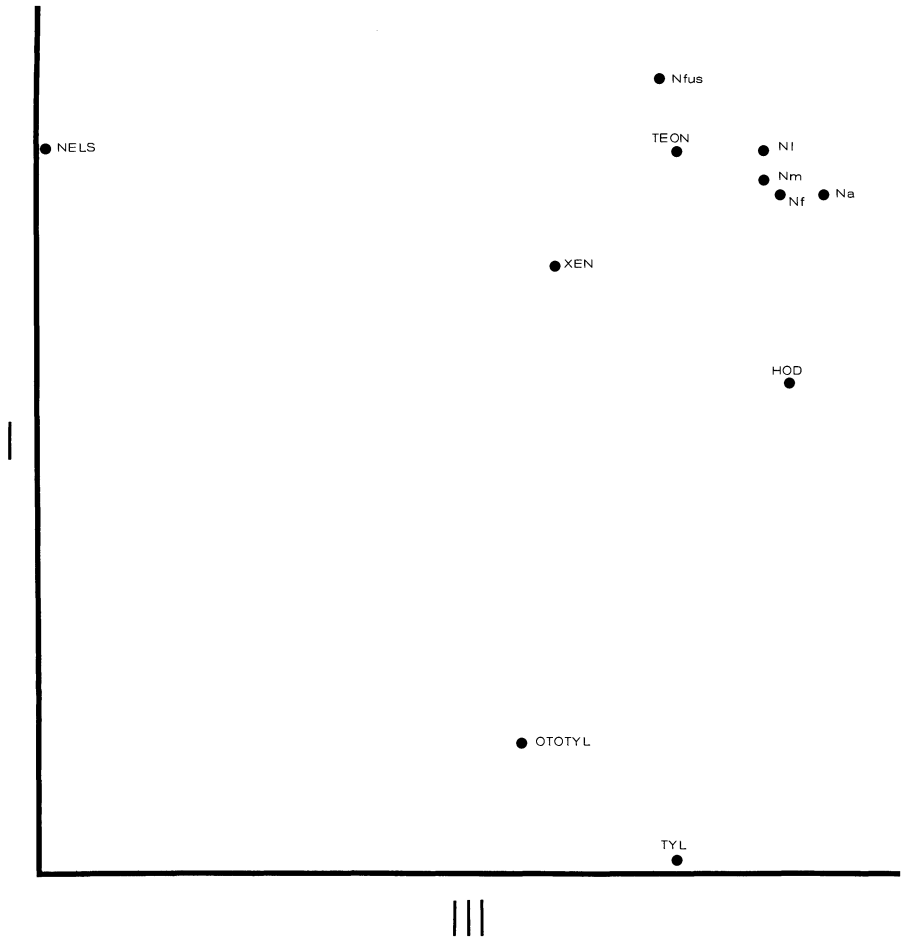


Fig. 26. Scatter plot of principal component I versus II and I versus III using 11 species of Neotomini and *Nelsonia* as described by 31 characters (see Table 12).

I repeated the Wagner tree program by varying the number of species, inserting HTUs and their hypothesized character state values, and differentially weighting characters. The first trial, using the same 44 samples as employed in the Prim network, yielded a tree of 353 steps and a consistency index of .343 (Fig. 28). *Tylomys* and *Ototylomys* diverge basally from all other neotomine-peromyscines. The next furcation separates *Baiomys* and *Scotinomys* as a monophyletic group, and *Ochrotomys* forms an isolated branch. A major phyletic unit, and one that remained intact throughout all replications of the Wagner tree analysis, consists of *Nelsonia* and species of *Neotoma*. Within the latter genus, the predicted early divergence and great patristic distance of *N. (Hodomys) alleni* are noteworthy. Also, *N. lepida* is patristically highly differentiated from other *Neotoma*. The re-

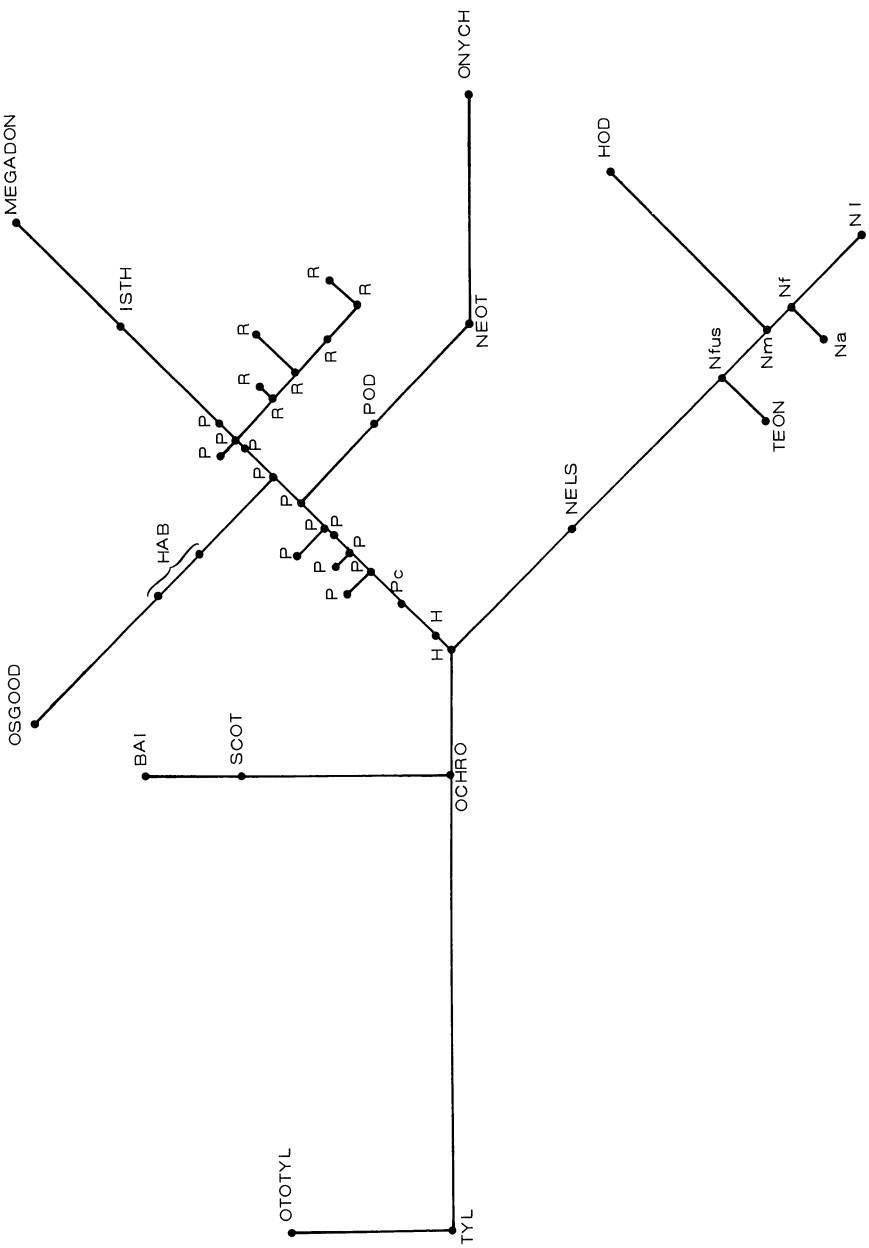


Fig. 27. Shortest connection network (Prim) of 44 species of neotomine-peromyscines. Distances between OTUs are proportional to the absolute sum of differences over all characters.

maining forms are arranged as offshoots of a basal complex comprised of species of *Peromyscus (Peromyscus)* and *P. (Haplomylomys).* All members of *Reithrodontomys* are singularly derived from one line of *Peromyscus (Peromyscus).* The subgenera *Isthmomys, Megadontomys* and *Osgoodomys* arise from another side branch of *Peromyscus (Peromyscus),* and a third segment leads to the subgenera *Habromys* and *Podomys* and the genus *Neotomodon. Onychomys* represents the most highly derived OTU of the latter clade.

In another trial, I eliminated some samples because I suspected that much of the homoplasy occurs at the distal or finer branches and could alter major cladistic relationships. Consequently, the number of OTUs was reduced from 44 to 34 by considering only the nominate species of each species group in the subgenus *Peromyscus* (namely, *boylii, leucopus, maniculatus, crinitus, truei, melanophrys* and *mexicanus*) instead of all 14; also, I omitted one species of *Habromys* and two of *Reithrodontomys.* Predictably, the Wagner tree generated is shorter (322 steps), but the index of consistency (.376) is not appreciably raised nor is the topography of the tree substantially changed. The major alterations involve the displacement of *Osgoodomys,* which now shares an ancestor with *Onychomys,* and the union of *Podomys* and *Neotomodon* (Fig. 29). I have summarized the number of derived character state changes predicted by this run of the Wagner program for certain intervals and taxa (Table 13).

In an effort to test further the stability of the primary furcations, I substituted the postulated common ancestors of certain genera and subgenera and applied the Wagner tree analysis to only 18 samples. I selected the values of five HTUs (from the first Wagner tree, Fig. 28) that subtended certain taxa as "primitive" for those taxa as follows: 1) *Baiomys* and *Scotinomys;* 2) the subgenus *Haplomylomys* of *Peromyscus;* 3) the subgenus *Peromyscus;* 4) *Reithrodontomys;* and 5) the subgenera *Teonoma* and *Neotoma* (except *N. lepida*) of *Neotoma.* The tree based on the reducd set of 18 OTUs has a length of 252 steps and a consistency index of .432. The basic tree shape departs little from the trees calculated previously. Rearrangements include the position of *Isthmomys* and *Megadontomys* on the stem leading to *Nelsonia* and *Neotoma* and the transposition of *Haplomylomys* proximal to the *Neotoma* branch (Fig. 30). The derived characters responsible for the former rearrangement are a character reversal of the sphenopalatine vacuities (2–1) and the formation of an "incipient" crater (0–1).

As stated above, I did not initially employ any weighting factor for the characters. All were treated equally. However, an *a posteriori* method of character weighting described by Farris (1969) was attempted. In the same manner that one derives a consistency measure of the entire data set with a tree (see MATERIALS AND METHODS and Farris, 1969), one can define an analogous index for individual characters. For example, the range of character one, index of complexity, is given as two (Table 8), but the total length of the character on the first tree generated (Fig. 28) is eight steps, which equals a consistency index of .250 for this character. By multiplying the original character values for each species by the individual

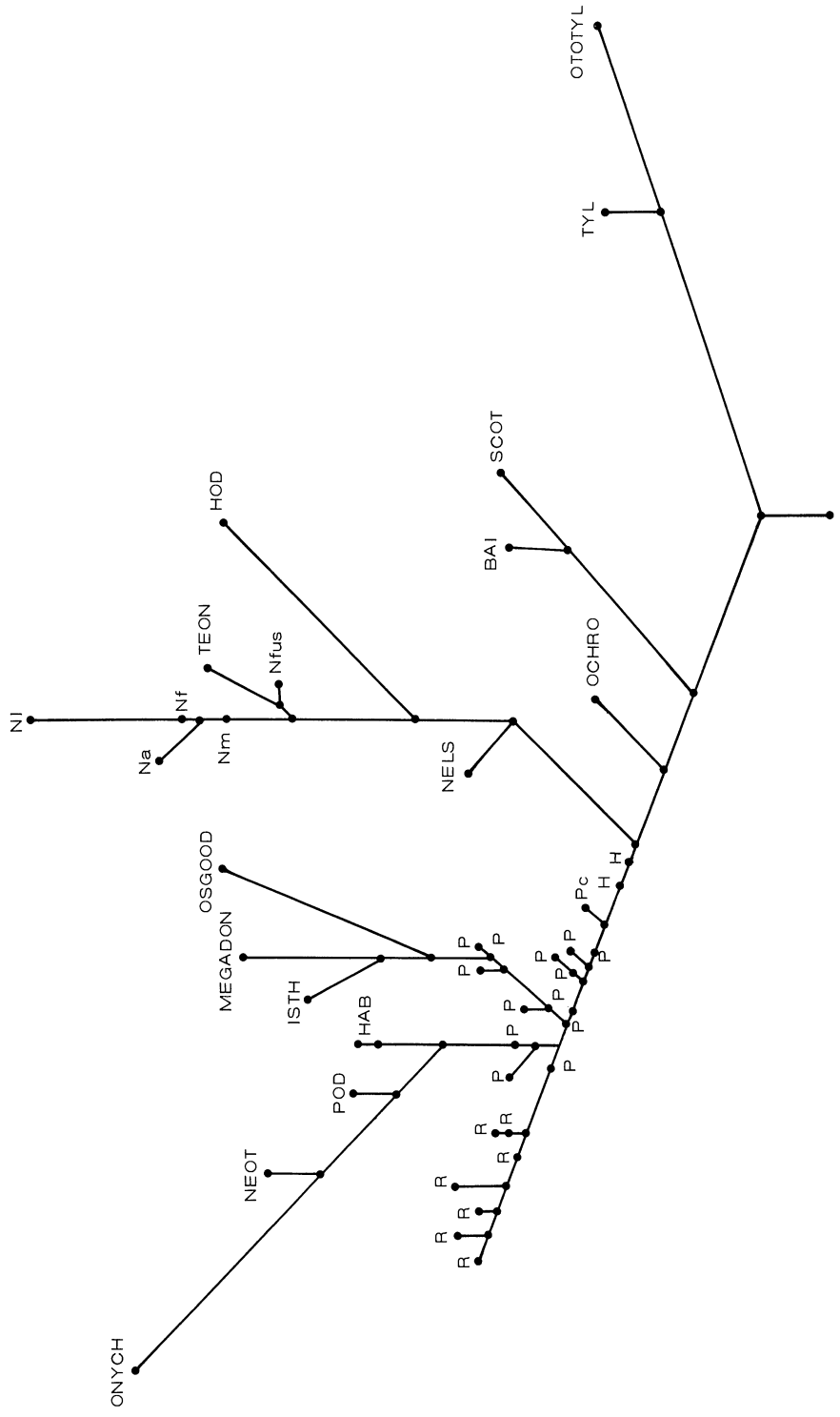


Fig. 28. Wagner tree analysis of 44 species of neotomine-peromyscines based on 59 characters. Index of consistency = .343.

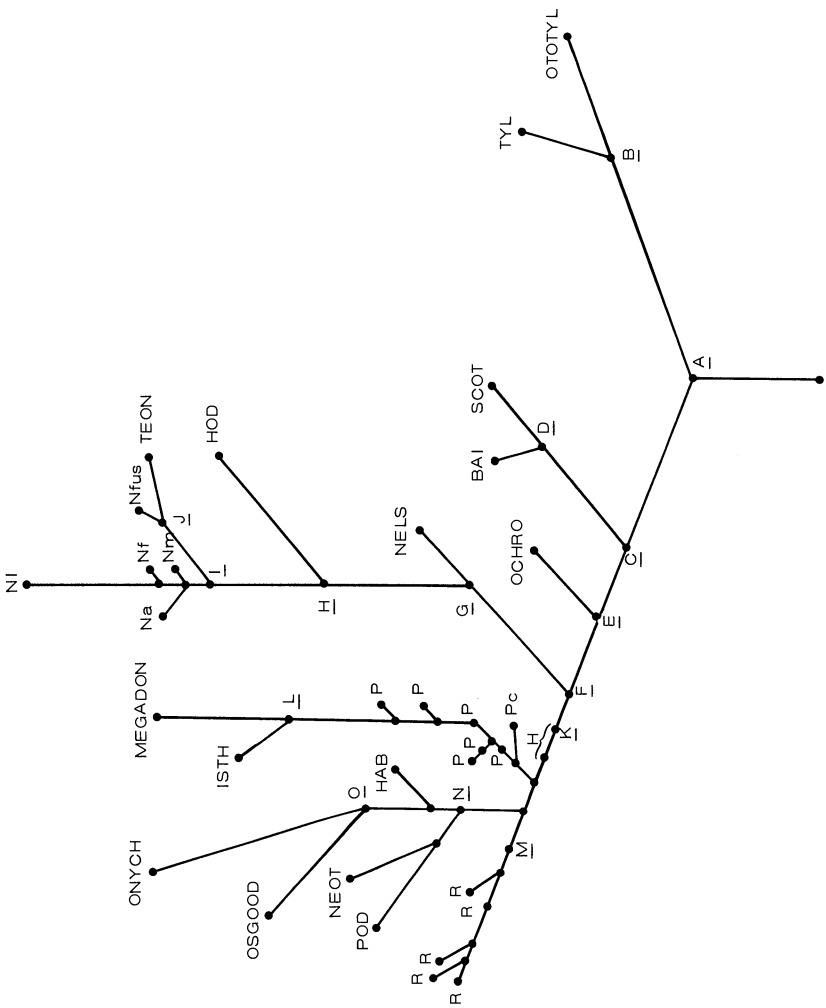


Fig. 29. Wagner tree analysis of 34 species of neotomine-peromyscines based on 59 characters. Underlined letters indicate HTUs for which apomorphic changes are given in Table 13. Index of consistency = .376.

TABLE 13

APOMORPHIC CHARACTER STATE CHANGES PREDICTED BY ESTIMATE OF PHYLOGENY OF NEOTOMINE-PEROMYSCINES (see Fig. 29).

Taxa	Total Changes	Character Reversals	Character (and character state changes)
HTU A	10	0	1(0-1); 2(0-1); 19(0-1); 20(0-1); 33(0-1); 42(0-1); 65(0-1); 70(0-1); 79(0-[1]-2)
HTU B	18	0	2(1-2); 10(0-[1]-2); 11(0-3); 16(0-[1,2]-3); 24(0-[1,2]-3); 29(0-2); 36(0-1); 44(0-1); 45(0-1); 49(0-1); 51(0-2); 67(0-1); 76(0-1)
Tylomys	7	3	19(1-0); 20(1-0); 42(1-0); 58(0-1); 73(0-[1]-2); 75(0-6)
Ototylomys	11	0	33(1-2); 36(1-2); 55(0-1); 61(0-1); 67(1-[2]-3); 72(0-1); 75(0-[1,2,3]-4)
HTU C	14	0	1(1-2); 3(0-[1]-2); 5(0-[1]-2); 6(0-1); 18(0-[1]-2); 19(1-2); 20(1-2); 39(0-1); 42(1-[2]-3); 77(0-1)
HTU D	10	1	16(0-[1,2]-3); 33(1-0); 35(0-1); 40(0-1); 45(0-2); 51(0-1); 67(1-2); 77(1-2)
Baiomys	4	2	42(3-[2]-1); 75(0-1); 78(0-1)
Scotinomys	6	0	8(0-[1]-2); 10(0-[1]-2); 65(0-1); 67(2-3)
HTU E	6	3	2(1-0); 46(0-1); 47(0-1); 55(0-1); 67(1-0); 70(1-0)
Ochrotomys	8	2	1(1-0); 35(0-1); 49(0-1); 58(0-1); 74(0-1); 75(0-1); 78(0-1); 79(2-1)
HTU F	3	0	46(1-[2]-3); 47(1-2)
HTU G	12	1	4(0-[1]-2); 20(2-1); 33(1-2); 39(1-0); 50(0-1); 51(0-2); 65(1-2); 67(0-[1,2]-3); 70(0-1)
Nelsonia	6	0	50(1-2); 52(0-1); 53(0-1); 67(3-4); 68(0-2); 78(0-1)
HTU H	11	4	16(0-[1,2]-3); 18(2-1); 23(0-1); 24(0-1); 25(0-1); 42(3-[2]-1); 58(0-1); 77(1-0)
Hodomys	13	5	8(0-[1]-2); 10(0-1); 11(0-3); 19(2-1); 20(1-0); 29(0-2); 33(2-1); 35(0-1); 46(3-2); 59(0-1); 65(2-1); 67(3-2)
HTU I	10	1	5(2-1); 20(1-2); 33(2-3); 60(0-1); 71(0-2); 74(0-2); 75(0-[1,2,3]-4)
HTU J	6	3	16(3-[2]-1); 24(1-0); 52(0-1); 65(2-3); 67(3-4)
N. lepida	10	3	18(1-2); 44(0-1); 50(1-0); 52(0-[1]-2); 58(1-0); 63(1-[2]-3); 64(0-1); 65(2-1)
HTU K	2	1	65(1-0); 66(0-2)
HTU L	8	6	24(1-2); 42(3-2); 44(0-1); 56(1-0); 63(2-[1]-0); 64(2-1); 67(0-1)
Isthmomys	5	1	19(1-2); 35(0-1); 55(1-0); 70(0-1); 75(0-5)
Megadontomys	10	4	9(0-1); 39(1-0); 42(2-1); 46(4-3); 50(0-1); 51(0-2); 54(0-1); 58(0-1); 61(0-1); 79(2-1)
HTU M	4	1	7(0-1); 45(0-2); 47(2-1); 52(0-1)

TABLE 13
(Continued)

Taxa	Total Changes	Character Reversals	Character (and character state changes)
HTU N	5	1	55(1-0); 70(0-1); 75(0-[1,2]-3)
Podomys	8	2	24(0-1); 52(1-2); 63(1-2); 64(1-2); 70(1-0); 73(0-1); 75(3-2); 77(1-4)
Neotomodon	7	2	4(0-1); 11(0-[1]-2); 25(0-1); 45(0-2); 52(1-0); 66(2-0)
Habromys	4	0	36(0-3); 52(1-[2]-3); 69(0-2)
HTU O	5	3	52(1-0); 66(2-0); 68(2-0); 72(0-1); 75(3-4)
Osgoodomys	11	2	16(0-[1,2]-3); 20(1-0); 24(0-[1]-2); 42(3-2); 64(1-2); 73(0-1); 74(0-2); 79(1-2)
Onychomys	17	3	1(1-2); 5(1-5); 6(1-2); 11(0-1); 20(1-2); 33(1-0); 40(0-1); 45(0-3); 46(3-[4]-5); 47(2-1); 51(0-1); 63(1-0); 74(0-1); 77(4-5); 78(0-[1]-2)

consistency indices observed in the initial Wagner tree (Table 14), a second data matrix, in which characters are devalued relative to the amount of homoplasy exhibited, is obtained and can be used to formulate a second tree. Thus, the same number of characters is incorporated into the successive tree, but those traits displaying less parallelism and fewer reversals assume greater importance in defining the tree's conformation.

I used this weighting procedure on the consistency results produced in the first Wagner tree (Fig. 28, Table 14). A noticeable effect of the method is dilation of some patristic distances and contraction of others. For instance, the distances separating some of the primary clades are substantially increased (compare Figs. 28 and 31). Also, the divergence of *Teonoma cinerea* and *Neotoma fuscipes* is increased to match that of *N. lepida,* but the 14 species of the subgenus *Peromyscus* are condensed into a tighter cluster. In addition to affecting patristic distributions, the weighting scheme caused some cladistic alterations. The most significant change is the association of *Onychomys* in a clade containing *Baiomys, Scotinomys* and *Ochrotomys* (Fig. 31), where before it linked with *Neotomodon* or *Osgoodomys* (Figs. 28, 29). The basal separation of *Ochrotomys* from this group is not strikingly different from its former position. *Neotomodon* and the subgenera *Podomys* and *Habromys* form one monophyletic assemblage, and *Osgoodomys* has reassumed its former union with *Megadontomys* and *Isthmomys* The cladistic status of *Reithrodontomys* remains unchanged, but its patristic separation from *P. (Peromyscus)* is augmented.

More dramatic modifications of branching patterns were realized by implementation of the WISS program. Again, *Tylomys* and *Ototylomys* are distinctively separated at the first bifurcation (Fig. 32). However, the next clade is largely unlike any divulged by Wagner tree analyses and contains

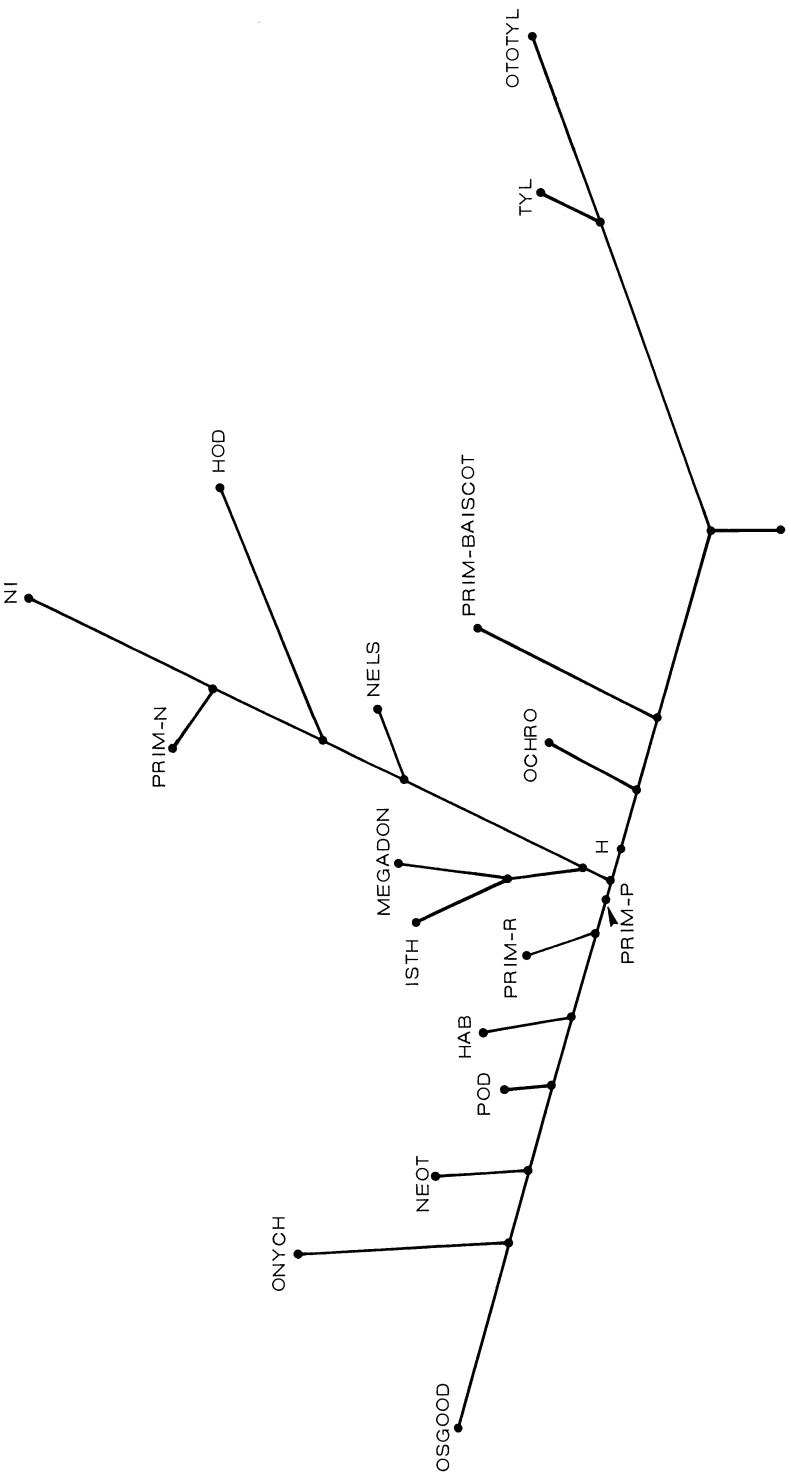


Fig. 30. Wagner tree analysis using hypothesized common ancestors of certain taxa. Index of consistency = .432.

TABLE 14

SUMMARY OF CONSISTENCY INDICES FOR 59 CHARACTERS USED TO ESTIMATE PHYLOGENY OF NEOTOMINE-PEROMYSCINES (see Fig. 28).

Range of Consistency Indices	Character Frequency	Character Number
Less than .20	2	55, 70
.20–.29	22	1, 2, 11, 16, 18–20, 33, 35, 39, 42, 46, 52, 56–8, 63, 64, 68, 75, 78, 79
.30–.39	6	24, 44, 61, 65, 67, 72
.40–.49	3	10, 50, 51
.50–.59	9	6, 8, 24, 29, 45, 47, 49, 66, 73
.60–.69	6	3–5, 9, 74, 77
.70–.79	0	
Greater than .80	11	7, 13, 23, 36, 40, 53, 54, 59, 69, 71, 76

Baiomys, Scotinomys, Ochrotomys, Reithrodontomys and *P. (Haplomylomys).* Within this group, *Baiomys* still constitutes the nearest sister-group of *Scotinomys.* The membership of *Ochrotomys, Reithrodontomys* and *P. (Haplomylomys)* results from derived changes in the sphenopalatine vacuities, subsquamosal and postglenoid foramina, shape of the third molar and position of the plantar pads. Perhaps a more revealing factor for their association is the similarity due to shared primitive states, namely the retention of preputial glands (*Baiomys, Scotinomys, Ochrotomys* and *Haplomylomys*) and generalized stomach morphology (*Baiomys, Scotinomys, Ochrotomys* and *Reithrodontomys*). The composition of the *Nelsonia–Neotoma* lineage has not changed but certain cladistic relationships have. Notably, the separation of *Nelsonia* follows that of *N. (Hodomys) alleni* as a result of loss of preputial glands and evolution of a discoglandular stomach in the former. Moreover, *Neotoma lepida* arises basally to other species of *Neotoma* in the WISS tree. An interesting transposition of branches occurs with regard to the remaining species. The ramification of *Neotomodon, Onychomys,* and the other subgenera of *Peromyscus* is depicted as early relative to the differentiation of the subgenus *Peromyscus* (compare Figs. 28 and 32). This contrast in cladistic portrayal consistently appeared in every iteration of the Wagner and WISS programs attempted.

The method of character compatibility was applied to the reduced set of 34 species used in the second Wagner trial (Fig. 29). I obtained four largest cliques of 15 characters as follows:

Clique A: 9, 13, 23, 25, 36, 40, 49, 53, 54, 56, 57, 59, 66, 69, 71;
Clique B: 7, 13, 23, 25, 36, 40, 49, 53, 54, 56, 57, 59, 66, 69, 71;
Clique C: 4, 9, 13, 23, 36, 40, 49, 53, 54, 56, 57, 59, 66, 69, 71;
Clique D: 4, 7, 13, 23, 36, 40, 49, 53, 54, 56, 57, 59, 66, 69, 71.

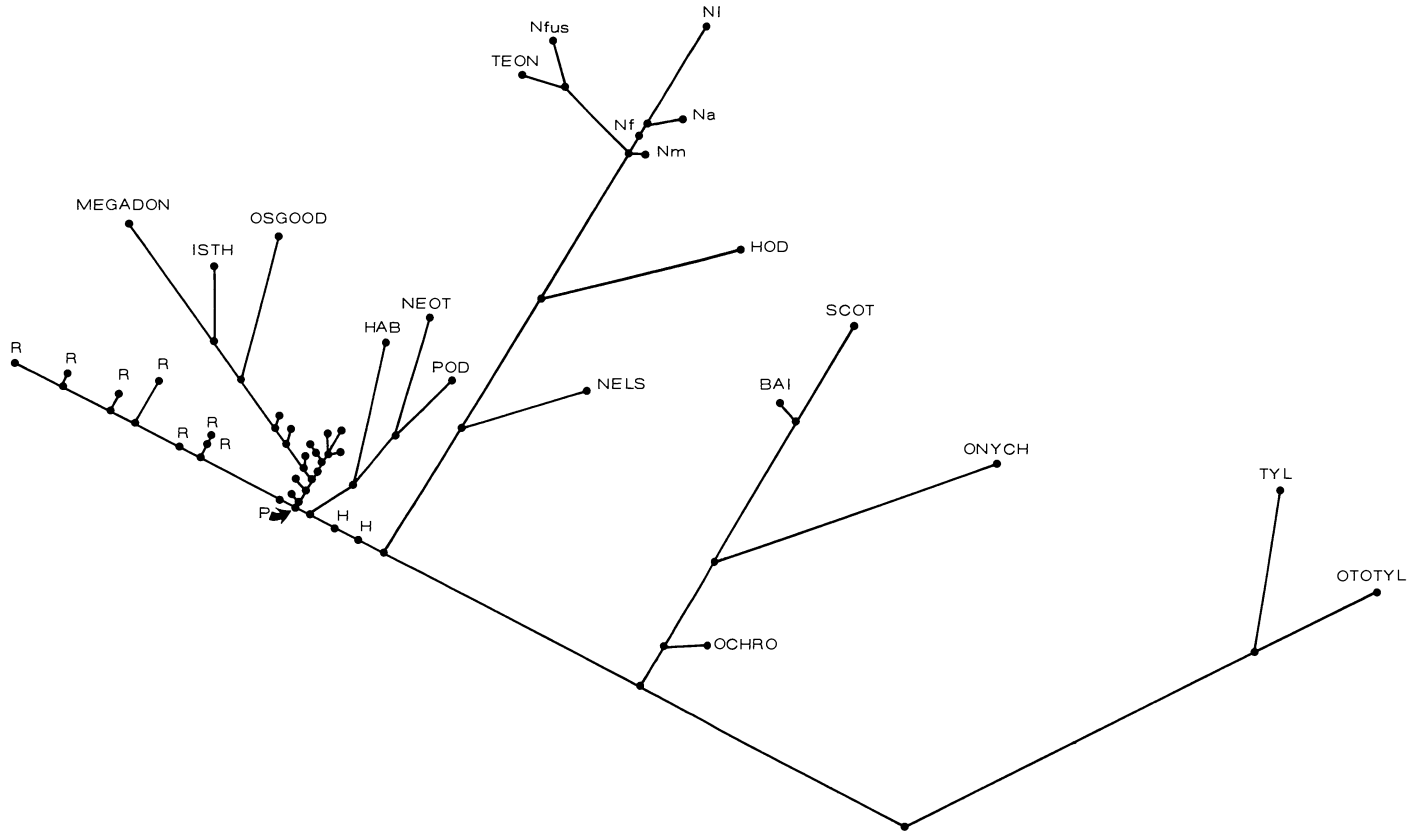


Fig. 31. Weighted Wagner tree analysis of 44 species of neotomine-peromyscines. Original characters weighted according to individual consistency indices (Table 14) obtained in first Wagner tree generated (see Fig. 28).

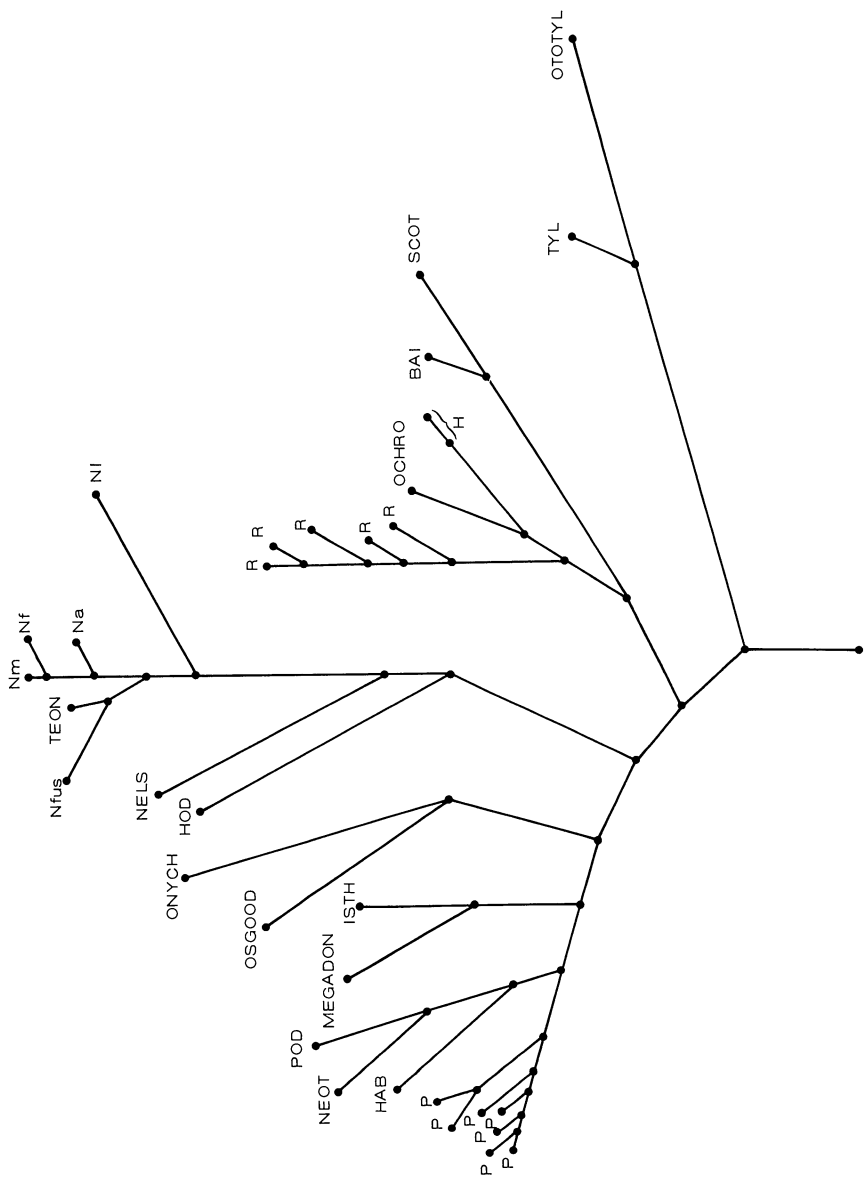


Fig. 32. Tree produced by weighted invariant step strategy (WISS). Index of consistency = .321.

The cliques are identical for 13 of the 15 characters (13, 23, 36, 40, 49, 53, 54, 56, 57, 59, 66, 69, 71), differing only with regard to numbers 4, 7, 9, and 25. Of the 13 redundant characters in the four cliques, five (13, 53, 54, 59, 69) are trivial in the sense that they are derived states characterizing single OTUs (autapomorphies) and therefore contribute no resolution to primary cladistic patterns. I selected only cliques B and D for illustration.

In contrast to the results obtained with the Wagner and WISS programs, character compatibility analysis discloses multiple radiations from a common ancestor (Fig. 33). *Osgoodomys* is in an equivalence class with the hypothetical ancestor; that is, the two OTUs are identical with reference to this set of 15 mutually compatible characters. Several points of similarity hold for the phylogenies based on the cliques presented. *Ochrotomys* is in a line leading to *Tylomys* and *Ototylomys* on the basis of loss of the gall bladder; *Baiomys, Scotinomys* and *Onychomys* constitute an unresolved monophyletic assemblage derived from the ancestor; and *Reithrodontomys* and the six other subgenera of *Peromyscus* comprise a third phyletic unit. Cliques B and D are dissimilar with respect to the disposition of *Nelsonia,* which either separates basally from the ancestor or diverges from the *Neotoma* lineage. The latter relationship agrees with that predicted by the Wagner trees. *Neotomodon* unexpectedly falls in the *Nelsonia–Neotoma* clade as a result of the transition from bunodont to planar to hypsodont molars.

In other studies employing the method of character compatibility (*e.g.* Cichocki, 1976 and Strauch, 1978), it has been profitable to reapply the method to smaller subsets of specimens, preferably ones identified as clades in the initial analysis. Thus characters found to be incompatible over the entire data set become compatible over restricted numbers of samples. This procedure assumes that much incompatibility results from homoplasious events at the distal branches in the phylogeny.

I first analyzed the relationships of *Nelsonia* and species of *Neotoma* and then samples representing *Peromyscus, Reithrodontomys, Ochrotomys* and *Neotomodon.* In the first case, character compatibility analysis yielded a single maximal clique of 16 characters (8, 11, 23, 24, 25, 29, 35, 42, 53, 59, 61, 64, 66, 71, 75, 77) out of 30 relevant ones. The early divergence of *Nelsonia* relative to species of *Neotoma* is corroborated (Fig. 34). *Neotoma (Hodomys)* is separated at the next furcation and the remaining species of *Neotoma* are pictured as highly derived.

Cladistic resolution of the second group of genera is less satisfactory. Sixteen largest cliques of 19 characters each were found for the 48 characters applicable to this restricted data set. Characters redundant for all 16 cliques include numbers 4, 13, 15, 16, 25, 36, 40, 46, 50, 54, 56, 57, 61, 67, and 69; variation in clique membership is accounted for by characters 3, 5, 7, 44, 48, 51, 52, 72, 73, and 74. The only relationships repeatedly confirmed are the common ancestry of the subgenera *Megadontomys* and *Isthmomys* of *Peromyscus* (in all 16 cliques) and the derivation of *Onychomys* either from the ancestor (7 of 16 cliques) or from a common ancestry shared with *Peromyscus (Osgoodomys)* (8 of 16 cliques). In the majority of

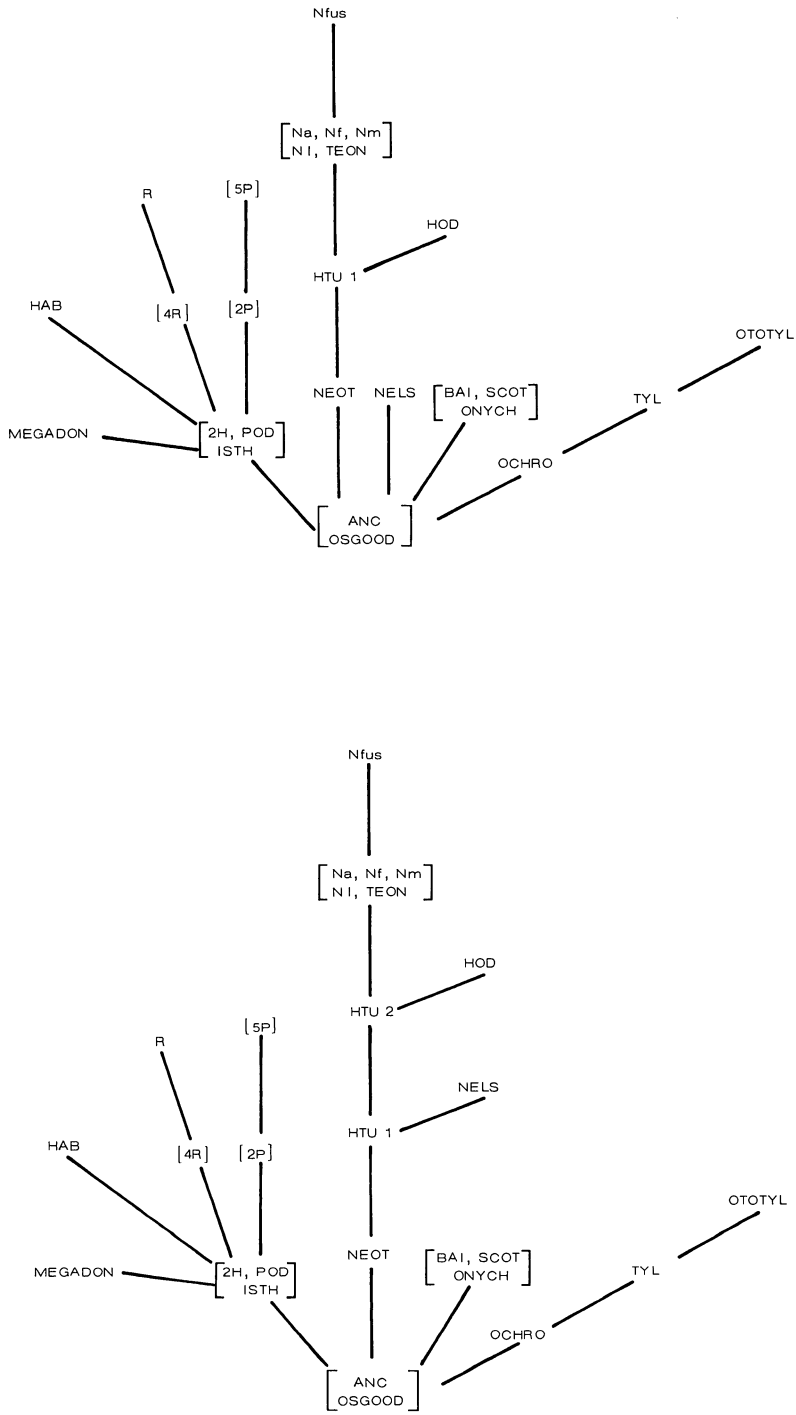


Fig. 33. Estimate of phylogeny obtained with character compatibility analysis of 34 species of neotomine-peromyscines. Diagrams are based on Cliques B (top) and D (bottom), each consisting of 15 mutually compatible characters (see text). Brackets enclose species in same equivalence class.

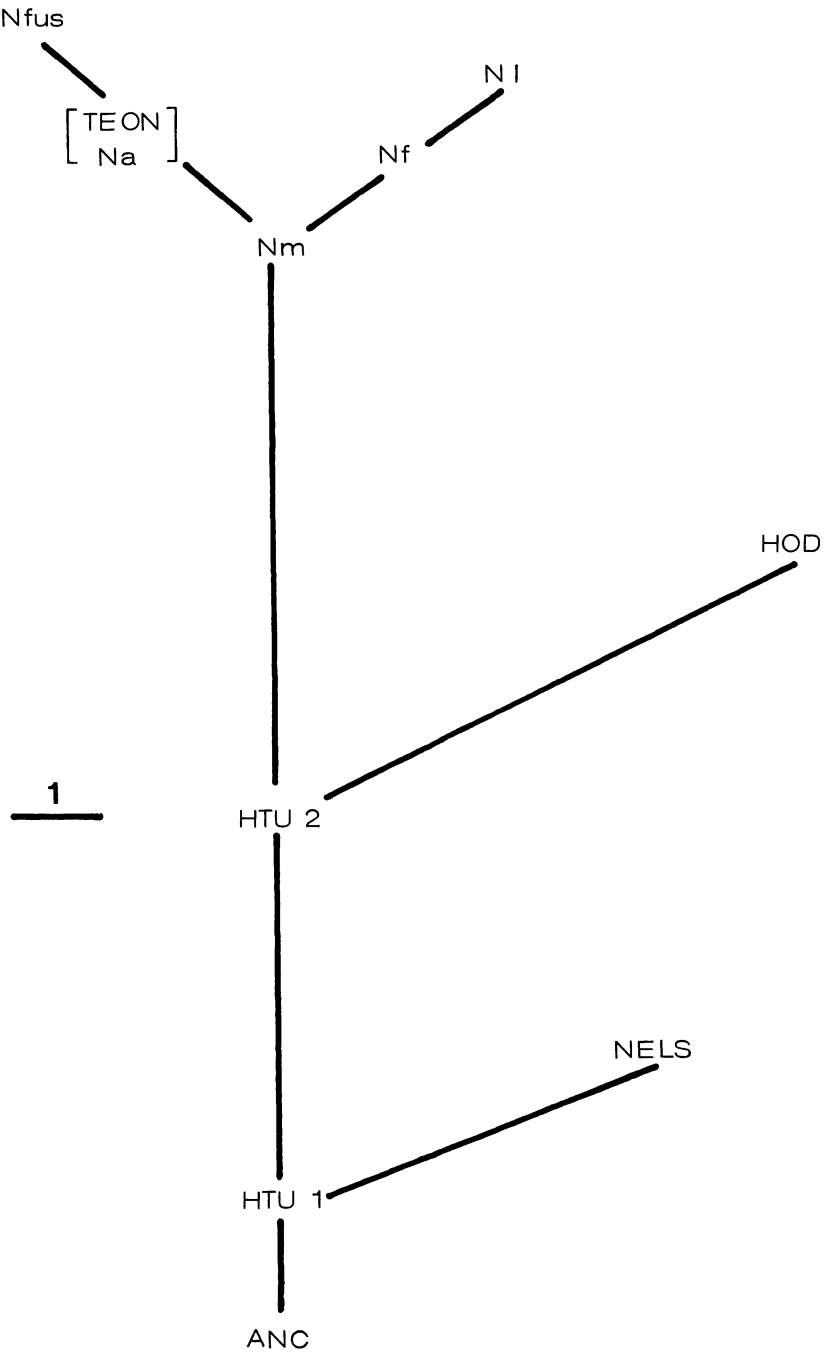


Fig. 34. Estimate of phylogeny obtained with character compatibility analysis of 9 species of *Neotoma* and *Nelsonia neotomodon*. Diagram is based on single maximal clique of 16 compatible characters (see text). Scale is proportional to one character state change between nodes. Brackets enclose species in same equivalence class.

cliques, the other forms are arranged as unresolved radiations from either *Peromyscus (Haplomylomys)* or an HTU.

Morphological Variation of the Glans Penis in New World Cricetines and Other Muroidea

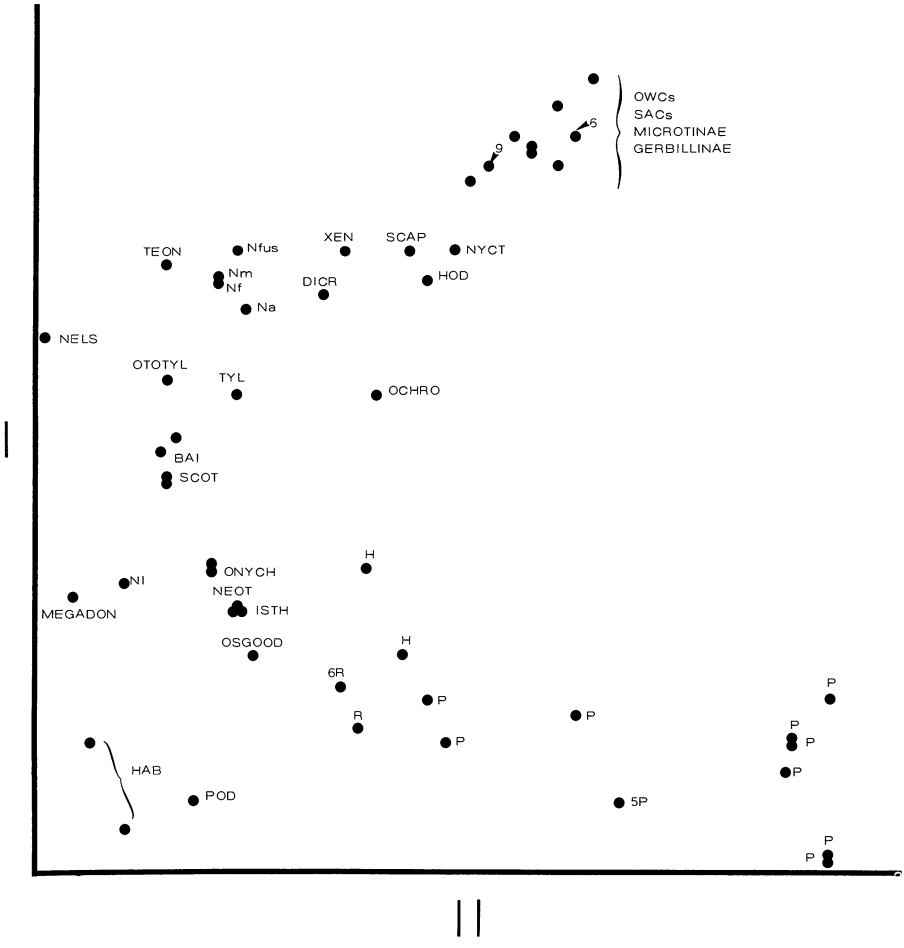
I have examined variation in phallic anatomy in greater detail because the postulated existence of two fundamental kinds of glandes, termed simple and complex, is integral to the notion of a dichotomy within New World Cricetinae (Hooper, 1960; Hooper and Musser, 1964). In defining features of the glans penis, I have tried to convey the trenchant differences between the two plans, which primarily involve development of a terminal crater, dorsal papilla, urethral process, and lateral bacular mounds and digits in the complex type and their absence in the simple kind. A total of 16 characters were recognized (see SURVEY OF CHARACTERS), which I analysed (using all 75 OTUs) by principal component analysis, a shortest connection network and the Wagner tree program.

Principal component analysis discloses interesting patterns of character covariation. Most of the species samples are sorted into two large ellipses (Fig. 35). The upper one contains forms with a complex glans, namely Old World cricetines, South American cricetines, microtines and gerbillines, as well as some neotomine-peromyscines (*Xenomys, Hodomys* and *Neotoma*). The lower constellation consists exclusively of neotomine-peromyscines (examples of *Neotomodon, Onychomys, Reithrodontomys* and the seven subgenera of *Peromyscus*). The genera *Baiomys, Scotinomys, Ochrotomys* and *Tylomys,* all neotomine-peromyscines, are positioned intermediately. The dispersion of specimens in the upper ellipse along principal components one and two reflects presence of a urethral process and dorsal papilla, subterminal urinary meatus, lateral bacular mounds, occurrence of a crater, and some shape characters (Table 15). Traits influencing the distribution of cases in the lower ellipse on the same axes include the possession of dorsal and ventral lappets, a subterminal urinary opening, and shape characters, particularly a long, narrow glans and baculum. The development of a crater hood, deep crater and relatively long cartilaginous tip largely accounts for the separation of samples of *Nelsonia, Neotoma* and *Ototylomys* on principal component three (Fig. 35, Table 15).

The construction of a shortest-connection network based on the same 16 characters employed in principal component analysis reveals that ordination has not severely distorted nearest neighbor relationships (Fig. 36). (The conformation of points in Fig. 36 differs slightly from that in Fig. 35 because I omitted certain species, *e.g.* from *Baiomys* and *Scotinomys;* however, the basic pattern is not disturbed). In general, the connectivity of the major clusters is largely internal. There are three conspicuous exceptions, one involving the samples of *Nelsonia* and *Neotoma,* which link to *Scapteromys.* The other two, *Neotoma lepida* and *Peromyscus (Megadontomys) thomasi,* represent species that possess highly modified glandes in comparison to their congenors. That found in specimens of *N. lepida* is long and

narrow, wholly unlike the proportions in other species of *Neotoma* (Hooper, 1960). *P. (Megadontomys) thomasi* is unique among species of *Peromyscus* in having a strongly corrugated glans, crater hood and urethral flap (Hooper, 1958; Hooper and Musser, 1964b)

As stated above, the polarities of certain characters of the glans penis that I recognized in the analyses of relationships within neotomine-peromyscines depart from the conventionally accepted viewpoint. My coding schemes for these characters assert an evolutionary transition from what is called the "simple" penis to a "complex" one. The current view of morphological change of the glans penis is exactly the opposite, namely the complex penis represents the ancestral type (Hooper and Hart, 1962; Hooper and Musser, 1964a; Hershkovitz, 1966a, b, 1972). The pertinent characters include numbers 55 (position of the urinary meatus), 58 (urethral process), 59 (dorsal papilla), 60 (lateral bacular mounds), 65 (length of cartilaginous tip divided by bacular length), and 67 (depth of crater). I



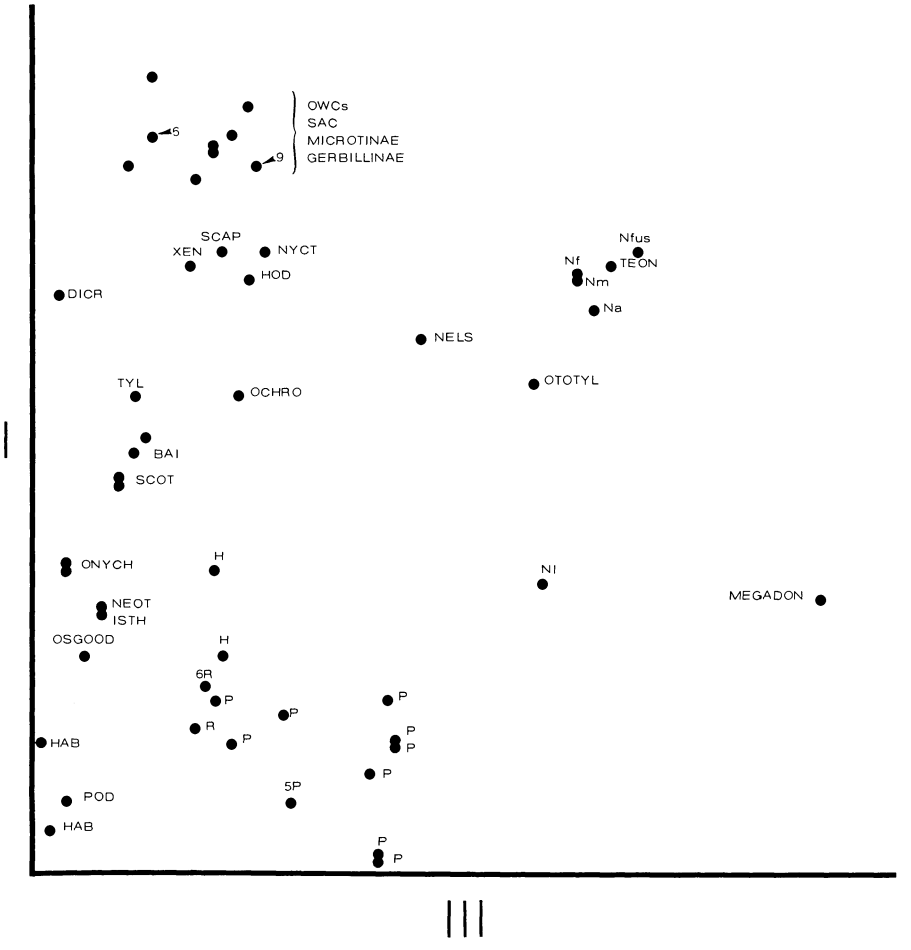


Fig. 35. Scatter plot of principal component I versus II and I versus III using all 75 species as described by 16 characters of the glans penis (see Table 15).

recoded these six characters (as numbers 80–85) for all 75 species to correspond to the accepted complex to simple sequence as follows.

Character 80: Position of Urinary Meatus.

(0) Subterminal.
(1) Terminal.

Character 81: Urethral Process.

(0) Present.
(1) Absent.

Character 82: Dorsal Papilla.

(0) Present.
(1) Absent.

TABLE 15

RESULTS OF PRINCIPAL COMPONENT ANALYSIS OF PHALLIC CHARACTERS AND CORRELATIONS OF CHARACTERS WITH FIRST THREE COMPONENTS EXTRACTED (see Fig. 35).

	Component		
	I	II	III
Eigenvalue	6.5	2.0	1.6
Cumulative % variation explained	38.5	50.6	60.2
Character			
52. Distribution of spines	-.33	-.42	-.13
53. Occurrence of spines within crater	.05	-.22	.13
54. Corrugation of body	.07	-.20	.43
55. Position of urinary meatus	.23	.55	.53
56. Dorsal lappets	-.57	.66	.24
57. Ventral lappet	-.38	.60	.25
58. Urethral process	.88	.22	.08
59. Dorsal papilla	.82	.36	-.20
60. Lateral bacular mounds	.79	.36	-.22
61. Crater hood	.12	-.42	.81
62. Ventral shield	.44	.25	-.28
63. L divided by W of glans penis	-.78	.18	.14
64. L divided by W of baculum	-.89	.15	-.05
65. L cartilaginous tip divided by baculum	.88	.09	.27
66. L baculum divided by L glans penis	-.85	.19	.06
67. Depth of crater divided by L glans penis	.84	-.19	.30

For $P \leq .05$, $r = .23$; for $P \leq .01$, $r = .30$

Character 83: Lateral Bacular Mounds.

(0) Present, strongly defined, free of crater walls.
(1) Present, weakly defined.
(2) Absent.
(3) Present, strongly defined, buried in tissue adherent to crater walls; derived from state (0).

The condition described by character-state (3) is restricted to the species of Gerbillinae examined and therefore treated as derived from the ancestral state.

Character 84: Length of Cartilaginous Tip Divided by Bacular Length.

(0) 0.4–0.6 : 1.
(1) 0.1–0.3 : 1.
(2) Less than 0.09 : 1.
(3) Greater than 0.8 : 1; derived from state (0).

The rare occurrence of species with extremely long cartilaginous tips (only some species of *Neotoma*) suggests that the condition is apomorphic.

Character 85: Depth of Crater Divided by Length of Glans Penis.

(0) 0.3–0.4 : 1.
(1) 0.1–0.2 : 1.

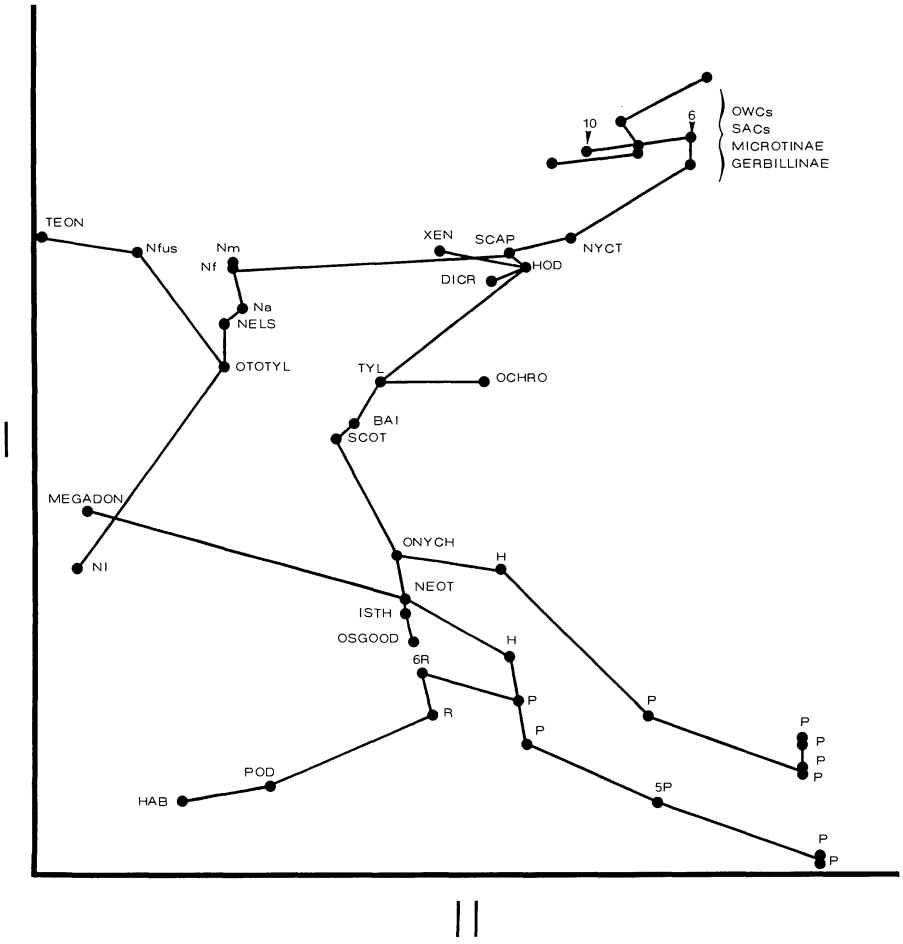


Fig. 36. Scatter plot of principal component I versus II and shortest-connection network overlay, using 71 species as described by 16 characters of the glans penis.

(2) "Vestigial" crater.
(3) Crater absent.
(4) Greater than 0.5:1; derived from state (0).

I have assumed that the extremely deep craters found in *Nelsonia* and some *Neotoma* evolved secondarily from the plesiomorphic condition.

As a result of these redefinitions in character polarity, I obtained two data sets, one reflecting the traditional complex to simple transformation and the other corresponding to the reverse sequence, simple to complex. I applied the Wagner tree analysis to each set. Thus, 16 characters of the male phallus were entered in each trial, differing only with respect to the polarity recorded for the six characters mentioned above. Ten characters (numbers 52–54, 56–57, 61–64, 66) remained unmodified. I do not intend to rigidly interpret these results as indicative of phylogenetic relationship (although there are clearly distinct associations of OTUs that agree with

the relationships predicted on the basis of my complete data set). Rather, I am interested in the patterns revealed by assuming that one or the other of the alternative evolutionary pathways, complex to simple or vice versa, is "correct". In particular, I want to ascertain the existence of two structural modalities that correspond to the complex and simple glandes penis as conventionally recognized.

In the first trial (complex to simple), the tree length is 71 steps and the consistency index is .408. The samples are arrayed in a linear fashion with most examples of South American cricetines equivalent in morphology to the proposed ancestor (Fig. 37). Some neotomine-peromyscines (*e.g. Hodomys* and *Xenomys*) are patristically near those with a complex penis. The largest hiatuses along the longest axis of the tree occur between *Ochrotomys* and an example of *Peromyscus (Haplomylomys)* and between *P. (Isthmomys)* and *P. (Megadontomys),* both intervals within forms having a simple phallus.

The tree obtained in the second trial (simple to complex) consists of the identical number of steps, 71, and consequently yields the same consistency index, .408. The ancestral condition conforms to the phallic morphology observed in specimens of *Onychomys,* a neotomine-peromyscine. An initial bifurcation is predicted, but this division does not separate the forms according to simple and complex glandes (Fig. 38). The right branch contains samples of *Peromyscus* (except the subgenus *Isthmomys*), *Reithrodontomys,* and *Neotomodon.* The left branch encompasses all forms with a complex penis as well as many neotomine-peromyscines (*Scotinomys, Baiomys, Tylomys, Ochrotomys, Xenomys, Ototylomys* and all *Neotoma*). Interestingly, the separation of specimens at the first bifurcation largely corresponds in membership to the two major ellipses divulged in principal component analysis (compare Figs. 35 and 38).

Neotomine-Peromyscines, South American Cricetines, and Other Groups of Muroidea

This section is intended to provide a rough estimate of the differentiation of neotomine-peromyscines from other assemblages of muroids, especially their hypothesized nearest sister-group, South American cricetines (see Fig. 1). I included only a few representatives of other muroid divisions (nevertheless, species were selected to represent a broad range of diversity). Consequently, the analyses in this section are less rigorous in contrast to my evaluations of neotomine-peromyscine relationships. Again, I restricted representation of the genera *Baiomys, Scotinomys* and *Onychomys* to single species, and I omitted *Xenomys, Thomasomys,* and *Peromyscus (Isthmomys) flavidus* because of missing characters. With the additional muroid species, the basic data matrix expanded to 69 species and 74 variables, which I evaluated using principal component analysis, a Prim network, and Wagner tree analysis.

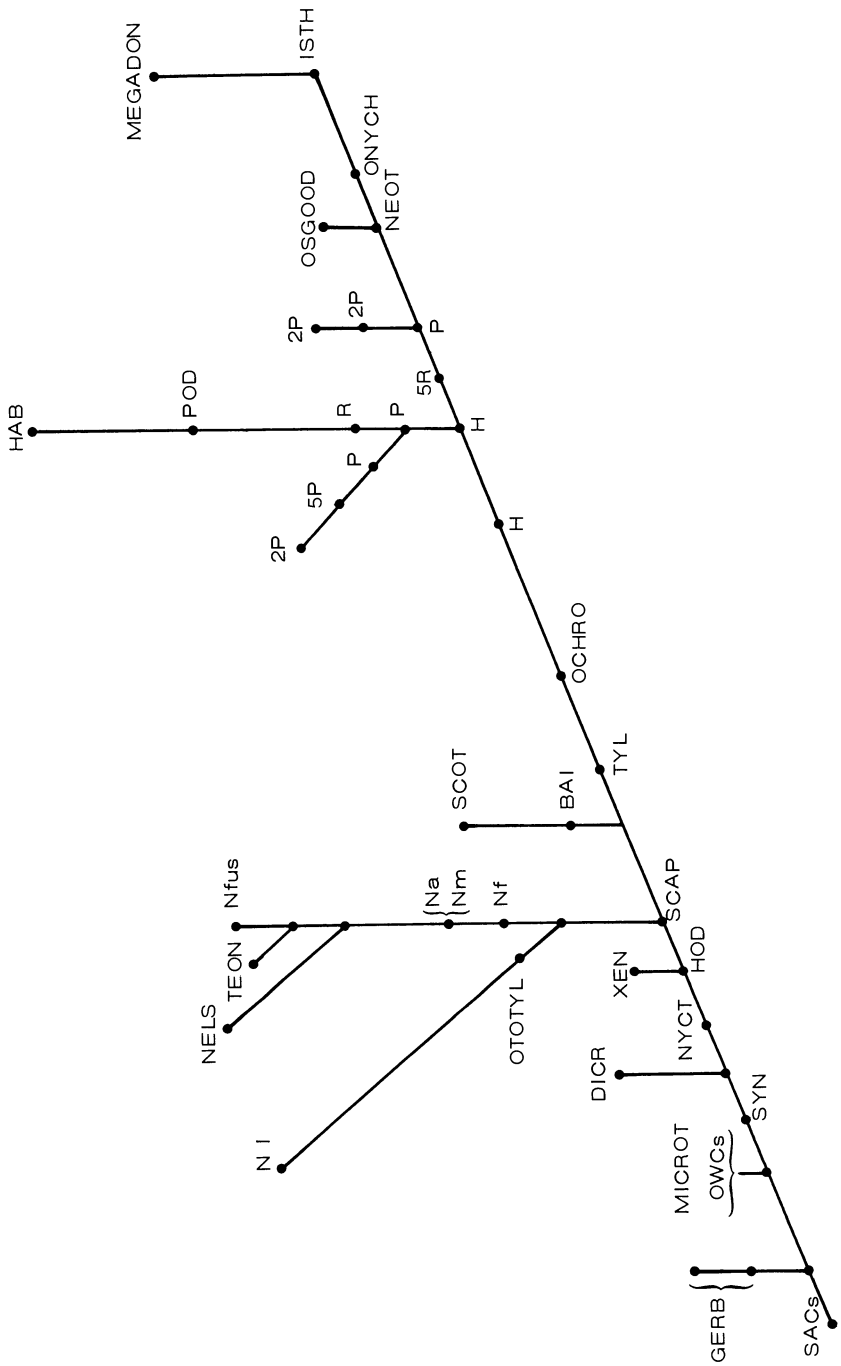


Fig. 37. Wagner tree analysis of all 75 species based only on the 16 characters of the glans penis and assuming the "complex" type is ancestral. Index of consistency = .408.

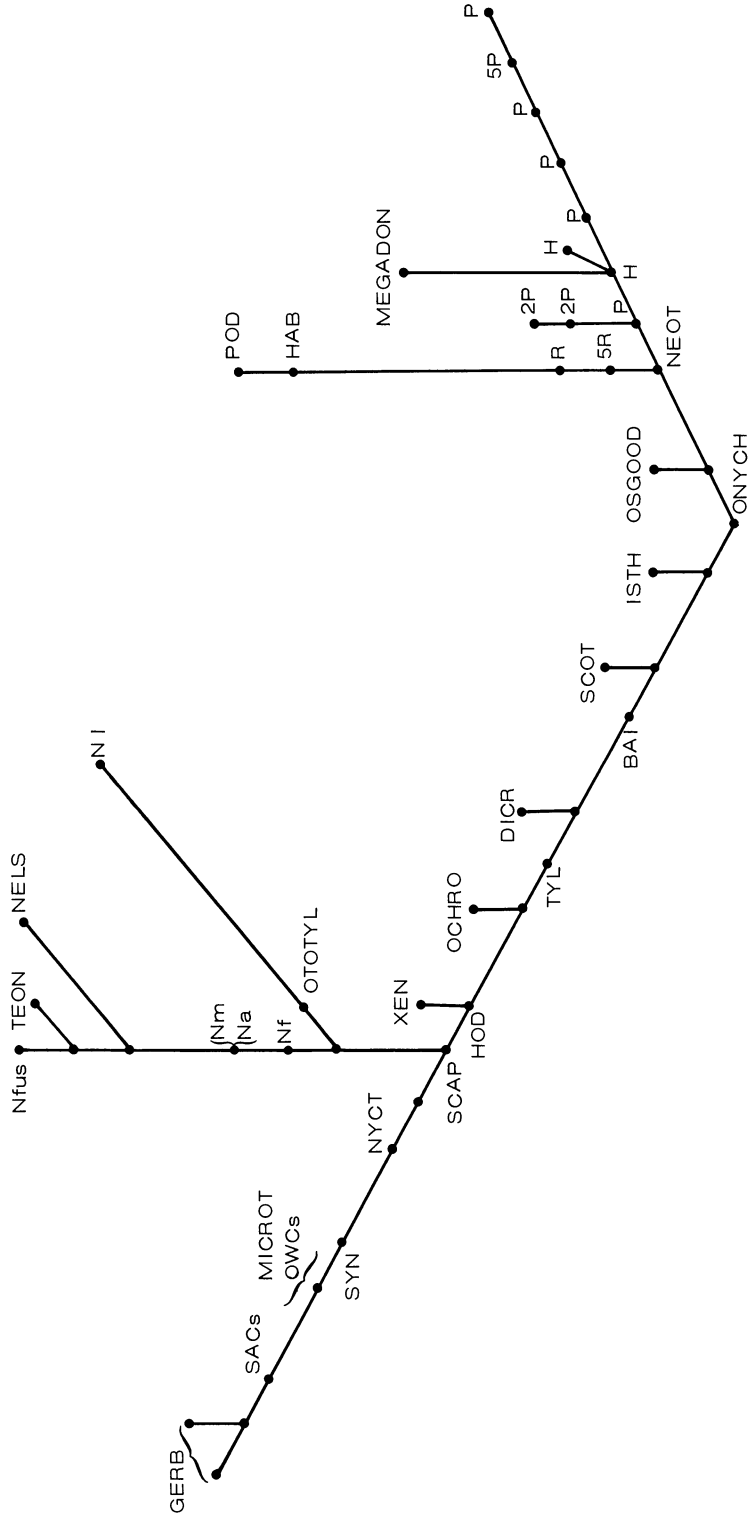


Fig. 38. Wagner tree analysis of all 75 species based only on the 16 characters of the glans penis and assuming the "simple" type is ancestral. Index of consistency = .408.

Principal components one, two and three summarize 29.2, 12.9 and 10.7 (= 52.8) percent of the variation among samples, respectively. Representatives of the subfamilies Microtinae and Gerbillinae form tight clusters that are set apart from those of neotomine-peromyscines, South American cricetines and Old World cricetines (Fig. 39). Although their centroids differ, the latter three groups are not as distinct as the Gerbillinae and Microtinae. Old World cricetines are closest to South American Cricetinae. Some neotomine-peromyscines, namely *Baiomys, Scotinomys, Hodomys,* and *Ochrotomys,* are dispersed near the periphery of South American cricetines (Fig. 39). The differentiation of species of *Neotoma* from the central cluster of neotomine-peromyscines almost matches that of South American cricetines with respect to neotomine-peromyscines. *Tylomys, Ototylomys,* and *Nyctomys* are the most distant outliers of the 58 species representing neotomine-peromyscines, South American cricetines and Old World cricetines.

In the shortest-connection network (Fig. 40), the isolated position of *Tylomys* and *Ototylomys* is reaffirmed. The sample of *Nyctomys* connects to *Ototylomys* but at a great distance. *Nelsonia* and species of *Neotoma* constitute a recognizable cluster, and the generic representatives of South American cricetines are more or less regularly spaced on another major axis of the network. *Baiomys* and *Scotinomys* connect to *Ochrotomys,* which also forms the vertex linking South American cricetines and the genera *Peromyscus, Reithrodontomys, Onychomys* and *Neotomodon.* The distances separating the various subgenera of *Peromyscus* and *Neotoma* are worthy of note in comparison to those observed between genera of South American cricetines.

A Wagner tree analysis was performed on the 58 species representing neotomine-peromyscines, South American cricetines and Old World cricetines using 62 characters (as coded in Table 7). The resulting tree (length = 455 steps; consistency index = .288) discloses three major points of interest (Fig. 41). For one, *Tylomys, Ototylomys* and *Nyctomys* diverge basally from all OTUs, other South American cricetines and neotomine-peromyscines alike. Second, the samples of *Ochrotomys, Baiomys* and *Scotinomys* are positioned on that branch leading to Old World cricetines and South American cricetines. Finally, the integrity of the major clades of neotomine-peromyscines persists and agrees with results presented above, even though the number of species and characters in the data matrix increased.

DISCUSSION

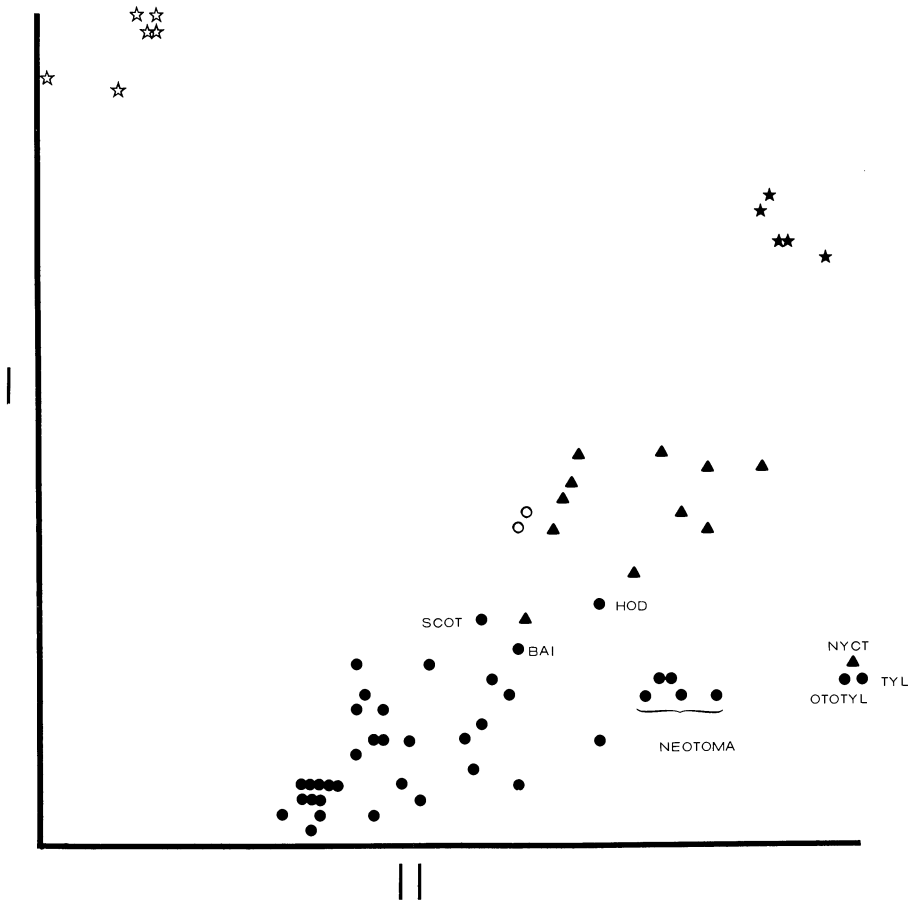
Relationships Within Neotomine-Peromyscines

In formulating a phylogeny of neotomine-peromyscine rodents, I have not relied exclusively on one line of evidence, a single set of characters, or a particular numerical program. Although the hypothesis of relationships I recognize (Fig. 42) is not exactly duplicated in any one analysis, it reflects in most essential features the results obtained with Wagner tree

analyses. Still, my phylogenetic hypothesis embraces some elements of similarity, which I regard as additional corroboration, from the results of the WISS, character compatibility and phenetic programs. Thus, I have sought to represent those relationships that were predicted repeatedly or demonstrated robustness to the various quantitative perturbations.

The phylogeny of neotomine-peromyscines advanced by Hooper and Musser (1964a) consists of twelve genera arranged in two phyletic lines, the Neotomini and Peromyscini. They included *Tylomys, Ototylomys, Xenomys* and *Neotoma* in the Neotomini and assigned *Baiomys, Scotinomys, Onychomys, Ochrotomys, Neotomodon, Peromyscus,* and *Reithrodontomys* to the Peromyscini (Fig. 42). Curiously, they identified *Nelsonia* as a member of the Neotomini in their text (1964a:54) but cladistically portrayed the genus in the Peromyscini (1964a:55, Fig. 9b), stating (1964a:56) that "*Nelsonia* appears to be somewhat removed toward the peromyscines".

The phylogenetic hypothesis proposed herein departs in several aspects from that of Hooper and Musser. I favor recognition of 18 genera, five of



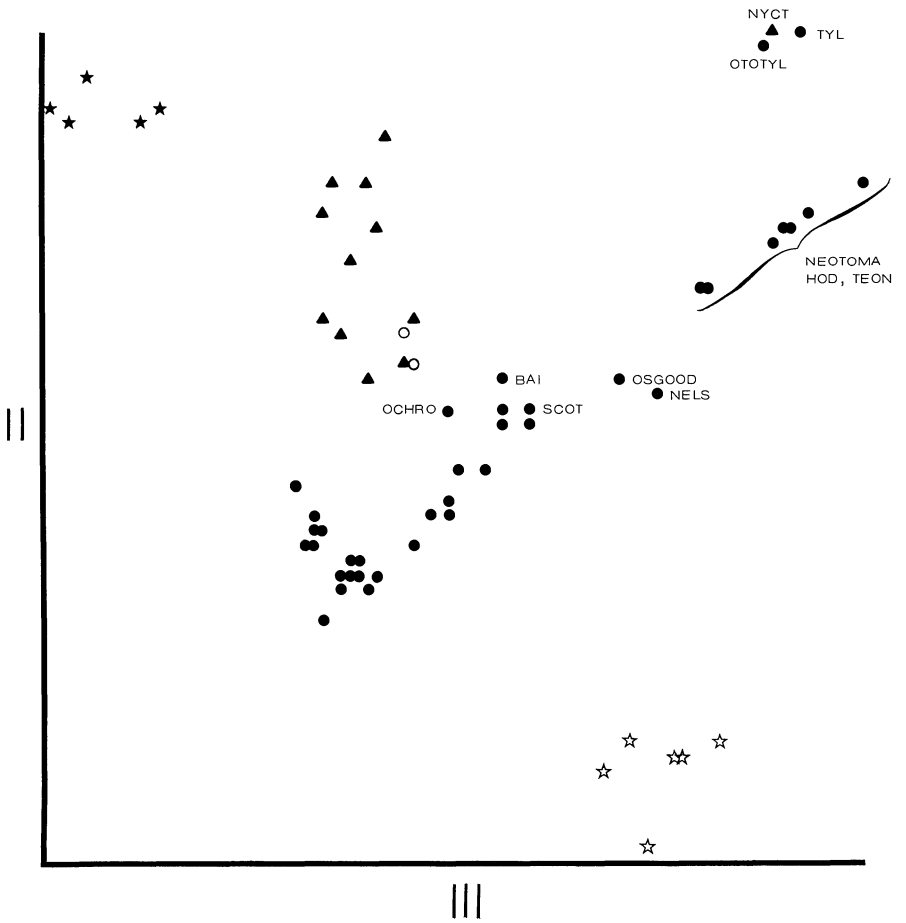


Fig. 39. Scatter plot of principal component I versus II and II versus III using 69 species as described by 74 characters. Symbol codes: open stars, Microtinae; closed stars, Gerbillinae; open circles, Old World cricetines; closed circles, neotomine-peromyscines; closed triangles, South American cricetines.

which are currently listed as subgenera of *Peromyscus* and one as a subgenus of *Neotoma.* Moreover, the genera are arrayed in four major clades of tribal level as follows: A) *Tylomys* and *Ototylomys;* B) *Baiomys* and *Scotinomys;* C) *Nelsonia, Xenomys, Hodomys* and *Neotoma;* and D) *Ochrotomys, Isthmomys, Megadontomys, Osgoodomys, Onychomys, Habromys, Podomys, Neotomodon, Reithrodontomys* and *Peromyscus* (Fig. 42). Few uniquely derived characters define these cladistic groups within neotomine-peromyscines. When other species of Muroidea are considered, the number of uniquely derived traits is reduced further. I feel more certain about the content of the first three groups. I am less confident of the definition and interrelationships suggested for the last. This uncertainty arises from the suspicion that certain forms may be farther removed from *Peromyscus* (here restricted

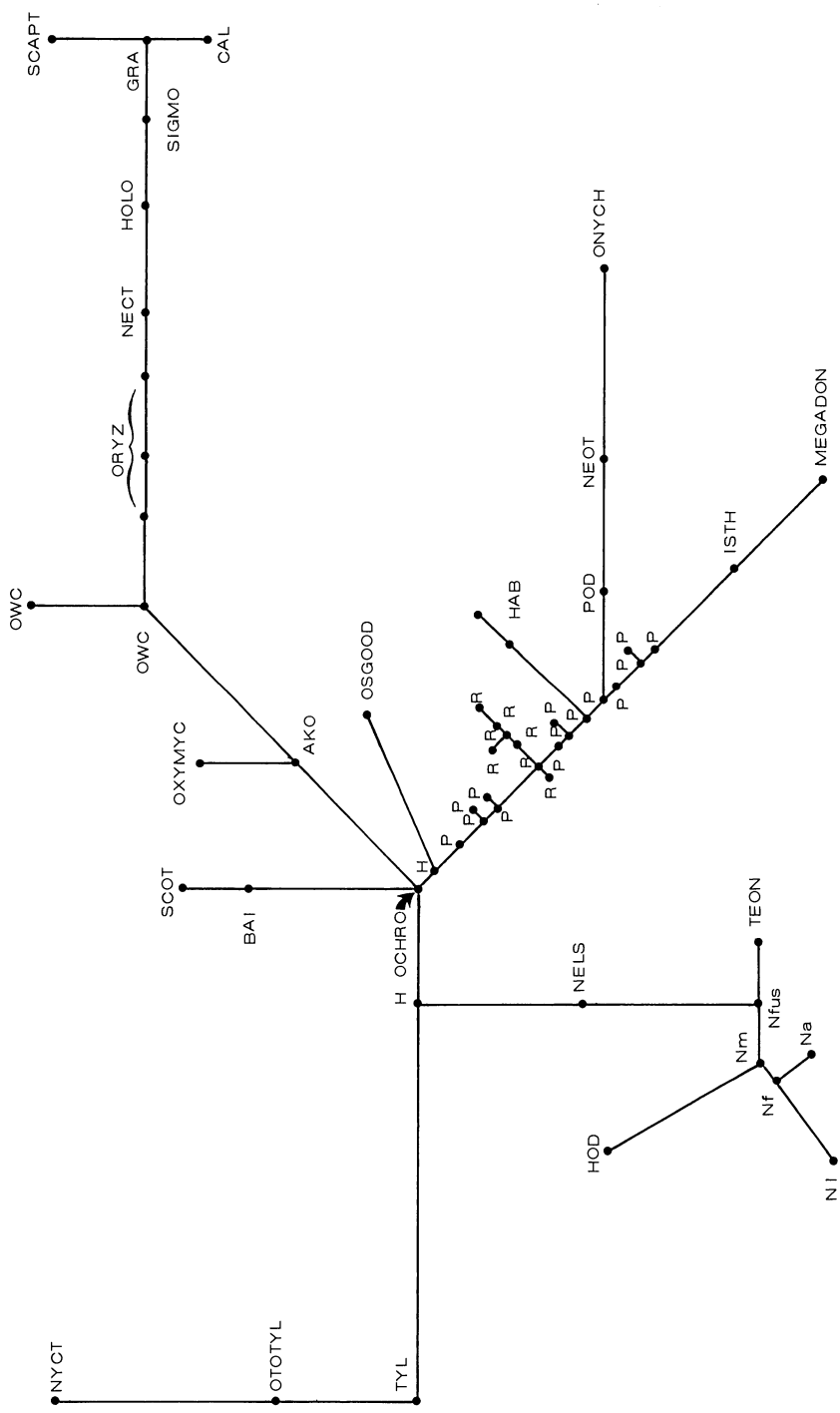


Fig. 40. Shortest connection network (Prim) of 56 species representing neotomine-peromyscines, South American cricetines and Old World cricetines. Distances between samples are proportional to the absolute sum of differences over all characters.

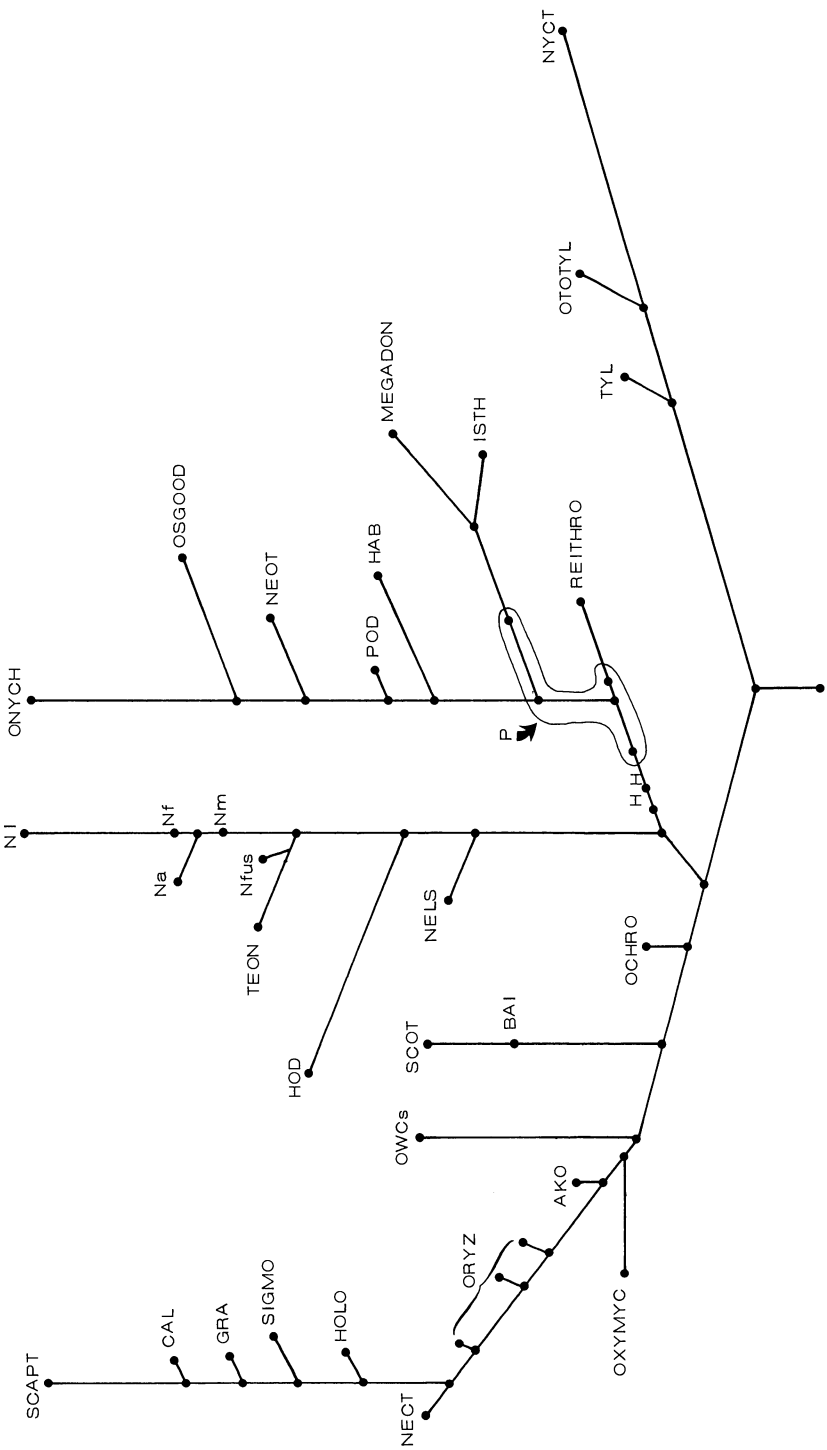


Fig. 41. Wagner tree analysis of 58 species representing neotomine-peromyscines, South American cricetines, and Old World cricetines based on 62 characters. Index of consistency = .288.

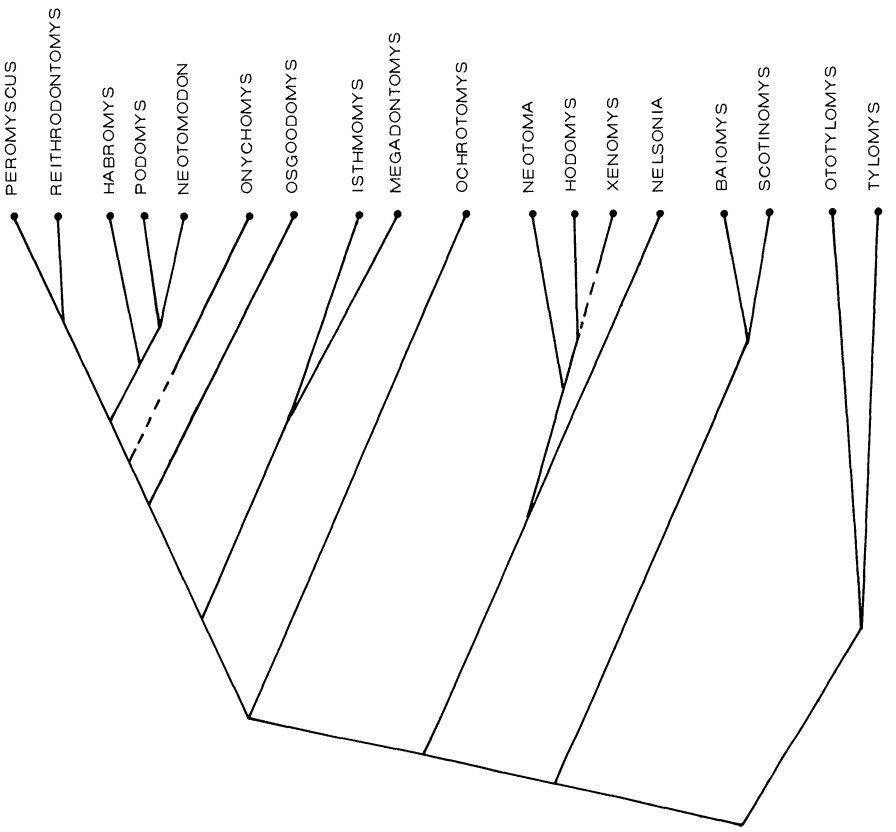


Fig. 42. The phylogeny of neotomine-peromyscine rodents proposed herein; compare with that formulated by Hooper and Musser, 1964 (Fig. 4).

to the subgenera *Peromyscus* and *Haplomylomys*) than I have arranged them.

Tylomys and *Ototylomys* possess numerous derived characters that suggest their near relationship. Among these are a deeply bifurcated anterocone (character 2), four-rooted upper M2 (10), auxillary rootlet on upper M3 (11), loss of the sphenofrontal and stapedial foramina (16), development of heavily rugose supraorbital and temporal ridges (24), attenuate entoglossal process (29), augmented rib count (36), reduction of the anterior longitudinal ridge (44) and increase in palatal rugae (45), loss of the gall bladder (49), complex caeca (51), and enlarged ampullae of the deferent ducts (76). Only characters 2, 45, and 76 are unique transformations among neotomine-peromyscines, but 10, 11, 29, 36, and 49 occur in just a few taxa. Symplesiomorphic resemblances include their hemiglandular stomachs, relatively complicated dentition, oppositely placed molar cusps, unmodified third molars, possession of an entepicondylar foramen, and arrangement of the plantar pads. Despite their many similarities, the two forms are highly divergent with respect to spermatozoan morphology

(Helm and Bowers, 1973), complement of accessory glands (Lawlor, 1969), and phallic anatomy (Hooper, 1960).

Although authors (*e.g.* Merriam, 1901) have long recognized the morphological similarity of *Tylomys* and *Ototylomys,* the first definitive statement of their affinities was provided by Hooper (1960) and Hooper and Musser (1964a), who viewed them as primitive members of the Neotomini (see Fig. 42). I agree that the two genera display many plesiomorphic traits but doubt that they share more recent common ancestry with *Xenomys* and *Neotoma.* Instead the separation of the progenitor of *Tylomys* and *Ototylomys* probably occurred prior to the differentiation of other neotomine-peromyscines. The basal divergence of *Tylomys* and *Ototylomys,* together with *Nyctomys* in analyses using South American cricetines as well as neotomine-peromyscines, further attests to the archaic nature of these genera. In aspects of dental morphology, especially the large third molars with unreduced posterior cingula, *Tylomys* and *Ototylomys* recall certain extinct genera of Oligocene and Miocene Eumyinae (Alker, 1967; Wood, 1937). Comparison with fossil material is recommended to ascertain if *Tylomys* and *Ototylomys* are descended from some ancient group.

In contrast to *Tylomys* and *Ototylomys,* the predicted sister-group relationship of *Baiomys* and *Scotinomys* was not anticipated by early workers. Some species of *Scotinomys* were initially described in *Akodon* (Allen, 1904; Bangs, 1902), a genus of South American cricetines, until Thomas (1913) formally recognized their distinctiveness. In like manner, species of *Baiomys* were included as a subgenus of *Peromyscus* for some time. Blair (1942) cogently argued for their generic status, and in his revision, Packard (1960) speculated that *Baiomys* is more closely related to some South American cricetines, such as *Calomys,* than a North American form. However, Hooper (1960) noted resemblances of the phalli of *Baiomys* and *Scotinomys,* and subsequently, Hooper and Musser (1964a) suggested their derivation from a common ancestor, a viewpoint strongly supported in my analyses.

Synapomorphic character state changes that delineate the *Scotinomys–Baiomys* clade include loss of the sphenofrontal and stapedial foramina (16), absence of the entepicondylar foramen (35), more distal location of the trochlear process (40), acquisition of two complete and five incomplete palatal ridges (45), reduction of the caecum (51), formation of a shallow crater (67), and shift in position of the plantar pads (77). Character 77(2) is unique among neotomine-peromyscines and numbers 35(1), 40(1), 45(2) and 51(1) are shared with a few OTUs. Although I did not code them as a separate state, the simplified ampullary glands observed in *Baiomys* and *Scotinomys* are singularly distinctive within neotomine-peromyscines (Arata, 1964; Carleton *et al.,* 1975). Interestingly, mice of both genera utter a trilling call and males have well-developed midventral glands (Blair, 1941; Hooper and Carleton, 1976). Resemblances due to shared primitive conditions involve possession of unilocular, hemiglandular stomachs, short, broad bacula and phalli with a terminal urinary

meatus, and retention of large preputial glands. Members of the two genera differ more strikingly in their dentitions than my simplistic coding of crown morphology conveys. The teeth of *Scotinomys* are elongate and narrow, relatively hypsodont, and selenodont in crown pattern. The latter diagnostic trait apparently results from union of the mesostyle with the paracone, as suggested by Hooper (1972). The molars of pygmy mice, *Baiomys,* are brachyodont and lack accessory styles and lophs. Other dissimilarities include the supernumerary roots in *Scotinomys* and the contrast in diploid numbers of chromosomes, 48 in species of *Baiomys* (Hsu and Benirschke, 1967; Lee and Elder, 1977) and 58 in *Scotinomys* (Carleton *et al.,* 1975).

The genera *Nelsonia, Hodomys, Xenomys* and *Neotoma* consistently formed a well-defined clade in most Wagner tree, WISS and character compatibility analyses. Derived characters that associate these OTUs are rooted, hypsodont molars (4), moderate inflation of the tympanic bullae (33), intermediate reduction of gastic glandular epithelium (46), three to four coils of the large intestine (50), a large, sacculated caecum (51), relatively long cartilaginous tip (65), deep terminal crater of the glans penis (67), and loss of lateral ventral prostates (70). Of these characters, 4(1–2), 50 (0–1), and 65(1–2) represent autapomorphic modifications. In addition, the first rib of all members contacts only the transverse process of the first thoracic vertebra, a condition interpreted as primitive.

The affinity of *Nelsonia* is ambiguous based on the various phenetic comparisons. In fact, the genus is phenetically closest (as determined by the Manhattan distance) to *Haplomylomys* of the genus *Peromyscus.* Merriam, in his diagnosis (1897), compared the genus both to species of *Peromyscus* and *Neotoma* but refrained from assigning it to his previously erected (1894) subfamily Neotominae. Later, Goldman (1910) included *Nelsonia* with other woodrats (*Neotoma, Xenomys, Hodomys,* and *Teanopus*). As a result of his studies on the cranium, dentition and phallus of specimens of *Nelsonia,* Hooper (1954, 1959, 1960) allied the form with *Neotoma* and *Xenomys* but subsequently emphasized its separation from them by deriving it from the base of the lineage including *Peromyscus* (Hooper and Musser, 1964a). The latter systematic position is untenable. All phylogenetic programs, Wagner tree, WISS and character compatibility alike, unequivocally disclose a cladistic association of *Nelsonia* with *Neotoma* and its relatives. *Nelsonia* is separated early relative to other members of the group because it retains certain primitive traits, such as a relatively complete assortment of accessory reproductive glands and retention of the stapedial and sphenofrontal foramina. My results endorse Hooper's (1954:12) earlier estimation that the diminutive wood rat, *Nelsonia neotomodon,* "... meets many of the requirements that might be expected in an ancestor of *Neotoma.*"

Hodomys alleni has been alternatively treated as a genus or a subgenus of *Neotoma.* Merriam (1892) described *alleni* as a species of *Neotoma,* and then (1894) included it in a separate genus, *Hodomys,* which he primarily com-

pared to *Xenomys*. Goldman (1910) followed Merriam in listing *Hodomys* as a genus of Neotominae. Burt and Barkalow (1942) significantly expanded the definition of *Neotoma* by relegating *Hodomys alleni* and *Teanopus phenax* to subgenera of *Neotoma,* and this arrangement is conventionally accepted today (Genoways and Birney, 1974; Hall and Kelson, 1959). Nevertheless, others have noted anatomical features of *alleni* that separate it from *Neotoma* (*e.g.* Sprague, 1941; Hooper, 1960; Carleton, 1973), and Schaldach (1960) and Carleton (1973) suggested reinstating *Hodomys* to its former generic status. The evidence reported here clearly warrants this action. Certain characters, notably the intermediate grade of the stomach and the possession of preputial, vesicular and unmodified dorsal prostate glands indicate that the ancestor of *Hodomys* separated prior to the differentiation of *Neotoma* proper. I tentatively have represented *Hodomys* as sharing a more recent common ancestor with *Xenomys* (Fig. 42) because the two display several resemblances (for example, absence of the entepicondylar foramen, an s-shaped lower third molar, and dorsal papilla) not observed in species of *Neotoma.*

The branching patterns intimated for species of *Neotoma* accord with certain subgeneric alignments but question others. *Neotoma albigula, floridana* and *mexicana* of the subgenus *Neotoma* were repeatedly associated closely.

Neotoma fuscipes, another member of the nominate subgenus, was predicted to share common ancestry with *N. (Teonoma) cinerea.* This relationship surprised me because no previous author had suggested any special kinship between the two. In fact, Goldman (1910:86) expressly denied a close relationship of *fuscipes,* which he isolated in the subgenus *Homodontomys,* either to species of *Neotoma* or *Teonoma cinerea.* Burt and Barkalow (1942) synonymized Goldman's subgenus *Homodontomys* into *Neotoma* but retained *Teonoma* as a subgenus for the bushy-tailed wood rat. Characters that associate *cinerea* and *fuscipes* include the persistence of the squamosal groove and large stapedial foramen (16), reduced spiny covering of the glans penis (52), exceptionally long cartilaginous tip (65) and deep crater (67). *Neotoma fuscipes* and *cinerea* have diploid counts (2N = 56 and 2N = 54, respectively) that differ from the typical number of 52 reported for most species (Baker and Mascarello, 1969; Lee and Elder, 1977). Other deviations from 2N = 52 include *Hodomys alleni* (2N = 48, Genoways and Birney, 1974; Lee and Elder, 1977) and *N. (Teanopus) phenax* (2N = 38, Baker and Mascarello, 1969).

The large patristic separation of *lepida* from other *Neotoma* suggests at least subgeneric status for that species. This conclusion was anticipated by Burt and Barkalow (1942) and Hooper (1960). Many of the unique features of *lepida* involve aspects of the phallus, namely the long narrow glans (63) and baculum (64), and limited distribution of spines (52); however, I also observed distinctions in the development of the anterior longitudinal ridge (44) and less complicated caecum (50) in specimens of *lepida.* The karyotype of *lepida* consists of 52 chromosomes as in most species of

the subgenus *Neotoma* (Baker and Mascarello, 1969). I have not proposed formal taxonomic recognition of *lepida* until the extent of its differentiation is evaluated in more detail. Indeed, the entire tribe Neotomini invites additional study to explore the relationship between *fuscipes* and *cinerea* revealed here, to include fluid examples of *Xenomys nelsoni* in order to refine its cladistic position to other wood rats, and to examine other species not surveyed, especially *N. stephensi, N. goldmani* and *N. (Teanopus) phenax.*

The last major group recognized largely corresponds to the Peromyscini of Hooper and Musser (1964a), except for the removal of *Baiomys* and *Scotinomys* and the recommended elevation of five subgenera of *Peromyscus* to genera (Fig. 42). This assemblage of ten genera is the least satisfactorily delimited of the four cladistic groups. An intermediate grade in stomach morphology (46), moderate depth of the incisura angularis (47), a baculum longer than the glans penis (66, except for *Ochrotomys*) and shift in plantar pad position (77) are the only derived traits characterizing the group and none of these evolutionary changes is unique. The cohesiveness of the assemblage appears to result more from a variety of symplesiomorphies: bunodont molars (except *Neotomodon*); three-rooted upper and two-rooted lower molars; complete carotid circulatory pattern (except *Osgoodomys*); thirteen thoracic and six lumbar vertebrae (except *Habromys*); presence of an entepicondylar foramen (except *Ochrotomys* and *Isthmomys*); proximal location of the trochlear process (except *Onychomys*); three complete and four incomplete transverse palatal ridges (except *Onychomys* and *Reithrodontomys*); retention of a gall bladder (except *Ochrotomys*); a poorly developed spire of the intestine; and a unremarkable caecum (except *Onychomys* and *Megadontomys*).

In addition to lacking definition based on many derived traits, the various quantiative phylogenetic techniques disclosed inconsistent, conflicting statements of relationship for certain members of this group, particularly *Onychomys* and *Ochrotomys.* For these reasons, their allocation here is considered provisional. Of the three phylogenetic methods employed, the WISS algorithm seemed most sensitive to slight alterations in number of OTUs or characters, a finding in agreement with Mickevich (1978).

The generic distinctiveness of golden mice, *Ochrotomys,* is clearly apparent in my results. Although once included as a subgenus of *Peromyscus* (Osgood, 1909), numerous authors have drawn attention to features that suggest a very distant relationship of *Ochrotomys* to *Peromyscus* proper. A short, wide baculum (Blair, 1942) and presence of a urethral process (Hooper, 1958), lack of an entepicondylar foramen (Rinker, 1960), transitional stomach morphology (Carleton, 1973), lack of a gall bladder, presence of large preputials but absence of ampullary glands (Arata, 1964), and a diploid number of 52 (Patton and Hsu, 1967) are among the combination of traits that distinguish the genus. I placed *Ochrotomys* closer to the base of Peromyscini than indicated in the Wagner trees because all phenetic treatments suggested a nearer position to this tribe rather than Neotomini.

The cladistic disposition of *Onychomys* remains dubious. Hence, its relationship in Figure 42 is indicated by a dashed line. In the Wagner trees, the sample of *Onychomys* was contained in a clade including *Habromys, Podomys, Neotomodon,* and sometimes *Osgoodomys,* usually as the most highly derived cladistic member. In contrast, the weighted Wagner program suggested a relationship to *Baiomys* and *Scotinomys,* a position also asserted by results of character compatibility because *Onychomys* fell into the same equivalence class with *Baiomys* and *Scotinomys.* I believe the erratic cladistic portrayal of *Onychomys* in the various analyses issues from the almost uniformly large distances separating that form from every other species. As a result, its connection to one OTU or another reflects any trivial character resemblance depending upon the program implemented. For instance, the first relationship mentioned above emphasizes derived changes in the accessory gland complement (loss of ampullary, anterior prostate and vesicular glands), and the latter reflects the modification of the calcaneum, reduction of the caecum and possession of preputial glands. The reduction of the third molars (5, 6) and concomitant coalescence of their roots (11), acquisition of two complete and four incomplete palatal rugae (45), evolution of a pouched stomach (46), loss of plantar pads (77), and development of a furry tarsum (78) constitute other apomorphic modifications demarcating the genus *Onychomys.* Grasshopper mice emit a piercing call (Hafner and Hafner, 1979), which is apparently unlike the staccato-like call of *Baiomys* and *Scotinomys;* however, mice of the three genera assume the same stance when calling. An equally plausible hypothesis of relationship is to consider *Onychomys* arising from the stem leading to *Baiomys* and *Scotinomys.*

Contrasting relationships also were predicted for *Osgoodomys banderanus.* Nonetheless, unlike *Onychomys, Osgoodomys* consistently remained within the peromyscine group, sometimes in a clade including *Habromys, Podomys,* and *Neotomodon* and other times with *Isthmomys* and *Megadontomys.* Again, these disparate cladistic associations are due to different character complexes, the former modification and loss of accessory reproductive glands and the latter elaboration of pronounced supraorbital crests. Other features that discriminate *Osgoodomys* include reduction of the carotid circulatory pattern (16) and lack of sphenopalatine vacuities (20). Hooper (1958) recognized the unusual nature of the phallus of *banderanus,* and subsequently, Hooper and Musser (1964b) underscored that distinctiveness by erecting the subgenus *Osgoodomys* for *banderanus.* On the basis of my analyses, I think generic recognition more appropriately reflects the large patristic distance separating *Osgoodomys* from other *Peromyscus.*

The seven remaining genera were regularly associated in clades as follows: *Megadontomys* and *Isthmomys; Habromys, Podomys,* and *Neotomodon;* and *Reithrodontomys* and *Peromyscus.* The sister-group relationship of *Isthmomys* and *Megadontomys* is not unexpected. Merriam (1898) diagnosed the subgenus *Megadontomys* of *Peromyscus* to contain the species *thomasi* and *nelsoni,* the latter now considered a subspecies of *thomasi* (Musser, 1964).

Bangs (1902) described *flavidus,* now the type species of *Isthmomys,* as a species of *Megadontomys,* which he viewed as a genus distinct from *Peromyscus.* In his monumental revision, Osgood (1909) retained *Megadontomys* as a subgenus within *Peromyscus* but explicitly considered the allocation of *flavidus* to the genus as provisional.

Except for Goldman's (1912) naming of *P. pirrensis,* a form allied to *flavidus,* the content of the subgenus *Megadontomys* remained unchanged until 1964. In that year, Hooper and Musser proposed the subgenus *Isthmomys* to encompass *flavidus* and *pirrensis,* based on the differentiation of their phalli from other *Peromyscus.* In addition to their distinctive glandes, specimens of *Isthmomys* lack an entepicondylar foramen (35), possess a stomach intermediate to the discoglandular and pouched stages (46), have only a single pair of ventral prostates (70), and exhibit elaborate, finely dissected vesicular glands (75). The usual occurrence of an accessory root on the upper M1 (9), singular articulation of the first rib (39), low extent of tibiafibular fusion (42), moderate number of coils in the intestinal spire (50), complicated caecum (51), fluting of the glans surface, and presence of a weakly developed urethral process (58) and crater hood (61) comprise the array of traits that distinguish *Megadontomys.* The two genera have the following characters in common: relatively pronounced supraorbital and temporal riding (24); low relief of the anterior longitudinal ridge of the diastemal palate (44); and relatively wide glandes and bacula (63, 64). Certain proportions of the phallus are uniquely combined in *Megadontomys* and *Isthmomys.* Although their glans and baculum are relatively broad, the length of the baculum is much greater than the length of the glans penis, a situation found in many other *Peromyscus.* Typically, a wide glans penis contains a baculum that is shorter than, or only as long as, its own length. In view of this distribution of characters, I have arranged *Megadontomys* and *Isthmomys* as separate genera.

Habromys, Podomys, and *Neotomodon* always were united cladistically, sometimes in a group containing *Onychomys* and *Osgoodomys,* but also in a lineage by themselves (weighted Wagner and WISS trees). The lack of a distinct pair of lateral ventral prostates (70) and diminution in size of the vesicular glands (75) are derived traits that characterize the three genera. Also, all exhibit an approximately terminal urinary meatus, a location considered ancestral. With regard to certain characters of the glandes and accessory glands, the three covary in an interesting reticular fashion. For instance, the distribution of spines is complete (52:0) in *Neotomodon,* but reduced (52:2) in *Podomys,* and spines are absent (52:3) in *Habromys;* the length of the glans penis and baculum (63, 64) is moderately long in *Neotomodon* and very long in *Podomys* and *Habromys;* the baculum is shorter than the glans penis (66) in *Neotomodon* but longer than the glans in *Podomys* and *Habromys;* the medial ventral prostates (69) are elaborate in *Habromys,* whereas the ampullary glands (74) are hypertrophied in *Neotomodon* and *Podomys;* finally the vesicular glands (75) of *Podomys* are short and saclike, while those of *Neotomodon* and *Habromys* resemble minute blebs from

the cephalic urethra. Generally *Podomys* and *Neotomodon* shared a more recent heritage due to derived similarities of the ampullary glands (74) and simplified dentition (1), a position in accord with the karyological evidence of Yates *et al.* (1979).

Although their descent from a common ancestor seems reasonable, *Habromys, Podomys* and *Neotomodon* are each markedly differentiated in their own way. Therefore, I favor recognition of their divergence at the generic level. *Habromys,* only recently described as a subgenus of *Peromyscus* (Hooper and Musser, 1964b), contains the only species of neotomine-peromyscines having modal numbers of thirteen thoracic and seven lumbar vertebrae (36), a glans penis entirely divested of spines (52) and elaborate medial ventral prostates (69). Moreover, Linzey and Layne (1974) discovered that species of *Habromys* lack an acrosomal hook on their sperm, a condition unique among the 27 species of *Peromyscus* (representing all seven subgenera) they surveyed. The presence of an interorbital shelf (24), reduction of spiny distribution (52), small vesicular glands (75) and absence or reduction of the hypothenar pad (77) distinguish the genus *Podomys.* Diagnostic traits of *Neotomodon* include the planar molars (4), single-rooted state of the upper M3 (11), moderate zygomatic notch (25), and occurrence of two complete and five incomplete palatal ridges (45).

Examples of *Reithrodontomys* were connected to species of *Peromyscus* (the subgenera *Haplomylomys* and *Peromyscus*) in iterations of the Wagner tree, including the weighted Wagner, and character compatibility analyses. Results of the various phenetic methods also indicated the nearness of *Reithrodontomys* and *Peromyscus,* but the WISS program placed *Reithrodontomys,* together with *P. (Haplomylomys),* on a stem subtending *Baiomys* and *Scotinomys.* Few derived traits unite *Reithrodontomys* and *Peromyscus,* and those that do, development of a subterminal urinary meatus (55) and proportional traits of the glans penis (63, 64), are not unique. Here is another instance of taxa whose affinity is suggested by a mixture of shared primitive traits (in a large part, the same ones common to Peromyscini) as well as some nonunique apomorphies. Derived states common to most species of *Peromyscus, sensu strictu,* are a bilocular, discoglandular stomach (46, 47) and a long, narrow phallus with a protrusible tip (except some species of the subgenus *Haplomylomys*). Many, but not all, species of *Peromyscus* possess glandes with ventral and/or dorsal lappets.

Synapomorphies that separate species of *Reithrodontomys* from those of *Peromyscus* involve grooved upper incisors (7), occurrence of two complete and five incomplete palatal rugae (45) and partial spiny investment of the glans' body (52). Although the monophyletic nature of *Reithrodontomys* is supported in the phylogenetic analyses, large patristic distances separated some of the species. The characters responsible for these gaps are complexity of the molars (1), size and shape of the third molars (5,6), presence of accessory roots (9, 13), occurrence of the entepicondylar foramen (35), and distribution of gastric glandular epithelium (46). Considerable divergence has also been reported in diploid numbers of chromosomes (Carle-

ton and Myers, 1979). In contrast, the morphology of the glans penis and complement of accessory reproductive glands is astonishingly uniform in species of *Reithrodontomys*. In all phylogenetic methods, the first bifurcation divided species of the subgenus *Aporodon* (*creper* and *mexicanus*) from those of the subgenus *Reithrodontomys* (*fulvescens, humulis, sumichrasti, megalotis* and *montanus*) in accordance with Hooper's (1952) taxonomic scheme.

As a result of their chromosomal banding study of *Baiomys, Neotomodon* and *Peromyscus* (8 species representing three subgenera), Yates *et al.* (1979) reduced *Neotomodon* to subgeneric status in *Peromyscus*. I do not dispute the cladistic relationship they present for *Neotomodon* and *Podomys*. I strongly disagree that the only interpretation of this cladistic disposition is consignment of *Neotomodon alstoni* to the genus *Peromyscus*. The critical question provoked by their finding, and the information revealed herein, is whether *Podomys* (and by extention the other highly differentiated subgenera of *Peromyscus*) is really closely related to *Peromyscus sensu strictu*. In my opinion, *Podomys* and the other subgenera (except *Haplomylomys*) are not; at least they are not more nearly related than some other mice currently allocated to separate genera. If *Neotomodon* is demoted to subgeneric status under *Peromyscus,* then it necessarily follows (assuming that consistency and equivalence in content are important criteria in defining systematic taxa) that *Reithrodontomys* and *Ochrotomys* be included too, that *Scotinomys* and *Baiomys* should be congeneric, and that *Neotoma* should encompass *Xenomys* and perhaps *Nelsonia*.

Such a broad generic definition seems overly cumbersome and unwieldy in comparison to generic standards employed in other groups of muroid rodents (except, perhaps, for Ellerman's 1941 concept of the genus *Rattus*). In particular, the patristic and phenetic distances delimiting the subgenera of *Peromyscus* in question (and the subgenus *Hodomys* of *Neotoma*) fully equal, or exceed, the separation of some currently recognized genera of South American Cricetinae (see Figs. 40, 41). Perhaps this only indicates that the assemblage of South American cricetines is generically oversplit. Yet, to judge from the recent literature, the number of South American cricetine genera at least has remained stable, and the trend appears to be toward proliferation of genera (for a recent compendium, see Gardner and Patton, 1976).

The seeming imbalance in delineation of genera of neotomine-peromyscines compared to those of South American cricetines reflects a historical shift in use of character suites considered important by rodent systematists in assessing relationships. In the earlier descriptive phase of study, glirologists emphasized attributes of the skin, cranium, and dentition as evidence of relationships, while they have relied only recently upon characters of the baculum, glans penis, accessory glands and other soft anatomical parts for clues to kinship. This historical change illuminates apparently different levels of variability of certain character complexes among neotomine-peromyscines as compared to South American cricetines. The protean nature of South American cricetines in regard to their dentitions,

crania and body forms is eminently apparent; nevertheless, in structure of the glans penis, assortment of accessory glands, and gastric morphology, the assemblage as a whole is remarkably uniform (Arata, 1964; Carleton, 1973; Hooper and Musser, 1964a; Voss and Linzey, 1980). On the other hand, the diversity in genital structures within neotomine-peromyscines is at least as striking as their cranial or dental differentiation. It is a telling observation that populations of *Peromyscus mexicanus* and *Osgoodomys banderanus,* forms distantly related to one another in my results, have been confused until the past decade (Musser, 1969). Voss and Linzey (1980) develop this theme of levels of morphological variability in greater detail. The point raised here is that much of the phenotypic diversity within neotomine-peromyscines has been revealed comparatively recently. And if one incorporates this additional variation between species into a classification, thus using a wide variety of characters as the best estimate of phylogenetic relationship, then generic distinction seems the preferable course to follow for those subgenera of *Peromyscus* and *Neotoma.* Linzey and Layne (1969) debated this same taxonomic conclusion with regard to the subgenera of *Peromyscus* but refrained from recommending it.

The phylogenetic hypothesis developed here (Fig. 42) constitutes a framework for further study of relationships of neotomine-peromyscine rodents. My recognition of four groups of tribal level—tylomyines, baiomyines, neotomines and peromyscines—actually corresponds more favorably to Hooper's (1960) ealier discernment of four basic divisions within neotomine-peromyscines than to the later arrangement of Hooper and Musser (1964a). An obvious course in testing these alternative phylogenies involves the examination of other species, the survey of more characters, and the inclusion of different kinds of data, such as karyological and electrophoretic evidence. However, I believe an equally profitable approach is to examine more carefully some of the characters I used. In particular, histological and embryological investigation of the glans penis and male accessory glands could contribute better understanding of homologies and polarities of those organs. I am acutely aware that my coding of some characters was overly simplistic and masked finer points of dissimilarity. I defend this elementary approach by observing that the range of morphological diversity in my study collection was truly immense and that my intent was to delineate major phyletic units. In view of the spectrum of dental variation from the rooted, bunodont, brachyodont molars of a *Baiomys taylori* to the evergrowing, hypsodont, prismatic teeth of a *Dicrostonyx groenlandicus,* I felt a simplified coding scheme was the only reasonable treatment. Consequently, another worthwhile course is to evaluate restricted phyletic units, especially those seemingly well delimited, and employ more detailed character state trees as a means of more finely resolving cladistic relationships.

The Simple Versus Complex Penis and a Reappraisal of the Neotomine-Peromyscine and South American Cricetine Dichotomy

Perhaps no other series of studies has so significantly influenced our concepts of New World cricetine evolutionary relationships, and indeed those of all Muroidea, than the anatomical surveys of the phallus undertaken by Hooper (1958, 1959, 1960, 1962) and colleagues (Hooper and Hart, 1962; Hooper and Musser, 1964a, b). The occurrence of simple and complex phalli is fundamental to the notion of a phyletic breach between neotomine-peromyscines, on the one hand, and South American cricetines on the other. For this reason, I devoted attention to the morphological variation in the muroid glans penis, which I shall review here. The basic theses I wish to develop are:

1) There exists a structural continuum between the traditionally defined "complex" and "simple" penes. As a result one cannot objectively identify a basic division in phallic structure that corresponds to the separation of genera of New World cricetines into neotomine-peromyscines and South American cricetines as those assemblages are currently recognized.

2) The hypothesis of the simple penis as ancestral is an equally plausible, if not more harmonious, interpretation than the "complex" type as primitive for Muroidea. The terms embody a heterogeneity of phallic types that probably evolved independently from a simplified glans penis within various lines of Muroidea.

3) Based on the two observations given above, and a review of the evidence purporting to validate the dichotomy, it is premature to nomenclaturally formalize the groups as Peromyscini and Sigmodontini (or Peromyscinae and Sigmodontinae).

Although Hooper (1959) mentioned the existence of two kinds of phalli, the first definitive characterization of the "two different architectural schemes" was contained in his study of *Neotoma* and related genera (1960: 16–17). The two kinds differ primarily with regard to five features (see Figure 19): structure of the baculum; development of a crater; presence of lateral and medial bacular mounds; presence of crater embellishments, especially a dorsal papilla and urethral process; and complicated vascular sinuses and sacs. In the complex glans penis, the baculum has four parts, a long proximal element and three shorter distal ones termed the medial and lateral bacular digits. The baculum of the simple type is usually a single bone, presumably homologous to the proximal element of the complex, capped with a cartilaginous tip, but in some species, this cartilaginous segment is well developed. A terminal crater is found in the complex type and is usually absent in the simple. Mounds of soft tissue, usually a medial and two lateral ones, protrude into the crater, and generally the medial and lateral bacular digits of the baculum extend into the mounds. Such mounds do not occur in the simple glans; however, in those simple-penile forms having a terminal crater, the long cartilaginous tip projects into the crater and would seem to constitute a medial bacular digit and bacular mound. Other processes, such as crater-rim papillae, dorsolateral papillae, dorsal papillae, and urethral processes, occur within the crater,

or at the crater's edge, of the complex penis. Of these, the dorsal papilla and urethral process are standard traits. The dorsal papilla arises from the crater floor behind the medial bacular mound. The urethral process is situated at the ventral lip of the urinary meatus. It should be noted that the urethral process, found in species with a complex penis and also some species of *Neotoma,* and the ventral lappet of some *Peromyscus,* are not homologous structures, even though they are positioned similarly with regard to the urethral orifice. A ventral lappet is epidermal tissue that is clearly an extention of the body of the glans above the urinary opening; whereas, the urethral process is continuous with the corpus cavernosum urethrae and appears erectile. Lastly, a complex system of vascular sinuses and sacs occupies the interior of the complex phallus and is lacking or only rudimentary in the simple type. A complex penis was observed in species of South American cricetines and other muroid groups (microtines, gerbillines, and murines), and the simple penis was demonstrated in those 12 genera eventually known as "neotomine-peromyscines".

There exist numerous exceptions to the co-occurrence of these traits both within muroid groups having complex phalli and within neotomine-peromyscines. Complex phalli do not always contain the trident baculum; if not, it is usually the lateral bacular digits that are missing (Anderson, 1960; Hamilton, 1946; Hooper and Hart, 1962). Lidicker (1968) observed lateral bacular digits in only two of the 28 species of Hydromyinae and Murinae from New Guinea. A deep terminal crater typifies *Hodomys, Xenomys* and species of *Neotoma,* and a shallow crater characterizes *Baiomys* and *Scotinomys,* all genera of neotomine-peromyscines. Lateral bacular mounds occur more regularly than the lateral digits; however, *Scapteromys,* a South American cricetine, lacks lateral bacular mounds (Hooper and Musser, 1964a), and they are indistinctly developed in *Dicrostonyx,* a microtine, and the South American cricetine *Nyctomys* (Hooper and Hart, 1962a; Hooper and Musser, 1964a). Among neotomine-peromyscines, urethral processes are present in *Xenomys, Hodomys,* some *Neotoma,* and *Megadontomys thomasi.* The urethral processes of these forms are usually simpler than those found in complex glandes but some, as in *Xenomys* and *Hodomys,* are elaborate. The glandes of *Hodomys* and *Xenomys* contain dorsal papillae, apparently the only neotomine-peromyscines that do, and the glans of the microtine *Dicrostonyx* lacks a dorsal papilla.

All of these variations and others have been previously reported, but I have recounted them here to emphasize the diversity of the glans penis and the numerous departures from the simple and complex plans. The results of the principal component analyses of the 16 phallic variables substantiate this diversity (Figs. 35, 36). However, the remarkable aspect of these analyses is the phenetic divergence revealed among those phalli labeled as "simple". I did not obtain any clear separation between groups of muroids defined as having simple (neotomine-peromyscines) or complex (South American cricetines, microtines and gerbillines) penes. Many species of the former and latter groups clustered close to one another. In-

stead, the amount of differentiation between some forms with a simple glans (*e.g.* species of *Neotoma* versus *Peromyscus*) matched and even surpassed that observed between some complex and simple-penile species (*e.g.* South American cricetines versus *Xenomys, Hodomys* and *Tylomys*). These findings suggest that the simple and complex glandes intergrade imperceptibly when analysed in terms of their unit characters. Furthermore, they indicate that the term "simple" embraces a heterogeneity of structural forms, some of them highly divergent, and that this heterogeneity is not consonant with a singular descriptive label.

The tight cluster of species possessing complex glandes disclosed in the principal component analyses (Fig. 35) is at least partially artifactual. Because my study focused upon neotomine-peromyscine rodents, I underrepresented the variation in complex glandes. For example, I did not record the occurrence of lateral bacular digits in my analysis. Lateral bacular mounds (Character No. 60) usually occur in complex types, but, as noted above, lateral bacular digits are frequently missing. I did not tabulate the variety of junctions between the distal bacular elements and the proximal bone. In some species, the distal elements are strongly ankylosed or fused, while in others, they appear highly mobile with formation of a synovial joint (see Arata *et al.,* 1965). I did not note the disposition of the dorsal papilla, only its presence/absence. The dorsal papilla is recessed within a pocket in species of Gerbillinae (except *Tatera indica*), but it arises from the crater floor in most forms. Substantial variety in shape, manner of subdivision, and development of spiny armament obtains for urethral processes. I coded this process only as present or absent. I did not code parotoid lobes, features of the body of the glans in some South American cricetines (Hooper and Musser, 1964a). I did not document the occurrence of crater-rim papillae, which may be absent in some species or numerous in others. They exist on the glandes of many Microtinae (Hooper and Hart, 1962) and Hydromyinae (Lidicker, 1968). I did not include species of Hydromyinae, which have phalli with two craters, one situated within the other (Lidicker, *op. cit.*). The addition of such characters and species would certainly increase the dispersion among forms with complex phalli and impart the notion that the appellation "complex" embodies heterogeneous morphologies as well.

The issue of vascular sinuses and sacs deserves special mention. Earlier, Hooper (1960) cited vascular sinuses as a diagnostic trait of the complex glans penis, but only one of five central features. Later, Hooper and Musser (1964a) laid greater stress upon the internal circulatory structure as an integral component of the complex type and de-emphasized the importance of traits such as lateral bacular digits and crater papillae. The vascular sinuses consist of a lattice-like labyrinth of connective tissue inside the walls of the body of the glans penis. They occur in most short, broad glandes, including some neotomine-peromyscines (*Scotinomys, Tylomys, Isthmomys, Megadontomys, Hodomys* and *Neotoma*) and probably most muroids with a complex glans. The development of such sinuses, there-

fore, seems to be associated with phalli of a certain conformation and not strictly with simple or complex types. I tried to convey the presence of such sinuses by recording proportional features of the glans.

These circulatory sinuses are not to be confused with the vascular sacs of Hooper (1962) and Hooper and Musser (1964a). The sacs arise from near the base of the baculum and project distad, just beneath the floor of the crater. Pearson (1958:424), Hershkovitz (1962:59) and Hooper (1962: 3) illustrate their position. The origin and nature of the sacs remain unclear. Hooper (1962) thought they were continuous with the deep dorsal vein, and subsequently, Hooper and Musser (1964a) speculated that they were interconnected to similar tissues that extend into the lateral bacular mounds and appear to surround the lateral bacular digits. My own examinations suggest a confluence with the walls of the corpus cavernosum urethrae, but I am unconvinced. As noted by Hooper and Musser, such sacs are apparently lacking in simple glandes. Extremely elongate sacs occur in all species of Gerbillinae examined, and in *Sigmodon, Graomys* and *Calomys* of South American Cricetinae. Poorly developed sacs appear to be present in Microtinae. I could not verify to my satisfaction their existence in the phalli of *Oryzomys, Nectomys, Holochilus* and *Nyctomys*. Lidicker (1968) assumed the interior sinuses of hydromyine rodents were equivalent to Hooper's (1962) vascular sacs; however, to judge from Lidicker's descriptions, they are not. His misinterpretation is interesting because it suggests that true sacs are either missing in hydromyines or only rudimentary. When present, the vascular sacs are usually conspicuous, recognizable structures. Clearly, the significance of the vascular sacs must await detailed histological study. Based on evidence to date, they are absent in the simple-penile neotomine-peromyscines, but their presence cannot be confirmed in all complex kinds and their development may vary.

The lack of unambiguous recognition of simple and complex glans penes compels a re-examination of the direction of evolution assumed for this organ. Although Hooper (1958, 1959, 1960, 1962) refrained from speculating on primitive and advanced states of the glans penis, Hooper and Hart (1962) and Hooper and Musser (1964a) advanced several arguments supportive of the complex type as ancestral for Muroidea. Basically, their evidence reduces to four points, which I consider below.

1) The poorly developed lateral bacular mounds with little cartilage or bone have the aspects of vestiges.

As the authors themselves note, however, such structures may embody incipient stages in evolutionary development. One must appeal to other evidence.

2) The occurrence of a particular variant of the complex penis is found in species that qualify as an ancestral morphotype on the basis of cranial and dental features.

Hooper and Hart (1962) used this inference in their microtine study to argue that the relatively ornate glandes of *Clethrionomys* and *Phenacomys* are

primitive. This reasoning is equivalent to observing that a state is primitive if it occurs in taxa that are estimated to be primitive on other evidence. As noted by Lundberg (1972) and Kluge (1976), this postulate is probably the weakest for determining character polarities. Moreover, one could reach the opposite conclusion within microtines by noting the simplified glandes of *Dicrostonyx* and *Ellobius,* two genera believed to represent ancient lineages (Kretzoi, 1955; Repenning, 1968). Do they instead retain the primitive morphology of the glans?

3) The complex glans penis is the cosmopolitan type within Muroidea.

This is the most powerful of the arguments generated for the complex as ancestral, and one cannot dispute their judgment based on this criterion. The notion of a primitive character as being more widespread within a group is commonly accepted (Wagner, 1961; Kluge and Farris, 1969; Kluge, 1976), but it is not infallible.

Outgroup comparisons to the Muroidea and to the Muridae are illuminating. The phalli of species of Dipodoidea, the probable sister-group of Muroidea, are fundamentally simple in that they lack a trident baculum, terminal crater, and crater processes (Vinogradov, 1925; Wrigley, 1972). A pair of pouches occur lateral to the urethral opening in some Dipodidae (Vinogradov, 1925), but these do not resemble the craters found in muroids.

Tachyoryctes (Rhizomyidae), *Spalax* (Spalacidae) and *Myospalax* (Myospalacini) represent taxa of Muroidea considered by some more distantly related to the Muridae (Fig. 1), or to represent early offshoots of Eurasiatic Cricetodontinae (Chaline *et al.,* 1977). A single-unit baculum, terminal urinary meatus, absence of a crater, and lack of attendant crater structures (bacular mounds, urethral process and dorsal papilla) characterize the glandes of all three genera. The phallus of *Spalax* possesses a midventral cleft near the urinary opening; this does not appear homologous to the crater of Muridae. Interestingly, the glans penis in *Tachyoryctes* resembles that observed in *Tylomys nudicaudus,* with the exception of the tiny urethral processes in the latter.

Such outgroup comparisons do not necessarily exclude the hypothesis that the complex type constitutes the ancestral morphology for Muridae *(sensu latu).* However, the occurrence of dissimilar kinds of complex phalli within Muridae prompts additional questions. Is the most complex perforce the most primitive? For instance, is the double crater seen in some Hydromyinae ancestral to single-cratered forms? If not, and the formation of a second crater is considered derived, then one must admit the possibility of the initial evolution of a crater from a craterless form. Raising such questions underscores the arbitrariness even in selecting an ancestral plan from within complex types and establishes in a reciprocal fashion the plausibility, at least, of a simple to complex transition.

4) It seems less likely that the complex type could evolve in parallel within each of the several groups of muroids (gerbillines, microtines, murines and South American cricetines).

This argument follows a parsimony theme: to posit the simple penis as ancestral invokes more parallel evolutionary events than the alternative hypothesis. To explore this notion further, I constructed several two-way contingency tests involving the glans penis (simple versus complex) and five other morphological features surveyed above (Fig. 43). These comparisons implement Le Quesne's method (1969, 1972, 1974) of discovering a uniquely derived character. If for any pair of dichotomous characters, one finds all four character state combinations collectively exhibited by OTUs within a group (in this case Muroidea), then one cannot cladistically unite those OTUs without predicting some parallelism or character reversal. That is to say, either one or the other of the characters is not uniquely derived, or neither of them is. It is evident that all possible squares are occupied (Fig. 43). Perhaps just the five other characters selected are homoplasious and the states of the glans penis are uniquely evolved, but this seems unlikely. One must recognize the alternative implication that either the complex or simple glans has evolved independently within various muroid lineages regardless of the assumption of polarity.

In addition, I used the method of character compatibility to tabulate incompatibilities of the six characters of the glans penis coded in reverse order (see RESULTS). I applied the character compatibility program, using 74 characters and 58 species (including 25 with a complex penis and 33 neotomine-peromyscines), first with the six characters coded in the complex to simple order and next in the reverse sequence. As a result, the same kind of pair-wise comparisons discussed in the last paragraph were generated for each of the six characters against the remainder of the data set for the two coding schemes. The results indicate that either hypothesis of primitiveness predicts considerable incompatibility (Table 16). This does not prove that the simple penis represents the ancestral morphology. Nevertheless, it effectively disputes the charge that the simple penis as primitive necessarily involves much more parallelism.

In summary, I regard the first, second and fourth arguments for the primitive nature of the complex glans penis as unconvincing or, at best, equivocal. The third reason, the within-group distribution of types of glandes in Muridae, constitutes the strongest evidence for ancestry of the complex architectural plan. However, outgroup comparisons of other families within Muroidea, namely Spalacidae and Rhizomyidae, support the simple as primitive as does reference to the Dipodoidea, the probable sister-group of the Muroidea.

As an alternative hypothesis, I suggest that the ancestral morphotype of the muroid phallus lies within that range of morphologies defined as "simple". However, the ancestral condition is not like the conventional portrayal of the simple glans; for example, the long, narrow baculum and glans with dorsal and ventral lappets of a *Peromyscus boylii*. I regard that combination of traits as highly derived. Instead, it more closely resembles the phallic anatomy of extant *Onychomys* or perhaps *Tylomys*. The intersec-

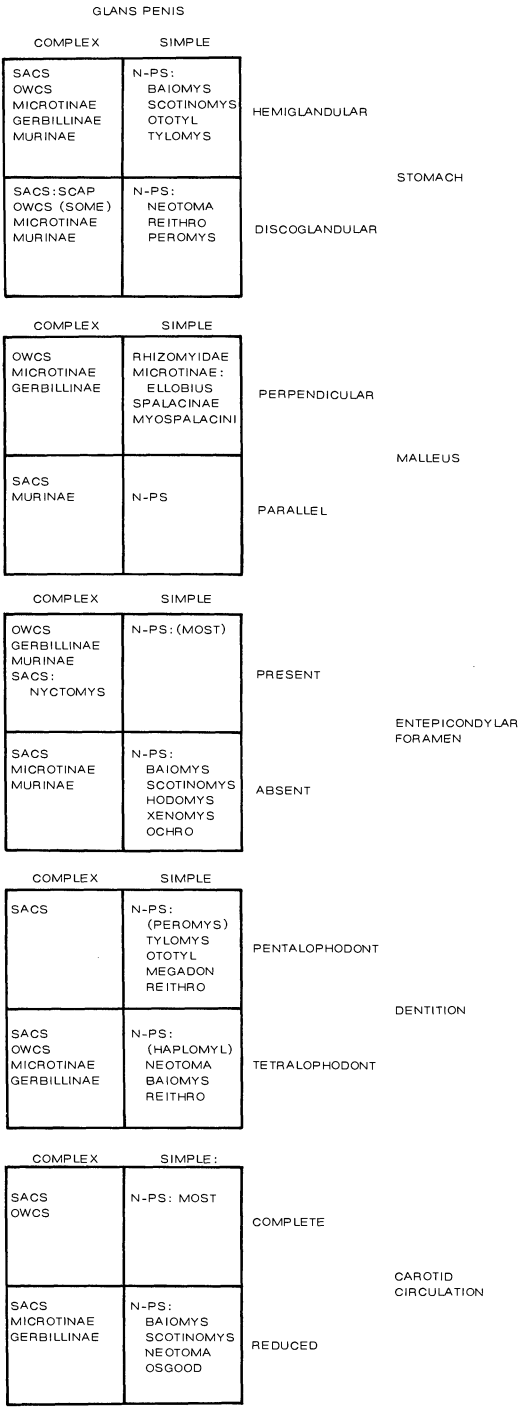


Fig. 43. Character compatibility of the glans penis with five other anatomical features for taxa of Muroidea. Occupation of every square in any dichotomous character comparison indicates that either one or the other character is not uniquely derived or, alternatively, neither of them is (see Discussion).

TABLE 16

COUNTS OF INCOMPATIBILITY OF SIX CHARACTERS OF THE GLANS PENIS OBTAINED WHEN CODED IN OPPOSITION (see DISCUSSION).

Character	POLARITY Complex ↓ Simple	Simple ↓ Complex
Position of Urinary Meatus	58	58
Urethral process	47	49
Dorsal papilla	52	52
Lateral bacular mounds	53	53
Length of cartilaginous tip divided by bacular length	64	65
Depth of crater divided by length of glans penis	63	63
Total number of incompatibilities observed	337	340
Maximum number of incompatibilities possible	438	438
Mean percent incompatibility	76.9	77.6

tion of the two major clouds of points in the plot of principal components one and two (Figs. 35, 44) circumscribes that morphology: a glans that is relatively short and broad; a baculum only as long as, or shorter than, the length of the glans' body; a terminal urinary meatus; lack of a crater (but perhaps development of a distinct shoulder at the margin of the soft tissue enclosing the bacular tip); absence of medial and lateral bacular mounds and digits, urethral process and dorsal papilla; and lack of a protrusible tip, ventral and dorsal lappets. Even within my limited survey of muroid species, several trends of phallic modification are apparent as exemplified by the glandes of *Peromyscus, Habromys, Neotomini* and South American cricetines (Fig. 44). A glans with two craters, lacking lateral bacular digits and possessing multiple rim papillae, as seen in Hydromyinae (Lidicker, 1968), represents another trend within Muroidea. I am convinced that as more groups of Muroidea are surveyed, other variations will be revealed, and a hypothesis of adaptive radiation from a relatively simple ancestral condition will constitute the most parsimonious interpretation.

Regardless of the correctness of this viewpoint, the morphological intergradation documented for the simple and complex phalli questions the propriety of formally recognizing the neotomine-peromyscines and South American cricetines as separate tribes or subfamilies. The distinction in phallic anatomy is less clear-cut than formerly supposed and warrants a conservative taxonomic approach until more information accumulates. In retrospect, some of the other investigations purporting to substantiate the dichotomy within New World cricetines are less persuasive and decisive than one would desire.

Rinker's (1954) myological survey included only 8 species representing four genera of the approximately 300 species and 58 genera of New World cricetines. Regretfully, I could not include myological characters in my data set. Nevertheless, on the basis of limited dissections of some neo-

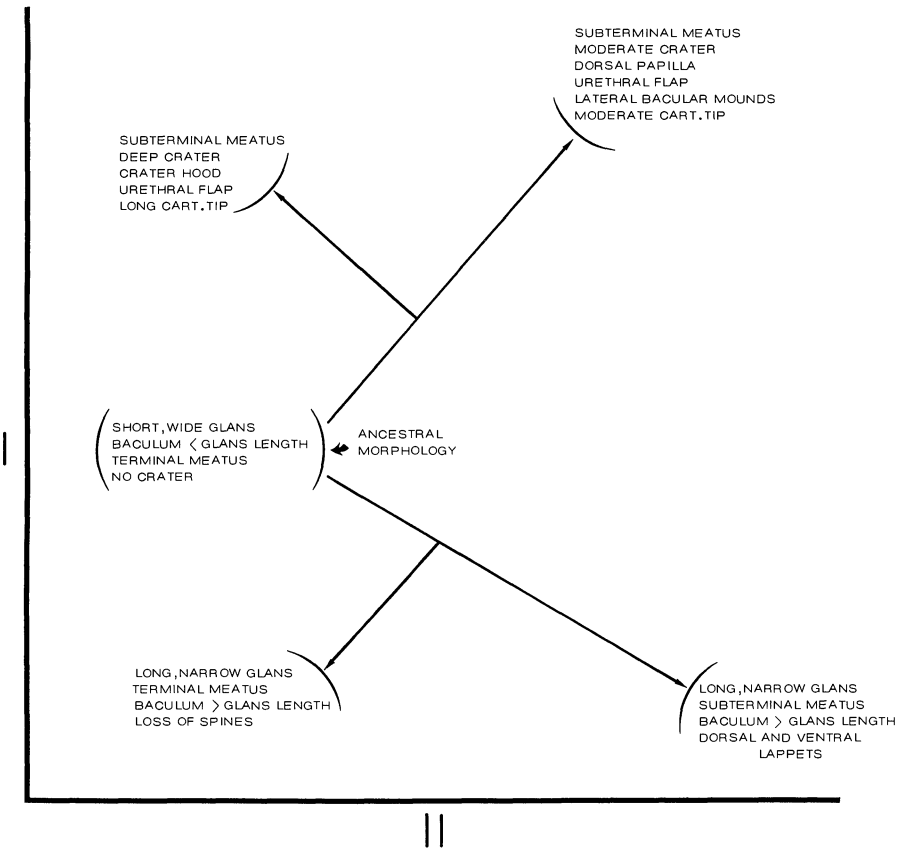


Fig. 44. Summary of principal trends in evolution of the glans penis based on my interpretation of character polarities and superimposed on the results of principal component analysis (see Fig. 35A).

tomine-peromyscines (*Baiomys, Scotinomys,* and *Tylomys*), I discovered that certain muscular features did not associate these genera with Rinker's "*Neotoma-Peromyscus* complex". Moreover, one wonders how much the inclusion of *Thomasomys* and *Akodon* as examples of South American cricetines instead of *Oryzomys* and *Sigmodon* would have altered Rinker's conclusions. The richness of diversity of the muscular system potentially offers many characters for evaluation of New World cricetine relationships.

The contributions of Arata (1964) and Carleton (1973) document differences in the frequency of occurrence of certain features within neotomine-peromyscines as compared to South American cricetines. Yet neither study identifies any derived characters that delimit either of the cricetine assemblages. *Baiomys, Scotinomys, Peromyscus* and *Reithrodontomys* possess almost complete sets of accessory reproductive glands like those found in South American cricetines (Arata, 1964; Voss and Linzey, 1980). The unilocular, hemiglandular stomach pattern typical of most South American cricetines does not differ from the stomachs in examples

of *Baiomys, Scotinomys, Tylomys* and *Ototylomys* (Carleton, 1973). At best, these two organ systems suggest polythetic taxa, but taken alone, they do not critically resolve the notion of a dichotomy.

Considerable attention has been devoted to the simple-penis and complex-penis assemblages and the dispersion of cricetine rodents into South America (Hershkovitz, 1966b, 1972; Patterson and Pascual, 1972; Savage, 1974; Marshall, 1979). Yet most of this zoogeographic debate does not pertain directly to the schism within New World cricetines but rather centers on the recency (late Pliocene or Miocene) and the manner of entry (closure of the land bridge or waif dispersal) into South America. If several stocks of South American cricetines existed in North America by late Miocene time, as maintained by Baskin (1978), then the matter of Latin American faunal interchange is largely irrelevant to the initial differentiation of neotomine-peromyscines from South American cricetines. Perhaps one factor associating Latin American faunal history to the simple and complex-penile cricetines is an *a posteriori* desire to link what is perceived as a major taxonomic division with an equally significant zoogeographic event. As it stands, the connection of zoogeographical events to the hypothesized phyletic rift within New World cricetines is unclear, and traditional opinions may have to be drastically revised as evidence from the renewed paleontological interest (*e.g.* Baskin, 1978 and Marshall, 1979) is synthesized.

The occurrence of various ectoparasites (primarily mites, ticks and fleas) on their rodent hosts has been cited as supportive of a fundamental division within New World cricetines (Wenzel and Tipton, 1966; Hershkovitz, 1972). Presumably, the long-term coevolution of the ectoparasites and their hosts leads to increased host specificity; as a result, parasites with restricted distributions may serve as indicators of the phylogenetic relationships of the hosts. Thus, Wenzel and Tipton (1966) have interpreted the assortment of ectoparasites found on complex-penile cricetines as belonging to groups whose origin or center of distribution lies in South America and whose taxonomic composition differs, in some significant regard, from those parasites residing upon simple-penile forms. In my opinion, a number of possible alternatives must be addressed before one attributes differences in ectoparasite loads to phylogenetic affinities of the hosts.

For example, what influence does the environment of the host exert upon the assemblage of ectoparasites? Seemingly, interrelated environmental factors (such as elevation, climate, humidity, structure of the plant community, and slope-exposure) play a major role. In a study of the parasites of *Peromyscus floridanus,* Layne (1963) identified habitat difference as the most important factor accounting for patterns of parasitism among the host populations. Furthermore, he (1971) noted that the southern limits of some northern fleas are apparently related to climatic variables rather than the occurrence of suitable hosts. Similarly, Tipton and Mendez (1966:318) considered that "Climatic factors probably influence the distri-

bution of the fleas [of the genus *Kohlsia*] to a much greater extent than that of the hosts." Wenzel and Tipton (1966) have noted a strong association of ectoparasites with elevation. Generally, the elevational range of the rodent hosts surpasses that of their poikilothermic ectoparasites. The association of elevation and the ectoparasite fauna is significant because, as recognized by Wenzel and Tipton *(op. cit.),* the distribution of cricetine rodents is stratified altitudinally, complex-penis species found predominantly in tropical and subtropical zones and simple-penile kinds restricted to lower-montane and montane belts. This relationship introduces another gamut of factors that vary with elevation (rainfall, temperature, habitat, seasonality, etc.) and that may affect the distribution of the ectoparasites. Variance in phylogenetic affinity of the rodents, therefore, is only one among a suite of variables that could account for the patterns of occurrence of these ectoparasites.

The siphonapteran genus *Polygenis* illustrates the ambiguity involved in applying the ectoparasitological data to problems on higher taxonomic levels. Wenzel and Tipton (1966:718) viewed *Polygenis* as ". . . an 'expanding' South American genus which has . . . dispersed into Middle America along with complex-penis-type Cricetinae and caviomorph rodents from South America." If the rarity of this genus on *Peromyscus* (a few fleas of two species were recovered—Tipton and Mendez, 1966) provides corroboration of a distant relationship of complex and simple-penile cricetines, then does the abundance of these fleas on South American cricetines and caviomorphs qualify as evidence of a close relationship between them? The absurdity of this suggestion emphasizes the importance of the broad elevational overlap of many complex-penile cricetines and caviomorphs in Panama and the lack of such between those groups and the montane peromyscines. Interestingly, a relatively high incidence of infestation by *Polygenis klagesi* was recorded for *Tylomys,* a genus assigned to the simple-phallic group; specimens of this rodent were collected below 4000 feet. In Florida, Layne (1971) found *Polygenis gwyni* on *Sigmodon hispidus* and *Oryzomys palustris,* both representatives of South American cricetines, as well as *Reithrodontomys humulis, Neotoma floridana* and three species of *Peromyscus,* all examples with a simple penis. *Sigmodon hispidus* is the most important reservoir for this flea, but it is as common on *Neotoma, Reithrodontomys* and *Peromyscus* as on *Oryzomys.* Moreover, Layne (1963) described a new species *(Polygenis floridanus)* that is primarily limited to *Peromyscus floridanus,* an occurrence which Wenzel and Tipton (1966:709) explained as resulting from transferral to *Peromyscus.* With what regularity do such transferences or adoptions of new hosts occur, and what reliance should be placed on this data without some feeling for the probability of such occurrences? The lack of firm answers to these questions and the complexity of factors influencing ectoparasite loads demand a cautionary approach. The problem elegantly lends itself to a factor analysis in which the proportion of variance in ectoparasite distributions attributable to phylogenetic affinity of the hosts can be compared to that due to environ-

mental and other variables. At this point, I question whether the data presented by Wenzel and Tipton (1966) in fact suggest a specificity of the ectoparasites at a high order of taxonomic relationship comparable to the neotomine-peromyscines versus South American cricetines.

The results of the Wagner tree analysis using species of neotomine-peromyscines and South American cricetines also cast doubt on the division as it is usually understood (Fig. 41). An unexpected finding is the cladistic union of *Nyctomys,* a South American cricetine, with *Tylomys* and *Ototylomys* at the first bifurcation.

The systematic position of *Nyctomys* has long remained enigmatic. Hershkovitz (1944) placed the genus in the thomasomyine group of South American cricetines. Hooper and Musser (1964a) noted the peculiar features of the phallus of *Nyctomys* and arranged it as a distant outlier to the mass of South American cricetines. Arata (1964) reached a similar conclusion but considered it an annectent form between South American cricetines and neotomine-peromyscines. As a result of their survey of accessory reproductive glands, Voss and Linzey (1980) suggested complete divorcement of *Nyctomys* from South American cricetines. Derived characters responsible for the relationship of *Nyctomys* to *Tylomys* and *Ototylomys* include bifurcation of the lingual root of M2 (10), reduced carotid circulation (16), development of supraorbital crests (24), increase in palatal ridges (45), absence of the gall bladder (49), and greater caecal complexity (51). Unlike other South American cricetines examined, *Nyctomys* retains an entepicondylar foramen, a primitive condition shared with *Tylomys* and *Ototylomys.* The basal divergence of *Nyctomys* supports Hershkovitz's (1966b) interpretation of the archaic nature of *Nyctomys.* Although they are highly differentiated from *Nyctomys, Tylomys* and *Ototylomys* must be considered its closest living relatives. The possibility that the three (and presumably *Otonyctomys*) represent survivors of a phyletically ancient group requires investigation.

The next division of the Wagner tree largely corresponds to the neotomine-peromyscines and South American cricetines, except for the disposition of *Ochrotomys, Baiomys,* and *Scotinomys* at the base of the branch including South American cricetines. I do not intend to attach formal taxonomic significance to the cladistic position of these genera. I do attach significance to my continued inability to demonstrate a biphyletic arrangement of genera corresponding to the recognized neotomine-peromyscine and South American cricetine assemblages, whether employing the entire suite of characters or just the 16 traits of the glans penis. Certainly there are major cladistic groups, such as the Neotomini and most Peromyscini, that appear more closely related to one another than to South American cricetines. Still, the predicted early divergence of *Ototylomys, Tylomys,* and *Nyctomys* departs from the conventional alignment of neotomine-peromyscines and South American cricetines. And there are the intermediate forms (for instance, *Baiomys* and *Scotinomys*) whose phylogenetic affinity is ambiguous. The uncertain position of such genera

prompts the suspicion that the two groups of New World cricetines are not monophyletic assemblages as presently constituted. As a result, I am no longer comfortable with the assumption that the 18 genera of neotómine-peromyscines shared a more recent common ancestor different from that shared by all 40 genera of South American cricetines, which I believe is the logical phylogenetic implication of erecting the subfamilies (or tribes) Peromyscinae and Sigmodontinae to contain those genera.

In reading Hooper (1959, 1960), Hooper and Hart (1962) and Hooper and Musser (1964), it is abundantly clear that they phrase their ideas as an hypothesis and that they invite testing of their hypothesis. Unfortunately, the notion of the simple versus complex glans penis became canonized in the literature without the critical testing they invited. Hooper and associates identified a singular variant of the muroid phallus when they characterized the simple-type glans penis, but I question whether it is inherently more different than any of the other variations in muroid phallic morphology.

On the basis of the evidence at hand, it is premature to taxonomically formalize a division within New World cricetines. The separation of neotomine-peromyscines and South American cricetines clearly does not match the differentiation of the Microtinae and Gerbillinae. It seems preferable to use informally the four tribes suggested above (tylomyine, baiomyine, neotomine, and peromyscine) at the same level as the eight identified for the South American forms (akodont, ichthyomyine, oryzomyine, oxymycterine, phyllotine, scapteromyine, sigmodont, and thomasomyine) until further studies illuminate more clearly their interrelationships.

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