A SYNOPSIS OF FOSSIL GRASSHOPPER MICE, GENUS *ONYCHOMYS*, AND THEIR RELATIONSHIPS TO RECENT SPECIES

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ABSTRACT

Grasshopper mice, genus *Onychomys*, are known from the Hemphillian to the Recent. Seven fossil forms (*bensoni, fossilis, gidleyi, jinglebobensis, larrabeei, martini* and *pedroensis*) have been described, and in this paper, a new species (*O. hollisteri*) is named from the late Blancan Borchers local fauna. The new form differs from its sympatric congenor, *O. fossilis*, mainly in smaller size. The taxonomic status and phylogenetic affinities of these eight nominal fossil species were examined with respect to each other and to the two living species, *leucogaster* and *torridus*. In addition to conventional univariate treatments, several multivariate numerical techniques (shortest connection network, principal component and cluster analyses) were employed to assist our evaluation; time, or stratigraphic position, was secondarily introduced into the phylogenetic analysis. It is concluded that only two lineages, each consisting of three successional species, are represented in the study material: *gidleyi* (with *larrabeei* in synonomy) → *pedroensis* (with *fossilis* and *jinglebobensis* in synonomy) → *leucogaster*; and *bensoni* → *hollisteri* new species → *torridus*. *Onychomys martini* is phenetically closest to *bensoni* but more material is required to elucidate its status more fully. The two lineages have closely paralleled one another in dental modifications, including increase in height of the primary cusps and reduction in relative length of the third molar with concomitant increases in the relative lengths of the first and second molars. Rates of evolution and the functional significance of these evolutionary changes are discussed.

INTRODUCTION

The investigation reported herein emerged from the discovery of two species of grasshopper mice, genus *Onychomys*, in the late Blancan White Rock local fauna, Belleville Formation, Kansas (Eshelman, 1975). One form was questionably identified as *O. fossilis*, but the specimens from the White Rock fauna are too few and fragmentary to allow an adequate description and diagnosis of the second species. Preliminary examination of the slightly younger Borchers local fauna (first reported by Hibbard, 1941c) also disclosed a second species of grasshopper mouse among the abundant *Onychomys* material recovered there and encouraged us to rigorously substantiate this find. The coexistence of two species of fossil *Onychomys* and the possibility that they may be ancestral to the two living grasshopper mice, *leucogaster* and *torridus*, provided impetus to systematically review all seven named fossil species of *Onychomys* (listed in approximate stratigraphic order):

Hemphillian
   O. martini (Hibbard, 1937), Edson Quarry local fauna;
   O. larrabeei (Hibbard, 1953), Saw Rock Canyon local fauna;
Blancan
   O. gidleyi (Hibbard, 1941a), Rexroad local fauna;
   O. bensoni (Gidley, 1922), Benson local fauna;
   O. fossilis (Hibbard, 1941c), Borchers local fauna;
Irvingtonian
   O. pedroensis (Gidley, 1922), Curtis Ranch local fauna;
Rancho la Brean
   O. jinglebobensis (Hibbard, 1955), Jinglebob local fauna.

In order to interpret differences between the seven nominal fossil species of grasshopper mice, we first required knowledge of the morphological limits of the two recent species. Our initial protocol was to evaluate the phenetic relationships of all samples, both fossil and living, as if they were contemporaneous forms. For purposes of analysis, we accepted populations of *torridus* and *leucogaster* as representative examples of "good" biological species and assumed that they documented the normal range of intra- and interspecific variation expected (as will become apparent, this assumption quickly proved suspect). The various fossil "populations" were viewed as unknowns whose taxonomic status and phylogenetic relationships must yet be ascertained. The time vector was secondarily introduced to elucidate possible character chronoclines and to examine ancestor-descendant polarities or relationships of common ancestry.

From our initial goal of simply reporting a new species of *Onychomys*, our study expanded to its present form wherein we:

(1) taxonomically revise the nominal fossil species of *Onychomys*, drawing upon a variety of numerical techniques commonly applied to neontological problems of the same kind,

(2) evaluate the phylogenetic relationships of the extinct taxa, particularly with respect to the two living species,

(3) examine patterns of variability and morphological rates of evolution, and

(4) interpret the functional significance and selective milieu which may have accounted for the character modifications and resulted in the modern species.

Our study has benefitted greatly from the papers of Rowell (1970), Cracraft (1974), Gingerich (1976a,b), Harper (1976), Engelmann and Wiley (1977), Szalay (1977) and Patterson and Rosen (1977), although our methodology and data interpretation may depart to a greater or lesser degree from each of them.

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MATERIALS AND METHODS

Specimens utilized in the various multivariate analyses consisted entirely of mandibular fragments with complete or partial tooth rows. We limited our multivariate treatments to lower jaws because they are more frequently preserved and recovered as fossils than are the more fragile maxillaries, and because most holotypes of the fossil species are lower jaws with intact molar series. Maxillary fragments were initially examined and measured, but too few were encountered with complete tooth rows. Eleven mandibular and tooth dimensions were measured as follows: (1) length of M_1-M_3 (LM_1-M_3); (2) length of M_1 (LM_1); (3) length of M_2 (LM_2); (4) length of M_3 (LM_3); (5) length of the talonid heel (hypoconid and entoconid) of M_3 (LM_3 tal.) — from the narrowest point formed by the reentrant valleys to the posterior margin of M_3; (6) anterior width of M_1 (AWM_1) — across the metaconid and protoconid; (7) posterior width of M_1 (PWM_1) — across the hypoconid and entoconid; (8) width of M_2 (WM_2) — across the metaconid and protoconid; (9) width of M_3 (WM_3) — across the metaconid and protoconid; (10) height of protoconid of M_1 — from the inflexion formed by the base of the anteroconid and anterior root (as viewed laterally) to the apex of the protoconid; (11) depth of ramus below M_1 — measured on the labial side of the dentary. All measurements were taken to 0.01 mm using a craniometer (Anderson, 1968) at 45 x magnification.

Specimens of both living and fossil *Onychomys* were assigned to six general age-classes based on the degree of wear of the first molar. These six age-classes are broadly comparable to those established by Van Cura and Hoffmeister (1966) for *Onychomys* in Arizona. Precise correspondence of their age-classes with ours is not likely, however, since they employed characteristics of wear of the entire tooth row. We restricted our assignments to criteria of the M_1 because few complete dentitions were available for many of the fossil examples.

Consequently, recognition of wear-stages III-VI is based only on a progressive widening of the dentine basins and reduction of the cusps. To reduce the subjectivity in assignment to wear-class, six individuals from one of the larger samples (*O. leucogaster* from Texas) were selected as representative standards; thus, every other specimen was compared to these six (listed below) for "age" classification. From youngest to oldest, our six wear stages are defined below:

I.   —cusps well elevated and conical; dentine tract of protoconid separate from that of the metaconid; enamel edges of the ridges connecting the primary cusps touching or nearly so — especially noticeable between the metaconid and protoconid and between the entoconid and hypoconid (UMMZ 67012).

II. —wear increased such that dentine of anteroconid and metaconid is confluent; narrow line of dentine visible on ridges connecting metaconid and protoconid, and hypoconid and entoconid (UMMZ 67004).

III. —dentine tracts broader; cusps lower and less defined (UMMZ 66975).

IV. —dentine tracts broader, cusps lower and less defined (UMMZ 65511).

V.   —dentine tracts broader; cusps lower and less defined (UMMZ 66959).

VI. —heavily worn; tooth "dished out" (UMMZ 66963).

The 10 samples (= operational taxonomic units, OTUs) of extant *Onychomys* included in the phenetic studies are listed below. In some instances, specimens from nearby localities were pooled to increase sample size. Allocation of individuals to subspecies follows Hollister (1914) and Hall and Kelson (1959). The number in parentheses preceding each locality corresponds to that given on the map in Figure 1; the number after the locality indicates sample size. Since only one OTU of a

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species occurs in any given state, the OTUs are subsequently referenced by the standard two-letter state abbreviations preceded by "*l*" or "*t*" (*leucogaster* or *torridus*) in the various tables and figures.

    O. leucogaster arcticeps:
       (1) Hooker, Cherry and Sheridan Counties, Nebraska, 24 (*l*-NE).
       (2) Bailey Co., Texas, 34 (*l*-TX).
       (3) Sweetwater and Uinta Counties, Wyoming, 12 (*l*-WY).
    O. l. breviauritus:
       (4) Woods Co., Oklahoma, 16 (*l*-OK).
    O. l. brevicaudus:
       (5) Elko Co., Nevada, 4 (*l*-NV).
    O. l. leucogaster:
       (6) Benson, Kidder and Stutsman Counties, North Dakota, 17 (*l*-ND).
    O. torridus longicaudus:
       (7) Clark Co., Nevada, 23 (*t*-NV).
    O. t. torridus:
       (8) Pima and Cochise Counties, Arizona, 16 (*t*-AZ).
       (9) Otero Co., New Mexico, 9 (*t*-NM).
     (10) Jeff Davis Co., Texas, 12 (*t*-TX).

Most samples of extinct *Onychomys* utilized in the multivariate analyses originate from the vertebrate faunal sequences of either the San Pedro Valley, Arizona or southwestern Kansas (Fig. 1). Many more specimens covering a wider geographic range were actually examined (see species summaries for an enumeration), but are not included in the phenetic treatments due to inadequacy of the samples (*i.e.*, only isolated teeth or dentary fragments with incomplete dentitions). The list of fossil species studied (arranged alphabetically) contains their general provenance and cites the major studies in which the species is either named or the local fauna described. More complete stratigraphic information may be obtained from those studies. Sample sizes given below indicate only the number of specimens with intact molar rows; nevertheless, mean dental dimensions may have been actually calculated on larger sample sizes, since many mandibles possessed at least some teeth (see tables of measurements, Appendix 1). Still, some of the fossil species are known only by the holotype. Species and locality abbreviations for fossil OTUs are provided below in parentheses.

    O. bensoni: Benson local fauna, San Pedro Valley Formation, Arizona, 1 (Gidley, 1922; Gazin, 1942).

    O. fossilis: Borchers local fauna, Crooked Creek Formation, Kansas, 19 (Hibbard, 1941c).

    O. gidleyi: Fox Canyon local fauna, Rexroad Formation, Kansas, 13 (*g*-FC) (Hibbard, 1950); Rexroad local fauna, Wendell Fox locality, Rexroad Formation, Kansas, 6 (*g*-WF) (Carleton, unpub.); Rexroad local fauna, locality No. 3, Rexroad Formation, Kansas, 5 (*g*-RR) (Hibbard, 1941 a,b); Beck Ranch local fauna, Yellow Quarry, Texas, 2 (*g*-BR) (Dalquest, 1978).

    O. jinglebobensis: Jinglebob local fauna, Kingsdown Formation, Kansas, 1 (Hibbard, 1955).

    O. larrabeei: Saw Rock Canyon local fauna, Rexroad Formation, Kansas, 1 (Hibbard, 1949, 1953, 1964).

    O. leucogaster: Schulze Cave, Layer C 1, Edwards Co., Texas, 10 (*l*-SC) (Dalquest, *et al.*, 1969); Friesenhahn Cave, Bexar Co., Texas, 9 (*l*-FC) (Lundelius, 1967).

    O. pedroensis: Curtis Ranch local fauna, San Pedro Valley Formation, Arizona, 1 (Gidley, 1922; Gazin, 1942).

    O. sp. nov.: Borchers local fauna, Crooked Creek Formation, Kansas, 4 (Hibbard, 1941c; Carleton and Eshelman, this study).

Standard descriptive statistics (mean, standard deviation, standard error of the mean, coefficient of variation, and range) were calculated for the 11 quantitative variables for each of the extinct and extant OTUs listed above. The coefficient of variation was multiplied by (1 + 1/4N), a factor derived by Haldane (1955) to correct for underestimation of the coefficient of variation due to small sample sizes. Product-moment correlation coefficients were derived for all possible pairs of variables, and linear regressions were performed for various pairs of variables and for the morphometric variables against the six wear-classes defined. Student's *t*-tests were executed for each dental measurement of the living species to test for possible sexual dimorphism. A multiple, linear discriminant function analysis was also performed using the eleven quantitative variables to identify those variables which give best separation of *O. leucogaster* and *torridus*. Phenetic relationships among the samples were summarized by a shortest connection network, principal component analysis and cluster analysis. Locality means (or individual measurements in cases where a fossil species is known by a single specimen) were employed as the character states, and characters were standardized in all three methods.
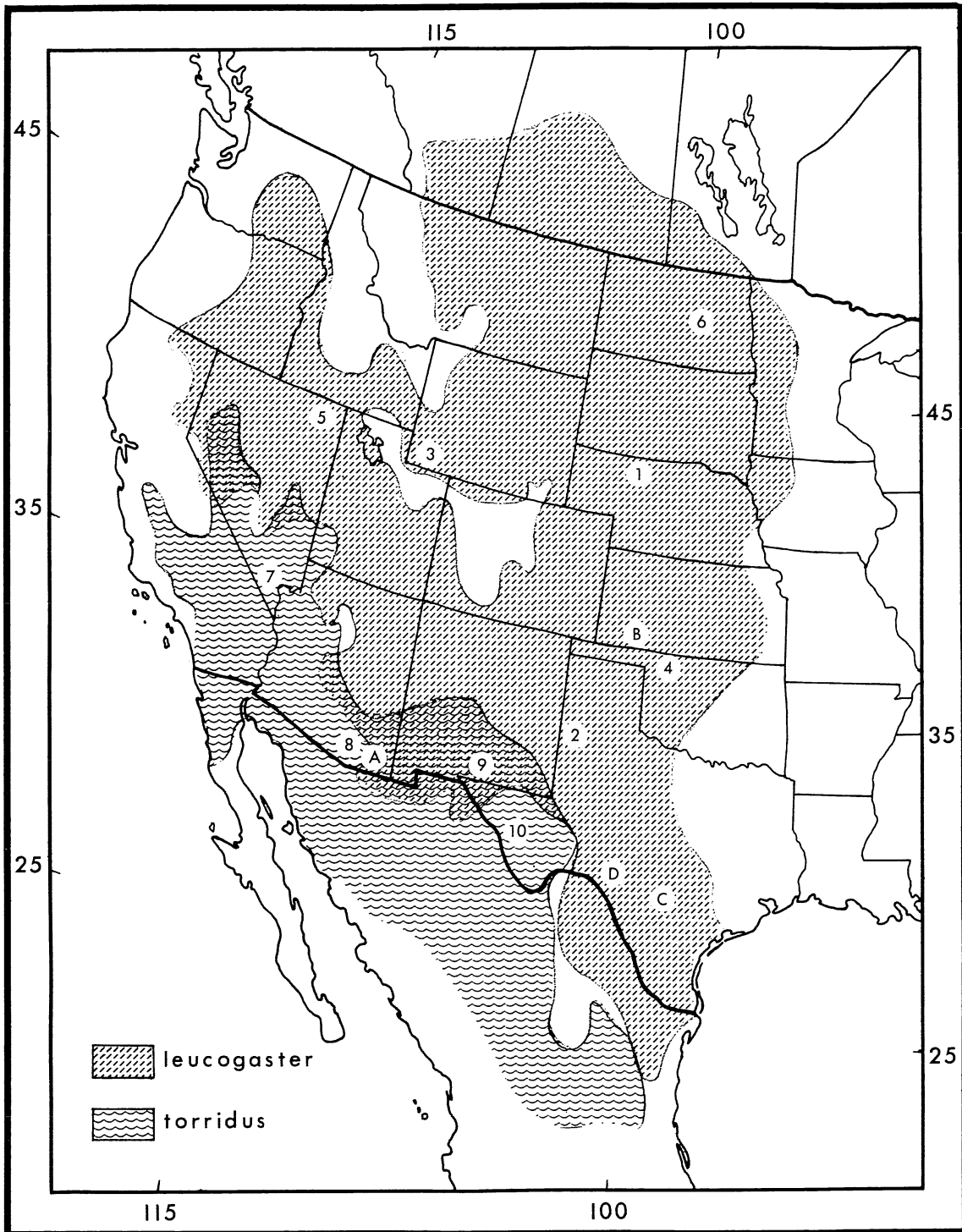
Figure 1. Distribution map (adapted from Hall and Kelson, 1959) showing geographic ranges of the two living species of *Onychomys*. Ten numbered localities refer to samples of Recent *torridus* and *leucogaster* listed in the Materials and Methods. The four lettered localities signify major fossil localities as follows: A) San Pedro Valley Formation, Arizona; B) Pliocene/Pleistocene strata in Meade Co., Kansas; C) Friesenhahn Cave, Bexar Co., Texas; D) Schulze Cave, Edwards Co., Texas.

Principal components were extracted from both the correlation and variance — covariance matrices; loading of each variable on the principal components is expressed by a correlation coefficient (Morrison, 1967). Cluster analyses were generated from both correlation and distance matrices and phenograms produced by the unweighted pair-group method using arithmetic averages (for discussion, see Sneath and Sokal, 1973); coefficients of cophenetic correlation were calculated for each phenogram. Data processing was performed by the Michigan Interactive Data Analysis System (MIDAS), a series of computer programs developed by the Statistical Research Laboratory of the University of Michigan.

Rates of evolution were calculated in *darwins* using the formula advanced by Haldane (1949):

$$\frac{\log \text{ natural } X_t - \log \text{ natural } X_0}{T}$$

where a character has the value X_t at time t and X_0 at time 0 and T is expressed in units at one million years (=crons). Since the change in log natural of a character per million years is generally quite small, evolutionary rates have been converted to millidarwins.

Institutions from which we borrowed specimens have been abbreviated as follows:

MCZ	Museum of Comparative Zoology, Harvard
MSU, TX	Midwestern State University, Texas
UA	Dept. Geological Sciences, University of Arizona
UKMVP	University of Kansas Museum of Vertebrate Paleontology
UMMP	University of Michigan Museum of Paleontology
UMMZ	University of Michigan Museum of Zoology
USNM	U.S. National Museum of Natural History, Dept. of Paleobiology
UT	Texas Memorial Museum, University of Texas, Austin

RESULTS

Dental Features of
O. leucogaster and *O. torridus*

In order to interpret variation in our fossil samples of *Onychomys* more knowledgably, we have attempted first to document patterns of variation within and between populations of the two living species.

While *torridus* and *leucogaster* are relatively easy to distinguish on the basis of skin and skull features, identification using dental traits is less obvious. Most apparent differences are size-related, especially as manifested in the length of the tooth row, widths of teeth, depth of ramus (and overall stoutness of the mandible), height of the primary cusps (in specimens with comparable tooth-wear), and wider incisors. In each instance, specimens of *leucogaster* exceed those of *torridus*, but the ranges of measurements may substantially overlap (see Appendix 1). The results of the discriminant function analysis corroborate our impressions derived from visual inspection of lower jaws of the two species. The four variables with the largest discriminant multipliers, that is, those variables that exhibit the least variation and overlap, include two width measurements (WM_2 and AWM_1), length M_1-M_3, and height of the protoconid (Table 1). Because the differences are on a larger scale, length of M_1-M_3 and depth of ramus are more readily apparent and therefore more practical to use.

Given the discriminant functions generated, specimens of *torridus* and *leucogaster* were individually classified by the computer as one or the other species using their posterior probabilities of classification. Only four specimens, all from Nevada identified as *leucogaster brevicaudus*, were "incorrectly" classified. Re-examination of the dentition, skulls and skins of these particular specimens (of course, the paleontologist doesn't enjoy such recourse to another suite of characters) substantiated their identification as *l. brevicaudus* and emphasized the importance of the size factor in the discriminant function analysis. Individuals of this subspecies (together with the westernmost form, *l. fuscogriseus*) are the smallest examples of *leucogaster* and fall well within the size range of *torridus*. Only judging proportional characters of the teeth (discussed below) and traits of the skin and skull reveals an affinity with *leucogaster*. The enigmatic position of these specimens will become more apparent upon further analysis.

In addition to contrast in size, *torridus* and *leucogaster* also differ in proportional aspects of their dentitions. For one, the M_3 is relatively smaller in samples of *torridus*; this is especially evident in the smaller size of the talonid portion (Table 2, Fig. 2). As a result, the M_3 appears subcircular in outline in *torridus* and slightly more oblong in *leucogaster*. The M_1 of *torridus* is relatively longer compared to that of *leuco-*

TABLE 1. Discriminant multipliers derived for each variable through discriminant function analysis of all *torridus* (N=60) and *leucogaster* (N=107).

LM_1-M_3	6.71
LM_1	-4.60
LM_2	-3.75
LM_3	-1.58
LM_3 talonid	4.15
AWM_1	4.86
PWM_1	3.76
WM_2	-8.95
WM_3	0.97
Height of protoconid	4.80
Depth of ramus	2.13

TABLE 2.   Ratios of selected mean dental lengths of living *Onychomys*.

Species and Locality (N)	$\frac{M_1}{M_{1-3}}$	$\frac{M_2}{M_{1-3}}$	$\frac{M_3}{M_{1-3}}$	$\frac{M_2}{M_1}$	$\frac{M_3}{M_1}$	$\frac{M_3}{M_2}$	$\frac{M_3\text{ tal.}}{M_3}$
leucogaster							
Texas(34)	42.7	35.4	22.0	83.0	51.6	62.2	41.2
Oklahoma(16)	42.6	35.6	22.4	83.7	52.6	62.9	44.0
Nebraska(24)	42.8	35.5	21.9	82.8	51.1	61.7	46.3
North Dakota(17)	42.7	35.6	22.2	83.3	52.2	62.6	42.3
Wyoming(12)	42.6	35.5	22.0	83.3	51.7	62.0	41.9
Nevada(4)	42.8	35.8	22.2	83.5	51.8	62.0	43.5
torridus							
New Mexico(9)	44.4	36.4	20.2	81.9	45.6	55.7	34.6
Arizona(16)	43.8	35.9	21.4	82.1	48.8	59.4	35.4
Texas(12)	45.4	36.2	19.2	79.8	42.2	52.9	32.9
Nevada(23)	44.3	35.9	21.2	81.1	47.8	58.9	39.5

Figure 2.   Crown views of left lower molar rows of: left — *O. torridus* (UMMZ 95873, Jeff Davis Co., Texas); right — *O. leucogaster* (UMMZ 67010, Bailey Co., Texas).

gaster (Table 2), but the difference is less striking than relative size of M_3. Another proportional dissimilarity involves the pronouncement of the knob found at the base of the incisor. In specimens of *leucogaster*, a distinct knob (usually termed the capsular process) projects laterally from the dentary at the origin of the incisor; thus, a sulcus is formed between the capsular process and the base of the coronoid process. The capsular process is weakly developed, with only a faint sulcus in examples of *torridus* (Fig. 3). This interspecific distinction is quite consistant based on examples of each species that we examined. Some variation is recognized: *leucogaster* from Texas possessed a smaller capsular process than other *leucogaster* studied; and *torridus* from Nevada exhibited a moderately sized capsular process (although still less pronounced than *leucogaster* from Texas) compared to other *torridus*. It should be noted that specimens of *leucogaster* from Nevada (= *l. brevicaudus*) agree with other *leucogaster* with regard to each of the differences in proportion described above.

No significant differences between the sexes of either species were discovered for any dental variable (Table 3). In fact, differences in mean measurements were extremely minute, generally on the order of 0.01 mm. This lack of sexual dimorphism in size agrees with the findings of Van Cura and Hoffmeister (1966), who measured 16 variables of the skin and skull, including length of maxillary tooth row, of both species in Arizona. In addition, the growth and development studies of Horner and Taylor (1968) on *O. t. longicaudus* and Pinter (1970) on *O. t. torridus* and *O. l. articeps* revealed no significant difference between the sexes in body weight or total length of newly-born to adult-sized animals. Accordingly, we have combined measurements of the sexes of the living species in the various statistical treatments. Furthermore, we feel encouraged to interpret any bimodal heterogeneity in our fossil samples as indicative of the presence of two species rather than a single, sexually dimorphic one. While we cannot eliminate the possibility that the ancestors or other fossil relatives of the two extant species exhibited strong sexual dimorphism, these findings increase our confidence that they did not.

The six wear-stages defined previously are assumed to be rough approximations of relative age. As noted by
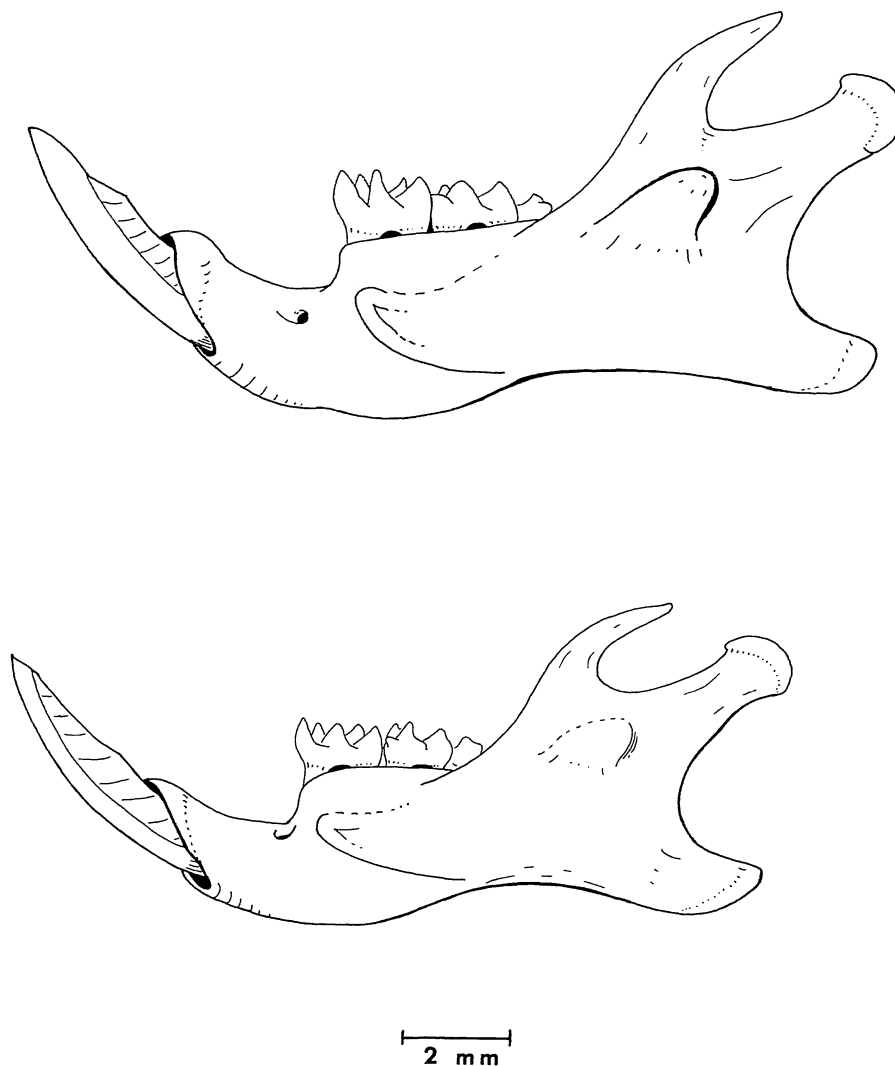
Figure 3.   Lateral views of left mandibles of: top — *O. leucogaster* (UMMZ 76054, Woods Co., Oklahoma); bottom — *O. torridus* (UMMZ 95873, Jeff Davis Co., Texas).

Van Cura and Hoffmeister (1966), length of the tooth row in *Onychomys* changes little with age and thus serves as a useful diagnostic character for separating the two species in Arizona.   In like manner, nine of the ten dental measurements we recorded showed no obvious or consistent relation with increasing age (Table 4). We observed a predictable, consistent trend only in height of the protoconid and depth of the ramus. As expected, protoconid height decreased significantly with age ($r = -.88$, $P < .0001$ in *leucogaster* and $-.84$, $P < .001$ in *torridus*), and depth of ramus increased ($r = .67$, $P < .001$ in *leucogaster* and $r = .45$, $P < .001$ in *torridus*). Curiously, correlations of LM_1, LM_3 tal., AWM_1, and WM_3 with stage of wear were significant at $P < .05$ in *leucogaster* but not *torridus*. Our interpretation of these unexpected correlations follows.   There exist

TABLE 3.   Results of Student's *t*-tests for differences between sexes.

Species	variable	$\male\male\ \bar{X}$	$\female\female\ \bar{X}$	t	P
leucogaster ($N\male\male$=61; $N\female\female$=42)	LM_1-M_3	4.36	4.38	.50	.61
	LM_1	1.87	1.88	.53	.59
	LM_2	1.55	1.56	1.10	.27
	LM_3	0.97	0.96	.62	.53
	LM_3 tal.	0.41	0.42	.33	.74
	AWM_1	1.04	1.05	.85	.39
	PWM_1	1.20	1.20	.23	.81
	WM_2	1.22	1.23	.80	.42
	WM_3	0.96	0.96	.13	.89
torridus ($N\male\male$=32; $N\female\female$=26)	LM_1-M_3	3.69	3.72	.58	.56
	LM_1	1.63	1.66	1.31	.19
	LM_2	1.33	1.35	1.01	.32
	LM_3	0.76	0.76	.16	.86
	LM_3 tal.	0.27	0.28	.76	.45
	AWM_1	0.92	0.91	1.05	.29
	PWM_1	1.07	1.06	.69	.49
	WM_2	1.09	1.09	.02	.98
	WM_3	0.81	0.80	.29	.76

significant size differences between OTUs within a species; for example, *leucogaster* from Texas and Oklahoma are bigger mice than those from North Dakota or Wyoming (see Appendix 1). Inspection of the distribution of wear states in Texan *leucogaster* revealed a disproportionate number with heavy wear (categories 4-6). Conversely, individual specimens of *leucogaster* from North Dakota and Wyoming are almost all classified as wear stages 1-3. Thus, sampling bias may account for some of the anomalous correlations of tooth size and wear stages. To check this, we calculated correlations of wear stage and dental measurements within the Texan sample (N=34) of *leucogaster*. Only depth of ramus (r = .79, P < .001) and height of protoconid (r = -.88, P < .001) were significantly correlated; no other variable even approached the level of significance, *i.e.*, P ⩽ .05.

Many of the dental variables used as characters in

our multivariate analyses are highly correlated with one another (Table 5). Intratooth length-width measurements are strongly correlated in all teeth as are most between-teeth width and length measurements. Only LM_3 and LM_3 tal. are consistently weakly correlated with length measurements of the anterior teeth. A similar pattern of correlations, particularly with regard to the weak integration of M_3 with M_1 and M_2, was revealed in the study of Gould and Garwood (1969) on the dental battery of *Oryzomys couesi*.

As indicated by others (*e.g.*, Gingerich, 1974; Gould and Garwood, 1969; and Van Valen, 1962), the M_3 is typically the most variable tooth in the tooth row. Coefficients of variation of the M_3 in OTUs of *torridus* and *leucogaster* generally range from 6 to 8. The LM_3 tal. is quite variable with values ranging from 8.1 to 20.0. In contrast, coefficients of variation of length and width measures of the M_1 and M_2 usually fall between 3 and 5 (see Appendix 2). The generalization that coefficients of variation less than four suggest an inadequate sample size for assessing variability in the population (Simpson, Roe and Lewontin, 1960: 91) seemingly does not apply well to measurements of individual teeth.

Onychomys of the Borchers Local Fauna

Hibbard (1941c) described *Onychomys fossilis* from the Borchers local fauna in Meade Co., Kansas and characterized it as a mouse the size of *leucogaster arcticeps* but with a relatively larger M_3 and a more weakly developed capsular process. The Borchers local fauna has yielded a rich collection of small mammals, and abundant remains of *fossilis* were recovered among them. Closer examination by Eshelman (1975: 33) suggested the presence of a second species of *Onychomys*, one much rarer in occurrence than *fossilis* and differing from it primarily in smaller size. The following sections provide substantiation of this viewpoint. In doing so, we shall frequently draw comparisons of the OTUs of *torridus* and *leucogaster* from Texas to demonstrate the degree of difference and patterns of variation between two morphologically similar, congeneric species.

The ranges of measurements of the Borchers form exceed that observed in populations of the living species. For example, LM_1-M_3 ranged from 4.02 to 4.92 mm, an interval of 0.90 mm; the largest interval in populations of *leucogaster* is only 0.67 mm for LM_1-M_3. In like manner, the LM_1 of the Borchers form measured 1.64 to 2.11 mm, an interval of 0.47 mm; the greatest difference

TABLE 4. Mean size of dental variables according to wear-stage in living *Onychomys*.

Species	Wear stage	N	LM_1-M_3	LM_1	LM_2	LM_3	LM_3 tal.	AWM_1	PWM_1	WM_2	WM_3	Height protoconid	Ramus depth
leucogaster	1	39	4.37	1.86	1.56	.96	.42	1.04	1.19	1.23	.94	.99	3.15
	2	30	4.33	1.84	1.55	.96	.43	1.04	1.19	1.21	.96	.95	3.27
	3	12	4.39	1.90	1.55	.95	.41	1.04	1.18	1.23	.97	.85	3.45
	4	11	4.36	1.88	1.54	.98	.39	1.08	1.23	1.25	1.00	.74	3.54
	5	9	4.48	1.94	1.56	.99	.39	1.06	1.22	1.25	.99	.68	3.55
	6	2	4.42	1.88	1.52	1.00	.38	1.06	1.18	1.22	.94	.60	3.72
torridus	1	7	3.70	1.62	1.34	.77	.30	.93	1.05	1.07	.80	.87	2.54
	2	14	3.74	1.66	1.36	.77	.29	.91	1.08	1.09	.81	.80	2.71
	3	17	3.66	1.67	1.31	.74	.27	.90	1.07	1.10	.81	.72	2.71
	4	15	3.69	1.67	1.34	.75	.25	.92	1.06	1.09	.80	.67	2.84
	5	5	3.79	1.65	1.35	.82	.30	.92	1.07	1.12	.83	.60	2.92
	6	2	3.68	1.60	1.32	.84	.26	.93	1.04	1.07	.82	.56	3.14

within populations of *leucogaster* examined is 0.36 mm. Furthermore, pooling individuals of *leucogaster* and *torridus* from Texas into one heterogeneous sample yielded ranges of measurements similar to that observed in the Borchers material. LM_1-M_3 of the mixed sample covered 3.69 to 4.63 mm, a span of 0.94 mm, while LM_1 measured 1.63 to 2.07 mm, a range of 0.44 mm.

Coefficients of variation for dental variables of the Borchers material are generally higher than those recorded in populations of living *Onychomys*. Discounting the M_3, which is typically highly variable anyway, coefficients of variation fall between 5 and 6 for dimensions of the teeth of the Borchers "population" (Appendix 2, Table 6). Coefficients of variation are usually less than 5 for the same variables in samples of *leucogaster* and *torridus*. Although coefficients of variation between 5 and 6 are not unusually high for most morphometric variables (see Long, 1969), mixed-species samples may nevertheless fall in this range (Table 6). The generalization that coefficients above 10 are indicative of mixed samples (Simpson, Roe and Lewontin, 1960: 91) must be applied carefully and the overall pattern of variability ascertained first.

A bimodality can be discerned for certain measure-

ments of the Borchers material. This is most evident in the regression of height of protoconid on depth of ramus. Both of these variables change markedly with age, and a strong negative correlation exists between them (Fig. 4). Two clouds of points are apparent: a large one that includes examples of *fossilis* and another that consists of only five specimens representing a smaller, less abundant species. This pattern of regression closely mimics that observed for the two extant species (Fig. 5).

Gingerich (1974, 1976 a,b) advocates construction of histograms plotting the logarithm of L x W of the first molar, typically the tooth having the smallest coefficient of variation, for diagnosing the sympatric occurrence of closely similar fossil species. Visual inspection of such histograms may disclose two or more peaks in the distribution suggesting the coexistance of morphologically close species. His approach was applied to the *Onychomys* of the Borchers local fauna, and two modes were detected in the distribution. Appreciable overlap of log scores is evident when specimens believed to represent the two sympatric fossil forms are indicated on the graph (Fig. 6). Histograms of log transformations of the L x W of first molars of *torridus*

TABLE 5. Matrices of correlation coefficients (r) for dental measurements of *Onychomys*.

	LM_{1-3}	LM_1	LM_2	LM_3	LM_3 tal.	AWM_1	PWM_1	WM_2
LM_{1-3}	1.00							
LM_1	.81	1.00			*leucogaster* N=103			
LM_2	.76	.53	1.00					
LM_3	.65	.22*	.49	1.00				
LM_3 tal.	.47	.11*	.44	.63	1.00			
AWM_1	.52	.49	.47	.27	.09*	1.00		
PWM_1	.50	.44	.46	.27	.15*	.55	1.00	
WM_2	.65	.53	.55	.36	.26	.67	.69	1.00
WM_3	.52	.29	.47	.59	.40	.51	.50	.63

	LM_{1-3}	LM_1	LM_2	LM_3	LM_3 tal.	AWM_1	PWM_1	WM_2
LM_{1-3}	1.00							
LM_1	.83	1.00			*torridus* N=60			
LM_2	.81	.62	1.00					
LM_3	.37	.05*	.20*	1.00				
LM_3 tal.	.10*	-.17*	.01*	.67	1.00			
AWM_1	.50	.42	.50	.08*	-.13*	1.00		
PWM_1	.63	.53	.51	.27*	.09*	.64	1.00	
WM_2	.70	.59	.64	.15*	-.05*	.62	.67	1.00
WM_3	.17*	-.09*	.09*	.38	.45	.06*	.29*	.18*

* = r *not* significant at $P \leqslant .01$.

and *leucogaster* from Texas did not disclose distinct peaks, however. Instead, the histogram has an irregular profile which is slightly skewed to the left (Fig. 7). In this instance, the identity of specimens as to species is known, but the coexistance of two fossil species could not be clearly inferred from this graph alone. Larger sample sizes obviously increase the efficacy of this method. Otherwise, the peak of a species occurring in relatively low density may be obscured by the tail of the distribution of a plentiful species. Furthermore, it is noteworthy that the M_1 is not necessarily the least variable tooth of the molar row among our samples. Coefficients of variation of the M_2 closely approximate those recorded for the M_1, such that no consistent greater-than/less-than relationship is apparent (Appendix 2). Still the M_1 possesses greater information content in the sense that it is larger and its crown pattern is usually more complex.

TABLE 6. Coefficients of variation of selected dental dimensions in "mixed-species" samples.

Species and Locality	LM_1-M_3	LM_1	LM_2	LM_3
torridus, Texas	2.0	3.3	3.6	6.4
leucogaster, Texas	3.3	4.6	4.0	5.0
All Texan *Onychomys*	6.8	5.6	6.5	13.0
fossilis	3.7	4.2	4.5	6.3
sp. nov.	2.0	2.5	2.0	2.3
All Borchers *Onychomys*	5.2	5.9	5.1	7.2

Simple scatter diagrams of LM_1 versus PWM_1 are presented in Figures 8 and 9. Two distinct clouds of points are not readily obvious even in the plot of Texan *leucogaster* and *torridus* whose identifications can be certified on the basis of other than dental traits. In fact, separate densities of points are more apparent in the scatter-plot of the Borchers material. We cannot positively allocate individuals which fall in the range of overlap of the two species. This is especially true for specimens consisting of only isolated molar teeth or fragmented dentary bones; more complete material can be more reliably identified.

The possibility that *fossilis* was an extremely variable species cannot be entirely discounted; however, on the basis of the several lines of evidence related above, we interpret this broad variation as the presence of a second species. Accordingly, we here describe and name this form in honor of Ned Hollister, the first revisor of the genus.

Onychomys hollisteri, new species
(Fig. 10)

Holotype.— University of Michigan Museum of Paleontology No. 72000, a left dentary with broken incisor and M_1-M_3. Collected in summer of 1953 by C. W. Hibbard and field party from the University of Michigan Museum of Paleontology.

Paratypes.— UMMP No. 72001, a left mandible with M_1-M_2 and UMMP Nos. 72002 and 72003, right mandibles with M_1-M_2.

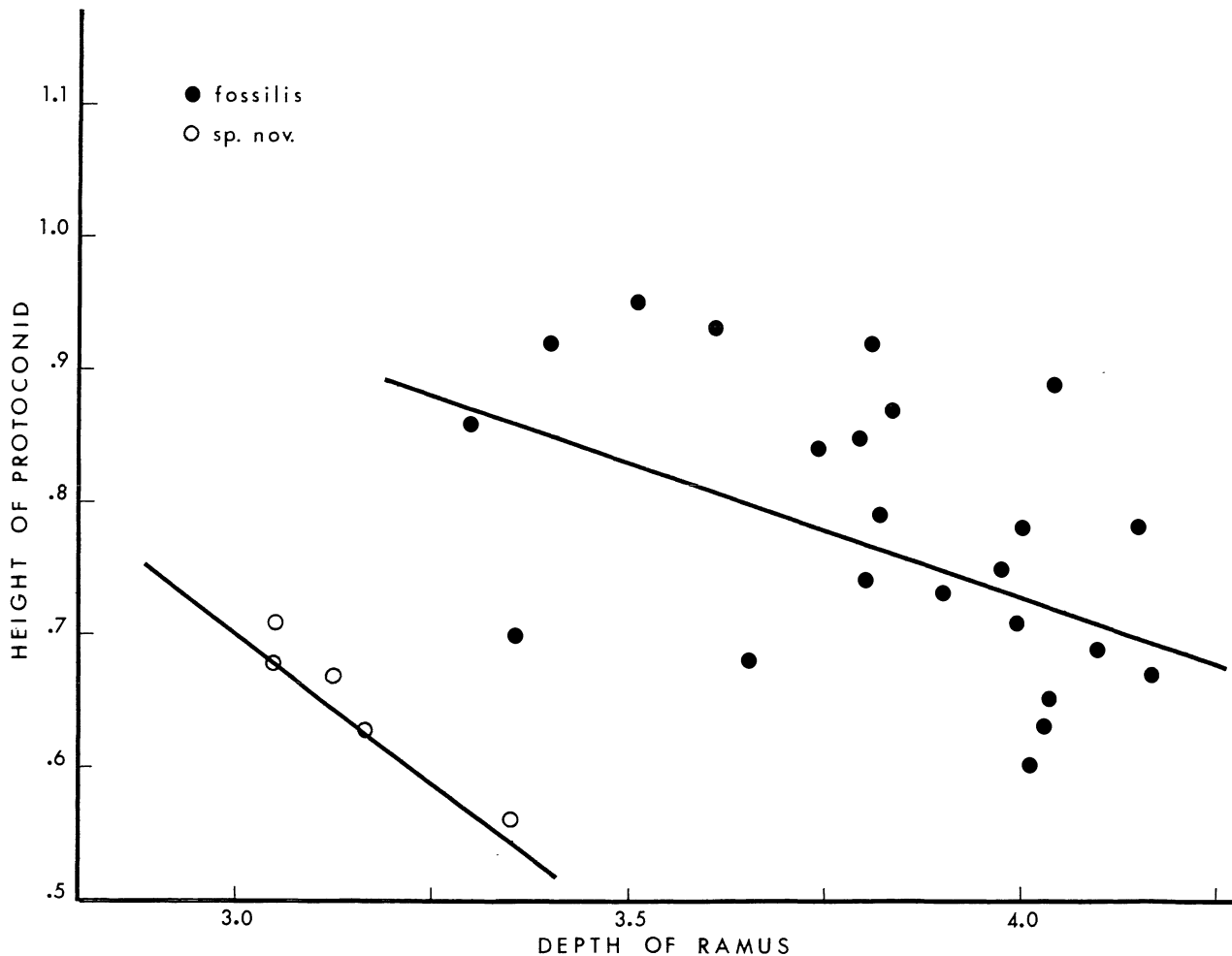*Horizon and type locality.*— Pliocene (Late Blancan

Figure 4.   Regression of height of the protoconid and depth of ramus for *Onychomys* of the Borchers local fauna.

Land Mammal Age), Crooked Creek Formation, Borchers local fauna, Borchers Pasture, NE¼ Sec. 21, T 33 S, R 28 W, Meade County, Kansas. Although Hibbard (1941c) originally assigned the Borchers local fauna to the Yarmouth interstadial of the Pleistocene, recent evidence suggests an older age (for review, see Zakrzewski, 1975).

Diagnosis.— A grasshopper mouse intermediate in size to living *leucogaster* and *torridus*. M_3 relatively larger than in *leucogaster* or *torridus* but more reduced than in early Blancan *gidleyi* and *bensoni*. The poorly developed capsular process resembles that seen in Recent *torridus*. Compared to its sympatric congenor *fossilis*, *hollisteri* is distinguished by its shorter tooth row and

narrower teeth (Fig. 10, Appendix 1), shallower, less robust mandible and weakly pronounced capsular process. Judgement of the affinities of *hollisteri* is deferred to following sections of this study.

Description of holotype.— No. 72000 is a young adult (wear-stage II). The anterior portion of the ramus is broken exposing the incisor, and the angle, coronoid and articular processes are missing. The masseteric ridge extends to the level of the anterior root of the first molar. Measurements of the type are: LM_1-M_3, 4.02; LM_1, 1.70; LM_2, 1.40; LM_3, 0.98; LM_3 tal., 0.46; AWM_1, 0.99; PWM_1, 1.10; WM_2, 1.19; WM_3, 0.93. Descriptive statistics of the entire series are given in Appendix 1.
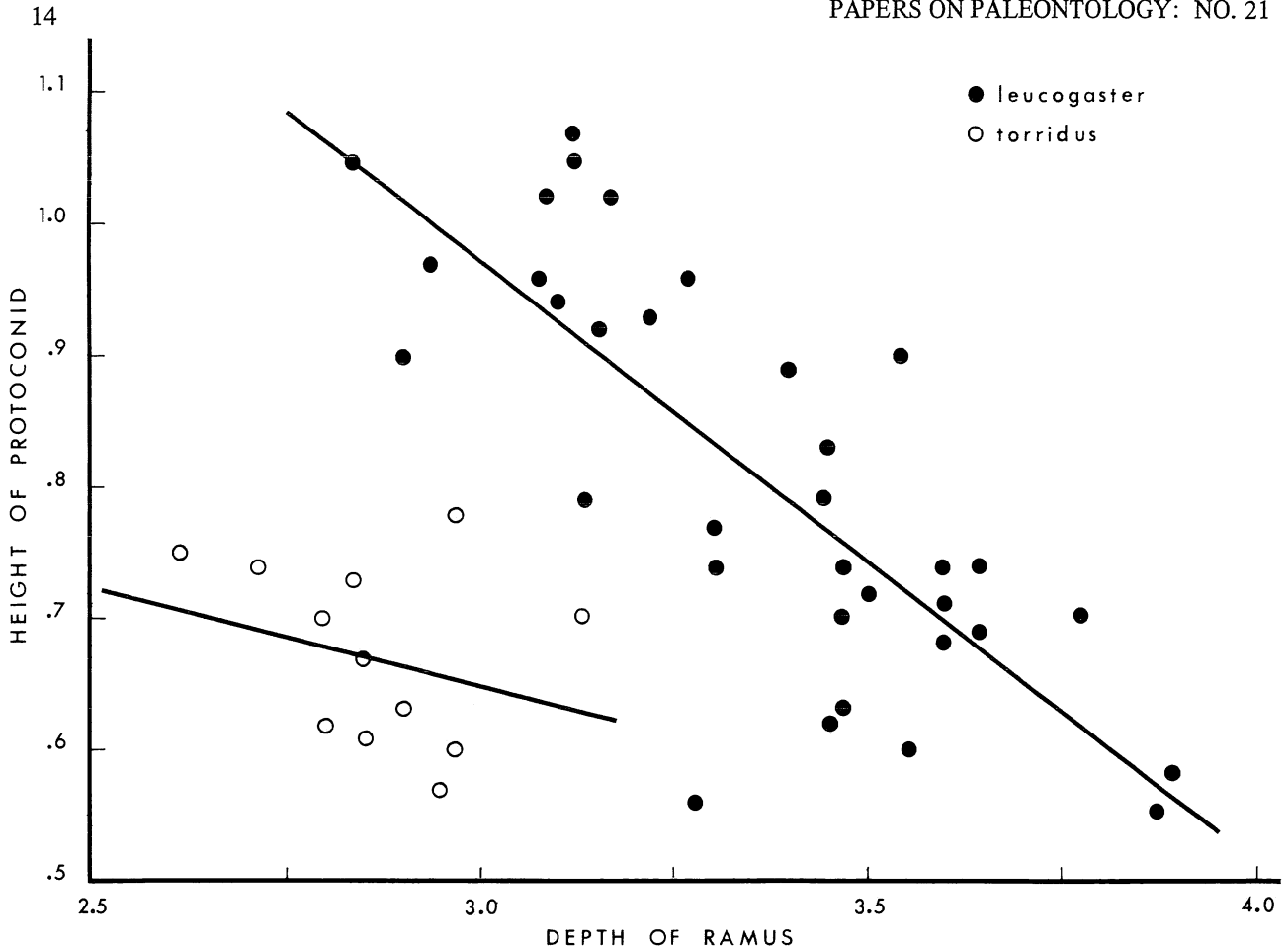
Figure 5.   Regression of height of the protoconid and depth of ramus for samples of *O. leucogaster* and *torridus* from Texas.

Referred material.— In addition to other jaws with incomplete dentitions (UMMP Nos. 72004-12) in the University of Michigan Museum of Paleontology, three of the paratypes in the original description of *fossilis* are here allocated to *hollisteri*. These are University of Kansas Museum of Vertebrate Paleontology Nos. 5237, 6159 and 6160; all are mandibles with intact tooth rows. Several isolated teeth from the White Rock fauna (UMMP Nos. 61695-7), judged slightly older than the Borchers local fauna (Eshelman, 1975), are referred to *hollisteri*. Also several partial mandibles and isolated molars (UA Nos. 4358-60, 4503) from the Wolf Ranch locality in the San Pedro Valley sequence of Arizona are assigned to *hollisteri*. These specimens are definitely larger than *bensoni*, named from the older Post Ranch locality, and fit within the size range observed for *hollisteri*.

Phenetic Analyses

In the various multivariate treatments, locality means served as the character states of the OTUs. Since height of the protoconid changes with increased wear and presumably age, differences between OTUs were rendered comparable by only utilizing teeth with little wear; that is, those assigned to wear-stages I and II. This procedure could not be applied to depth of ramus, also an age-related variable, because specimens of *bensoni* and *pedroensis* lacked complete mandibles. Thus, 10 morphometric variables were employed in the multivariate programs.

One qualitative character, the development of the capsular process, was also included. As discussed above, *torridus* and *leucogaster* differ in the pronouncement of the capsular process, its size ranging from a slight swell in *torridus* to a distinct lateral projection in most *leuco-*
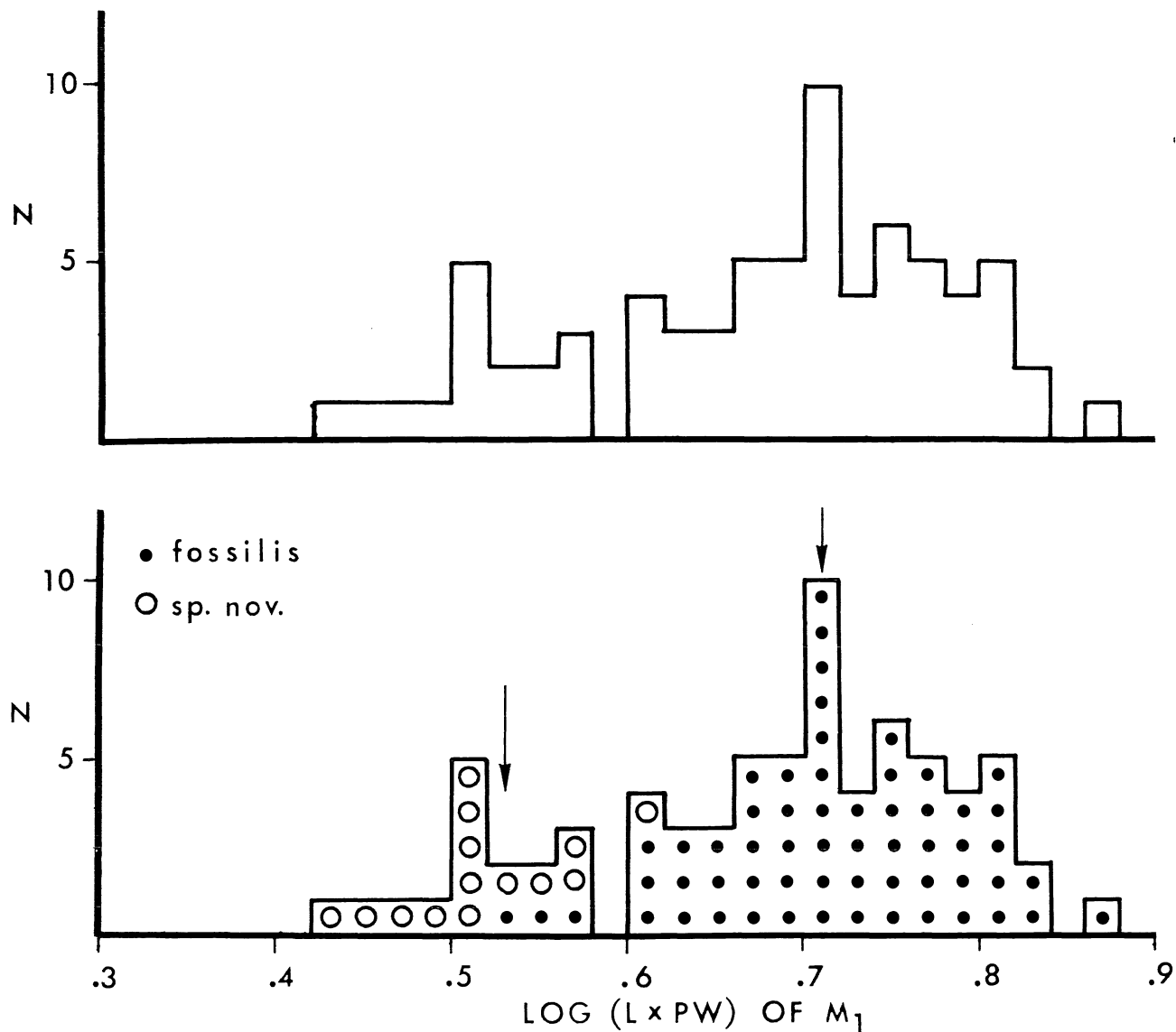
Figure 6. Histogram of the logarithm of length x posterior width of the first molar for specimens of *Onychomys* from the Borchers local fauna. The top figure only portrays the data profile, while the bottom includes species identities. Arrows denote the mean log (LxPW) of M_1 for each species.

gaster (Fig. 3). OTUs of fossil *Onychomys* also contrast in this character. Two annectant grades are recognized as intermediate to the character states observed for *torridus* and *leucogaster*; the distribution of these character states among all samples is as follows:

(0) minute bump or swell: *bensoni*, all *gidleyi*, *hollisteri*, and *torridus* from Arizona, New

Mexico, and Texas.

(1) larger with incipient sulcus: *fossilis* and *torridus* from Nevada.

(2) distinct bump with moderate sulcus: *jinglebobensis*, *leucogaster* from Texas, and *pedroensis*.

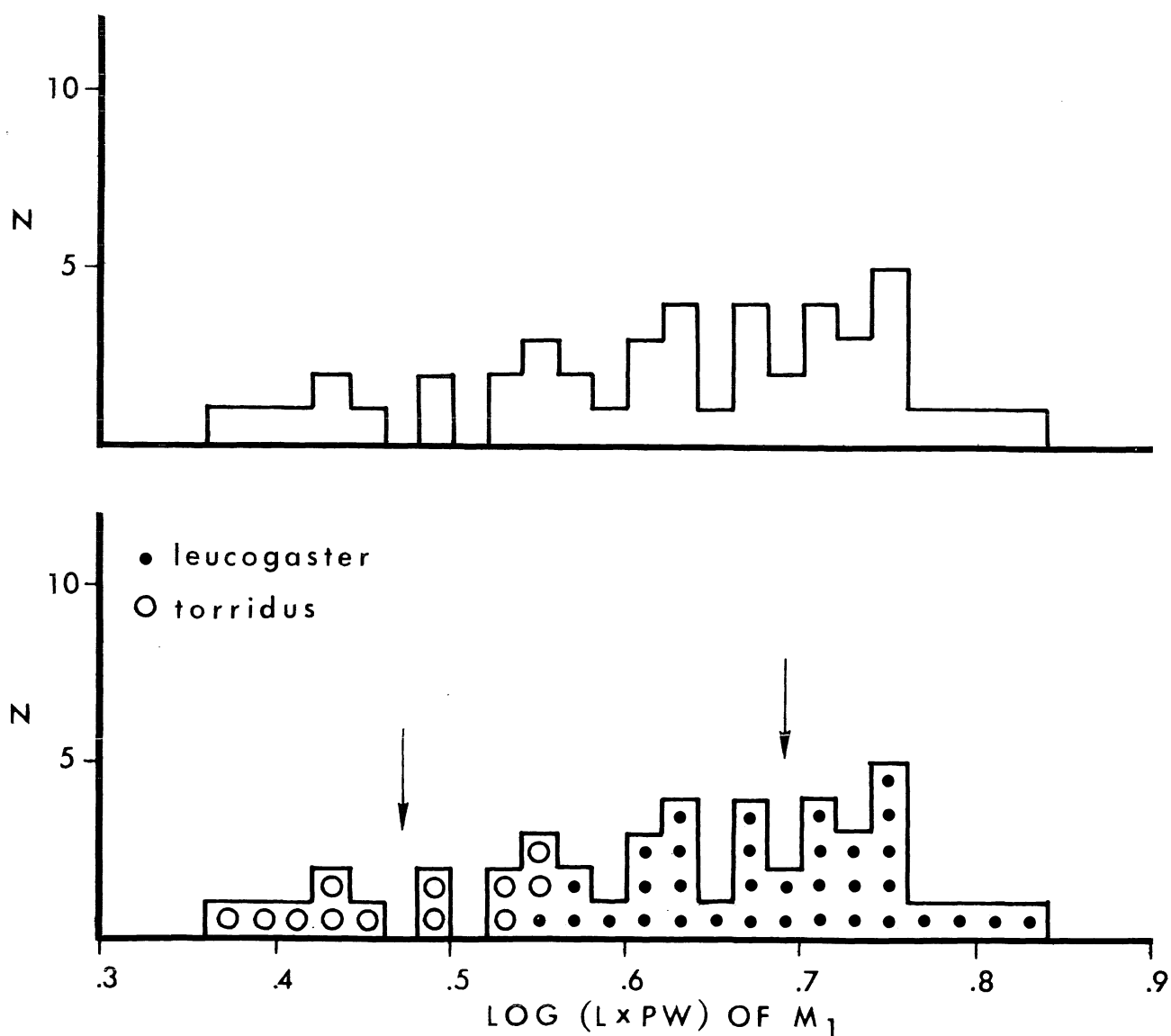(3) projection with well-defined sulcus: all other

Figure 7.   Histogram of the logarithm of length x posterior width of the first molar for specimens of *O. torridus* and *leucogaster* from Texas.   Other information as in Fig. 6.

leucogaster, including specimens from Schulze Cave and Friesenhahn Cave.

The various phenetic analyses were performed using only the 10 morphometric variables and then adding the one qualitative variable.   Principal components were derived from a correlation matrix when the data set included the capsular process.

The cluster analyses (UPGMA) produced quite different aggregations of OTUs depending on what coefficient was selected as the estimator of phenetic resemblance.   The cluster analysis employing a taxonomic distance coefficient (d_{jk}) disclosed five major groups (Fig. 11).   One consists of *larrabeei, hollisteri* and samples of *gidleyi*.   *Onychomys larrabeei* is interspersed with OTUs of *gidleyi*, but *hollisteri* is set somewhat off as an outlier to these taxa.   The large forms,
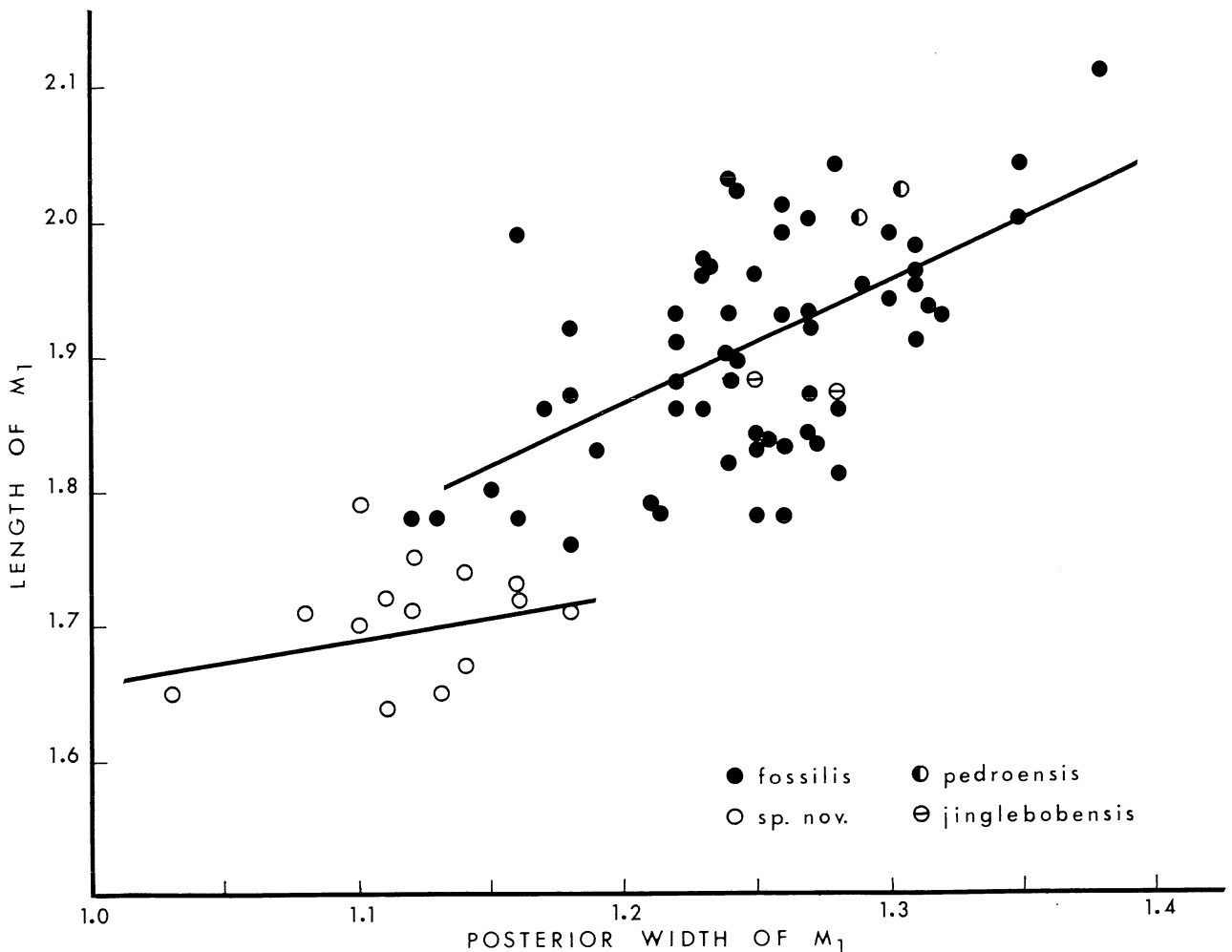
Figure 8.   Bivariate scatter plot of length of M_1 versus posterior width of M_1 for specimens of *Onychomys* from the Borchers local fauna. Examples of *O. pedroensis* and *O. jinglebobensis* are also plotted.

fossilis, jinglebobensis and *pedroensis* comprise a second, rather loose cluster. The latter three OTUs form a pair-group with a large cluster consisting of five of the six samples of Recent *leucogaster* and the two Pleistocene cave representatives of *leucogaster*. Within this cluster the two late Pleistocene samples are dispersed among populations of Recent *leucogaster*, not set apart from them. The Nevada sample of *leucogaster* and those of *torridus* constitute a fourth association of OTUs; the Nevada sample joins with *torridus* at a later clustering cycle. The lone example of *bensoni* is clearly more isolated than other OTUs, but it does pair with *leucogaster* from Nevada and the four samples of *torridus*.

The major bifurcation in the phenogram suggests a *leucogaster* group and a *torridus* group. The coefficient of cophenetic correlation obtained for this phenogram (cc = .804) is lower than that generated using the correlation coefficient as a measure of similarity (cc ≐ .899).

The cluster analysis using the correlation coefficient (1 - *r*) yielded a markedly disparate picture (Fig. 12). Again, a major bifurcation segregates the OTUs, but minor groups are not as readily apparent within each major cluster as occurred in the clustering exercise utilizing taxonomic distance. Two primary rearrangements of OTUs can be discerned. *Onychomys*
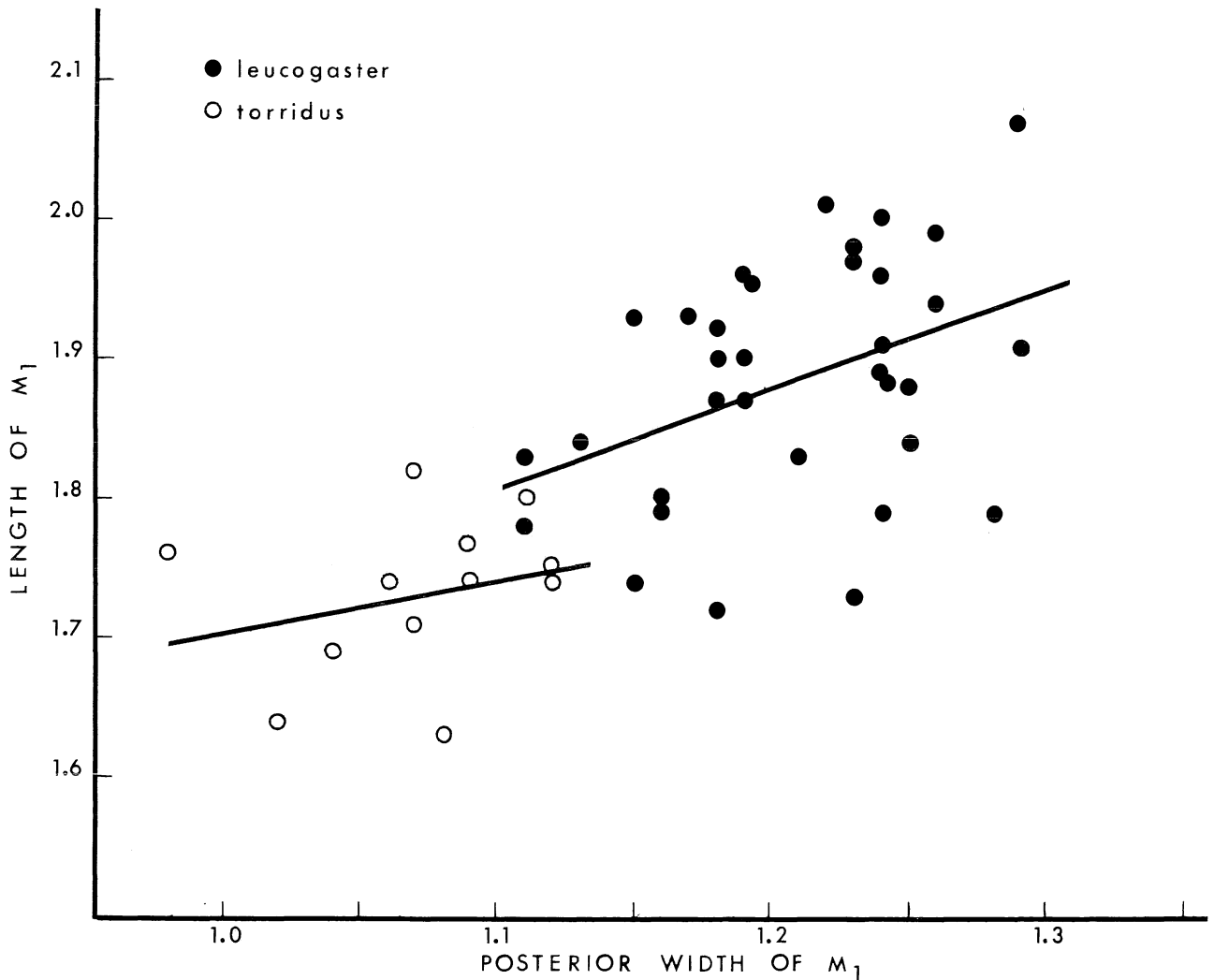
Figure 9.   Bivariate scatter plot of length of M_1 versus posterior width of M_1 for specimens of *O. leucogaster* and *O. torridus* from Texas.

bensoni is completely disassociated from examples of *torridus* and instead links closely with an OTU of *gidleyi*. A discrete separation of OTUs of *leucogaster* (excluding that from Nevada) from those of *torridus* is no longer evident: *torridus* from Texas and New Mexico cluster among examples of *leucogaster*. At the risk of prematurely interjecting time into our analysis, it is necessary to comment upon the large discrepancy between the two phenograms (Figs. 11, 12).

Several workers (*e.g.*, Eades, 1965; Minkoff, 1965; Rowell, 1970) have questioned the adequacy of the correlation coefficient as a measure of taxonomic resemblance.   In particular, Minkoff (op. cit.) noted that two OTUs which differ greatly in size may nonetheless be strongly correlated if the linear dimensions of one depart from the corresponding dimensions of the second by a uniform amount. As discussed above, the major differences between *torridus* and *leucogaster* are size-related; the same holds for separation of *bensoni* from OTUs of *gidleyi*.   Instead, the correlation coefficient is more successful as a measure of shape and proportion.   Viewed from this perspective, the phenogram derived using the correlation coefficient assumes greater relevance.   The first major bifurcation divides extinct
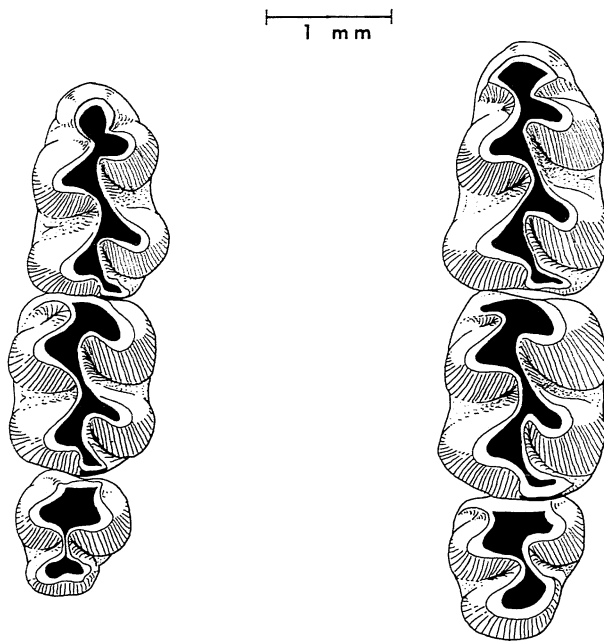
Figure 10. Crown views of left lower molar rows of: left — the holotype of *O. hollisteri* (UMMP 72000, Borchers Local Fauna, Kansas); right — specimen of *O. fossilis* (UMMP 35762, Borchers Local Fauna, Kansas).

TABLE 7. Results of principal component analysis using variance-covariance matrix.

Component	I	II
Eigenvalue	0.167	0.017
Cumulative % variation explained	88.0	97.1
Degrees freedom	44	35
Significance	0.0	0.0
LM_1-M_3	.99	.02
LM_1	.91	.37
LM_2	.91	.37
LM_3	.85	-.52
LM_3 tal.	.79	-.58
AWM_1	.93	.27
PWM_1	.95	.18
WM_2	.91	.24
WM_3	.90	-.28
Height protoconid	.56	.70

OTUs from extant ones, with the exception of the two late Wisconsin samples of *leucogaster*, that is, those OTUs possessing a relatively large M_3 are segregated from those having a relatively small one. At least among the Recent OTUs, there is no separation according to conventional taxonomic alignment.

The basic clusters evident in principal component analyses correspond closely to those produced by clustering with the distance coefficient. In the principal component analyses, however, the OTU of *hollisteri* assumes a much more isolated position — one approximately equidistant to the constellations of OTUs representing *bensoni, gidleyi, torridus,* and *leucogaster* — in contrast to its close association with *larrabeei* and samples of *gidleyi* as revealed by the clustering results (Fig. 13). Again the *leucogaster* from Nevada is positioned much nearer samples of *torridus* than other conspecifics. The separation of OTUs along the first principal component indicates a general size factor, grading from the smallest sample of *torridus* to the largest form, *pedroensis.* Most dimensions of the teeth are predictably correlated with principal component I (Table 7). Height

of the protoconid and measurements of the M_3 load significantly on the second principal component (Table 7); thus, dispersion of OTUs along this axis mainly reflects relatively smaller size of the M_3 and greater height of the protoconid. Inclusion of the qualitative character (development of the capsular process) did not substantially alter the conformation of OTUs. One difference involves a translocation of the *leucogaster* from Nevada to the right of samples of *torridus* because pronouncement of the capsular process contributes mainly to principal component II. Secondly a greater hiatus is apparent between *fossilis* and *jinglebobensis.*

Discrete clusters of OTUs are not as visibly obvious in the shortest connection network (Fig. 14). The association of *leucogaster* from Nevada with samples of *torridus* is repeated in this analysis. The isolated positions of *bensoni* and *hollisteri* are also apparent, although *hollisteri* is somewhat closer to an example of *gidleyi* than to *torridus* from New Mexico. The remaining OTUs — including those of *gidleyi, larrabeei, fossilis, jinglebobensis, pedroensis* 'and *leucogaster* — grade almost uniformly. Two size polarities can be detected along the network length. Beginning from the right, size increases from *bensoni,* the smallest

Figure 11.   Cluster analysis (UPGMA) of 22 OTUs of fossil and living *Onychomys* generated from a distance matrix using ten morphometric and one qualitative character. Coefficient of cophenetic correlation = 0.804.

OTU, through *fossilis* to the largest form *pedroensis*. A decrease in size occurs from *fossilis* through *leucogaster* from the late Pleistocene to the smallest sample of Recent *leucogaster* (*l*-WY).

At this point, some comment is required concerning the status of our OTU of *leucogaster* from Nevada.

When we initiated this study, we did not anticipate any difficulty with the alpha taxonomy of the two extant species; our attention was focused on evaluating consanguinity among the fossil populations. In retrospect, this assumption seems naive, for the genus had not been intensively reviewed since Hollister's 1914 revision,
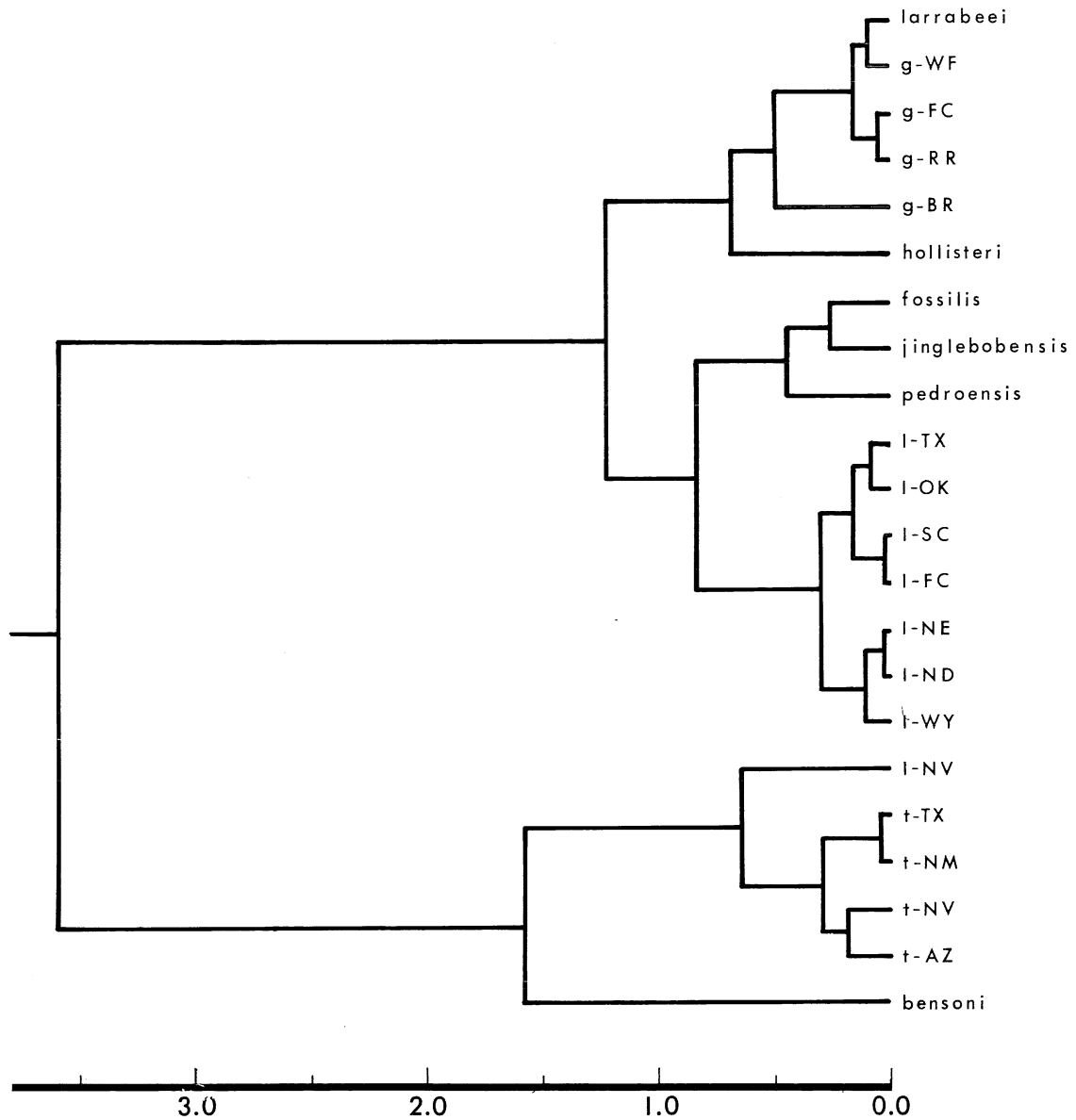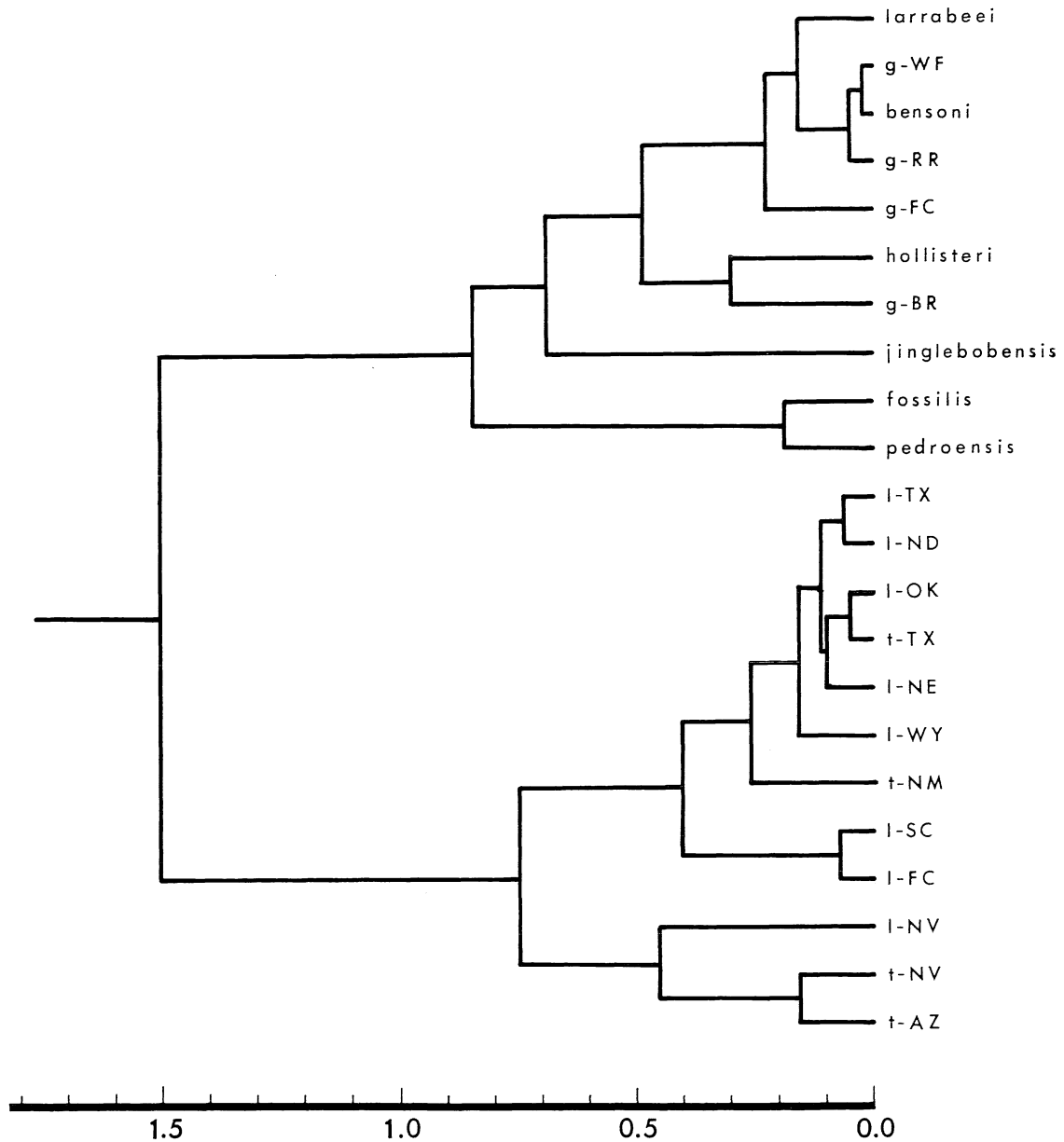
Figure 12.　Cluster analysis (UPGMA) of 22 OTUs of fossil and living *Onychomys* generated from a correlation matrix using only the ten morphometric characters. Coefficient of cophenetic correlation = 0.899.

except for Van Cura and Hoffmeister's (1966) restricted study in Arizona. The specimens of *leucogaster* from Nevada, as well as those of *l. fuscogriseus* contained in UMMZ, are as phenetically distinct from other *leucogaster* as are OTUs of *torridus*. In certain qualitative and proportional features, however, these specimens resemble typical *leucogaster*. Populations of *brevicaudus* and *fuscogriseus* together occupy the Great Basin province in contrast to the essentially Great Plains distribution of other *leucogaster* included in the study; therefore, some geographic isolation and differentiation might be expected. We are not arguing separate species
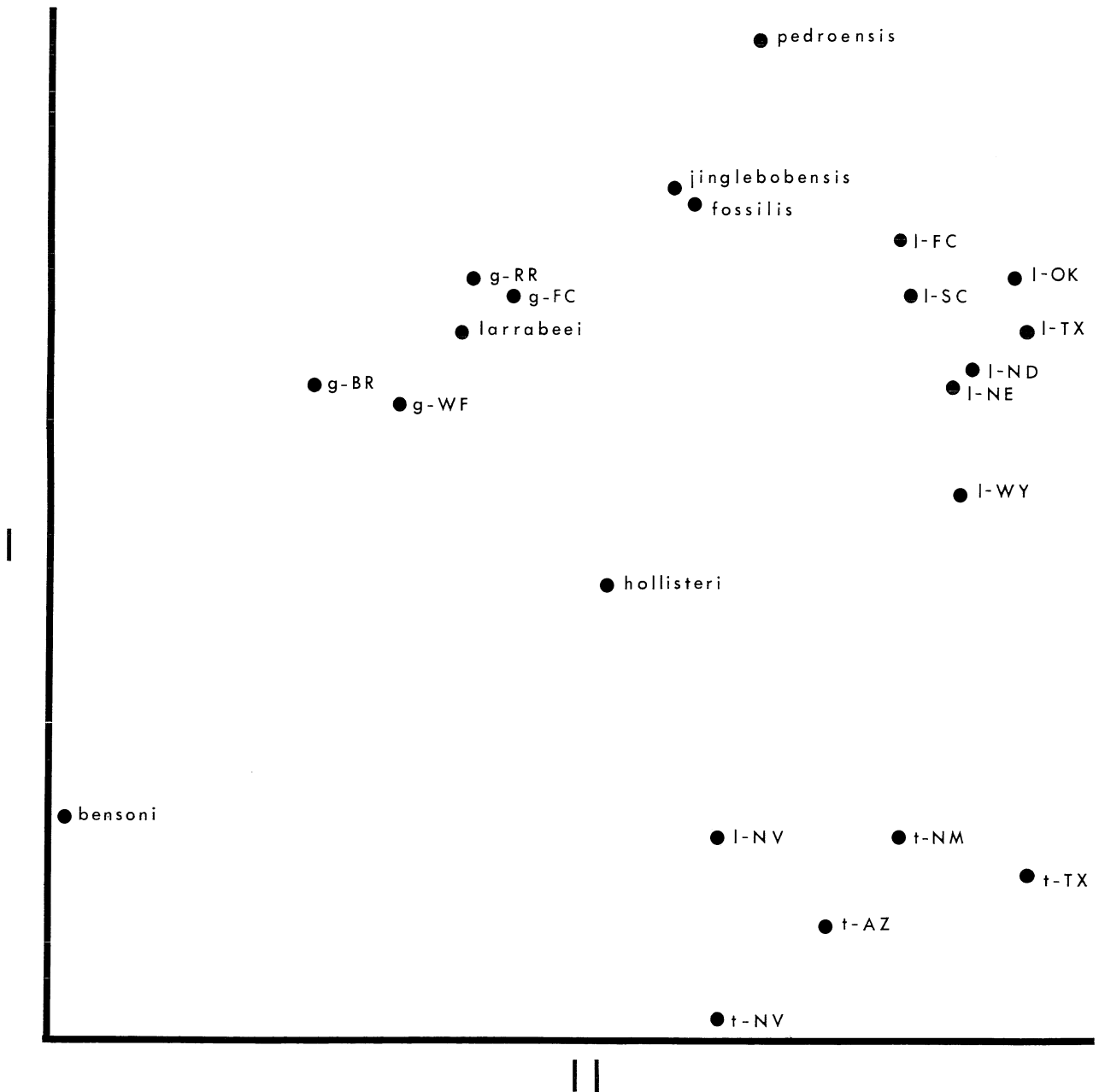
Figure 13.   Scatter plot of Principal Component I versus II using the 22 OTUs as cases as described by the ten morphometric characters.

recognition for those populations; our sample size is wholly inadequate. We are pointing out the need for further systematic re-examination of these subspecies, and indeed, the genus *Onychomys* as a whole. Such is clearly beyond the scope and original intent of our

study.

Procedurally, these specimens present another problem. If we adhere strictly to our stated protocol, that is, to utilize populations of the living species as a yardstick for interpreting differences between fossil
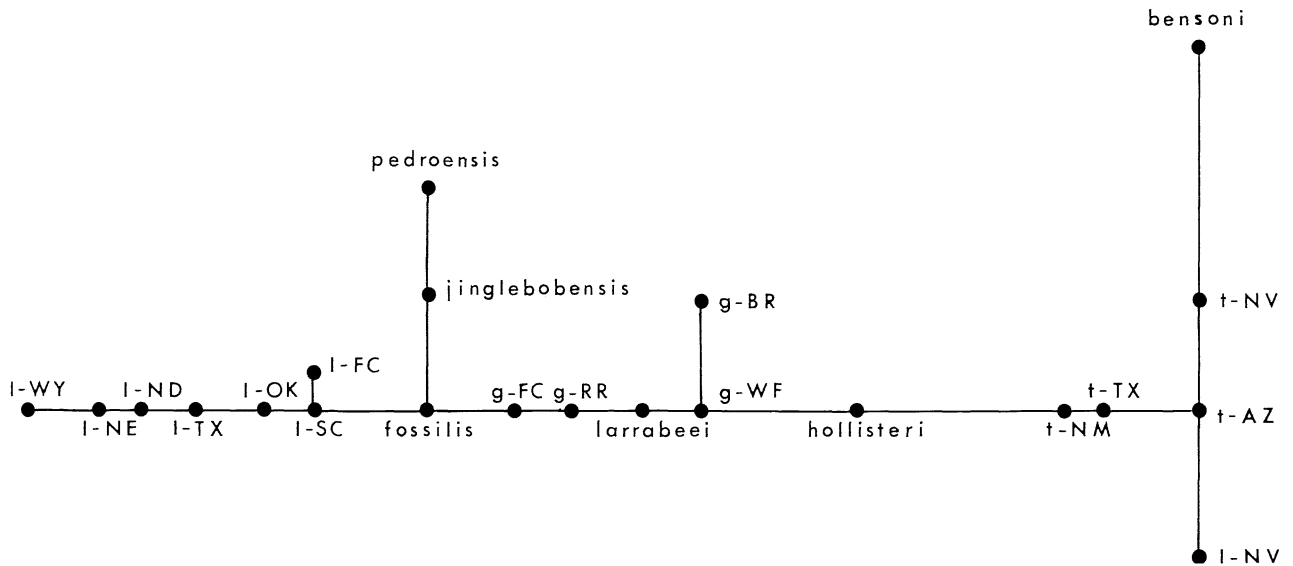
Figure 14. Shortest connection network of 22 OTUs of fossil and living *Onychomys* based on ten morphometric and one qualitative character. The distance between OTUs is proportional to the amount of dissimilarity over all characters.

OTUs, then we lose all resolution by including the Nevadan *leucogaster*. Not only do we lose discrimination between samples of extinct *Onychomys* but also between the Recent ones. Because we originally selected populations of Recent *Onychomys* to serve as examples of "good" biological species and because this assumption is now strongly suspect, we feel justified in eliminating this OTU from further analyses. Determination of the status of *brevicaudus* and *fuscogriseus* is more properly a task for neontologists.

Chronological Perspective

The stratigraphic order of the fossil faunas and the chronological correlations of the Kansas and Arizona sequences are drawn mainly from the papers of Zakrzewski (1975) and Lindsay, *et al.* (1975). The ages of the two late Pleistocene cave deposits are 9,680 years B.P. for Schulze Cave, Layer Cl (Dalquest, *et al.*, 1969) and 9,640 years B.P. for Friesenhahn Cave (R.W. Graham, per. comm.). While the geomagnetic dating scheme presented by Lindsay, *et al.* perhaps alters previous conceptions of the amount of time elapsed between certain faunas (Fig. 15), it has not significantly modified the order of these fossiliferous strata as perceived by earlier authors using other information (see, *e.g.*, Hibbard,

1970). We are not as concerned here with absolute time spans between the extinct faunas as with the correctness of their temporal succession. On this latter account, there appears to be concensus, one derived from and bolstered by several different kinds of evidence.

One possible phylogeny utilizing information from the phenetic analyses is illustrated in Figure 16. The precise points of bifurcation and angle of branching cannot be, nor are they intended to be, vigorously defended. Yet neither are they random or capricious. Distribution of taxa along the time vector accords with Lindsay, *et al.*'s (1975) chronology, and dispersion of the forms on the morphology axis corresponds to their mean scores on the first principal component. The pattern of branching is suggested by the results of the clustering exercise and shortest connection network. In this version, *bensoni* qualifies as the probable ancestor of *torridus* on the basis of size; *gidleyi* occupies a central stem position giving rise to *hollisteri*, *leucogaster*, and a side line that terminates with the large form *jinglebobensis* in the Pleistocene. Clearly, other interpretations are possible, but this phylogeny is basically harmonious with the phenetic analyses.

Even when viewed within this chronological framework, certain doubts exist concerning the status and cladistic relationships of the various named forms.

CORRELATION OF FAUNAS
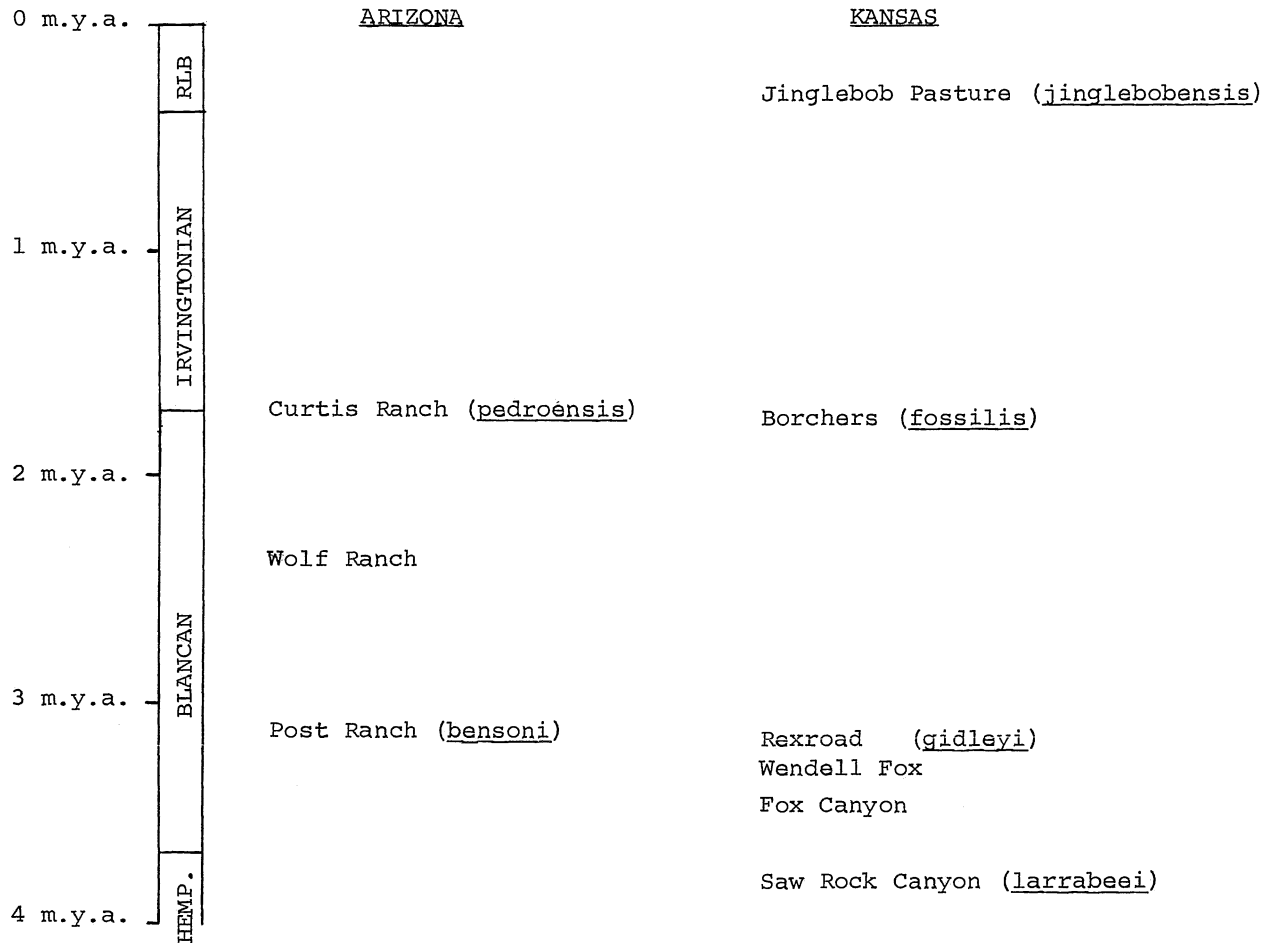
Figure 15. Correlation of fossiliferous strata from Arizona and Kansas (adapted from Lindsay, *et al.*, 1975). Species of extinct *Onychomys* are enclosed in parentheses next to the horizon from which they were described.

Three questions in particular need further consideration and clarification:

1) What is the status of *pedroensis* with regard to *fossilis* and *jinglebobensis*? *Onychomys fossilis* from the Borchers local fauna in Kansas is approximately contemporaneous with *pedroensis* from the Curtis Ranch in Arizona, yet *fossilis* is phenetically more divergent from *pedroensis* than from the much younger *jinglebobensis* (Jinglebob local fauna in Kansas).

2) Does *jinglebobensis* represent a species of *Onychomys* that disappeared in the Pleistocene or did it evolve into *leucogaster*? The latter interpretation postulates a rather rapid rate of evolutionary change.

3) What is the relationship of *hollisteri*? In the clustering program, *hollisteri* is linked with samples of *gidleyi*, but in the principal component analysis, the hiatus between *hollisteri* and *gidleyi* is as large as that between *bensoni* and *hollisteri*.

Interestingly, the second principal component partitions the OTUs according to their relative antiquity (Fig. 13). Proceeding from left to right, one first encounters *bensoni, larrabeei* and OTUs of *gidleyi* from the late Hemphillian and early Blancan, then *hollisteri, fossilis* and *pedroensis* from the late Blancan and early
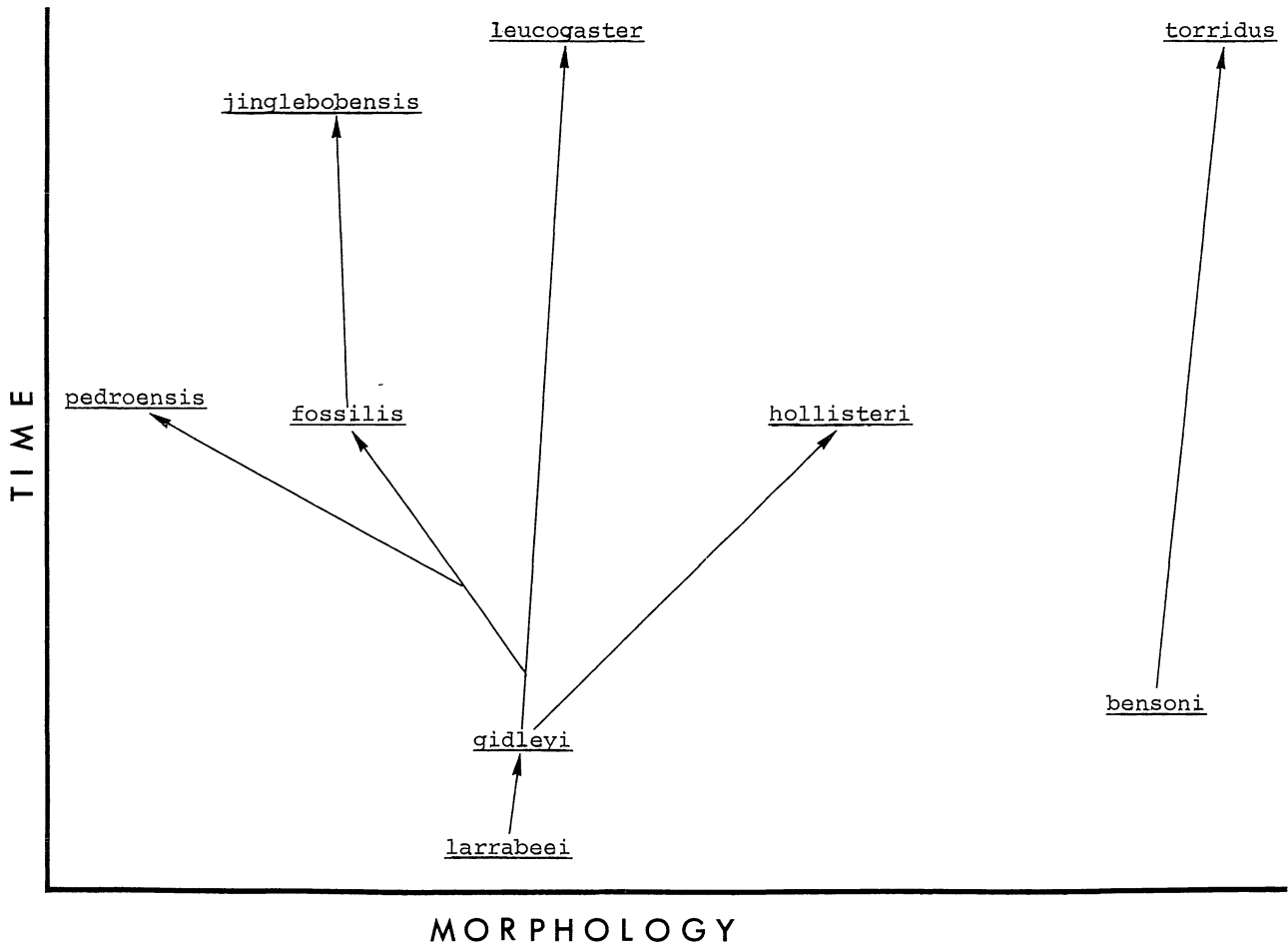
Figure 16.   Preliminary phylogeny based mainly on phenetic analyses but following Lindsay, *et al.*'s (1975) chronology. See text for discussion.

Irvingtonian, and finally OTUs of living *leucogaster* and *torridus*. It should be stressed that "time" was never coded as a character and used as input for the principal component or any other phenetic analysis. When one closely inspects the temporal relationships, however, it becomes apparent that the separation of OTUs along principal component II only loosely corresponds to their ages. For example, OTUs of *gidleyi* from Beck Ranch and Wendell Fox are undoubtedly slightly younger than either *larrabeei* from Saw Rock Canyon or *gidleyi* from Fox Canyon, yet the former two are dispersed to the left of the latter. Similarly, *jinglebobensis* of the

Rancho La Brean Land Mammal Age is aligned with the much older forms *fossilis* and *pedroensis*. The interpretation of the second principal component as a general time factor may be explained by considering the variables which contribute most to it. Those characters that seemingly have undergone the greatest evolutionary change (LM$_3$, LM$_3$ tal., WM$_3$, height of protoconid and capsular process) all load significantly on principal component II (Table 7). Recognition of this relationship lends some resolution to the three questions mentioned above.

There are generally two sets of OTUs evident at any time period suitably represented. This is more readily
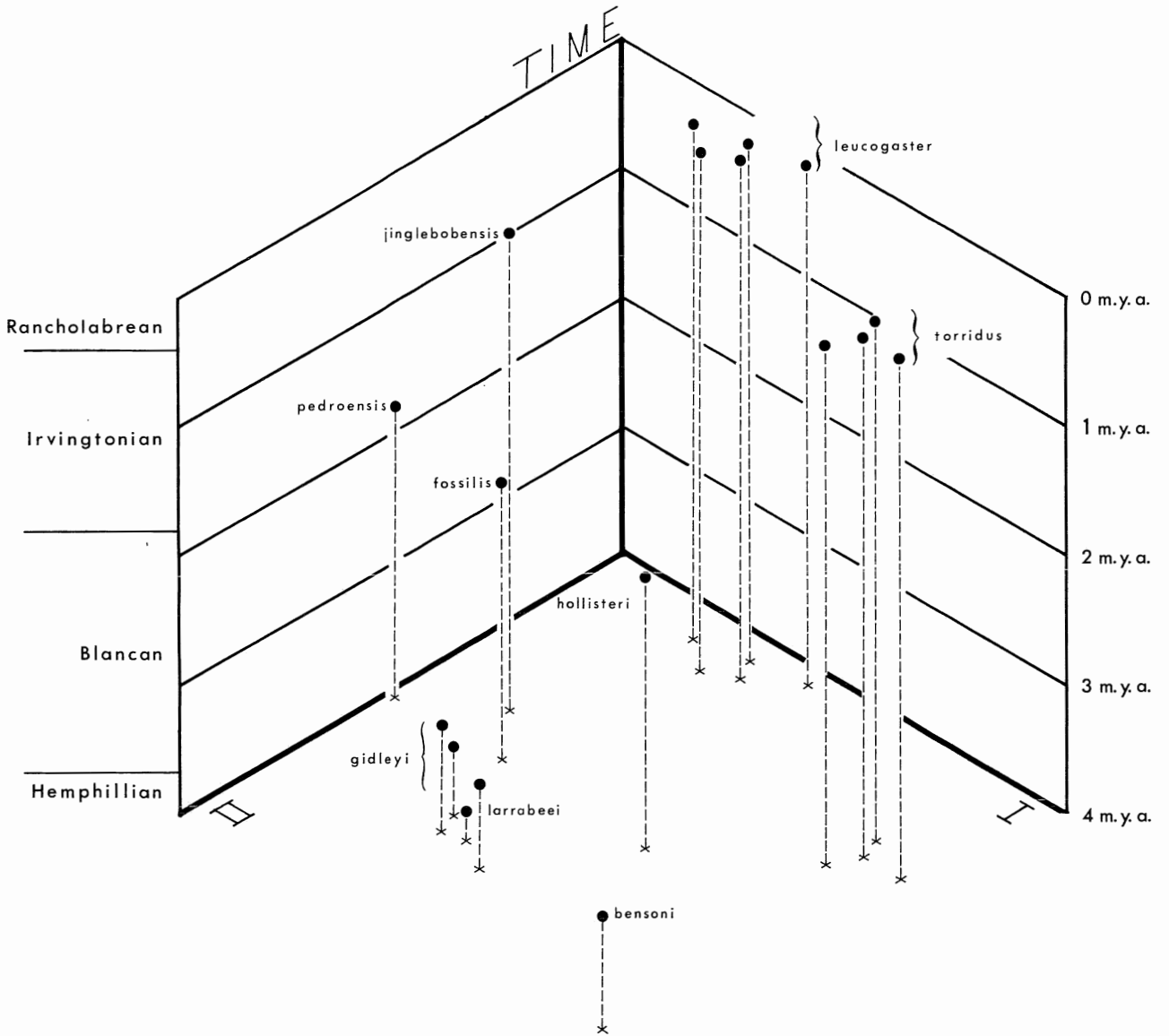
Figure 17. Projection of Principal Components I and II onto the time scale adopted in our study. See text for discussion.

apparent in the projection of principal components I and II onto a time axis (Fig. 17). In the early Blancan, *bensoni* stands apart from *larrabeei* and examples of *gidleyi*. *Onychomys larrabeei*, named from the Saw Rock Canyon local fauna in Kansas, is obviously not remarkably differentiated from *gidleyi*. In like manner, the new species *hollisteri* contrasts with the larger forms *fossilis* and *pedroensis* in the late Blancan – early Irvingtonian interval (the gap between *hollisteri* and *fossilis* does, in fact, exceed that between *fossilis* and *pedroensis*, although this is not visibly obvious from the perspective shown in Fig. 17). The degree of difference between *pedroensis* and *fossilis* resembles that evident between the largest (*l*-OK) and smallest sample (*l*-WY) of Recent *leucogaster*. The taxonomic distance between *pedroensis* and *fossilis*, for instance, is 0.58 compared to 0.50 between *l*-OK and *l*-WY. If one includes the two late Wisconsin cave samples of *leucogaster* in this comparison (on the assumption that the 10,000 year differential is much less than that between the time of existence of the Curtis Ranch and Borchers local faunas), then the maximum distance figure between OTUs of *leucogaster* is actually greater ($d_{jk} = 0.75$). This suggests that *pedroensis* and *fossilis* represent geographic variants of a single species. Finally, the hiatus between OTUs of *leucogaster* and *torridus* in the Recent approximates that separating *fossilis/pedroensis* and *hollisteri* or *gidleyi/larrabeei* and *bensoni*. Unfortunately, we lack examples of smaller *Onychomys* from the time period of *jinglebobensis*.

The evolutionary fate of *jinglebobensis* is still problematic. On the one hand, it is morphologically quite similar to *fossilis* and appreciably different from *leucogaster*; on the other hand, *jinglebobensis* is temporally farther removed from *fossilis* ($\sim$1.5 million years) than from living *leucogaster* ($\sim$ 300,000 years). This juxtaposition of near time and distant morphology could argue for the disappearance of *jinglebobensis* toward the end of the Pleistocene, and the derivation of modern *leucogaster* at some earlier cladistic event, as suggested in the first phylogeny (Fig. 16). Alternatively, the argument for an ancestral-descendant relationship of *jinglebobensis* and *leucogaster* presupposes a relatively rapid rate of change, involving both reduction of the third molar and diminution in overall size. We regard the phenetic disposition of the two late Wisconsin OTUs of *leucogaster*, as revealed in the principal component analyses, as crucial support for this interpretation. Although these two cave samples are only 10,000 years

in age, and undoubtedly referrable to *leucogaster*, there exist fine differences in morphology, especially in relative size of the M_3, that separate them from living *leucogaster* along principal component II (Figs. 13, 14). Furthermore, some decrease in general size is indicated during this brief time interval.

A synopsis of the foregoing phenetic and chronological observations yields a phylogeny markedly different from that initially proposed (Fig. 18). The major features of our phylogenetic hypothesis include the following:

1) Only two lineages, one leading to modern *leucogaster* and the other to *torridus*, are represented in the material examined. Thus, both of these phyletic lines are extended back to very early Blancan (late Hemphillian in the case of *larrabeei* from the Saw Rock Canyon).

2) Each lineage consists of three temporally successive species: *gidleyi* (including *larrabeei*) – *pedroensis* (including *fossilis* and *jinglebobensis*) – *leucogaster*; and *bensoni–hollisteri–torridus* (Fig. 18).

3) These lineages have paralleled one another quite closely; there is no evidence of substantial divergence from their first appearances in the fossil record. For example, the mean taxonomic distances between successive pairs of paleospecies are: *bensoni – gidleyi*, 3.08; *hollisteri – pedroensis*, 2.31; *torridus – leucogaster*, 2.97.

4) The significant character trends include reduction in relative size of the third molar (especially evident in the talonid heel), concomitant increase in relative size of the first and second molars (Appendix 3), increased height of primary cusps (tubercular hypsodonty). The capsular process becomes more pronounced in the *leucogaster* line but typically remains small and inconspicuous in the *torridus* line.

5) An increase in size has occurred from the early Blancan to the late Blancan, apparently followed by a period of stability throughout most of the Pleistocene, and then a relatively rapid diminution in size in late Pleistocene times resulting in the living species. Such a parallel increase in size would account for the phenetic coupling of late Blancan *hollisteri* of the *torridus* lineage with early Blancan *gidleyi*, a member of the *leucogaster* line, in the clustering program.

6) There is no need to invoke vicariance events associated with the last glacial epoch to account for the origin of the modern species, as is sometimes done for pairs of morphologically similar, congeneric species;
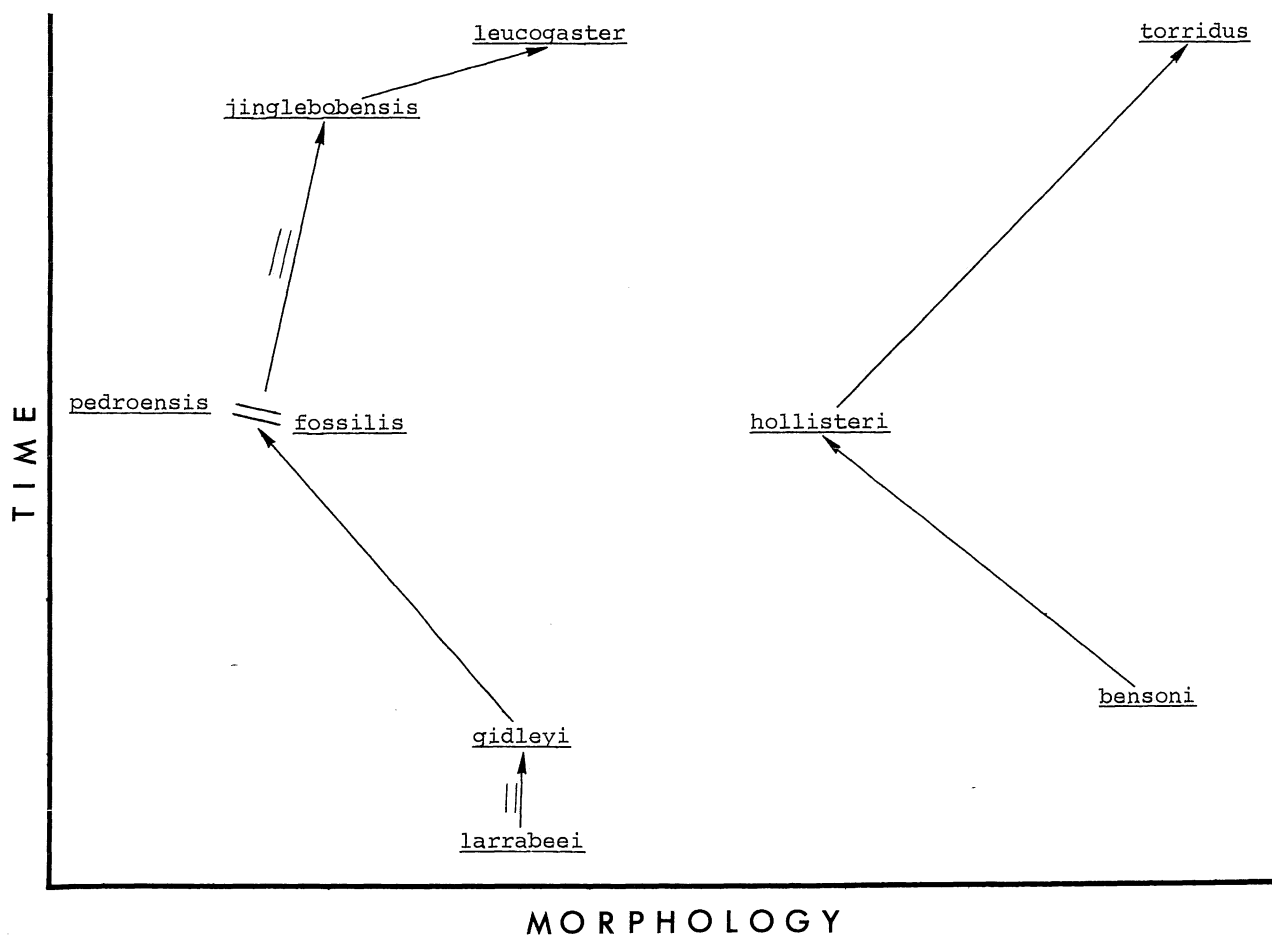
Figure 18.   Phylogenetic hypothesis incorporating phenetic analyses with chronological perspective.   Equality signs indicate proposed synonomies.   See text for discussion.

two distinct lines are indicated from the earliest appearance of *Onychomys* in the fossil record.

<div style="text-align:center">

Systematic Revision

Onychomys leucogaster Group

Onychomys gidleyi Hibbard

</div>

Onychomys gidleyi Hibbard, 1941a:281.
Onychomys larrabeei Hibbard, 1953:401, Fig. 4c.

Holotype.— Univ. of Kansas Museum of Paleontology No. 4669, an incomplete left ramus with incisor and M_1-M_3; from the Rexroad fauna, locality No. 2, Rexroad Formation in Meade Co., Kansas.

Emended diagnosis.— A grasshopper mouse approximately the size of Recent *O. leucogaster*, but differing from that species in larger size of the M_3 (primarily as revealed in the greater size of the talonid heel), lower-crowned molars, and poorly developed capsular process. *O. gidleyi* is smaller in overall size than *pedroensis* but possesses a relatively larger M_3 and smaller capsular process compared to that form.   *O. gidleyi* differs from the early Blancan *bensoni* in being much larger.

Discussion.— Hibbard (1953) named *larrabeei* from the Saw Rock Canyon local fauna, Rexroad Formation of Kansas, and distinguished it from *gidleyi* on the basis of possessing narrower molars.   *O. larrabeei* is known
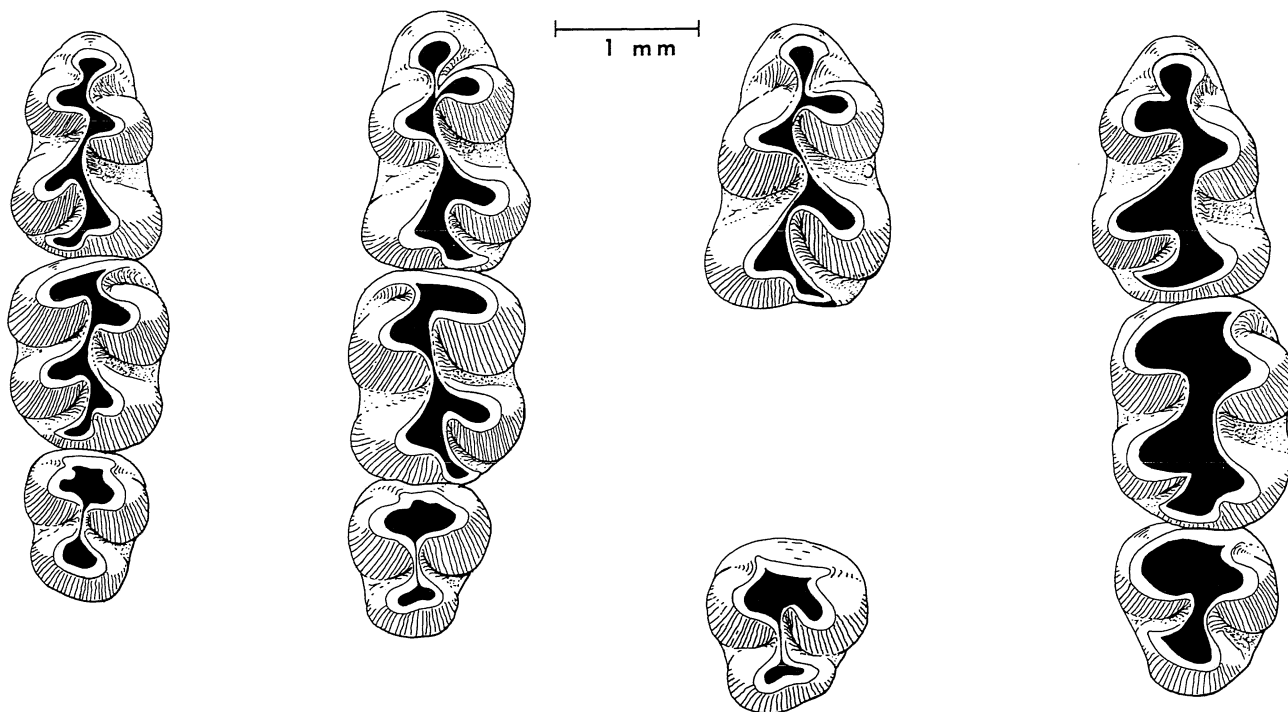
Figure 19. Crown views of molar rows of several holotypes of fossil *Onychomys* (listed from left to right): *O. bensoni* (USNM 10509, Post Ranch, San Pedro Valley Formation, Arizona); *O. larrabeei* (UMMP 27486, Saw Rock Canyon local fauna, Rexroad formation, Kansas); *O. pedroensis* (USNM 10506, Curtis Ranch locality, San Pedro Valley Formation, Arizona); *O. jinglebobensis* (UMMP 29254, Jinglebob local fauna, Kingsdown Formation, Kansas).

only by the holotype (Fig. 19), but the molar widths as well as all other dental measurements of that specimen, clearly fall within the range recorded for samples of *gidleyi* (see Appendix 1). Hibbard obviously considered the two forms closely related as he later (1964) proposed that *gidleyi* of the Rexroad local fauna was derived from *larrabeei*. We accept this lineage, but the lack of any morphological differentiation of *larrabeei* from our samples of *gidleyi* persuades us to place *larrabeei* in synonymy under *O. gidleyi* Hibbard, 1941a.

The known time span of *gidleyi* thus extends from the late Hemphillian Saw Rock Canyon local fauna to the early Blancan Rexroad local fauna. *O. gidleyi* is viewed as ancestral to the larger form *pedroensis* of the late Blancan.

Material examined.— Saw Rock Canyon local fauna, Rexroad Formation, Kansas (UMMP); Fox Canyon local fauna, Rexroad local fauna, Wendell Fox and Rexroad No. 3 localities, Rexroad Formation, Kansas (UMMP);

Beck Ranch local fauna, Yellow Quarry, Texas (MSU, Tx.). The number of specimens examined from each of these localities is indicated in the tables of measurements, Appendix 1. In addition to the more complete specimens that were measured, numerous isolated teeth have been recovered from the Wendell Fox and Fox Canyon localities.

Onychomys pedroensis Gidley

Onychomys pedroensis Gidley, 1922:125, Plate 35, Fig. 1.
Onychomys fossilis Hibbard, 1941c:208, Plate 2, Figs. 2,6,8.
Onychomys jinglebobensis Hibbard, 1955:208, Fig. 5f.

Holotype.— U.S. National Museum No. 10586, a partial left mandible with broken incisor and bearing M_1 and M_3 (Fig. 19); from the Curtis Ranch local fauna, San Pedro Valley Formation, Arizona.

Emended diagnosis.— A grasshopper mouse slightly

larger in size than Recent *O. leucogaster*. *O. pedroensis* also differs from *leucogaster* in having a deeper, more robust dentary, relatively larger M_3 and talonid portion of M_3 and smaller capsular process. Compared to *gidleyi*, *pedroensis* is larger with a deeper lower jaw, possesses a relatively smaller M_3, especially as evident in the more reduced talonid heel, and has a moderately developed capsular process. Specimens of *pedroensis* exceed those of *bensoni*, *hollisteri* and *torridus* both in size and in development of the capsular process.

Discussion.– In his diagnosis of *O. fossilis*, Hibbard (1941c) contrasted the new form mainly with *leucogaster* and *torridus*. He relied on a personal communication from C. Lewis Gazin (one paragraph quoted verbatim by Hibbard, 1941c:209) for distinctions between *pedroensis* (Fig. 19) and the grasshopper mouse from the Borchers local fauna. In that paragraph, Gazin cited the primary differences as a "more slender jaw with narrower teeth" in the Borchers form and the greater development of the capsular process in *pedroensis*. The two agreed in relative reduction of the M_3 and position of the masseteric crest.

It is unfortunate that only a few specimens of *pedroensis* have been recovered, thus discouraging a more rigorous evaluation of its level of differentiation from Hibbard's *fossilis*. On the basis of the material at hand, however, it seems more appropriate to consider the two conspecific. In size and narrowness of teeth, specimens of *pedroensis* fall within the range of variation observed for the larger sample of *fossilis*, albeit at the larger end of the size scale for any particular measurement (see, *e.g.*, Fig. 9 and Appendix 1). In this regard, a bivariate scatter-plot including specimens of *pedroensis* and *fossilis* presents a distribution similar to one that would be obtained by plotting a couple of specimens from the sample of *leucogaster* from Oklahoma (which averages the largest in size of all *leucogaster* examined) together with the entire sample of *leucogaster* from Wyoming (which averages smaller in size). Furthermore, the degree of difference between *pedroensis* and *fossilis* revealed in the various phenetic analyses corresponds closely to that observed between populations of *leucogaster* (excluding that from Nevada) or *torridus*. Also, the distinction in pronouncement of the capsular process is not sufficient to justify specific separation; specimens of *leucogaster* from Texas possess a relatively smaller capsular process compared to other representatives of *leucogaster* studied. Since *pedroensis* and *fossilis* are approximately contemporaneous, *fossilis* could

be retained as a subspecies of *pedroensis*, and treated in the same context as present-day subspecies, rather than as a chrono-subspecies or stratum-label. We see no practical benefit for doing so and, therefore, place *fossilis* in complete synonymy with *pedroensis*.

Hibbard (1955) described *jinglebobensis* (Fig. 19) from the late Pleistocene Kingsdown Formation of Kansas and separated it from *pedroensis* on the basis of slightly larger jaw and M_3, and from *fossilis* on the basis of overall larger size of dentition and mandible. Neither of these diagnoses serve to distinguish *jinglebobensis* from either *pedroensis* or *fossilis*. In fact, the M_3 of *jinglebobensis* is slightly smaller (but not significantly so) than that of *pedroensis* (Appendix 1), and the mandible of *jinglebobensis* fits within the pattern of variation observed for *fossilis* and actually averages smaller in size (Appendix 1). Morphologically, *jinglebobensis* closely resembles *fossilis*, and if one accepts that *pedroensis* and *fossilis* are conspecific, as we have argued, then the specific status of *jinglebobensis* is even less defensible.

On the basis of material examined, we recognize *pedroensis* from the late Blancan Borchers local fauna through the late Pleistocene Jinglebob local fauna (late Sangamon or early Wisconsin) and consider *pedroensis* the antecedent of Recent *leucogaster*.

Material examined.– Borchers local fauna, Borchers Pasture, Crooked Creek Formation, Kansas (UMMP, UKMVP); Curtis Ranch local fauna, San Pedro Valley Formation, Arizona (USNM); Jinglebob local fauna, Kingsdown Formation, Kansas (UMMP). Sample sizes for these localities are given in Appendix 1. In addition, we have examined isolated teeth and jaws in UMMP from the Sandahl local fauna, McPherson Formation, Kansas (Semken, 1966); Cragin Quarry local fauna, Kingsdown Formation, Kansas (Hibbard and Taylor, 1960); and White Rock local fauna, Belleville Formation, Kansas (Eshelman, 1975).

Onychomys leucogaster (Wied-Neuwied, 1841)

Holotype.– According to Hollister (1914), the whereabouts, or even the existence, of the specimens which Wied-Neuwied used in his description is unknown. The type locality is Mandan Indian village, near Fort Clark, Oliver Co., North Dakota.

Diagnosis.– Since our study focuses on the status and relationships of named fossil taxa, we have restricted our diagnosis of *leucogaster* to features of the dentition

and lower jaw. For a complete characterization, refer to Hollister (1914).

Compared to *gidleyi, bensoni,* and *hollisteri,* the teeth of *leucogaster* are more noticeably hypsodont, the M_3 is greatly reduced (especially the talonid portion) and the capsular process is moderately to strongly developed. In size, specimens of *leucogaster* approximate those of *gidleyi* but surpass those of *bensoni* and *hollisteri.* *O. leucogaster* is slightly smaller than *pedroensis* and possesses a more reduced M_3. Distinctions between *leucogaster* and .*torridus* have been summarized above and by Hollister (1914) and Van Cura and Hoffmeister (1966).

Discussion.− The tentative allocation of *Onychomys* from the Cragin Quarry local fauna (Kingsdown Formation, Meade Co., Kansas) to *leucogaster* by Hibbard and Taylor (1960) is debatable. Since the Cragin Quarry material is presumed older than the Jinglebob local fauna (Hibbard and Taylor, *op. cit.*; Zakrzewski, 1975) this identification implies the existence of *leucogaster* prior to *jinglebobensis* (= *pedroensis*), a sequence contrary to our proposed lineage. Their identification rests on the smaller size (compared to *jinglebobensis*) of two specimens consisting of lower jaws with first molars. The size differential is only slight, and without the M_3 to ascertain its degree of reduction, the placement of these samples to species is impossible. Interestingly, Dalquest (1967) referred the *Onychomys* obtained (three isolated first molars) from the Slaton Quarry in Texas, a fauna he considered slightly older than either Cragin Quarry or Jinglebob, to *jinglebobensis.*

These examples underscore the subjectiveness of attempting species' identifications using small sample sizes and few characters, which unfortunately are common traits of a paleontological sample. More complete specimens may be more reliably classified. Also, if the chronological sequence *gidleyi−pedroensis−leucogaster* does represent an evolutionary lineage, then the uncertainty of identification could reflect the arbitrariness inherent in dividing a phyletic continuum into successional species.

Material examined.− Schulze Cave, layer C1, Edwards Co., Texas (MSU, TX); Friesenhahn Cave, Bexar Co., Texas (UT). Numerous teeth and jaw fragments were recovered from these caves, in addition to the relatively intact specimens measured (Appendix 1). Other late Wisconsin sites which were examined include: Schulze Cave, Layer C2, Edwards Co., Texas (MSU, TX) (Dalquest, *et al.*, 1969); Klein Cave, Texas (MSU, TX);

Good Creek, Foard Co., Texas (MSU, TX) (Dalquest, 1962); Groesbeck Creek, Hardeman Co., Texas (MSU, TX) (Dalquest, 1965); Cueve de Abra, Tamaulipas, Mexico (MSU, TX) (Dalquest and Roth, 1970); Rattlesnake Cave, Zone 1, Kinney Co., Texas (UT) (Lundelius, 1967); Pratt Cave, Level 2, Texas (UT); Jones local fauna, Vanhem Formation, Meade Co., Kansas (UMMP). Numbers and localities of extant *leucogaster* studied are given in the Materials and Methods.

Onychomys torridus Group

Onychomys bensoni Gidley

Onychomys bensoni Gidley, 1922:125, Plate 34, Fig. 15.

Holotype.− U.S. National Museum No. 10509, an incomplete right ramus with M_1-M_3 (Fig. 19) from the Benson local fauna, Post Ranch locality, San Pedro Valley Formation, Arizona.

Emended diagnosis.− A grasshopper mouse approximately the size of *O. torridus,* but differing from that species in greater size of the M_3 (especially the talonid heel) and more brachyodont molars. The distinctly smaller size of *bensoni* separates it from the contemporaneous form *gidleyi*; otherwise, the two are similar in proportional features of their dentitions. The molars of *bensoni* (Fig. 19) are slightly lower crowned, the M_3 less reduced, and the teeth are smaller in most dimensions compared to *hollisteri.* Specimens of *pedroensis* and *gidleyi* exceed *bensoni* in overall size, greater development of capsular process and height of teeth; however, the M_3 of *bensoni* is proportionately larger than that in those forms.

Discussion.− Gazin (1942) noted that the plate and figure numbers of the holotypes of *Eligmodontia* (= *Bensonomys*) *arizonae* and *Onychomys bensoni* were switched in Gidley's (1922) original descriptions; the plate/figure numbers given above observe Gazin's corrections.

Onychomys bensoni is viewed as ancestral to the larger form *hollisteri* from the late Blancan Borchers local fauna.

Material examined.− The holotype constitutes the only known specimen of *bensoni.*

Onychomys hollisteri Carleton and Eshelman

Discussion.− Since this species is described in this study, information on the holotype and the diagnosis

are not repeated here.

The discovery of two fossil species of *Onychomys* at the same locality was first reported by Eshelman (1975) for the White Rock local fauna. Although only isolated first molars were recovered, the measurements and features of these teeth closely match those recorded for the more abundant series of *hollisteri* obtained from the slightly younger Borchers local fauna; these teeth contrast in size with two other first molars questionably assigned to *fossilis* (Eshelman, 1975). The sympatric occurrence of two species of fossil *Onychomys*, presumably ancestral to living *torridus* and *leucogaster*, is not unexpected, since the ranges of the two Recent forms overlap. However, present-day zones of contact and sympatry lie 400-600 miles to the southwest (in Texas or New Mexico) of these late Blancan records from Kansas (Fig. 1).

Known examples of *hollisteri* cover a time interval approximately equivalent to the late Blancan (Wolf Ranch locality, Arizona through the Borchers local fauna, Kansas). In our view, *hollisteri* evolved into modern *torridus*. This transition implies substantial decrease in overall size and reduction of the M_3, changes parallel to the ones that can be more convincingly documented with the better fossil record of the *leucogaster* lineage.

Material examined.— Borchers local fauna, Borchers Pasture, Crooked Creek Formation, Kansas (UMMP, UKMVP); sample sizes indicated in Appendix 1. Numerous isolated teeth were also recovered from the Borchers local fauna. Several isolated teeth are recorded from the White Rock local fauna, Belleville Formation, Kansas (UMMP) and the Wolf Ranch locality, San Pedro Valley Formation, Arizona (UA).

Onychomys torridus (Coues, 1874)

Holotype.— U.S. National Museum No. 9886, a skin-only, adult (sex not recorded) from Camp Grant, Graham Co., Arizona; collected 10 June 1867 by Dr. Edward Palmer.

Diagnosis.— Our diagnosis only covers traits of the dentition and mandible; for additional information, see Hollister (1914).

The small size of individuals of *torridus*, particularly as reflected in the length of toothrow and depth of ramus (Appendix 1), readily separates them from specimens of *gidleyi* and *pedroensis*. Furthermore, the M_3 of *torridus* is much more reduced than in either of those forms.

O. torridus approximates *bensoni* in overall size, but the M_3 of *torridus* is relatively much smaller and its teeth more hypsodont compared to *bensoni*. Specimens of *torridus* can be distinguished from those of *hollisteri* on the basis of smaller size and more reduced M_3. Diagnostic features of *torridus* and *leucogaster* are discussed above and by Hollister (1914) and Van Cura and Hoffmeister (1966).

Specimens examined.— Several jaw fragments with first molars from Pratt Cave, Level 2, Culberson Co., Texas (UT). Sample sizes and localities of Recent *torridus* examined are listed in Materials and Methods.

Onychomys, Incertae sedis

Onychomys martini (Hibbard)

Peromyscus martini Hibbard, 1937:464, Fig. 4.
Onychomys martini Hoffmeister, 1945:191.

Holotype.— Univ. of Kansas Museum of Paleontology No. 3850, a partial right maxillary with M_2 and M_3; from the Edson Quarry, Ogallala Formation, Sherman Co., Kansas.

Discussion.— Hibbard (1937) named *maritni* as a species of *Peromyscus* and later (1939) reported a right dentary bearing the incisor, M_1 and M_2, which he also assigned to *Peromyscus martini*. Hoffmeister (1945) referred *martini* to the genus *Onychomys* and we agree with his reallocation. Subsequently, Hibbard (1953), in his description of *O. larrabeei*, stated that *martini* is smaller than his new species and considered *larrabeei* to be more closely related to *gidleyi* than to *martini*.

We did not have the opportunity to study the holotype of *martini* but did examine the right dentary (Museum of Comparative Zoology No. 6201) mentioned by Hibbard (1939). Based on this specimen, *O. martini* is phenetically closest to *bensoni*. The dentary lacks an M_3, but the size of the alveolus indicates that this tooth was relatively large, as in other Pliocene *Onychomys*. The alveolar length of the tooth row measures 3.89 mm in *martini* and 3.79 mm in *bensoni*. Other measurements of *O. martini* (MCZ No. 6201) are as follows: LM_1, 1.52; AWM_1, 0.96; PWM_1, 1.00; LM_2, 1.27; WM_2, 1.04; height of protoconid, 0.57, and depth of ramus below M_1, 3.22. These dimensions closely resemble those of the holotype of *bensoni* (see Appendix 1). The height of the protoconid is less in *martini*, but the teeth of this specimen are more heavily worn compared to *bensoni*. The two contrast in shape

of the M_1: that of *martini* is oval, the width across the anterior cusps only slightly less than the posterior width, while that of *bensoni* tapers more abruptly anteriorly, such that the distance across the anterior cusps is noticeable less than that for the posterior cusps.

Phenetically, *martini* is small like other members of the *O. torridus* group and perhaps even conspecific with *O. bensoni*. The older stratigraphic horizon from which *martini* was described (base of the Ogallala Formation, middle Pliocene) and the incompleteness of the few known specimens, however, make such a formal taxonomic judgement premature. Until the Edson Quarry material is re-examined and additional examples of *martini*, hopefully ones with intact molar rows, are recovered, we have retained *martini* as *Onychomys, Incertae sedis*.

Related Genera

In addition to the named forms of *Onychomys* discussed above, two other taxa deserve mention because of their near relationship to *Onychomys*.

One, *Miochomys niobrarensis*, was described by Hoffmeister (1959) from the Niobrara River fauna (late Miocene) in Cherry Co., Nebraska. Hoffmeister viewed this form as closely allied, possibly ancestral, to *Onychomys*, but exhibiting some traits intermediate to *Onychomys* and *Peromyscus*. Clark, *et al.* (1964) formally derived *Onychomys* from *Miochomys* and *Peromyscus* from *Copemys*, both groups descended from a *Leidymys* stock in the early Miocene. Klingener (1968), however, disputed the distinctiveness of *Miochomys niobrarensis* and provisionally referred it to *Copemys kelloggae*. Lindsay (1972) basically endorsed Klingener's viewpoint, but retained *niobrarensis* as a species of *Copemys* and mentioned no special relationship between *Copemys* and *Onychomys*. Thus, the descendant relationship of *Onychomys* from either *Miochomys* or *Copemys* is largely unresolved.

More recently, Jacobs (1977) described *Paronychomys* from the Redington local fauna (Hemphillian age) in San Pedro Valley, Arizona. The new form is characterized by more alternate cusps than in *Copemys* or *Peromyscus* and high crowned cheek teeth. The hypsodonty observed in *Paronychomys* is apparently achieved by elongation of that portion of the tooth between the base of the cusps and the base of the crown. This type of hypsodonty contrasts with that recorded for *Onychomys*, which mainly involves vertical relief of the cusps. Jacobs (1977:516) suggests that "*Paronychomys* may have been derived from *Copemys* or from some as yet undiscovered primitive species of *Onychomys*."

DISCUSSION

Rationale for our Phylogenetic Hypothesis
and Classification

The paleontologist is obviously restricted in his character analysis and his resultant phylogenetic inferences to those parts of the organism frequently preserved in the fossil record, in our case jaw fragments and teeth. This underscores what we consider the critical drawback of the paleontological sample: the paucity of characters for numerical analysis and phylogeny reconstruction. As noted by Cracraft (1974) and Farris (1976), two otherwise similar fossil forms occurring in successive strata may differ in some uniquely derived character(s) not preserved in the fossil record and therefore unknown to the investigator. Knowledge of the distribution of such characters could drastically alter one's estimation of relationships of those forms. Our characterization of the phenotypes of the extinct populations is limited to several measurements of the lower jaw and dentition; moreover, these measurements record a single character complex, the masticatory apparatus, and most are predictably strongly intercorrelated. We would feel more confident basing our phylogeny on a greater number of characters from a variety of organ systems.

Gingerich (1976a,b), on the other hand, identifies several advantageous properties of mammalian teeth in reconstructing phylogenies, including their lack of appreciable ontogenetic change once erupted, their high heritability and their reflection of the bearer's trophic niche and ecological adaptations. Examination of fossil material further offers what Van Valen (1969: 193) termed the advantage of "direct extension in time" and the opportunity to study rates of character transformation and to delineate the functional significance of documented character modifications. On balance then, we regard objections concerning the fewer potential characters discernable from fossils as reasons for judiciously interpreting fossil information rather than

entirely discarding it. Fortunately, there is a growing literature, derived from both theoretical considerations and practical experience, that specifically addresses the utilization of fossils in phylogeny reconstruction (for example, Bretsky, 1975; Cracraft, 1974, 1975; Engelmann and Wiley, 1977; Gingerich, 1976a,b; Harper, 1976; Patterson and Rosen, 1977; and Szalay, 1977).

We employed several populations of each living species of *Onychomys* to assist us in evaluating the distinctiveness of the several named extinct forms. Our survey of *torridus* and *leucogaster* was by no means exhaustive, either in size of sample or geographic coverage; obviously, much larger samples could have been amassed by visiting other museums. Our intent, however, was not a revision of the recent species (although such an undertaking is clearly warranted and could offer further insight to the relationships of the fossil taxa). Furthermore, inequality of sample sizes and disparity in geographic origins are common attributes of paleontological samples, and therefore, we simply accepted for analysis what was locally available. In doing so, we could weigh the bias, if any, of small sample size and disjunct geographic origin on the taxonomic structure revealed in the various multivariate programs and on patterns of variation and correlation. This is precisely the situation faced when interpreting differences between fossil taxa, some known by only a few specimens (*e.g., jinglebobensis*) or by many (*e.g., fossilis*) and from widespread geographic localities (Kansas, Texas and Arizona).

Some may object to our use of the extant populations, collected in essentially a single temporal plane, as a yardstick for measuring the differentiation of populations evolving through time. We justify this application for two reasons. First, in the absence of other criteria to evaluate specific discontinuities, we had to rely on a degree-of-morphological-difference criterion, specifically as observed for the lower jaws and dentition of the two living species. This assumes that the extinct

populations were no more or no less variable than the extant ones. Second, there were several instances where fossil taxa were approximately contemporaneous (but certainly not to the same extent as our recent samples) but from widely separated geographic sources. Thus, we emphasized the use of the intra- and interspecific differentiation revealed by the living species in taxonomic decisions involving a relatively narrow time interval, for example, the status of *pedroensis* and *fossilis* from late Blancan/early Irvingtonian or early Blancan *gidleyi* found in Kansas and Texas.

In our study, we initially treated all samples, fossil and living, as contemporaneous forms. Utilizing the results of the various multivariate analyses, we identified six phenetic clusters which we ultimately recognized as species. The secondary introduction of stratigraphic position (time) into the analysis helped us resolve some taxonomic difficulties (such as the status of *fossilis* with respect to *pedroensis*) and provided insight to the phylogenetic relationships of the species. The interjection of a time scale was particularly significant in illuminating the position of *hollisteri* in the Borchers local fauna (assuming of course that our estimation of relationships is correct). On strictly phenetic grounds, one could argue that *hollisteri* is more closely related to *gidleyi* than *bensoni*. However, viewing the differences in a chronological perspective —where in late Blancan time only two grasshopper mice, one large and one small, exist, and where both of these forms are larger than an otherwise similar pair of species in the early Blancan — we favored the derivation of *hollisteri* from *bensoni*. Our phylogenetic conclusion relates these species by an ancestry-descent model rather than some cladistic pattern of common ancestry. Our procedure adhered for the most part to what Gingerich (1976b) called the stratophenetic method and was generally consistant with the set of ordering principles elaborated by Harper (1976).

Cracraft (1974) noted that paleontologists may uncritically accept as primitive that morphological state which appears earliest in a stratigraphic section. It is possible, due to the vagaries of fossil formation and discovery, for a species originating relatively early to occur in younger fossiliferous strata; whereas, another related species, which in fact originated later, is found in the oldest beds. Mere acceptance of their stratigraphic position as indicative of ancestral or derived morphologies would result in erroneous conclusions about polarities of character evolution and relative primitiveness of

the species. Cracraft (*op. cit.*) urges that the analysis of ancestral-derived sequences should be based on evidence independent of the stratigraphic sequence in order to avoid such circularity in reasoning.

His arguments on this account are well-taken but difficult to accommodate. Given the fragmentary nature of the fossil specimens themselves, few characters are available which can be coded and subjected to the kind of phylogenetic systematic analysis Cracraft favors. For that very reason, many systematists restrict their studies to living animals, from which potentially innumerable characters can be tabulated and their direction of evolution decided. Our data set included mainly continuous variables and only one qualitative one. Perhaps we could have transformed some of the morphometric variables to qualitative ones. For instance, we could define the following characters: size of M_3 — relatively large (0), medium (1), or small (2); talonid heel of M_3 — relatively large (0), medium (1), or small (2); height of protoconid — relatively low (0), medium (1), or high (2); and development of capsular process — relatively weakly (0), moderately (1), or strongly pronounced (2). Examination of sister groups (*Peromyscus, Reithrodontomys* and *Baiomys*) to determine which states are primitive yielded the results already coded (*i.e.*, 0-1-2) above. In fact, Hershkovitz (1962) and Misonne (1969) view the reduction in size of the third molar as a major trend within many groups of Muridae; similarly, increases in height of teeth from brachyodont to hypsodont conditions are documented for many lines of murids. From this, we would conclude that *gidleyi* and *bensoni* exhibit the greatest degree of primitiveness, *pedroensis* and *hollisteri* are more advanced, and *torridus* and *leucogaster* possess the most derived features. This order corresponds to their succession of appearance in the fossil record: *gidleyi* and *bensoni* in the early Blancan; *pedroensis* and *hollisteri* in the late Blancan; and *leucogaster* and *torridus* in the late Pleistocene-Recent.

Although this exercise is restricted to a few characters and therefore rather simplistic, it does meet in principle some of Cracraft's (1974) objections. We could arrive at an estimation of the relative antiquity of these six species independent of their stratigraphic position. However, rather than represent these phylogenetic relationships as a succession of sister groups, it seems as reasonable to relate them in an ancestor-descendant sequence, because each pair of species with the next most derived character state is superpositioned in the

fossil record. We agree with Szalay (1977) that the potential loss of biological information (in terms of character origins, their rates of transformation, and perhaps their functional significance) may be great if one is automatically consigned to interpret relationships as bifurcating sister groups when an hypothesis of ancestor-descendant relationships is equally plausible. Furthermore, as emphasized by others (for example, Gingerich, 1976 a,b; Harper, 1976; Szalay, 1977), our phylogenetic hypothesis is clearly testable and certainly refutable by the accumulation of other fossil *Onychomys*, particularly from time intervals where we lacked specimens, and by additional study of characters.

Our final classification acknowledges three successional species in each lineage: *gidleyi—pedroensis—leucogaster* and *bensoni—hollisteri—torridus*. Bifurcation of the ancestral stock occurred prior to the appearance of *Onychomys* in the fossil record, and since their appearance, the two lineages have paralleled one another in direction of dental changes. Some may argue that only two species, *leucogaster* and *torridus*, deserve to be recognized since we have proposed only two lineages, each of which represents a temporal continuity of a gene pool. We decided otherwise because our phenetic analyses disclosed six distinctive morphologies, and the hiatus between each morphotype more or less resembled that observed between the two living species; hence, we chose to recognize each morphology by available specific epithets. Admittedly, our specific allocation of extinct samples was fortuitously aided by discontinuities in the fossil record. Decisions concerning specific placement of newly discovered fossil *Onychomys*, especially from intermediate time intervals, may prove more difficult. As alluded to in the systematic revision, we may have already met this problem in some of the late Pleistocene collections that have been assigned variously to *jinglebobensis* (=*pedroensis*) or *leucogaster*. Additional paleontological samples from this period may favor synonymy of *jinglebobensis* under *leucogaster*, but such a realignment would not alter our basic phylogenetic hypothesis.

Variation and Rates of Evolution

The following discourse on evolutionary rates and variation of course presupposes that the phylogeny we proposed is, in some sense, true or correct. The analysis of darwinian rates has been restricted to the *leucogaster* lineage since we have a better sampling through time than exists for the *torridus* sequence. In calculating darwins as the unit of evolutionary rates, we have used Lindsay, *et al.*'s (1975) time scale for assigning absolute ages to the various fossiliferous strata. We employed mean dimensions of all specimens of *leucogaster* examined (excluding only those from Nevada), instead of just one OTU, as the best estimate of the morphology of Recent *leucogaster*; similarly, we averaged the samples of *leucogaster* from the late Pleistocene. Samples of *gidleyi* and *pedroensis* utilized represent only the Kansan beds; samples of *gidleyi* and *pedroensis* from other localities are too small. As it stands, we are painfully aware that this same criticism pertains to the sample from the Jinglebob local fauna; we simply lacked any other suitable series from this particular time frame.

Based on this succession of species and localities, we have tabulated rates of evolution (in millidarwins) from a variety of sources, including several unit-character means, ratios of mean dimensions, and multivariate scores (Table 8). Each of these measurements records the same pattern of darwinian rates throughout our phyletic sequence. Differences in magnitude of the evolutionary rates do exist between variables. This is strikingly demonstrated by the high rates calculated for dimensions of the third molar as compared to the first, and underscores Simpson's (1953) observation that rates of evolution of unit characters may change independently within a single phyletic line. It is also noteworthy that metrics derived from the multivariate analyses (principal component scores, distance and correlation coefficients) yield similar patterns and magnitudes of darwinian rates (Table 8). This result is not surprising since most measurements describe a single character complex, that is, the dental battery, and are highly intercorrelated (Table 5). Compared to the range of rates based on raw character values, the multivariate metrics seem to have an averaging affect on rates of evolution. Lerman (1965) used another multivariate statistic (Mahalanobis' D^2) to measure rates of evolution of character complexes in a variety of animals.

Simpson (1944, 1953) first drew attention to differences in rates of evolution both between phyletic lines of descent and within a single phyletic lineage. He characterized three categories of evolutionary rates: bradytely, corresponding to very slow rates of evolutionary change (the existence of this class of rates was inferred more from the persistence of relatively unchanged, geologically ancient animals, *i.e.* "living fos-

TABLE 8.   Rates of Evolution (millidarwins).

Species, Locality, and Approximate Age (years)	Raw Mean Character Values					Mean Proportion			Principal Component Scores		Resemblance Coefficients		Grand Mean
	LM_1-M_3	LM_1	LM_2	LM_3	LM_3 tal.	$\frac{LM_1}{LM_1-M_3}$	$\frac{LM_3}{LM_1-M_3}$	$\frac{LM_3}{LM_1}$	I	II	d_jk	1-r	
O. gidleyi Fox Canyon 3,600,000	14	77	17	23	157	68	34	57	11	60	17	31	47
O. gidleyi Rexroad 3 3,250,000	18	15	23	30	64	3	50	41	13	76	12	15	30
O. pedroensis Borchers 1,800,000	3	7	17	12	41	5	17	20	3	13	15	13	14
O. pedroensis Jinglebob 300,000	45	72	131	317	72	131	276	413	66	379	151	186	186
O. leucogaster late Wisconsin 10,000	2,800	3,200	1,900	7,100	15,500	700	3,900	3,000	3,000	3,400	5,100	3,500	4,425
O. leucogaster Recent 0													

sils" than from documentation with the fossil record); horotely, representing "normal" rates of evolution that seem to typify a given group of animals (another group may exhibit its own characteristic range of evolutionary rates); and tachytely, extremely fast rates of evolution occurring as brief, explosive episodes (possibly, but not necessarily, resulting in the origin of new taxa). In an important paper, Kurtén (1960) surveyed distributions of evolutionary rates among Tertiary and Quaternary mammals and lent some quantification to Simpson's three classes. Using Haldane's (1949) measure of morphological rates of evolution, Kurtén (*op. cit.*) detected three modes of evolutionary rates,

which he termed simply A-, B-, and C- rates. A- rates averaged 12.6 darwins (R=3.7–43) and seemed to correspond to Simpson's tachytelic rates, while B-rates ($\bar{x}$=0.51 darwins, R=0.12–2.3) fit well with Simpson's notion of horotely. For various reasons, Kurtén (1960) declined to associate his C- rates ($\bar{x}$=0.023 darwins, R=0.003–0.2) with Simpson's bradytely.

Rates of evolution evident in our study correspond favorably to Kurtén's (1960) A-, B-, and C- rates both in magnitude and, to a lesser extent, in distribution of the rates according to geological age (Table 8). Whether based on unit characters or character complexes (principal component scores or coefficients of taxo-

TABLE 9. Rates of Evolution (millidarwins).

Species, Locality, and Approximate Age (years)	Raw Mean Character Values					Mean Proportion			Principal Component Scores		Resemblance Coefficients		Grand Mean
	LM_1-M_3	LM_1	LM_2	LM_3	LM_3 tal.	$\dfrac{LM_1}{LM_1\text{-}M_3}$	$\dfrac{LM_3}{LM_1\text{-}M_3}$	$\dfrac{LM_3}{LM_1}$	I	II	d_jk	1-r	
O. gidleyi Fox Canyon 3,600,000	17	27	15	20	21	10	60	44	13	50	4	4	24
O. pedroensis Borchers 1,800,000	25	12	44	80	108	13	52	67	24	69	50	53	50
O. leucogaster Recent 0													

nomic resemblance), rates of evolution for *Onychomys* throughout the late Tertiary to middle Pleistocene (Jinglebob) range from three to 157 millidarwins (mean is approximately 30 millidarwins); this class of rates matches the C- rates found by Kurtén (1960) for his much larger sample of Tertiary mammals. Rates of evolution approximating Kurtén's (*op. cit.*) B- rates are observed for the interval between *O. pedroensis* from the Jinglebob and *O. leucogaster* from the late Wisconsin. Finally, a high rate of morphological change (4,425 millidarwins) occurred between late Wisconsin and Recent times. This tachytelic rate of evolution falls within Kurtén's A- rate category, a set of rates that he recorded exclusively for postglacial intervals (approximately 8000 years B.P. to the present). In overview, it appears that grasshopper mice of this lineage remained relatively stable morphologically from early Blancan to sometime in the middle Pleistocene. Beginning in the middle Pleistocene, rates of evolutionary change were augmented slightly, then followed by a rapid period of change from late Wisconsin to Recent.

As glaringly evident here, however, and as cautioned by Kurtén (1960), the significance of these differences in evolutionary rates suffers from the inequality of the temporal sampling. Gaps between the Blancan samples far exceed those between the Pleistocene ones; there-

fore, bouts of tachytelic evolution may be overlooked because of the coarseness of our chronological survey. Furthermore, as emphasized by Simpson (1953) and Kurtén (1960), it is highly unlikely that sustained tachytely could persist for such long periods. To cite an illustrative example using length of tooth row: in order for a rate of 3000 millidarwins to have transpired between *O. gidleyi* of the Rexroad local fauna and *O. pedroensis* of the Borchers (an interval of 1.5 million years), the tooth row would have changed in length from 4.44 mm to 400 mm, a ninety-fold increase. Assuming that sufficient variation existed for selection to operate upon, the end result would hardly be identified as a grasshopper mouse. Ideally, one would desire large samples equally dispersed through time. The likelihood of obtaining such data, however, is minimized by the fact that the farther back in time one goes, the lower the confidence of age assignment; a 20,000 year gap can be accepted with some measure of confidence for two faunas from the late Pleistocene, but not for two from the early Pleistocene.

To partially overcome some of the criticisms recited above, we recalculated darwinian rates as if only three samples, approximately equidistant chronologically, were known to us: *O. gidleyi* from the Fox Canyon; *O. pedroensis* from the Borchers; and extant *O. leuco-*

gaster. The time intervals between Fox Canyon and Borchers and between Borchers and Recent equal about 1.8 million years. Rates of evolution determined in this exercise correspond to C- rates (Table 9). Moreover, the high rates of tachytely observed previously for the late Pleistocene-Recent period have been "averaged out" by extending our temporal perspective. Nevertheless, evolutionary rates maintained over the 1.8 million years following the Borchers are, on the average, double those recorded for the 1.8 million years preceding the Borchers (Table 9). Perhaps much of the morphological change during the post-Borchers interval occurred relatively late, such as within the past 200,000 years; if correct, this would agree with the pattern seen in several European mammals (Kurtén, 1960). Alternatively, additional samples of Pleistocene *Onychomys* may reveal fluctuations in size coincident with major climatic oscillations, as documented for European populations of *Ursus arctos* (Kurtén, 1960). Until a better distribution of Pleistocene examples of *Onychomys* is accumulated, either explanation must be admitted as possible.

Van Valen (1969) disputed (but later in the same paper accepted) whether Kurtén's (1960) data demonstrated populational changes of the ancestral-descendant sort or simply reflected large-scale shifts of climatically adapted races of a geographically widespread species. In fact, some variation in size, possibly clinal in nature, is suggested by our OTUs of living *leucogaster* (Appendix 1). At least for those populations inhabiting the Great Plains region, a decrease in average size is apparent from south to north (for sake of argument, we accept this as proven, but to convincingly substantiate such a trend requires larger samples covering a much broader latitudinal transect). The alternatives then become: have we really monitored rates of evolutionary change for species' populations through time; or have we by chance sampled various-sized individuals from populations that differed in average size, shifted their ranges due to climatic fluctuations, and actually remained morphologically stable through time. If the latter is correct, then the "rates of evolution" we derived are largely statistical artifacts.

We feel that Van Valen's criticism does not apply to our data for two reasons. First our study reveals changes other than simply overall size; for example, reduction in size of the third molar, increase in relative lengths of the first and second molars, and increase in cusp height. And these morphological changes occur independently of size trends in the *leucogaster* lineage;

that is to say, a polarity of reduction in relative size of the third molar is observed for the *gidleyi–pedroensis–leucogaster* sequence (Appendix 3), but this same sequence describes first an increase and then a decrease in size. Also, no cline of reduction of the third molar, paralleling the apparent size trend, is detectable in our examples of *leucogaster* (Appendix 3). Second, the two late Pleistocene collections of *leucogaster* from Texas surpass in average size any of the Recent populations we examined (Appendix 1). Our geographic survey is not exhaustive, but it seems adequate to document extremes in size within living *leucogaster*. Hence, the difference in size between late Pleistocene and Recent *leucogaster* (and by inference, the decrease in size from *pedroensis* to *leucogaster*) is viewed as the result of selection for smaller size, and not simply fortuitous sampling of larger-sized animals from a clinally varying species.

Inspection of coefficients of variation of the dental variables (Appendix 2) and their corresponding rates of evolution (Table 8) intimates a relationship between amount of intrapopulational variation and the degree of modification through time. Specifically, those dimensions that have undergone substantial reduction in relative size throughout our phyletic sequence (LM_3 and LM_3 talonid) consistently exhibit both higher coefficients of variation and rates of evolution. In particular, the late Wisconsin-Recent interval illustrates the much higher rates of change of LM_3 and LM_3 talonid compared to LM_1 and LM_2; coefficients of variation recorded for the former two variables exceed, sometimes by a large amount, those calculated for the latter (Appendix 2).

Moreover, there is some indication that the degree of variation of LM_3 and LM_3 talonid has increased from early Blancan to Recent times. Coefficients of variation of LM_3 and LM_3 talonid of samples of *gidleyi* are smaller than those of late Pleistocene and Recent *leucogaster* (Appendix 2). In fact, coefficients of LM_3 in *gidleyi* generally match those of LM_1 and LM_2, while in most species studied, the third molar usually exhibits the greatest variability (Gingerich, 1974; Gould and Garwood, 1969; Van Valen, 1962). Fewer specimens per sample cannot adequately account for this reduced variation since at least the examples of *gidleyi* from Fox Canyon and Wendell Fox compare in size to OTUs of *leucogaster*. Furthermore, if small sample size is accepted as the explanation, then the close correspondence of coefficients of variation of all other dental dimensions of *gidleyi* and *leucogaster* becomes

TABLE 10. Correlations (*r*) of Selected Dental Lengths.

Species and Locality	$M_1:M_2$	$M_1:M_3$	$M_2:M_3$	M_3tal:M_3	$M_1:M_1$-M_3	$M_3:M_1$-M_3
O. gidleyi Fox Canyon	.51*	.23	.41	.63*	.76**	.72**
O. leucogaster Texas	.51**	.05	.29	.31	.82**	.46**

* = P < .05, ** = P < .01

enigmatic and must also be addressed. The smaller absolute size of LM_3 in living *leucogaster*, and therefore an assumed greater imprecision in measurement, is an inadequate reason too, for other dimensions in that size range (*e.g.*, AWM_1, WM_3) do not display such large coefficients of variation. The generally weaker correlations involving the third molar in extant *leucogaster* as compared to *gidleyi* (Table 10) further bolster the notion that a real increase in variability of the third molar has occurred, somehow related to its accelerated rate of evolutionary change.

Diverse opinions exist concerning the interrelationship of rates of evolution and the amount of variation within a population. In his investigation of two lineages of oreodont artiodactyls, Bader (1955) found a pattern of lower variability in that line which exhibited higher rates of evolution. Other authors have not discerned any obvious association between rates of evolution and character variation (Downs, 1961; Kurtén, 1960). Guthrie (1965), however, has suggested a positive relationship between higher variation and rapidity of evolution. Working with Pleistocene and Recent populations of *Microtus*, Guthrie (*op. cit.*) demonstrated very high coefficients of variation for dental moieties that underwent the greatest change over that period, and generally low coefficients for those dental segments that remained phylogenetically stable. Our results, especially as documented by the late Pleistocene-Recent sequence, provide corroboration of Guthrie's observations. Other evidence is provided by Kluge and Kerfoot (1973), who examined distributions of character divergence over a wide variety of neontological vertebrate samples. Although they did not specifically treat rates of evolution, they did document significant positive correlations between the ranges of character divergence and local sample variation.

The Functional Significance of Morphological Trends

In this section, we shall attempt to elucidate the functional significance(s) of the character trends we have documented. Discussion about selective pressures on populations that existed several million years ago must admittedly remain largely speculative. Yet, since we have investigated fossil taxa that have living descendants, we feel insight to the habits of the fossil species can substantially profit from our knowledge of the biology of the living forms. At the least, our speculation can be more informed than commenting upon terminal groups. We have identified three primary morphological trends in our hypothesized phylogeny: changes in size, increase in the height of the major cusps, and reduction in relative size of the third molar.

An increase in average size is apparent in the phyletic sequences from *gidleyi* to *pedroensis* and *bensoni* to *hollisteri*, attended by diminution in size to Recent *leucogaster* and *torridus*. As a consequence of this evolutionary reversal in size, individuals of *leucogaster* and *torridus* compare closely to their progenitors in the Pliocene, *gidleyi* and *bensoni*, in some dimensions. For example, most OTUs of *gidleyi* do not differ significantly from samples of *leucogaster* in mean length of the tooth row (Appendix 1). As mentioned above, we cannot determine whether *Onychomys* of the *leucogaster* lineage remained large throughout most of the Pleistocene, or whether fluctuations in size occurred in concert with episodes of glaciation. Regardless of the course of size evolution for much of the Pleistocene, a marked decrease in measurements can be traced from *pedroensis* in the Jinglebob local fauna to late Wisconsin *leucogaster* to Recent *leucogaster*. Decreasing size chronoclines in the late Pleistocene have been reported for mammals other than *Onychomys*. Kurtén (1960)

demonstrated marked postglacial "dwarfing" in five of 12 species he studied from Europe (mostly larger mammals such as lynx, wolf and bear). Similarly, reduction in size has been suggested for bighorn sheep in North America (Harris and Mundel, 1974). Other species studied have remained either stable in size throughout the late Pleistocene or even exhibited a moderate increase (Kurtén, 1960; Semken, 1966). We cannot interpret the size trends evident in our *Onychomys* material, except only as a reflection of climatic alterations, perhaps in accordance with Bergman's rule.

The parallel set of lineages we propose both record an absolute and relative increase in molar height (Appendices 1, 3). This involved augmentations in the height of only the dental cusps (termed tubercular hypsodonty, *sensu* Hershkovitz, 1962) instead of a vertical elongation of the entire crown of the tooth (=coronal hypsodonty), such as occurred in microtine evolution. The pronounced vertical relief of the cusps above the base of the molars in *Onychomys* is reminiscent of the general topography of molars seen in insectivores or insectivorous bats. Indeed, we believe that the evolution of increased tubercular hypsodonty marks a shift in the diet of *Onychomys* from a more omnivorous or granivorous feeding niche toward more exclusive insectivory. As intimated by their trivial names, grasshopper mice and scorpion mice, both species of *Onychomys* consume large quantities of arthropods (chiefly Orthoptera, Coleoptera, Lepidoptera and Arachnida), which comprise about 70-80 percent by volume of their total diet (Bailey and Sperry, 1929; Horner, *et al.*, 1965; Flake, 1973). Grasshopper mice do utilize limited quantities of seeds, grasses and forbs. Flake (1973) established that the consumption of these food items by *O. leucogaster* inhabiting short-grass prairie in Colorado increased during winter, when insects are scarcer; still, animal matter constituted approximately 60 percent of their diet for that period. Presumably, the conical cusps of *Onychomys* molars serve as an adaptation for efficiently grasping, puncturing and crushing the hard chitinous exoskeleton of their insect prey.

The most obvious evolutionary modification of the dentition of *Onychomys* is the reduction in relative size of the third molar. This diminution is most strikingly apparent for the posterior moiety of the tooth (hypoconid and entoconid) as compared to its anterior half (protoconid and metaconid). What is less obvious is that this reduction in relative size was accompanied

by concomitant increase in the relative lengths of the first and second molars. For example, the lengths of the first, second and third molars in *gidleyi* comprise 41.0, 33.7, and 25.9 percent of the total length of the tooth row, respectively; whereas, in Recent *leucogaster*, the corresponding percentages are 42.6, 35.5, and 22.0. The incremental gains in relative length of both the first and second molars (1.6 + 1.7 = 3.4) roughly equal the percentage decrease of the third molar (-3.9). In like manner, percent lengths of the tooth row for the first, second and third molars of *bensoni* are 40.5, 32.5, and 26.5, respectively; these same figures are 44.4, 36.1, and 20.3 percent for Recent *torridus*. Again, the percent increase in the lengths of the first and second molars together (3.9 + 3.6 = 7.5) roughly approximates the net decrease in relative length of the third molar (-6.2). There is some suggestion that the second molar experienced a greater increase in length relative to the first molar in the *leucogaster* lineage (Appendix 3); such a trend is not as clearly evident for the *torridus* lineage. Because the amount of decrement of the third molar was apparently compensated by augmentation of the lengths of the two other molars, these increases are not as conspicuous when comparing specimens of *gidleyi* and *leucogaster*; one's attention focuses on the difference in size of the M_3.

Both Hershkovitz (1962) and Misonne (1969) identify the reduction of the third molar as a major evolutionary trend in the Muridae (*sensu latu*). The result has been the complete elimination of a third molar in some murid genera (for example, *Rhynchomys, Crossomys* and *Hydromys*). Misonne (1969) further recognized that reduction of the third molar has been attended by a lengthening of the first molar. He viewed the second molar as basically unchanged phylogenetically, but we believe that the increase in relative length of the second molar closely approximated, or even slightly exceeded, that of the first molar in *Onychomys*. According to Misonne (1969:52), the shift in relative sizes of the M_1 and M_3 in Muridae was precipitated by loss of the fourth premolar, a tooth possessed by most other Rodentia. As a consequence of this disappearance, the remaining cheek teeth were set somewhat back in the oral cavity, a position presumably inconvenient for effective mastication. Reduction of the M_3 and increase of the M_1 had the effect of bringing the whole molar series forward on the jaw, and this readjustment of the dental battery improved masticatory efficiency.

We can't evaluate the extent to which the modifica-

tion of the M_3 in *Onychomys* simply reflects some broader trend of third molar reduction observed for all Muridae, but we doubt the applicability of Misonne's hypothesis to our material. In some regards, Misonne's explanation raises more perplexing questions than it purports to satisfy. For instance, if the evolutionary disappearance of the fourth premolar resulted in a forward shift of the remaining cheek teeth to fill the vacated area, then it is not clear why the premolar was lost initially. A supression of the third molar and retention of the PM_4, M_1 and M_2 would have achieved the same functional length of tooth row. Or each of the three molars could have increased slightly by equal increments instead of reducing the third molar and lengthening the first by a corresponding amount. Furthermore, comparison of mandibular shapes in Pliocene and Recent *Onychomys* does not reveal any anterior translocation of the molar row with respect to the condylar process or the base of the incisor; however, we did not record appropriate measurements to critically test this possibility. Finally, it is important to recall that recognizable cricetines, having a dental formula of 1/1, 0/0, 0/0, 3/3, existed at least by the early Oligocene. If the loss of the fourth premolar created a less effective masticatory apparatus, then we expect that selection would rapidly adjust the tooth rows and populations would thus pass relatively quickly through this transitional stage until another adaptive mode is re-established. We doubt, therefore, that the changes in relative molar lengths in *Onychomys* from the late Pliocene to Recent are vestiges of this repositioning due to loss of the PM_4, an event which occurred sometime prior to the Oligocene.

In murid rodents, the first, second and third molars erupt and become functional sequentially from front to back. Moreover, Gaunt (1963) demonstrated that the delay between the time of eruption of the second and third molars significantly exceeds that between the first and second. In view of this, a greater selective premium may have been placed on those teeth which emerged earliest during ontogeny. For instance, selective advantage could have accued to recently-weaned individuals who possessed slightly longer first and second molars, thus providing them with a greater triturative surface at a crucial time in their life histories. Because its space in the molar field was supplanted by increases of the M_1 and M_2, the later developing third molar decreased correspondingly.

Upon re-examination of specimens of *gidleyi* with complete tooth rows, we discovered that the severity of wear on the M_3 is slightly more pronounced in *gidleyi* for a given wear-stage of the M_1 as compared to living *leucogaster*. Thus, in *leucogaster* the M_3 displays little or no abrasion for wear-classes I and II, while in *gidleyi*, appreciable wear of the M_3 is usually evident by stage II (a complicating factor in this comparison, and one not anticipated when we originally assigned stages of wear, is the greater height of the cusps in living as compared to fossil *Onychomys*). At first, we believed this indicated that fossil *Onychomys* were less precocial than their Recent descendants. Our observations on relative wear of the M_3 do not really address this possibility, but they do suggest that the timing of eruption of the molars, especially the M_3, was more synchronous in Pliocene *Onychomys*.

Like the increase in cusp height, the increase in surface area of the M_1 and M_2 at the expense of the M_3 may also reflect the predilection of living *Onychomys* for arthropods. Perhaps, selection intensities were strongest on young grasshopper mice, during the weaning process from their mother's milk to a diet containing the chitinous hardparts of insects, but a larger triturative surface in the front of the oral cavity may have benefitted adults too. The significance of such different proportions in molar lengths would profit immensely from investigations of synchrony of molar eruption in a variety of murids, in relation to such variables as degree of reduction of the M_3, ages at weaning, and food habits of the newly weaned young.

Functional studies of mastication in grasshopper mice would also lend much insight, but unfortunately such have not been attempted. However, elegant studies of the mechanics of chewing are available for two other murids, the rat *Rattus norvegicus* (Hiiemae, 1967, 1971) and the hamster *Mesocricetus auratus* (Gorniak, 1977). Of the two, Gorniak's study on the hamster seems most pertinent to our investigation because the structure of the skull and configuration of the dentition of *Onychomys* and *Mesocricetus* resemble one another in several aspects. The molar crowns of *Mesocricetus* are tubercular like those of *Onychomys*; the zygomatic arches of *Onychomys* and *Mesocricetus* are strongly bowed outward, so that the margins of the zygoma are set well laterad to the molar rows; the ascending ramus of the mandible in both genera diverges laterally from the vertical plane of the tooth row; and the zygomatic plate is relatively narrow and similarly inclined in *Onychomys* and *Mesocricetus*. From these compari-

sons, we are not advocating that grasshopper mice and hamsters chew their food exactly alike, only that, to the extent one can infer function from structure, mastication in *Onychomys* more nearly resembles mastication in *Mesocricetus* than *Rattus*. Therefore, we have abstracted some of the salient points from Gorniak's (1977) study.

The masticatory pattern of hamsters differs markedly from that of rats. The interlocking cusps of the hamster's cheek teeth restrict propalinal movement (anterior/posterior) of the mandibles (compared to the strong propalinal component observed in rats). Accordingly, a masticatory orbit in the hamster consists of the lateral translation of the mandibles to "unlock" the molar cusps as well as a short protrusive stroke of the mandible as it is being elevated. This upstroke of the mandible accomplishes food reduction as the lower molars move anteriorly during jaw closure. Gorniak (1977:452) tested hamsters on different consistencies of food (soft kernels of sunflower seeds versus hard food pellets) and suggested that ". . . trituration of relatively soft food involves primarily shearing forces, and hard foods are broken down by a combination of compressive and shearing forces."

The chitinous exoskeleton of the insects which comprise such a large proportion of the diet of *Onychomys* must afford even harder resistance during trituration and require generation of larger compressive forces than reducing food pellets. One might reasonably expect even less propalinal movement of the mandibles in *Onychomys* as compared to *Mesocricetus* and greater reliance on vertical compressive strokes to crush insects wedged between the molar cusps. The high conical shape of the molar tubercles also suggests reduced anterior/posterior excursions of the lower jaw during mastication.

If the progenitors of modern *Onychomys* were less narrowly adapted to insects in their food habits, one might predict greater protraction and retraction of the jaw in the Pliocene forms. We did not systematically study wear facets on the molar crowns to analyze this possibility, but another line of evidence indicates that this might be so. The zygomatic plate in examples of Pliocene *gidleyi* contrasts in size and shape with that of Recent *leucogaster*. In *gidleyi*, the anterior border of the zygomatic plate is usually convex but sometimes straight, and the lateral face of the plate is somewhat concave. In *leucogaster*, the anterior edge of the plate is more often convex, seldom straight, and the

lateral face is flatter. Furthermore, the width of the zygomatic plate of *gidleyi* surpasses that of *leucogaster*; in *gidleyi* from Fox Canyon, this width equals 2.30 mm (R=2.16–2.56; N=8), while in *leucogaster* the same dimension measures 0.97 mm (R=1.64–2.24; N=34). We selected these two samples for comparison because more maxillary fragments were collected from Fox Canyon, and because *gidleyi* from Fox Canyon and *leucogaster* from Texas are similar in length of tooth row (4.42 as compared to 4.40 mm, respectively). These differences in size and shape indicate greater surface area for muscular attachment in *gidleyi*. The *masseter lateralis profundus, pars anterior* originates on the lateral aspect of the zygomatic plate, and together with the infraorbital slip of the medial masseter, functions to protract and elevate the lower jaw during closing in mastication (Hiiemae, 1971). The changes in conformation and size of the zygomatic plate are slight, but they are consistent with the notion of reduction in propalinal movement in living *Onychomys*.

As the morphological changes are slight, so too is the glimpse of the evolutionary history of grasshopper mice that we have sampled. And we emphasize that these modifications of the dentition and zygomatic architecture are not viewed as indicative of a total shift in diet of *Onychomys*, for example, from granivorous food habits to insectivorous ones. Food studies have demonstrated that *torridus* and *leucogaster* regularly ingest some seeds and other plant parts. We only suggest that the diet of Pliocene *Onychomys* was more cosmopolitan, containing larger proportions of such food items, and that the trends apparent during the course of *Onychomys* evolution reflect a narrowing of their trophic niche to more exclusive insectivory.

Numerous collectors have noted the scarcity of grasshopper mice relative to other rodents trapped. For instance, Horner and Taylor (1968) reported only a six percent incidence of *Onychomys torridus* in their total catch of rodents over a five-year period. In Utah, Egoscue (1960) obtained only five *Onychomys leucogaster* (2.5%) out of 201 cricetine rodents collected for approximately 1800 trap-nights; other species collected were *Reithrodontomys megalotus* (44.8%), *Peromyscus maniculatus* (49.2%) and *Neotoma lepida* (3.5%). The lower density of grasshopper mice accords with their larger home range sizes (Blair, 1953; Ruffer, 1968). In mesquite desert habitat in New Mexico, Blair (1953) determined mean home-range areas of 4.7 acres for male *Peromyscus maniculatus*, 5.8 acres for

male *Onychomys leucogaster* and 7.8 acres for male *O. torridus*. The predatory habits of *Onychomys* and their position in the community as secondary level consumers predict the association of larger home ranges and lower densities in *Onychomys* compared to herbivorous or granivorous rodents (Burt, 1940; McNab, 1963).

Analyses of rodent remains in owl pellets also attest to the relatively low abundance of grasshopper mice. We have tabulated the frequency of occurrence (based on the total number of individuals of only cricetid rodents) of *Onychomys* in the regurgitated pellets of the Barn Owl (*Tyto alba*), Great-horned Owl (*Bubo virginianus*) and Long-eared Owl (*Asio otus*) from the Great Plains region. The percent occurrence of *O. leucogaster* ranges from 1.1 to 7.5; individuals of *Peromyscus*, *Microtus* or *Sigmodon* are more commonly captured by these owls (Table 11). Dalquest, *et al.* (1969) implicate the barn owl as the principal concentrator of the rich supply of small mammals found in late Pleistocene deposits in Schulze Cave, Texas. We have calculated the frequency of occurrence of cricetid rodents from Schulze Cave, Layer C_1, based on lower jaws, since Dalquest, *et al.* (1969) conveniently tallied this figure for every taxon recovered from the cave. The composition of cricetid rodents from Schulze Cave resembles the proportions of species identified from owl pellets (Table 11). Specimens of *Onychomys leucogaster* occur in relatively low numbers. The high percentage of *Sigmodon hispidus* (Cotton Rat) in Schulze Cave contrasts with the complete absence of this grassland rodent in studies conducted in Colorado, Wyoming and Nebraska; however, the cotton rat does not range that far north today. The other study of owl predation in Texas (Rainey and Robinson, 1954) does reveal a high proportion of *Sigmodon* in the diet.

We have dwelled upon the concurrence of human and owl censuses in divulging relatively low densities of *Onychomys*, because it has been suggested that many of the microvertebrate concentrations found in the Tertiary have resulted from the accumulation of owl pellets or carnivore scats in streams and ponds (Hibbard, 1941c, 1950; Mellet, 1974). Hibbard (1941c:218), in particular, noted the abundance of small mammal parts in owl pellets and described their deposition in streams flowing under owl roosts and subsequent burial as the banks eroded; he postulated such a sequence of events to account for the concentration and entrapment of small mammals comprising the Borchers local fauna.

Certainly owls belonging to the same genera that today hunt grasshopper mice existed during late Blancan times (Feduccia, 1975). In light of the above observations, it is interesting to note that grasshopper mice were the most abundant rodents Hibbard (1941c, 1970) found in the Borchers local fauna. *Onychomys* totaled 55.6 percent of all the cricetine rodents in the Borchers (as derived from Hibbard's 1941c, counts of the number of maxillae and rami for each species) compared to 43.8 percent for *Sigmodon hilli* and only a few specimens each of *Reithrodontomys, Neotoma* and *Synaptomys*. Have populations of *Onychomys* experienced an absolute decline in numbers, at least from late Blancan (Borchers local fauna) to the present? Such a decline is consistent, we think, with the hypothesis that living grasshopper mice have evolved from more granivorous or omnivorous ancestors.

Viewing the Borchers local fauna as a thanatocoenosis resulting from owl predation, one is struck by the absence of *Peromyscus* and the rarity of microtines, forms which constitute a significant portion of the diet of owls presently inhabiting the Great Plains. Abundant remains of fossil *Peromyscus* are not encountered until the middle to late Pleistocene (Hibbard, 1968), and *Microtus* appeared and underwent an impressive radiation in the Pleistocene (Guthrie, 1965; Martin, 1975). The evolutionary success of these two genera is reflected in their large numbers of species (approximately 50-60 in each) and their great ecological diversity. Further, the substantial number of *Microtus* and *Peromyscus* recovered in owl pellets testifies to their dominance in grassland communities, filling small-mammal herbivorous (*Microtus*) and omnivorous (*Peromyscus*) trophic niches. Although the evidence is only circumstantial, we speculate that the arisal and radiation of these forms in the early Pleistocene provided the competitive impetus that eventually restricted grasshopper mice to their present role of secondary consumers in the community.

In summary, we envision the following outline of *Onychomys* evolution. Grasshopper mice were more omnivorous in their dietary requirements during the Pliocene and early Pleistocene. With the flourishing of *Microtus* and *Peromyscus* in the Pleistocene and the successful invasion of grassland biomes by these rodents, populations of *Onychomys* gradually became more exclusive in their food habits, ultimately assuming an insectivorous trophic position. The larger proportion of insects in their diet favored the generation of

TABLE 11. Frequency of Cricetine and Microtine Rodents in Owl Pellets from the Great Plains.

Prey Species	Tyto alba? Dalquest et al., 1969 Schulze Cave, Texas	Tyto alba Rickart, 1972 Nebraska	Tyto alba Marti, 1974 Colorado	Bubo virginianus Long and Kerfoot, 1963 Wyoming	Bubo virginianus Rickart, 1972 Nebraska	Bubo virginianus Marti, 1974 Colorado	Asio otus Rainey and Robinson, 1954 Texas	Asio otus Marti, 1974 Colorado
Cricetinae								
Onychomys leucogaster	7.4	7.5	1.1	3.2	2.4	1.1	—	2.7
Peromyscus spp.	28.6	5.1	32.3	34.2	4.0	56.9	17.9	53.5
Reithrodontomys spp.	7.5	20.8	9.4	—	25.6	5.6	8.5	8.7
Baiomys taylori	1.0	—	—	—	—	—	—	—
Neotoma spp.	9.0	—	0.2	—	—	0.6	—	—
Sigmodon hispidus	41.6	—	—	—	—	—	33.4	—
Oryzomys palustris	0.1	—	—	—	—	—	—	—
Microtinae								
Microtus spp.	4.7	66.6	67.0	45.2	68.0	35.0	40.2	35.1
Synaptomys cooperi	0.1	—	—	—	—	—	—	—
Lagurus curtatus	—	—	—	17.2	—	—	—	—
Ondatra zibethicus	—	—	trace	—	—	0.8	—	—

Species of Owls

greater compressive forces during mastication; the lessened reliance upon propalinal chewing and shearing is reflected in the diminution in area of the zygomatic plate. An increase in height of the molar cusps afforded sharp, conical projections, to pierce and break the insects' chitinous exoskeleton. Increase in length of the first and second molars occurred at the expense of the third molar, either to equip newly-weaned young with a larger surface area for triturating their insect prey, or simply because it was uniformly advantageous to amplify the area of those teeth possessing high cusps for chewing insects. Extensive foraging for insects and other arthropods resulted in expansion of their home ranges, and consequently, with the narrow-

ing of their food habits to predominantly insects, populations of *Onychomys* experienced a decline in absolute numbers of individuals. The interaction of these factors accounts for the relative scarcity of *Onychomys* in rodent communities today. To a greater or lesser degree, there are assumptions and potential biases connected to each of the lines of evidence on which we constructed our overview of the recent evolution of *Onychomys*. Yet taken as a whole, a convincing paradigm emerges, one consistent with a heterogeneity of data, both paleontological and neontological, and one that we feel conveys some of the major features of the evolution of grasshopper mice, genus *Onychomys*.

ACKNOWLEDGEMENTS

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APPENDIX 1

Tables of Measurements. Fossil localities are listed according to suggested revision.

Length of M_1-M_3					Length of M_1				
Species and Locality	N	$\overline{X}$	1 S. D.	Range	Species and Locality	N	$\overline{X}$	1 S. D.	Range
O. gidleyi					*O. gidleyi*				
Saw Rock Canyon	1	4.40	—	—	Saw Rock Canyon	1	1.78	—	—
Fox Canyon	13	4.42	.14	4.23–4.72	Fox Canyon	35	1.81	.09	1.65–2.01
Rexroad 3	5	4.44	.12	4.31–4.58	Rexroad 3	9	1.86	.07	1.79–2.01
Wendell Fox	6	4.28	.09	4.11–4.38	Wendell Fox	15	1.78	.05	1.69–1.86
Beck Ranch	2	4.32	—	4.25, 4.39	Beck Ranch	5	1.73	.07	1.65–1.84
O. pedroensis					*O. pedroensis*				
Borchers	19	4.56	.17	4.26–4.92	Borchers	57	1.90	.08	1.76–2.11
Curtis Ranch	1	4.68	—	—	Curtis Ranch	2	2.01	—	2.00, 2.02
Jinglebob	1	4.54	—	—	Jinglebob	2	1.88	—	1.87, 1.88
O. leucogaster					*O. leucogaster*				
Friesenhahn Cave	9	4.51	.14	4.39–4.85	Friesenhahn Cave	25	1.93	.11	1.70–2.10
Schulze Cave	10	4.44	.13	4.17–4.59	Schulze Cave	21	1.92	.09	1.78–2.07
Texas	34	4.40	.14	4.12–4.63	Texas	34	1.88	.09	1.72–2.07
Oklahoma	16	4.46	.15	4.25–4.85	Oklahoma	16	1.90	.06	1.79–2.00
Nebraska	24	4.34	.16	4.01–4.68	Nebraska	24	1.86	.08	1.71–1.98
North Dakota	17	4.36	.13	4.18–4.61	North Dakota	17	1.86	.08	1.75–2.05
Wyoming	12	4.22	.17	3.92–4.53	Wyoming	12	1.80	.10	1.61–1.97
Nevada	4	3.83	.14	3.62–3.92	Nevada	4	1.64	.10	1.53–1.76
O. bensoni	1	3.85	—	—	*O. bensoni*	1	1.56	—	—
O. hollisteri	4	4.11	.08	4.02–4.20	*O. hollisteri*	13	1.70	.04	1.64–1.79
O. torridus					*O. torridus*				
New Mexico	9	3.85	.17	3.65–4.18	New Mexico	9	1.71	.13	1.51–1.91
Arizona	16	3.70	.13	3.38–3.92	Arizona	16	1.62	.08	1.48–1.75
Texas	12	3.81	.08	3.69–3.99	Texas	12	1.73	.06	1.63–1.82
Nevada	23	3.59	.12	3.34–3.81	Nevada	23	1.59	.06	1.48–1.73

| Length of M_2 ||||| Length of M_3 |||||
Species and Locality	N	$\overline{X}$	1 S. D.	Range	Species and Locality	N	$\overline{X}$	1 S. D.	Range
O. gidleyi					*O. gidleyi*				
Saw Rock Canyon	1	1.52	—	—	Saw Rock Canyon	1	1.12	—	—
Fox Canyon	24	1.50	.06	1.39−1.62	Fox Canyon	14	1.15	.05	1.07−1.23
Rexroad 3	7	1.49	.04	1.40−1.53	Rexroad 3	5	1.16	.05	1.10−1.23
Wendell Fox	15	1.45	.05	1.35−1.52	Wendell Fox	9	1.13	.04	1.06−1.20
Beck Ranch	3	1.39	.02	1.37−1.41	Beck Ranch	2	1.11	—	1.10, 1.12
O. pedroensis					*O. pedroensis*				
Borchers	45	1.54	.07	1.43−1.62	Borchers	32	1.11	.07	.96−1.22
Curtis Ranch	3	1.61	.02	1.58−1.64	Curtis Ranch	2	1.19	—	1.18, 1.20
Jinglebob	1	1.58	—	—	Jinglebob	1	1.13	—	—
O. leucogaster					*O. leucogaster*				
Friesenhahn Cave	28	1.52	.06	1.43−1.66	Friesenhahn Cave	12	1.04	.04	.98−1.10
Schulze Cave	23	1.52	.07	1.40−1.65	Schulze Cave	15	1.02	.06	.88−1.13
Texas	34	1.56	.06	1.44−1.73	Texas	34	.97	.05	.87−1.09
Oklahoma	16	1.59	.07	1.45−1.75	Oklahoma	16	1.00	.08	.90−1.22
Nebraska	24	1.54	.07	1.43−1.68	Nebraska	24	.95	.06	.88−1.08
North Dakota	17	1.55	.05	1.48−1.69	North Dakota	17	.97	.07	.85−1.09
Wyoming	12	1.50	.06	1.42−1.59	Wyoming	12	.93	.08	.75−1.02
Nevada	4	1.37	.09	1.23−1.44	Nevada	4	.85	.05	.82− .92
O. bensoni	1	1.25	—	—	*O. bensoni*	1	1.02	—	—
O. hollisteri	11	1.41	.03	1.36−1.45	*O. hollisteri*	6	.98	.02	.97−1.03
O. torridus					*O. torridus*				
New Mexico	9	1.40	.06	1.32−1.49	New Mexico	9	.78	.05	.74− .87
Arizona	16	1.33	.05	1.24−1.40	Arizona	16	.79	.04	.72− .85
Texas	12	1.38	.05	1.31−1.46	Texas	12	.73	.05	.67− .83
Nevada	23	1.29	.06	1.18−1.40	Nevada	23	.76	.06	.63− .84

Length of M₃ talonid						Anterior Width of M₁				
Species and Locality	N	$\overline{X}$	1 S. D.	Range		Species and Locality	N	$\overline{X}$	1 S. D.	Range
O. gidleyi						*O. gidleyi*				
Saw Rock Canyon	1	.57	—	—		Saw Rock Canyon	1	1.01	—	—
Fox Canyon	15	.53	.05	.43– .61		Fox Canyon	35	1.07	.04	.98–1.15
Rexroad 3	5	.56	.04	.52– .62		Rexroad 3	9	1.04	.04	.99–1.10
Wendell Fox	9	.55	.03	.50– .62		Wendell Fox	15	1.01	.05	.90–1.07
Beck Ranch	2	.58	—	.57, .59		Beck Ranch	5	1.00	.04	.96–1.05
O. pedroensis						*O. pedroensis*				
Borchers	32	.51	.06	.39– .65		Borchers	57	1.08	.04	.98–1.19
Curtis Ranch	2	.56	—	.55, .58		Curtis Ranch	2	1.16	—	1.14, 1.17
Jinglebob	1	.48	—	—		Jinglebob	2	1.10	—	1.09, 1.10
O. leucogaster						*O. leucogaster*				
Friesenhahn Cave	12	.51	.05	.44– .61		Friesenhahn Cave	24	1.10	.03	1.05–1.17
Schulze Cave	15	.48	.07	.33– .59		Schulze Cave	21	1.09	.05	.95–1.17
Texas	34	.40	.05	.31– .51		Texas	34	1.06	.04	.99–1.14
Oklahoma	16	.44	.06	.35– .55		Oklahoma	16	1.09	.03	1.06–1.14
Nebraska	24	.44	.05	.35– .54		Nebraska	24	1.03	.03	.99–1.12
North Dakota	17	.41	.04	.35– .59		North Dakota	17	1.02	.06	.94–1.14
Wyoming	12	.39	.06	.28– .47		Wyoming	12	1.00	.05	.94–1.10
Nevada	4	.37	.03	.33– .41		Nevada	4	.90	.03	.87– .93
O. bensoni	1	.48	—	—		*O. bensoni*	1	.82	—	—
O. hollisteri	6	.43	.02	.40– .46		*O. hollisteri*	13	.99	.04	.94–1.03
O. torridus						*O. torridus*				
New Mexico	9	.27	.05	.19– .36		New Mexico	9	.92	.04	.83– .96
Arizona	16	.28	.04	.18– .36		Arizona	16	.94	.03	.88– .99
Texas	12	.24	.05	.16– .30		Texas	12	.93	.04	.85–1.00
Nevada	23	.30	.04	.22– .35		Nevada	23	.89	.03	.83– .94

Posterior Width of M_1 Width of M_2

Species and Locality	N	$\overline{X}$	1 S. D.	Range	Species and Locality	N	$\overline{X}$	1 S. D.	Range
O. gidleyi					*O. gidleyi*				
Saw Rock Canyon	1	1.16	—	—	Saw Rock Canyon	1	1.19	—	—
Fox Canyon	35	1.25	.04	1.17–1.32	Fox Canyon	24	1.25	.04	1.17–1.32
Rexroad 3	9	1.20	.04	1.15–1.25	Rexroad 3	7	1.22	.06	1.14–1.32
Wendell Fox	15	1.17	.04	1.10–1.24	Wendell Fox	14	1.19	.04	1.13–1.28
Beck Ranch	5	1.14	.05	1.08–1.20	Beck Ranch	3	1.10	.03	1.08–1.13
O. pedroensis					*O. pedroensis*				
Borchers	57	1.24	.05	1.12–1.38	Borchers	45	1.26	.06	1.13–1.42
Curtis Ranch	2	1.30	—	1.29, 1.31	Curtis Ranch	3	1.31	.03	1.26–1.36
Jinglebob	2	1.26	––	1.25, 1.28	Jinglebob	1	1.23	–––	—
O. leucogaster					*O. leucogaster*				
Friesenhahn Cave	24	1.26	.05	1.17–1.36	Friesenhahn Cave	27	1.28	.07	1.16–1.40
Schulze Cave	21	1.23	.06	1.09–1.33	Schulze Cave	23	1.26	.06	1.16–1.36
Texas	34	1.21	.05	1.11–1.29	Texas	34	1.25	.06	1.11–1.36
Oklahoma	16	1.22	.05	1.11–1.30	Oklahoma	16	1.26	.05	1.18–1.34
Nebraska	24	1.18	.05	1.10–1.28	Nebraska	24	1.21	.05	1.11–1.29
North Dakota	17	1.19	.05	1.13–1.29	North Dakota	17	1.22	.04	1.15–1.28
Wyoming	12	1.18	.05	1.08–1.25	Wyoming	12	1.19	.06	1.12–1.29
Nevada	4	1.08	.04	1.02–1.10	Nevada	4	1.06	.05	.98–1.10
O. bensoni	1	1.04	—	—	*O. bensoni*	1	1.09	—	—
O. hollisteri	13	1.12	.04	1.03–1.18	*O. hollisteri*	11	1.16	.05	1.08–1.25
O. torridus					*O. torridus*				
New Mexico	9	1.07	.06	.97–1.19	New Mexico	9	1.12	.06	1.00–1.21
Arizona	16	1.08	.04	1.02–1.17	Arizona	16	1.10	.05	1.01–1.20
Texas	12	1.07	.04	.98–1.12	Texas	12	1.13	.05	1.04–1.20
Nevada	23	1.05	.03	1.00–1.12	Nevada	23	1.06	.03	1.00–1.11

Width of M$_3$					Height of Protoconid				
Species and Locality	N	$\overline{X}$	1 S. D.	Range	Species and Locality	N	$\overline{X}$	1 S. D.	Range
O. gidleyi					*O. gidleyi*				
Saw Rock Canyon	1	.99	—	—	Saw Rock Canyon	1	.79	—	—
Fox Canyon	14	1.03	.03	.97–1.08	Fox Canyon	35	.74	.13	.43– .93
Rexroad 3	5	1.03	.04	.98–1.09	Rexroad 3	9	.78	.09	.67– .94
Wendell Fox	9	.99	.05	.92–1.07	Wendell Fox	14	.77	.10	.56– .92
Beck Ranch	1	.98	—	—	Beck Ranch	3	.76	.10	.66– .87
O. pedroensis					*O. pedroensis*				
Borchers	31	1.00	.07	.88–1.12	Borchers	48	.77	.10	.57– .95
Curtis Ranch	1	1.11	—	—	Curtis Ranch	2	.84	—	.74, .93
Jinglebob	1	1.12	—	—	Jinglebob	1	.93	—	—
O. leucogaster					*O. leucogaster*				
Friesenhahn Cave	11	.96	.04	.91–1.04	Friesenhahn Cave	25	.85	.13	.55–1.00
Schulze Cave	15	.97	.06	.87–1.11	Schulze Cave	21	.83	.14	.57–1.11
Texas	34	.99	.05	.84–1.10	Texas	34	.99	.05	.84–1.10
Oklahoma	16	.98	.06	.87–1.12	Oklahoma	16	.98	.06	.87–1.12
Nebraska	24	.94	.04	.88– .99	Nebraska	24	.94	.04	.88– .99
North Dakota	17	.97	.05	.88–1.05	North Dakota	17	.97	.05	.88–1.05
Wyoming	12	.90	.06	.75– .98	Wyoming	12	.90	.06	.75– .98
Nevada	4	.78	.02	.75– .79	Nevada	4	.86	.05	.82– .94
O. bensoni	1	.87	—	—	*O. bensoni*	1	.65	—	—
O. hollisteri	6	.93	.04	.86– .97	*O. hollisteri*	14	.71	.09	.56– .90
O. torridus					*O. torridus*				
New Mexico	9	.81	.04	.73– .86	New Mexico	9	.78	.05	.74– .87
Arizona	16	.82	.03	.74– .87	Arizona	16	.82	.03	.74– .87
Texas	12	.79	.04	.68– .86	Texas	12	.79	.04	.68– .86
Nevada	23	.81	.04	.73– .86	Nevada	23	.81	.04	.73– .86

Depth of Ramus below M_1

Species and Locality	N	$\overline{X}$	1 S. D.	Range
O. gidleyi				
Saw Rock Canyon	1	3.41	—	—
Fox Canyon	17	3.26	.27	2.70−3.79
Rexroad 3	6	3.50	.15	3.24−3.67
Wendell Fox	16	3.29	.22	3.02−3.75
Beck Ranch	3	3.39	.27	3.08−3.57
O. pedroensis				
Borchers	29	3.83	.27	3.29−4.19
Curtis Ranch	—	—	—	—
Jinglebob	2	3.52	—	3.26, 3.79
O. leucogaster				
Friesenhahn Cave	22	3.48	.30	2.96−4.06
Schulze Cave	18	3.50	.28	3.07−4.02
Texas	34	3.36	.26	2.83−3.89
Oklahoma	16	3.37	.17	3.03−3.71
Nebraska	24	3.30	.18	2.98−3.68
North Dakota	17	3.22	.32	2.70−3.91
Wyoming	12	3.22	.14	3.10−3.51
Nevada	4	2.84	.16	2.62−2.96
O. bensoni	—	—	—	—
O. hollisteri	5	3.14	.12	3.04−3.35
O. torridus				
New Mexico	9	2.88	.15	2.64−3.06
Arizona	16	2.93	.19	2.52−3.22
Texas	12	2.86	.13	2.61−3.13
Nevada	23	2.53	.23	2.13−3.01

APPENDIX 2

Coefficients of variation; fossil localities listed according to suggested revision

Species and Locality	Variable										
	LM_1-M_3	LM_1	LM_2	LM_3	LM_3 tal.	AWM_1	PWM_2	WM_2	WM_3	height protoconid	depth ramus
gidleyi											
Fox Canyon	3.3	4.9	3.7	4.3	8.6	4.2	4.3	3.3	3.0	17.5	8.2
Rexroad 3	2.8	3.7	3.0	4.5	7.1	3.8	3.1	4.6	4.3	11.8	4.6
Wendell Fox	2.3	2.8	3.4	3.6	6.5	4.8	3.4	3.5	5.3	13.2	6.6
pedroensis											
Borchers	3.7	4.2	4.5	6.3	11.8	3.7	4.0	4.8	7.0	13.0	7.0
leucogaster											
Friesenhahn Cave	3.2	5.7	3.8	3.9	10.0	2.7	3.9	5.5	4.3	15.3	8.6
Schulze Cave	3.0	4.7	4.6	6.0	14.8	4.6	4.9	4.8	6.3	16.9	8.0
Texas	3.3	4.6	4.0	5.0	11.5	4.2	4.0	4.6	5.0	5.0	7.9
Oklahoma	3.4	3.3	4.6	7.7	14.0	2.6	4.3	4.0	6.5	6.1	5.2
Nebraska	3.7	4.2	4.4	6.0	11.9	3.2	4.3	4.0	4.2	4.2	5.5
North Dakota	3.0	4.5	3.4	7.3	9.5	5.4	4.4	3.1	4.8	5.2	10.0
Wyoming	4.1	5.6	4.0	8.8	14.1	4.8	3.7	4.9	7.0	6.7	4.4
Nevada	3.8	6.5	7.0	6.3	8.6	3.5	3.9	5.0	2.8	6.2	5.9
hollisteri											
Borchers	2.0	2.4	2.2	2.3	6.0	4.0	3.6	4.3	4.3	12.7	4.0
torridus											
New Mexico	4.6	8.0	4.6	6.4	18.0	4.2	6.3	5.6	4.7	6.4	5.4
Arizona	3.5	4.8	3.8	5.4	16.3	3.5	3.6	4.4	4.1	3.6	6.5
Texas	2.0	3.3	3.6	6.4	20.0	4.5	3.8	4.8	5.6	5.1	4.7
Nevada	3.2	3.5	4.6	8.1	13.5	3.3	3.2	2.7	4.9	4.9	9.1

Ratios of selected mean dental dimensions; fossil localities listed according to suggested revision

Species	$\dfrac{LM_1}{LM_{1-3}}$	$\dfrac{LM_2}{LM_{1-3}}$	$\dfrac{LM_3}{LM_{1-3}}$	$\dfrac{LM_2}{LM_1}$	$\dfrac{LM_3}{LM_1}$	$\dfrac{LM_3}{LM_2}$	$\dfrac{M_3 \text{tal.}}{LM_3}$	$\dfrac{\text{Ht. protoconid}}{LM_1}$
gidleyi								
Saw Rock Canyon	40.4	34.5	25.4	85.4	62.9	73.7	49.1	47.2
Fox Canyon	40.9	33.7	25.8	82.3	63.5	77.2	46.4	45.7
Rexroad 3	41.9	33.6	26.1	80.1	62.4	77.8	48.2	45.7
Wendell Fox	41.4	33.6	26.2	81.9	63.3	77.7	48.6	46.1
Beck Ranch	40.0	32.2	25.7	80.3	64.2	79.8	52.2	50.3
pedroensis								
Borchers	41.7	33.8	24.3	81.0	58.4	72.1	45.9	45.8
Curtis Ranch	42.9	34.4	25.4	80.1	59.2	73.9	47.0	46.3
Jinglebob	41.4	34.8	24.9	84.0	60.1	71.5	42.5	49.5
leucogaster								
Friesenhahn Cave	42.8	33.7	23.0	78.8	53.9	68.4	49.0	49.7
Schulze Cave	43.2	34.2	23.0	79.2	53.1	67.1	47.0	50.0
Texas	42.7	35.4	22.0	83.0	51.6	62.2	41.2	52.1
Oklahoma	42.6	35.6	22.4	83.7	52.6	62.9	44.0	51.3
Nebraska	42.8	35.5	21.9	82.8	51.1	61.7	46.3	51.1
North Dakota	42.7	35.6	22.2	83.3	52.2	62.6	42.3	52.7
Wyoming	42.6	35.5	22.0	83.3	51.7	62.0	41.9	53.9
Nevada	42.8	35.8	22.2	83.5	51.8	62.0	43.5	53.0
bensoni	40.5	32.5	26.5	80.1	65.4	81.6	47.0	41.4
hollisteri	41.4	34.8	24.9	82.9	57.6	69.5	43.9	50.3
torridus								
New Mexico	44.4	36.4	20.2	81.9	45.6	55.7	34.6	46.2
Arizona	43.8	35.9	21.4	82.1	48.8	59.4	35.4	52.2
Texas	45.4	36.2	19.2	79.8	42.2	52.9	32.9	53.7
Nevada	44.3	35.9	21.2	81.1	47.8	58.9	39.5	48.0

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