TAXONOMY AND GEOGRAPHIC DISTRIBUTION OF
PEROMYSCUS MANICULATUS NUBITERRAE RHOADS
(MAMMALIA: RODENTIA)

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INTRODUCTION

The deer mouse, *Peromyscus maniculatus*, is one of the most common and widely distributed small mammals in North America. Over its range, which extends from southern Mexico to the Arctic and from coast to coast, the deer mouse exhibits considerable morphological and ecological variation, with 28 continental and 38 insular subspecies recognized (Hall and Kelson, 1959). Some of these geographic races, quite distinct and associated with recognizable barriers, probably represent incipient or proto-incipient species. Other less distinct forms warrant serious re-evaluation so that a clearer picture of the systematics and taxonomy of the deer mouse may be obtained in the future. This paper presents the results of an examination of the taxonomic status and distribution of the cloudland deer mouse, *Peromyscus maniculatus nubiterra*, a little-studied form that inhabits the higher elevations of the Appalachian Mountains from New York to Georgia. Major emphasis is placed on the relationships between the cloudland deer mouse and the morphologically and ecologically similar woodland deer mouse, *Peromyscus maniculatus gracilis* (LeConte).

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LITERATURE

*P. m. nubiterrae* has been infrequently studied or used as a laboratory animal. Most work published on this form has concerned new localities and status reports in state mammal surveys, along with references to habitat selection (Bailey, 1946; Barbour; 1941; Cady, 1941; Coleman, 1948; Gifford and Whitebread, 1951; Golley, 1962, 1966; Grimm and Roberts, 1950; Handley and Patton, 1947; Kellogg, 1939; Komarek and Komarek, 1938; Odum, 1949; Paradiso, 1969; Richmond and Roslund, 1949; Roslund, 1951; Wilson, 1945; Wilson and Friedel, 1942). Notable exceptions are the coverage of this subspecies by Osgood (1909), plus Linzey's (1970) examination of early growth and development, Kirkland and Linzey's (1973) notes on reproductive success, and Bradshaw and George's (1969) description of the karyotype.

By comparison, *P. m. gracilis* is a well-known and much-studied form. King (1969) provides an overview of the abundant and varied research conducted on this subspecies.

METHODS AND MATERIALS

Data for this study were obtained from *Peromyscus maniculatus* specimens housed in Carnegie Museum of Natural History (CM), the National Museum of Natural History (USNM), the Museum at Michigan State University (MSU), and the Shippensburg State College Vertebrate Museum (SSC). External measurements (given in mm) for total length, tail length, body length (total length minus tail length), hind foot length, ear length, and weight (given in gm) were obtained from tags accompanying specimens. Because ear length and weight frequently were not recorded, these characters are represented in the statistics by smaller sample sizes than are other external characters. Only specimens judged to be adults, i.e., having a total length of at least 160 mm, as suggested by Linzey's (1970) data, were used in the study. A total of 806 specimens was examined: 595 *P. m. nubiterrae*...
and 211 *P. m. gracilis* (Table 1).

I examined 100 skulls of each subspecies (Table 1). Ten measurements were taken on each skull, using Helios dial micrometers (1/20 mm calibration). The skull measurements included:

1. Greatest length: from the anterior tip of the nasals to the posterior-most portion of the braincase.
2. Condylar length: from the anterior base of the incisors to the posterior point of the occipital condyle.
3. Interorbital breadth: the shortest distance between the orbits.
4. Cranial breadth: the width of the braincase at its widest point.
5. Maxillary tooth row: length of the cheek tooth row from the anterior base of $M^1$ to the posterior base of $M^3$.
6. Nasal: the greatest anterior-posterior length of the nasal bones.
7. Shelf of bony palate: length of the palate from the posterior edge of the incisive foramen to the posterior edge of the palate.
8. Diastema: length of the space between the anterior base of $M^1$ and the posterior-lateral base of the incisor.
9. Palatine slits: the greatest length of the incisive foramen.
10. Postpalatal length: distance from the posterior medial edge of the palate to the anterior edge of the foramen magnum.

| Subspecies        | No. skulls | No. skins | State      | Museum |
|-------------------|------------|-----------|------------|--------|
|                   | $M^1$ | $F^2$ | $M$ | $F$ |          |
| *P. m. nubiterrae* |        |         | Georgia    | USNM   |
|                   | 7     | 7       | 24         | 15     | Maryland | USNM   |
|                   | 4     | 6       | 14         | 13     | Kentucky | USNM   |
|                   | 27    | 23      | 183        | 144    | Pennsylvania | CM |
|                   | 9     | 1       | 30         | 33     | N. Carolina | USNM   |
|                   | 2     | 8       | 11         | 10     | N. Carolina | CM     |
|                   | 6     | 4       | 16         | 22     | Tennessee  | USNM   |
|                   | 1     | 11      | 6          | 6      | Virginia   | USNM   |
|                   | 6     | 4       | 28         | 21     | W. Virginia | USNM   |
|                   | 54    | 46      | 324        | 271    | Totals     |        |
| *P. m. gracilis*  | 15    | 5       | 6          | 4      | Michigan   | MSU     |
|                   | 6     | 4       | 14         | 14     | Michigan   | USNM    |
|                   | 2     | 1       | 10         | 9      | N. Hampshire | USNM   |
|                   | 7     | 6       | 11         | 19     | New York   | SSC     |
|                   | 1     | 3       | 17         | 11     | Ontario    | CM      |
|                   | 19    | 31      | 28         | 50     | Pennsylvania | CM |
|                   | 50    | 50      | 96         | 115    | Totals     |        |

$^1$M = Males.

$^2$F = Females.
EXTERNAL AND SKULL MORPHOLOGY

P. m. nubiterrae and P. m. gracilis are exceedingly similar in morphology and ecology. Hamilton (1943) describes P. m. nubiterrae as “not well characterized, but being a peripheral form, has slight differences which set it off from gracilis to the north.” Osgood (1909) describes P. m. nubiterrae as being similar to P. m. gracilis but slightly smaller and with a broader, better-defined middorsal dusky area. Osgood also notes that the skull of P. m. nubiterrae is similar to that of P. m. gracilis but decidedly smaller. The data obtained in this study confirm these previous observations. P. m. nubiterrae is, indeed, very similar to P. m. gracilis and possibly is better defined geographically than morphologically or ecologically.

Tables 2 and 3 contain the means, standard errors, standard deviations, coefficients of variation and ranges for six specimen tag measurements of 595 P. m. nubiterrae (324 males; 271 females) and 211 P. m. gracilis (96 males; 115 females). Comparisons of sexes within subspecies reveal that females tend to be larger than males. In both subspecies the hind foot measurement for males was greater than that for females, but the difference was not significant (Student’s t-test; Tables 2 and 3). Because of the significant sex differences in both species for total length, body length, weight, and tail length in P. m. gracilis, all comparisons between subspecies were made between samples of the same sex.

Statistical comparisons of the two subspecies using Student’s t-test reveal that female P. m. gracilis are significantly larger than female P. m. nubiterrae in all six measurements (Table 4). In males, P. m. gracilis averaged larger than P. m. nubiterrae in all measurements but weight. The differences were significant for total length, hind foot length, and body length. The overlap of the range of measurements for each character is large, ranging from 63% for the hind foot of females to 90% for the body length of males. In general, males of each subspecies seem to be somewhat less differentiated than the females. In males the overlap for the six characters averages 83.5%, while in females it averages 70.6%. The coefficients of difference for external measurements range from .12 to .32 (Table 4). This is far below the level of 1.28 suggested by Mayr (1969) for distinguishing subspecies. Thus, data from the external measurements confirm that on the average, P. m. nubiterrae is slightly smaller than P. m. gracilis.

The same size relationship between P. m. nubiterrae and P. m. gracilis is evident in the data from the 10 skull characters examined. Tables 5 and 6 contain, respectively, statistics for the skull measurements of P. m. nubiterrae and P. m. gracilis. The differences in skull measurements are not as pronounced as in the skin measurements. P. m. nubiterrae females average larger than males in nine of ten characters,
### TABLE 2
Univariate statistical comparison of external measurements of adult *P. m. nubiterrae*

| Measurement     | N   | Mean  | S.E. | S.D.  | C.V. | Range    | t-ratio |
|-----------------|-----|-------|------|-------|------|----------|---------|
| **Males:**      |     |       |      |       |      |          |         |
| Total length    | 324 | 174.88| .46  | 8.37  | 4.79 | 160-202  | 4.45*** |
| Tail length     | 324 | 89.34 | .36  | 6.49  | 7.27 | 70-111   | 1.95    |
| Hind foot       | 324 | 20.69 | .05  | .81   | 3.94 | 19-25    | 1.83    |
| Ear length      | 199 | 18.75 | .09  | 1.25  | 6.65 | 15-22    | 1.46    |
| Body length     | 324 | 85.50 | .27  | 4.94  | 5.78 | 74-102   | 5.27*** |
| Weight          | 189 | 17.79 | .08  | 1.07  | 6.03 | 13-24    | 2.18*   |
| **Females:**    |     |       |      |       |      |          |         |
| Total length    | 271 | 178.15| .58  | 9.58  | 5.38 | 160-205  |         |
| Tail length     | 271 | 90.38 | .39  | 6.47  | 7.15 | 70-109   |         |
| Hind foot       | 270 | 20.57 | .05  | .77   | 3.74 | 18-23    |         |
| Ear length      | 171 | 18.57 | .09  | 1.11  | 6.00 | 15-22    |         |
| Body length     | 271 | 87.79 | .34  | 5.64  | 6.43 | 74-101   |         |
| Weight          | 150 | 18.37 | .28  | 3.44  | 18.72| 12-29    |         |

*Significant at .05 level.
***Significant at .001 level.

### TABLE 3
Univariate statistical comparison of external measurements of adult *P. m. gracilis.*

| Measurement     | N   | Mean  | S.E. | S.D.  | C.V. | Range    | t-ratio |
|-----------------|-----|-------|------|-------|------|----------|---------|
| **Males:**      |     |       |      |       |      |          |         |
| Total length    | 96  | 176.79| .80  | 7.87  | 4.45 | 161-196  | 5.06*** |
| Tail length     | 96  | 88.19 | .57  | 5.56  | 6.30 | 74-105   | 4.32*** |
| Hind foot       | 96  | 21.29 | .12  | 1.16  | 5.45 | 18-25    | 1.17    |
| Ear length      | 67  | 19.04 | .13  | 1.08  | 5.70 | 14-21    | 1.43    |
| Body length     | 96  | 88.59 | .56  | 5.49  | 6.20 | 72-103   | 3.68*** |
| Weight          | 37  | 17.37 | .37  | 2.24  | 12.89| 14-23.5  | 4.37*** |
| **Females:**    |     |       |      |       |      |          |         |
| Total length    | 115 | 183.53| 1.02 | 10.89 | 5.90 | 160-221  |         |
| Tail length     | 115 | 91.96 | .64  | 6.89  | 7.50 | 74-117   |         |
| Hind foot       | 115 | 20.99 | .21  | 2.27  | 10.82| 17-25    |         |
| Ear length      | 96  | 19.36 | .16  | 1.60  | 8.25 | 14-24    |         |
| Body length     | 115 | 91.60 | .58  | 6.25  | 6.82 | 78-110   |         |
| Weight          | 63  | 20.42 | .50  | 3.88  | 19.02| 12-33.5  |         |

***Significant at the .001 level.
TABLE 4
COMPARISON\(^1\) OF MEANS OF SIX EXTERNAL MEASUREMENTS OF P. m. gracilis AND P.m. nubiterra (g.—n.).

| Variable         | Males:        | Females:      |
|------------------|---------------|---------------|
|                  | N            | g.—n. | t-ratio | % Overlap | C.D. | N            | g.—n. | t-ratio | % Overlap | C.D. |
| Total length     | 420          | 1.91  | 1.99*   | 83        | .12  |
| Tail length      | 420          | 1.51  | 1.57    | 76        | .13  |
| Hind foot        | 420          | .60   | 5.70*** | 86        | .30  |
| Ear length       | 266          | .29   | 1.70    | 75        | .12  |
| Body length      | 420          | 3.09  | 5.25*** | 90        | .30  |
| Weight           | 226          | -.42  | 1.76    | 86        | .13  |
| Total length     | 386          | 5.38  | 4.84*** | 74        | .26  |
| Tail length      | 386          | 1.58  | 2.15*   | 74        | .12  |
| Hind foot        | 385          | .42   | 2.70**  | 63        | .14  |
| Ear length       | 267          | .79   | 4.75*** | 70        | .29  |
| Body length      | 386          | 3.81  | 5.87*** | 64        | .32  |
| Weight           | 213          | 2.05  | 3.81*** | 79        | .28  |

*Significant at .05 level.
**Significant at .01 level.
***Significant at .001 level.

\(^1\)Student's t-test with percent overlap of range, and coefficient of differentiation after Mayr, 1969.

while P. m. gracilis females average larger than males in seven of ten characters. The only significant difference is in the cranial breadth of P. m. gracilis, in which males exceed females. The reason for this difference is not evident.

Comparison of the subspecies reveals that P. m. gracilis is significantly larger than P. m. nubiterra in seven of ten characters in each sex (Table 7). The width of the interorbital constriction is the only character in which the mean for both sexes is greater in P. m. nubiterra, but this greater difference is significant only in males. The overlap in measurements for the ten characters averages 61% in males and 70.3% for females. In this statistic, the females of the two subspecies appear to be about as equally differentiated as in skin measurements. However, the overlap range for skull-characters in males is much less than for skin measurements. This suggests that males may be more differentiated in skull morphology than in external anatomy. The coefficients of difference range from .05 for the cranial breadth in females to .62 (Table 7). The coefficients of difference average .40 in males and .31 in females. Once again these levels are below those normally accepted for subspecies differentiation (Mayr, 1969).

The analysis of skin and skull measurements verifies the observations of earlier workers. P. m. nubiterra is slightly smaller than P. m. gracilis. Although populations of the two subspecies may be distin-
### TABLE 5
Student's t-test of cranial measurements of *P. m. nubiterrae* by sex

| Measurement                  | N  | Mean | S.E. | S.D. | C.V. | Range          | t-ratio |
|-----------------------------|----|------|------|------|------|----------------|---------|
| **Males:**                  |    |      |      |      |      |                |         |
| Condylobasal length         | 54 | 21.88| .10  | .75  | 3.42 | 20.05-23.65    | 1.35    |
| Greatest length             | 54 | 24.46| .09  | .64  | 2.63 | 23.1-25.9      | .58     |
| Cranial breadth             | 54 | 11.33| .05  | .38  | 3.32 | 10.8-12.15     | .00     |
| Interorbital breadth        | 54 | 3.90 | .02  | .13  | 3.42 | 3.65-4.3      | .00     |
| Maxillary tooth row         | 54 | 3.42 | .02  | .13  | 3.91 | 3.1-3.65     | 1.81    |
| Nasal                       | 54 | 9.71 | .05  | .37  | 3.83 | 8.85-10.5     | .33     |
| Shelf of bony palate        | 54 | 4.02 | .04  | .26  | 6.55 | 3.55-4.85    | 1.73    |
| Palatine slits              | 54 | 4.58 | .04  | .27  | 5.80 | 3.85-5.25     | 1.77    |
| Diastema                    | 54 | 6.49 | .04  | .29  | 4.52 | 5.85-7.1    | .48     |
| Postpalatal length          | 54 | 8.56 | .05  | .34  | 4.02 | 7.7-9.6   | 1.80    |
| **Females:**                |    |      |      |      |      |                |         |
| Condylobasal length         | 46 | 22.10| .13  | .88  | 3.98 | 20.3-23.55     |         |
| Greatest length             | 46 | 24.55| .13  | .90  | 3.65 | 22.55-26.5    |         |
| Cranial breadth             | 46 | 11.33| .04  | .29  | 2.60 | 10.8-11.9     |         |
| Interorbital breadth        | 46 | 3.90 | .02  | .14  | 3.63 | 3.55-4.2     |         |
| Maxillary tooth row         | 46 | 3.48 | .03  | .19  | 5.53 | 3.2-4.45     |         |
| Nasal                       | 46 | 9.74 | .08  | .53  | 5.46 | 8.55-10.8   |         |
| Shelf of bony palate        | 46 | 3.93 | .04  | .26  | 6.53 | 3.35-4.5     |         |
| Palatine slits              | 46 | 4.73 | .04  | .30  | 6.33 | 4.1-5.85   |         |
| Diastema                    | 46 | 6.54 | .05  | .33  | 5.10 | 5.8-7.4   |         |
| Postpalatal length          | 46 | 8.69 | .06  | .38  | 4.33 | 8.05-9.6   |         |

**TABLE 6**
Student’s t-test of cranial measurements of *P. m. gracilis* by sex

| Measurement                  | N  | Mean | S.E. | S.D. | C.V. | Range          | t-ratio |
|-----------------------------|----|------|------|------|------|----------------|---------|
| **Males:**                  |    |      |      |      |      |                |         |
| Condylobasal length         | 50 | 22.71| .08  | .59  | 2.60 | 21.4-23.9     | .77     |
| Greatest length             | 50 | 25.19| .19  | .64  | 2.52 | 23.8-26.25    | .00     |
| Cranial breadth             | 50 | 11.53| .05  | .32  | 2.78 | 10.95-12.4    | 3.28**  |
| Interorbital breadth        | 50 | 3.80 | .03  | .18  | 4.69 | 3.5-4.3      | 1.81    |
| Maxillary tooth row         | 50 | 3.47 | .02  | .14  | 3.98 | 3.1-3.8      | 1.33    |
| Nasal                       | 50 | 10.02| .06  | .42  | 4.27 | 9.05-11.2    | .22     |
| Shelf of bony palate        | 50 | 4.10 | .03  | .21  | 5.17 | 3.6-4.5     | .49     |
| Palatine slits              | 50 | 4.88 | .04  | .29  | 5.93 | 4.3-5.6     | 1.12    |
| Diastema                    | 50 | 6.85 | .04  | .29  | 4.23 | 6.3-7.4     | 1.46    |
| Postpalatal length          | 50 | 8.92 | .04  | .31  | 3.52 | 8.2-9.45    | .82     |
| **Females:**                |    |      |      |      |      |                |         |
| Condylobasal length         | 50 | 22.81| .10  | .70  | 3.08 | 21.6-24.45   |         |
| Greatest length             | 50 | 25.19| .10  | .71  | 2.82 | 23.7-26.65   |         |
| Cranial breadth             | 50 | 11.36| .05  | .32  | 2.85 | 10.65-11.95  |         |
| Interorbital breadth        | 50 | 3.86 | .02  | .15  | 3.84 | 3.55-4.15   |         |
| Maxillary tooth row         | 50 | 3.43 | .02  | .16  | 4.56 | 3.1-3.85   |         |
| Nasal                       | 50 | 10.04| .07  | .49  | 4.87 | 8.95-11.4  |         |
| Shelf of bony palate        | 50 | 4.08 | .03  | .20  | 4.86 | 3.65-4.45  |         |
| Palatine slits              | 50 | 4.95 | .05  | .33  | 6.71 | 3.65-5.7   |         |
| Diastema                    | 50 | 6.94 | .05  | .33  | 4.69 | 6.1-7.6   |         |
| Postpalatal length          | 50 | 8.98 | .06  | .41  | 4.59 | 8.0-9.95  |         |

**Significant at .01 level.**
TABLE 7
COMPARISON\textsuperscript{1} OF MEANS OF TEN CRANIAL MEASUREMENTS OF P. m. gracilis AND
P. m. nubiterrae (g.—n.).

| Variable                      | N  | g.—n. | t-ratio | % Overlap | C.D. |
|-------------------------------|----|-------|---------|-----------|------|
| **Males:**                   |    |       |         |           |      |
| Condylobasal length          | 104| .88   | 6.24*** | 58        | .62  |
| Greatest length               | 104| .73   | 5.83*** | 67        | .57  |
| Cranial breadth               | 104| .24   | 3.50*** | 55        | .34  |
| Interorbital breadth          | 104| -.10  | 3.33*** | 81        | .32  |
| Maxillary tooth row           | 104| .05   | 1.89    | 39        | .19  |
| Nasal                         | 104| .31   | 4.01*** | 62        | .10  |
| Shelf of bony palate          | 104| .08   | 1.71    | 69        | .17  |
| Palatine slits                | 104| .30   | 5.48*** | 52        | .54  |
| Diastema                      | 104| .36   | 6.27*** | 52        | .62  |
| Postpalatal length            | 104| .36   | 5.56*** | 66        | .55  |
| **Females:**                  |    |       |         |           |      |
| Condylobasal length          | 96 | .71   | 4.39*** | 47        | .41  |
| Greatest length               | 96 | .64   | 3.90*** | 70        | .40  |
| Cranial breadth               | 96 | .07   | .48     | 85        | .05  |
| Interorbital breadth          | 96 | -.04  | 1.33    | 92        | .17  |
| Maxillary tooth row           | 96 | -.05  | 1.39    | 49        | .14  |
| Nasal                         | 96 | .30   | 2.89**  | 65        | .29  |
| Shelf of bony palate          | 96 | .15   | 3.20**  | 71        | .33  |
| Palatine slits                | 96 | .22   | 3.40*** | 73        | .35  |
| Diastema                      | 96 | .41   | 6.12*** | 72        | .62  |
| Postpalatal length            | 96 | .29   | 3.60*** | 79        | .37  |

**Significant at .01 level.
***Significant at .001 level.

\textsuperscript{1}Student’s t-test with percent overlap of range, and coefficient of differentiation after Mayr, 1969.

Distinguished statistically on the basis of most skull and skin measurements, it is difficult to assign individual specimens to either subspecies on the basis of these characters because of the extensive overlap between them. In identifying single individuals, characteristics other than skin and skull measurements should be used.

**Color Comparisons**

Some authors have used dorsal coloration as a key character in distinguishing between *P. m. nubiterrae* and *P. m. gracilis* (Osgood, 1909; Hamilton, 1943). *P. m. nubiterrae* is described as having a darker, broader middorsal stripe; however, both subspecies exhibit considerable variation in color intensity and width of the middorsal stripe.

The stripe in *P. m. nubiterrae* often exceeds one-half the width of the back, while in *P. m. gracilis* it is often less than one half. In addition, the contrast between the sides and the back stripe is often lacking in *P. m. gracilis*, so that no back stripe is evident.
Specimens of the two races from Pennsylvania are darker and more frequently have a noticeable middorsal stripe than do *P. m. gracilis* from New York and New Hampshire. In *P. m. nubiterrae*, the middorsal stripe becomes more distinct in populations south of Pennsylvania. This suggests a north-south gradient for dorsal coloration, with intermediate populations in Pennsylvania being the most similar.

On the basis of specimens at the National Museum of Natural History, it is possible to differentiate non-Pennsylvania specimens with regularity on the basis of dorsal coloration. *P. m. gracilis* from New Hampshire are consistently lighter than *P. m. nubiterrae* from Georgia, North Carolina, Tennessee, Kentucky, Virginia, Maryland, and West Virginia. Compared to a series of 28 from New Hampshire, only 10 of 326 specimens from Georgia to Maryland were lighter than the darkest specimen from New Hampshire.

Thus, with the exception of specimens from Pennsylvania, dorsal coloration and the appearance of the middorsal stripe are the best characters by which specimens of the two subspecies may be distinguished without long series. Over most of its range, *P. m. nubiterrae* has a conspicuously darker dorsum with a more distinct middorsal stripe.

**Breeding Characteristics**

Although there is no evidence that *P. m. nubiterrae* and *P. m. gracilis* differ in reproductive characteristics in the wild, they do exhibit marked differences in reproductive success in the laboratory. *P. m. nubiterrae* is an excellent breeder, while *P. m. gracilis* is fair to poor (Kirkland and Linzey, 1973). This differential breeding success under laboratory conditions is exhibited by Pennsylvania and non-Pennsylvania individuals of the two subspecies. The results of recent cross matings between males of one subspecies and females of the other suggest that the lack of breeding success in *P. m. gracilis* may be due to female inhibition. Male *P. m. gracilis* will successfully mate with female *P. m. nubiterrae*, but previously reproductively successful *P. m. nubiterrae* males do not mate successfully with female *P. m. gracilis*. This differential breeding success in the laboratory is one of the most important and consistent distinctions between *P. m. nubiterrae* and *P. m. gracilis*. It indicates that these two subspecies represent differentiated gene pools, in spite of obvious morphological similarities.

**Karyotypes**

Differences in karyotypes between *P. m. gracilis* and *P. m. nubiterrae* have been reported by Bradshaw and Hsu (1972). *P. m. nubiterrae* has either 34 or 36 biarmed autosomes, while *P. m. gracilis* has either
36 or 38. According to Bradshaw and Hsu, there appears to be a north-south cline for autosome number in these two subspecies. In *P. m. nubiterrae* from North Carolina, the autosome number is typically 34 to 36. In Pennsylvania 36 autosomes are present, and the number increases to 36 to 38 for *P. m. gracilis* specimens from Vermont and New Hampshire. In *P. m. nubiterrae*, specimens with 34 biarmed autosomes occur more frequently than do specimens with 36. These data provide further evidence of differentiated gene pools and of clinal gradients in *P. maniculatus* along the Appalachian Mountains.

**Distribution**

*P. m. nubiterrae* is restricted to the mountains of the Appalachian chain, and occurs in ten states: Georgia, South Carolina, North Carolina, Tennessee, Kentucky, Virginia, West Virginia, Maryland, Pennsylvania, and New York. A disjunct population of *P. m. nubiterrae* may exist adjacent to Pymatuning Swamp in Crawford County, Pennsylvania. Thirteen specimens (CM) collected in March and April, 1932, from 2 miles S.W. of Linesville and the south edge of Pymatuning Swamp are typical of *P. m. nubiterrae*. Although *P. m. nubiterrae*'s north-south range extends nearly 650 miles, its east-west distribution is probably less than 175 miles at its widest point. An examination of capture localities from the literature and museum specimens (see Specimen Localities and Literature Records below) reveals that the cloudland deer mouse is somewhat more restricted in its distribution than Hall and Kelson (1959) suggest (Figure 1). This is particularly true for its absence from the Tennessee Valley, although *P. m. nubiterrae* occurs in a small section of mountains in the eastern portion of Tennessee. *P. m. nubiterrae* tends to live at higher elevations, but the data of Wilson (1945) suggest that it may occur as low as a 900 foot elevation in Virginia. Most workers conclude that it is most abundant above the 2500-3500-foot level in the forests of the Canadian Zone. Its occurrence at lower elevations is limited to cool shaded valleys.

*P. m. gracilis* has a more northern distribution, which extends from northeastern Pennsylvania through New York and much of northern New England. It also extends westward through southern Canada to Michigan, Wisconsin, and Minnesota (Hall and Kelson, 1959). Within this range, *P. m. gracilis* inhabits cool, deciduous, boreal forests (Klein, 1960).

The interface between the ranges of *P. m. nubiterrae* and *P. m. gracilis* is located in north-central Pennsylvania. In this region there is undoubtedly some intergradation between the two subspecies (Grimm & Whitebread, 1952; Benton & Altman, 1964). The current boundary between the two subspecies, as drawn by Hall and Kelson (1959), is based on Roslund's (1951) designation of 23 deer mice from Bradford
Fig. 1. Range of *Peromyscus maniculatus nubiterrae.*
and Sullivan counties as *P. m. nubiterrae*. I believe that these specimens (CM 32281; 32300-03; 32519-21; 32523-24; 32526-27; 32529-30; 32532; 32534; 32535; 32539; 32541-44; 32553) should be redesignated as *P. m. gracilis*. There are no obvious color differences between the 23 specimens in question and specimens of either subspecies from Pennsylvania. However, the means of the skin measurements are more similar to those of the 78 *P. m. gracilis* from northern Pennsylvania than to the 307 *P. m. nubiterrae* from western Pennsylvania (Table 8). None of the differences are significant. The redesignation of these specimens results in a constriction of the northern and eastern borders of *P. m. nubiterrae* until the range corresponds more or less with the unglaciated portions of central Pennsylvania. Thus in Pennsylvania *P. m. gracilis* is restricted to the glaciated portions of the northeastern part of the state.

**TABLE 8**

|                      | **P. maniculatus** | **P. m. gracilis** | **P. m. nubiterrae** |
|----------------------|--------------------|--------------------|----------------------|
|                      | Bradford & Sullivan co.’s | Northeastern Pennsylvania | Central and western Pennsylvania |
| **n**                | 23                 | 78                 | 307                  |
| **Total length**     | Mean 179.96        | Mean (diff.) 182.27 (+2.31) | Mean (diff.) 176.88 (−3.08) |
| **Tail length**      | 92.61              | 93.01 (+ .50)      | 90.83 (−1.78)        |
| **Body length**      | 87.35              | 89.26 (+1.91)      | 86.04 (−1.31)        |
| **Hind-foot length** | 21.04              | 21.28 (+ .24)      | 20.74 (− .30)        |
| **Ear length**       | 19.61              | 19.07 (+ .54)      | 18.73 (− .88)        |
|                      | Σdiff 5.50 mm      | Σdiff 7.35 mm      |                      |

1Sexes combined.

**Subspecies Formation**

Using normal taxonomic criteria, it is difficult to justify the recognition of two extremely similar subspecies whose current range interface (Hall and Kelson, 1959) does not correspond with a major physiographic or biological barrier. An appropriate solution under these circumstances might be to designate *P. m. nubiterrae* and *P. m. gracilis* as a single subspecies, *P. m. gracilis*, which exhibits typical north-south character gradients. However, if the 23 previously mentioned Bradford and Sullivan counties, Pennsylvania, specimens (CM) are actually *P. m. gracilis* and not *P. m. nubiterrae*, then the subspecies boundary corresponds with the farthest advance of the Wisconsin Ice Front. The existence of the two forms as separate gene pools then may be justified on historical grounds.
The area now occupied by *P. m. nubiterrae* was not glaciated. However, *P. m. nubiterrae* was probably shifted southward along the Appalachians during the late Pleistocene. Guilday (1971) has documented the southward displacement of an arctic-subarctic mammal fauna into the central Appalachians. Any southward displacement of *P. m. nubiterrae* may have been tempered by altitudinal shifts into lowland areas.

The region now occupied by *P. m. gracilis* was totally covered by ice during the Pleistocene. During the Wisconsin glaciation, the stock from which the current *P. m. gracilis* is derived must have resided in the range of one or more of the other current subspecies of *P. maniculatus* (or their parental stocks), or in an area in the East or Midwest that was then ecologically suitable. In the East, *P. m. gracilis* may have resided in Pleistocene refugia in New Jersey. Braun (1947, 1964) has documented boreal forest elements in New Jersey during the Pleistocene. Wetzel (1955) has concluded that the presence of *Synaptomys cooperi* on the Delmarva Peninsula and southward on the Virginia-North Carolina coast provides evidence of an Atlantic Coast refugium for boreal species during the Pleistocene.

I propose that these subspecies were formed during the late Pleistocene when *P. m. gracilis* was pushed south and east into a coastal refugium, while *P. m. nubiterrae* continued to reside in the unglaciated part of the Appalachian Mountains. This period of separation during the Wisconsin permitted the development of the behavioral differences reflected in the independent breeding responses under laboratory conditions. The extremely similar morphology of the two forms has resulted from living under similar environmental conditions over a long period of time. The higher elevations in the southern Appalachians are and have been similar in vegetation and climate to the northern areas currently inhabited by *P. m. gracilis*.

**Other Subspecies**

In addition to its geographical proximity and close relationship to *P. m. gracilis*, *P. m. nubiterrae* is partially sympatric with the Prairie Deer Mouse, *Peromyscus maniculatus bairdii* (Hoy and Kennicott). The latter race has extended its range eastward, apparently in response to extensive clearing of forests (Paradiso, 1969). *P. m. bairdii* exhibits strong preferences for open grassland habitats and seldom ventures into forest areas (Harris, 1952; Wecker, 1963). Thus, although geographically sympatric, the two races are ecologically separated (Hall and Kelson, 1959; Paradiso, 1969).

*P. m. nubiterrae* and *P. m. bairdii* are also morphologically distinct. *P. m. bairdii* is one of the short-tailed grassland races of deer mice, and its external measurements markedly distinguish it from the longer-tailed, larger-bodied *P. m. nubiterrae*. In Pennsylvania the ranges of
the standard skin measurements for *P. m. bairdii* are: total length, 121-160 mm; tail length, 50-70 mm.; hind-foot length, 16-19 mm.; ear length, 12-14 mm. (Doutt, et al., 1973). There is thus no overlap with measurements of *P. m. nubiterrae*.

**Summary**

*Peromyscus maniculatus nubiterrae* occupies a range along the higher elevations of the Appalachian Mountains from New York to Georgia, predominantly in areas that were not glaciated. It is poorly differentiated from *P. m. gracilis*, which occupies a range to the north and east of *P. m. nubiterrae* that was once glaciated. On the basis of skull and external morphology, it is difficult to justify the retention of *P. m. nubiterrae* as a separate subspecies. Dorsal coloration is the best character by which to distinguish between these two forms. *P. m. nubiterrae* tends to have a darker and more distinct middorsal stripe.

An additional criterion for retaining *P. m. nubiterrae* as a subspecies separate from *P. m. gracilis* is the success attained in its differential breeding in the laboratory. This distinction suggests genetic differences between *P. m. nubiterrae* and *P. m. gracilis* that are not observed in external and skull morphology. Karyotypic differences have also been observed between the two subspecies. These differences were probably acquired during the late Pleistocene when, it is hypothesized, *P. m. gracilis* occupied a refugium in New Jersey, while *P. m. nubiterrae* occupied an Appalachian range.

**Specimen Localities and Literature Records**

The localities of the 595 skins and 100 skulls of *P. m. nubiterrae* examined in this study are listed below. Museums housing each group of specimens examined are listed at the end of these sections. County records from a search of the literature are also given.

**Georgia.** Specimens examined: Rabun County, Rabun Bald. Towns County, Brasstown Bald (USNM). Literature records: Lumpkin; Rabun; Towns; Union; White counties (Golley, 1962).

**Kentucky.** Specimens examined: Harlan County, Black Mountain (USNM).

**Maryland.** Specimens examined: Garrett County, Grantsville; 6 mi. N Frostburg (USNM). Literature records: Allegany; Garrett counties (Paradiso, 1969).

**North Carolina.** Specimens examined: Clay County, 12½ mi. E Hayesville (USNM). Haywood County, 7½ mi. S Waynesville (CM). Macon County, Highlands; 10 mi. W Franklin - Wayah Bald (USNM). Mitchell County, near summit Roan Mt. (CM); 7½ mi. SW town of Roan Mountain, Carter Co., Tennessee; and Glen Ayre, Roan Mt. (USNM). Rutherford County, Cove Creek. Transylvania County, Pisgah Forest - Bent Creek Experimental Station. Watauga County, Grandfather Mt.; 7½ mi. N Elk Knob. Yancey County, Mt. Mitchell; 3½ mi. S Mt. Mitchell summit (USNM). Literature records: Jackson; Macon counties (Odum, 1949). Buncombe; Henderson; Macon; Mitchell; Swain; Transylvania counties (Brimley, C.S., 1944-46).

**Pennsylvania.** Specimens examined: Bedford County, 6 mi. NW Immler; 7 mi. NW Immler; 2 mi. E Osterburg. Cambria County, 5 mi. N Ebensburg; 5 mi. NNE Ebensburg;
5½ mi. NE Ebensburg; 5 mi. NE Ebensburg; 1½ mi. SW Patton. Cameron County, 8 mi. NNW Emporium - Three Mile Run. Centre County, 2.3 mi. SE Woodward - Cherry Run. Clearfield County, McGees Mills; 4 mi. NW Cessna Run; 0.7 mi. SE McGees Mills. Crawford County, S edge Pymatuning Swamp; 2 mi. SW Linesville. Fayette County, ¼ mi. S Ohioyle; 4 mi. SE Ohioyle; 2½ mi. NW Markleysburg; 2 mi. E Markleysburg; 2 mi. NW Markleysburg. Forest County. Brookston. Huntingdon County, 5 mi. NE McAlveys Fort; 5½ mi. NE McAlveys Fort. Indiana County, 8½ mi. SE Indiana; Cessna Run - 4 mi. NW Glen Campbell; Glen Campbell. Jefferson County, 5½ mi. NE Sigel; 8 mi. NE Sigel - Heath Station. Lycoming County, 6½ mi. S Nisbet. McKean County, 10 mi. SW Bradford - Sugar Run; Sugar Run; 3 mi. N Clermont - Red Mill Run; 4 mi. E Clermont. Mifflin County, 5 mi. W Milroy. Potter County, 4 mi. SW Ulysses - Gold; 8 mi. NE Coudersport; 4 mi. NW Costello; Costello; 6½ mi. S Ulysses - Buckseller Run; 5½ mi. SW Ulysses - Cobb Hill; 5½ mi. SW Ulysses - Rapple Hollow; 7½ mi. SW Ulysses - Woodcock Run. Somerset County, 2 mi. SSE Somerset; ½ mi. W. Bakersville; 8 mi. NW Somerset; 10 mi. NW Somerset; 5½ mi. WSW Jennerstown; 5 mi. WSW Jennerstown; 4½ mi. NW Salisbury; 5 mi. NW Salisbury. Warren County, 5 mi. E Columbus - Benson Swamp; 5 mi. N Kinzua; 2½ mi. N Kinzua. Washington County, 6 mi. SSE Laughlintown; Laughlintown; 2½ mi. SSE Rector - Lynn Run; 3 mi. SSE Rector; 2 mi. SSE Rector; 7½ mi. S Laughlintown - Bald Knob Tower; 1½ mi. SSE Rector - Lynn Run; 5 mi. SE Rector; 6 mi. S Laughlintown; 4½ mi. SSE Rector; ½ mi. ESE Laughlintown (CM).

TENNESSEE. Specimens examined: Carter County. Cocke County, Snake Den Mt.; 4½ mi. SE Cosby - Low Gap; Old Black Mt.; Inadu Knob; Mt. Guyot. Johnson County, Holston Mts.; 3½ mi. NE Shady Valley - Holston Mt. (USNM). Literature records: Blount; Carter; Cocke; Johnson; Sevier; Sullivan counties (Kellogg, 1939).

VIRGINIA. Specimens examined: Bedford County, Peak of Otter. Giles County, Mountain Lake. Grayson County, Mt. Rogers - Troutdale. Page County, Skyland. Rappahannock County, Devil's Stairs - Washington (USNM). Literature records: Dickenson; Giles; Grayson; Highland; Page; Rappahannock; Smyth; Tazewell; Wise counties (Bailey, 1946). Augusta; Bedford; Giles; Grayson; Highland; Page; Rappahannock; Shenandoah; Smyth; Tazewell; Washington; Wise counties (Handley and Patton, 1947).

WEST VIRGINIA. Specimens examined: Greenbrier County, White Sulphur Springs. Mercer County, Flat Top. Pocahontas County, Cranberry Glades; Dubbin - Middle Mt. Raleigh County, SW of Pemberton - Windy Gulf; Flat Top Mt. Randolph County, Cheat Bridge. Pendleton County, Spruce Knob (USNM). Tucker County, 2 mi. S Parsons (SSC). Literature records: Monongalia County (Wilson, 1945).

REFERENCES CITED

BAILEY, J. W.
1946. The mammals of Virginia. Richmond, Williams Printing Co., 416 pp.

BARBOUR, R. W.
1941. Three new mammal records from Kentucky. Jour. Mammalogy, 22: 195-96.

BENTON, A. H., AND H. J. ALTMAN
1964. A study of fleas found on Peromyscus in New York. Jour. Mammalogy, 45: 31-36.

BRADSHAW, W. N., AND W. A. GEORGE, JR.
1969. The karyotype in Peromyscus maniculatus nubiterrae. Jour. Mammalogy, 50: 822-24.

BRADSHAW, W. N., AND T. C. HSU
1972. Chromosomes of Peromyscus (Rodentia, Cricetidae) III. Polymorphism in Peromyscus maniculatus. Cytogenetics, 11: 436-51.
BRAUN, E. L.
1947. Development of the deciduous forests of eastern North America. Ecol. Monog., 17: 211-219.
1964. Deciduous forests of eastern North America. New York, Hafner, 596 pp.

BRIMLEY, C. S.
1944-46. The mammals of North Carolina. Installment No. 12, reprinted from Carolina Tips.

CADD, E. R.
1941. Notes on certain mammals of the mountains of southwestern Virginia. Jour. Mammalogy, 22: 323-25.

COLEMAN, R. H.
1948. Some mammal notes from South Carolina. Jour. Mammalogy, 29: 293-94.

DOUGT, J. K., C. A. HEPPENSTALL, AND J. E. GUILDA
1973. Mammals of Pennsylvania, Harrisburg, Pa. Game Comm., 3rd edition, 283 pp.

Gifford, C. L., AND R. WHITEBREAD
1951. Mammal survey of southcentral Pennsylvania. Final Report Pittman-Robertson Project 38R. Harrisburg, Pa. Game Comm., 67 pp.

GOLDS, F. B.
1962. Mammals of Georgia. University of Georgia Press, 218 pp.
1966. South Carolina mammals. Charleston, The Charleston Museum, 181 pp.

GRIMM, W. C., AND H. A. ROBERTS
1950. Mammal survey of southwestern Pennsylvania. Final Report Pittman-Robertson Project 24R. Harrisburg, Pa. Game Comm., 99 pp.

GRIMM, W. C., AND R. WHITEBREAD
1952. Mammal survey of northeastern Pennsylvania. Final Report Pittman-Robertson Project 42R. Harrisburg, Pa. Game Comm., 82 pp.

GUILDA, J. E.
1971. The pleistocene history of the Appalachian mammal fauna. Blacksburg, Va., Research Division Monograph 4, Virginia Polytechnic Institute and State University, 233-261.

HALL, E. R., AND K. R. KELSON
1959. The mammals of North America. New York, Ronald Press, 2 vol., 1083 pp.

HAMILTON, W. J., JR.
1943. Mammals of the eastern United States. Ithaca, New York, Comstock Publishing Co., 432 pp.

HANDEY, C. O., JR., AND C. P. PATTON
1947. Wild mammals of Virginia. Richmond, Commission of Game and Inland Fisheries, Commonwealth of Virginia, 220 pp.

HARRIS, V. T.
1952. An experimental study of habitat selection by prairie and forest races of the deer mouse, Peromyscus maniculatus. Contr. Lab. Vert. Biol., Univ. Michigan, 56: 1-53.

KELLOGG, R.
1939. Annotated list of Tennessee mammals. Proc. U.S. Nat. Museum, 86 (3051): 245-303.

KING, J. A.
1969. Biology of Peromyscus (Rodentia). Special Publication No. 2, American Society of Mammalogists, 593 pp.

KIRKLAND, G. L., JR., AND A. V. LINZEY
1973. Observations on the breeding success of Peromyscus maniculatus nubiterrae. Jour. Mammalogy, 54: 254-55.

KLEIN, H. G.
1960. Ecological relationships of Peromyscus leucopus noveboracensis and P. maniculatus gracilis in central New York. Ecol. Monogr., 30: 387-407.
KOMAREK, E. V. AND R. KOMAREK
1938. Mammals of the Great Smokey Mountains. Bull. Chicago Acad. Sci., 5 (6): 137-162.
LINZEI, A. V.
1970. Postnatal growth and development of Peromyscus maniculatus nubiterrae. Jour. Mammalogy, 51: 152-55.
MAYR, E.
1969. Principles of systematic zoology. New York, McGraw-Hill, 428 pp.
ODUM, E. P.
1949. Small mammals of the Highlands (North Carolina) Plateau. Jour. Mammalogy, 30: 179-92.
OSGOOD, W. H.
1909. Revision of the mice of the American genus Peromyscus. North American Fauna 28, 285 pp.
PARADISO, J. L.
1969. Mammals of Maryland. North American Fauna 66, 193 pp.
RICHMOND, N. D., AND H. R. ROSLUND
1949. Mammal survey of northwestern Pennsylvania. Final Report Pittman-Robertson Project 20R. Harrisburg, Pa. Game Comm., 67 pp.
ROSLUND, H. R.
1951. Mammal survey of northcentral Pennsylvania. Final Report Pittman-Robertson Project 37R. Harrisburg, Pa. Game Comm., 55 pp.
WECKER, S. C.
1963. The role of early experience in habitat selection by the prairie deer mouse, Peromyscus maniculatus bairdii. Ecol. Monogr., 33: 307-325.
WETZEL, R. M.
1955. Speciation and dispersal of the southern bog lemming, Synaptomys cooperi (Baird). Jour. Mammalogy, 36: 1-20.
WILSON, L. W.
1945. The genus Peromyscus in West Virginia. Jour. Mammalogy, 26: 95-96.
WILSON, L. W., AND J. E. FRIEDEL
1942. A list of mammals collected in West Virginia. Proc. West Virginia Acad. Sci., 15: 85-92.
Kirkland, Gordon L. 1975. "Taxonomy and geographic distribution of Peromyscus maniculatus nubiterrae Rhoads (Mammalia: Rodentia)." *Annals of the Carnegie Museum* 45, 213–229. https://doi.org/10.5962/p.330510.

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