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Notes on Geographic Variation of Microtus pennsylvanicus (Mammalia, Rodentia) in New Mexico and Chihuahua

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The presence of a relict population of *Microtus pennsylvanicus* near Aragon in southwestern New Mexico, was reported by Anderson (1961) on the basis of two skins and one skull collected and prepared by J. Stokley Ligon in 1915. Two additional specimens, also obtained by Ligon in 1915, were recently found in the Bailey-Law Collection of the Rockbridge Alum Springs Biological Laboratory and Virginia Polytechnic Institute and State University. These specimens add to our knowledge of the characteristics of the relict population and enable us to compare this population with others in the region, including a distinctive population recently discovered in Chihuahua, Mexico, and named *Microtus pennsylvanicus chihuahuensis* by Bradley and Cockrum (1968). These relict populations are here compared with each other and with populations in northern New Mexico and southern Colorado. Some statistical infelicities in Anderson's earlier work (1956) that bear on the problem of the relationship of the Aragon population are also noted.

First, the infelicities. Dr. J. C. Barlow, a former student at the University of Kansas, kindly called to Anderson's attention the fact that a formula printed on statistical computation sheets formerly used had been

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misread, with consequent error in calculated values of standard deviations, standard errors, and coefficients of variation. The error involved reading part of the computational formula, $(\Sigma fd')^2/N$, as $(\Sigma fd'/N)^2$. Therefore statistics published by Anderson prior to 1960 (after which time he no longer used these sheets) were recalculated from the original data sheets to verify or correct the values. Errors were detected in the following publications and pages therein, all in the University of Kansas Publications of the Museum of Natural History: vol. 7, no. 7, p. 504; vol. 9, no. 4, pp. 100–101; vol. 9, no. 17, pp. 499–501. The recalculated standard deviations are in some cases larger but in most cases smaller than the erroneous values. In no case would the difference have led to taxonomic conclusions different from those drawn. A sheet with all recalculated values is available upon request from Anderson.

The two newly found specimens are Nos. 434, an adult female, and 435, an adult male, in the Bailey-Law Collection (now A.M.N.H. Nos. 217046 and 217047, respectively). They were taken 8 miles southwest (at 7000 ft.) and 7 miles southwest (at 6400 ft.), respectively, from Aragon, in what was then Socorro County (now Catron County), New Mexico, on February 16 and April 12. Each is a standard study skin and skull in good condition, except for slight damage to the bullae. The skins are slightly paler and redder in dorsal pelage than the skin of A.M.N.H. No. 90873 from the same population. The redness may in part result from changes since the specimens were prepared. All three have a buffy ventral hue.

Means \pm standard deviations (plus minimum and maximum, all measurements in millimeters) of the four skins and three skulls in the Aragon series are: total length 176.2 \pm 8.5 (168–187); tail length 42.2 \pm 2.1 (40–44); length of hind foot 22.2 \pm 0.5 (22–23); condylobasilar length 29.20 \pm 0.56 (28.6–29.7); zygomatic breadth 17.70 \pm 0.62 (17.0–18.2); lambdoidal breadth 13.07 \pm 0.50 (12.6–13.6); prelambdoidal breadth 9.37 \pm 0.32 (9.0–9.6); depth of braincase 8.57 \pm 0.32 (8.2–8.8); and alveolar length of molar tooth row 7.90 \pm 0.26 (7.6–8.1). Measurements were taken as described by Anderson (1954).

Besides the distinctive *chihuahuensis* already mentioned, two other forms require comparison with the Aragon population: *M. p. modestus* of southern Colorado and northern New Mexico and *M. p. aztecus* of northwestern New Mexico. *Microtus p. modestus* is a distinctive subspecies whose characters relative to *chihuahuensis* are smaller hind foot and skull measurements and paler coloration. *Arvicola modesta* was originally described as a distinct species (Baird, 1858), but Bailey (1900) rightly considered it a race of *M. pennsylvanicus*. *Microtus p. aztecus* was also described

as a distinct species and was characterized as being (1) large and as having (2) full and soft pelage, (3) short tail, (4) narrow skull, and (5) grayish brown dorsum with tinge of pale buff (Allen, 1873). Bailey (1900) recognized the affinity of aztecus with M. pennsylvanicus, but retained aztecus as a distinct species differing from pennsylvanicus in characters 3 and 4 (above) and in having (6) larger hind foot, (7) larger skull, (8) narrow braincase, and (9) longer interparietal. After comparisons with M. p. modestus, Hall and Cockrum (1952) reduced aztecus to a subspecies of M. pennsylvanicus, differing from modestus in characters 4 and 7 (above) and in having (10) narrower nasals. Bradley and Cockrum (1968), in their description of M. p. chihuahuensis, gave measurements of aztecus along with those of modestus, but did not critically review the situation in New Mexico. Present workers have accepted the merger of aztecus with M. pennsylvanicus as a valid subspecies.

The following series (see fig. 1) are compared here: (A) 32 M. p. modestus from near the type locality in southern Colorado, measurements from Anderson, 1956, p. 100, recalculated as mentioned above; (B) 18 M. p. modestus from north-central New Mexico, measurements from Bradley and Cockrum 1968; (C) 8 M. p. aztecus, measurements also from Bradley and Cockrum; (D) 9 M. p. aztecus, measured by Anderson in the Museum of Vertebrate Biology in Berkeley and the American Museum of Natural History, and including the holotype; (E) the Aragon series, now numbering four skins and three skulls; and (F) 27 M. p. chihuahuensis measured by Bradley and Cockrum, and three specimens examined by Anderson in the A.M.N.H. Measurements are plotted in a ratio diagram in figure 2. Larger measurements are at the right on the diagram. If the measurements of two dimensions are equidistant from the baseline O, then the ratio of those two measurements is equal to the ratio of the measurements of the same two dimensions in the standard. The "significant differences" discussed in text are those estimated from the data in this diagram to be significant at or above the 95 per cent level. These differences were not tested further because sample E is small and variances are unknown for samples B, C, and F.

The texture and length of pelage, character 2 above, may help in distinguishing *M. pennsylvanicus* from other species of *Microtus* in the area but these attributes of pelage are not noticeably different among the above populations within *M. pennsylvanicus*, except perhaps for F. Characters of the pelage need quantitative definition before they can be verified or used effectively, particularly as possible seasonal differences have not been adequately evaluated.

In color, chihuahuensis (F) is definitely darker throughout than series

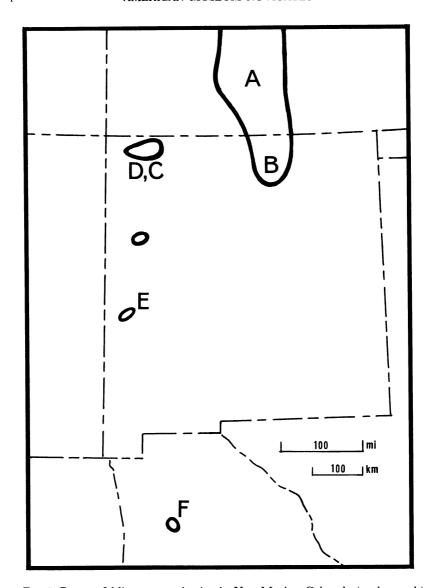


Fig. 1. Range of *Microtus pennsylvanicus* in New Mexico, Colorado (to the north), and northern Chihuahua. The origins of the samples A through F as discussed in text are shown. Within each area outlined in heavy black are populations presumed to be in more or less continuous genetic contact at present. Note the relict nature of the southern populations. The area between D and E without a letter is San Rafael (Anderson, 1961). Specimens from there were not used in the present study.

A through E. Series E and F have buffier bellies than those of other series in which gray predominates, but in F the blackness obscures the buffiness. The buffy belly is therefore, most noticeable in series E, which has a distinct reddish hue dorsally as well. Series E is slightly darker than series A through D, but is closer to these series in degree of darkness than to series F. The color does not differ noticeably in series A through D.

In external measurements there are no significant differences in total length or tail length. The mean length of hind feet in *chihuahuensis* (series F) is significantly greater than in *modestus* (series A and B). Series C and D (aztecus) and E are intermediate between *modestus* and *chihuahuensis* but probably not significantly different from either. Judgments here are based on the ratio diagram and the assumption that the variances for measurements by Bradley and Cockrum are comparable with those of the series for which variances were calculated.

In most cranial measurements as in length of hind foot chihuahuensis (F) is significantly larger than modestus (A and B), aztecus (C and D) tends to be intermediate, and the Aragon series (E) is near chihuahuensis. A few measurements provide exceptions to the general increase in size of cranial features from A to F. The term "relatively" as used below for cranial measurements means "as a ratio of condylobasilar length." The large measurements of zygomatic and lambdoidal breadth for chihuahuensis reflect the strength and distinctness of ridges and processes that develop in larger skulls. These dimensions are, therefore, consistent with wellknown allometric relationships (see Anderson, 1959, p. 434, for example). The teeth are large, but not relatively so, in chihuahuensis, compared to A through D. The sagittal length of the interparietal seems relatively small in chihuahuensis and relatively large in aztecus and the Aragon series, as shown by the relationship of length to width of interparietal and by the ratio of its length to condylobasilar length of skull. The length of the interparietal is one of the more variable dimensions, and there is some doubt whether Anderson has measured the width of interparietal in the same way as did Bradley and Cockrum. This doubt arises because measurements of certain specimens by Anderson (such as series D) are larger than comparable measurements by Bradley and Cockrum (such as those for series C) in this dimension. The relative length of nasals in chihuahuensis is less than in other series and the width of nasals is greater. The width of nasals is less in aztecus. The bullae are larger both actually and relatively in chihuahuensis. We did not measure bullae in the Aragon series because of uncertainty about the exact method of measurement, but visual comparison clearly indicates actually and relatively smaller bullae in this series than in chihuahuensis.

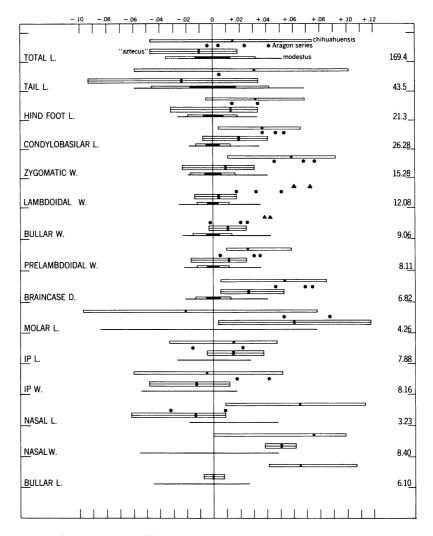


Fig. 2. Ratio diagram (Simpson, Roe, and Lewontin, 1960, here modified by adding ranges and statistics showing variation) for the comparison of four geographically separated populations of *Microtus pennsylvanicus*. The sample selected as the standard is of *M. p. modestus* (A as noted in text for those nine dimensions showing confidence intervals and sample B for the other six dimensions.) The range ± 2 S.E. is shown in black, and the range ± 1 S.D. is shown in open box. Samples C and D of "aztecus" were combined and mean and range are shown. Individual values (dots) from the Aragon series (sample E) are plotted. The mean and range are shown for *M. p. chihuahuensis* (sample F) except for two dimensions where two individuals only are shown by triangles. The values in millimeters of the means for the standard series are given at right. The numerical scale is the difference between the log₁₀ of the standard mean and the log₁₀ of the value being compared. *Abbreviations:* D. depth, IP. interparietal, L. length, W. width.

Among the series A through F, the most distinctive individually is F, followed by E, whereas A through D are more alike inter se and are distinct from E and from F. In some characters E is like F, in others like A through D, and vet in others intermediate between F on one hand and series A through D on the other. Over-all its characters bridge the differences between the distinctive F (chihuahuensis) and the more northern series A through D. In comparing C with D we find them inseparable, likewise in comparing A with B. A comparison of C and D (aztecus) with A and B (modestus) reveals at most a marginal degree of difference. Among differences numbered 1 through 10 above, characters 1 (based on length of skull, but not on external measurements), 4 (based on lambdoidal breadth), 7 (equivalent to 1), 9, and 10 (relatively at least) seem to be verified. Characters 2, 3, 5, 6, and 8 are not verified. The distinctness of the subspecies aztecus is thus seen to involve only half the characters reported to be diagnostic. Three of the characters in which aztecus differs from modestus, namely (1) greater condylobasilar length, (11) longer tooth row, and (12) perhaps longer bulla, are in the direction of the characters of the Aragon series and chihuahuensis to the south. Two other characters, (9) longer interparietal and (10) relatively narrow nasals of aztecus, are shared with the Aragon series and differ from both chihuahuensis and other modestus.

In taxonomic terms we can reflect the observed relationships, and by inference the genetic relationships, by synonymizing aztecus with modestus and by regarding the Aragon series as intergrades between chihuahuensis and modestus.

The term intergrade as used here refers to the morphological characteristics of the geographically intermediate Aragon population and does not imply that this and the other disjunct populations have been able to interbreed within the recent past. However, we postulate that the morphological gradient that exists now may have arisen in part as the result of such interbreeding, perhaps as recently as the late Wisconsin glacial period when one continuous population may have inhabited this region. Present morphological relationships among these populations would thus represent a certain durability of characteristics, even with disjunctions of hundreds of kilometers and after thousands of years. We recognize that selection has helped maintain the morphological relationships of these populations since disjunction occurred, and that the intergrade situation may reflect an environmental gradient at present, in spite of the discontinuity of habitats of these voles. An interesting parallel exists with certain southern, relict, marsh-dwelling, isolated, and small populations of M. montanus, which are also characterized by large size and dark pelage (Anderson, 1959). Probably this parallelism reflects important environmental selection for such characteristics.

In summary, newly found material of a relict population of *Microtus pennsylvanicus* once present in southwestern New Mexico was compared with other samples from Chihuahua, New Mexico, and Colorado. *Microtus pennsylvanicus aztecus* (Allen, 1893) is placed in the synonymy of *Microtus pennsylvanicus modestus* (Baird, 1858). The relict population near Aragon is interpreted as intergrade between *M. p. modestus* and *M. p. chihuahuensis* Bradley and Cockrum, 1968. The intergrades are nearer *M. p. modestus*, to which they are referred.

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