

**A CHROMOSOMAL SUBDIVISION IN *PEROMYSCUS LEUCOPUS*:
IMPLICATIONS FOR THE SUBSPECIES CONCEPT AS
APPLIED TO MAMMALS**

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ABSTRACT.—The application of Lidicker's (1962) definition of subspecies as evolutionary subdivisions gives the trinomen a biologically meaningful position in the nomenclatural hierarchy. We tested the validity of this application of the subspecies concept in *Peromyscus leucopus* by comparing limits of the two chromosomal races with Hall's (1981) proposed subspecific boundaries, and found no congruence. The implications of this lack of concordance are: 1) either chromosomal races do not indicate limits of evolutionary subunits in *P. leucopus*; or 2) the currently recognized subspecies in *P. leucopus* are not reflective of Lidicker's (1962) criteria.

The systematic value of assigning subspecies has been extensively debated (Corbet, 1970; Lidicker, 1962; Burt, 1954; and Wilson and Brown, 1953). Most critics of the trinomen probably would agree that if the concept of the subspecies is to have systematic value, then such designations must represent genetically distinct, evolutionary subunits within a species. Verification that subspecies boundaries, which are based on classical studies of morphology, actually represent limits of evolutionary subunits would strengthen the credibility of the usage of the subspecies concept within mammals.

As defined by Lidicker (1962, page 169), "A subspecies is a relatively homogeneous and genetically distinct portion of a species which represents a separately evolving, or recently evolved, lineage with its own evolutionary tendencies, inhabits a definite geographic area, is usually partially isolated, and may intergrade gradually, although over a fairly narrow zone with adjacent subspecies."

Chromosomal races are generally recognized as indicating such evolutionary subdivisions within a species. If this is true, then the limits of chromosomal races compared to classically conceived subspecific boundaries should comprise a proper test of the accuracy of subspecific boundaries. Such a test can be readily applied to the white-footed mouse, *Peromyscus leucopus*, a mammal with 17 recognized subspecies (Hall, 1981), and two major chromosomal races (Baker et al., 1983), representing a northeastern-southwestern subdivision of the species.

Karyotypes of the two chromosomal races of *Peromyscus leucopus* differ by three presumed pericentric inversions (Baker et al., 1983). Using the standard chromosome numbering system for *Peromyscus* (Committee, 1977), these marker chromosomes are pairs 5, 11, and 20. Animals of the northeastern race exhibit the acrocentric condition in pairs 5 and 11, and have banded 20's. Southwestern specimens are banded for 5 and 11, and

are acrocentric for 20. Intermediate, or hybrid karyotypes, are those in which three marker chromosomes do not conform to the above described parental conditions.

Although it may be an attractive alternative to conclude that the two races represent biological species, we find no indication in the morphological (Hall, 1981; Osgood, 1909) and genic (Kilpatrick and Zimmerman, 1975) data to suggest that two species are involved. Additionally, the magnitude of natural hybridization between the two races does not provide support for the idea that two species are represented.

METHODS AND MATERIALS

Mice from Kansas, Oklahoma, and northern Texas were collected with Sherman live traps, and transported alive to the laboratory, where they were karyotyped and G-banded (Lee and Elder, 1980), and analyzed to determine the condition of the three marker chromosomes (homozygous-acrocentric, homozygous-biarmed, or heterozygous).

Voucher specimens were prepared as standard museum skins accompanied by skulls, and were deposited in The Museum, Texas Tech University, Lubbock, Texas.

Distribution of the two chromosomal races, based on current data from throughout our three-state study area, were superimposed over the proposed boundaries of subspecies of Hall (1981), to determine any correlation (see Fig. 1).

RESULTS

Peromyscus leucopus is primarily a woodland mouse throughout the study area (Davis, 1974; Hall, 1954). In Kansas and Oklahoma, suitable habitat is relatively continuous in the eastern part of the states (Kuchler, 1974; Duck and Fletcher, 1943). Further west, grasslands predominate and *P. leucopus* is generally restricted there to the wooded borders of waterways and in man-made shelter belts, thus assuming a dendritic distribution pattern. Samples from along and north of the Arkansas River in Kansas contained mice with the northeastern karyotype. South of that river, mice with the southwestern cytotype were taken. Presumably, populations of mice inhabiting watersheds adjoining the Arkansas River to the south seldom come in contact with populations to the north, due to the unsuitable habitat separating them. Our general collecting indicates this to be the case in Kansas.

Mice from Oklahoma present another pattern. In the east-central part of the state, the northeastern cytotype appears south of the Arkansas River. Here too, specimens with an intermediate, or hybrid, karyotype were collected. Unlike in Kansas, where the two chromosomal races may be geographically isolated, in Oklahoma the two races form a zone of hybridization. However, at no locality have the two parental types been

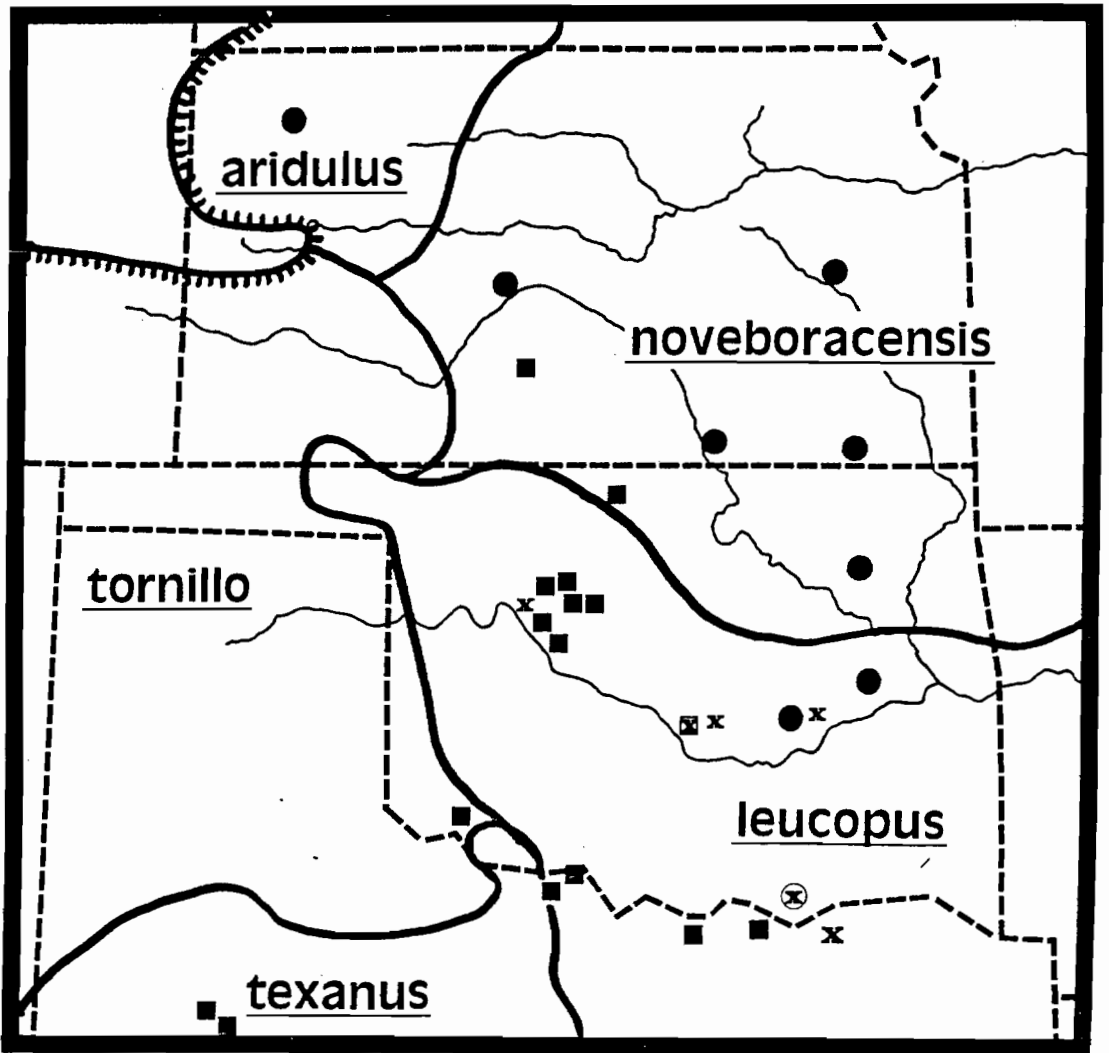


FIG. 1.—Subspecific boundaries of Hall (1981) for *Peromyscus leucopus* in Kansas, Oklahoma, and northern Texas. Dots indicate localities where animals of the northeastern cyotype were collected. Squares indicate localities where specimens of the southwestern chromosomal race were taken. Places where intermediate karyotypes were recorded are designated by an "X." Circles and squares enclosing an "X" indicate where intermediate and parental karyotypes were collected together. Hatched line indicates the extent of the range of *P. leucopus*.

found to be sympatric. Based on combinations of the three marker pairs of chromosomes, the 12 hybrid cytotypes encountered were possible F_2 or backcross individuals. This indicates that the two races freely interbreed and produce fertile offspring. No F_1 karyotypes have yet been recorded from within the three-state study area, although one of three mice from Tennessee (Baker et al., 1983) appears to be an F_1 (heterozygous for each of the three pairs or marker chromosomes). The width of the zone surely varies along its extent, but collecting in central Oklahoma, between Norman and near Henryetta, documents a width of at least 64 km in that area.

Based on our sample, mice from the western, central, and extreme southern parts of Texas are all examples of the southwestern race. Although

no specimens have yet been examined from the woodlands of extreme eastern Texas, it is possible that the northeastern race occurs in that area, based on the presence of a hybrid animal from 3 mi E Bonham, Fannin County. The Red River, separating Oklahoma from Texas, is a braided stream, in which the water level is often quite low, and is spanned by numerous bridges. This river probably is a barrier of limited consequence to *Peromyscus leucopus*.

Within the species *Peromyscus leucopus*, boundaries of the five recognized subspecies occurring in our study area clearly do not correspond to those of the two chromosomal races (see Fig. 1). The cytological boundaries transect the subspecific boundary separating *P. l. leucopus* and *P. l. noveboracensis*, indicating that the chromosomal races are composed of morphologically diverse phenotypes.

DISCUSSION

As applied to mammals, it has been alleged that the subspecies concept is often misused (Corbet, 1970; Lidicker, 1962; Burt, 1954). Our test for correlation of the limits of currently recognized subspecies to the limits of chromosomal races indicates to us that the subspecies concept, as defined by Lidicker (1962), has been misapplied in *Peromyscus leucopus*. This misapplication can be traced back to Osgood's (1909) monumental revision of the genus *Peromyscus*. In that work, Osgood (page 16) stated that "Local and geographic variations are great, so great, indeed, that excepting a few species with limited range, all the species have developed geographic peculiarities by means of which they have been subdivided into more or less numerous (geographic) races or subspecies." The tradition of using subspecies to identify extreme phenotypic variants is perpetuated in the literature through Hall (1981), whose subspecific boundaries as applied to *P. leucopus* simply are modifications of those proposed by Osgood (1909). Given the degree of intergradation of morphotypes and the clinal variation cited by Osgood, it is apparent that subspecific boundaries as proposed by Hall (1981) are often arbitrary. We propose that this is the case in *P. leucopus*, but clearly this situation is not restricted to *Peromyscus*. Another obvious example is found in much of the *Ursus* complex.

In dealing with the problem of clinal variation and the recognition of subspecies, Corbet (1970) claimed that the concept of the subspecies is meaningless, unless it is restricted to "discrete" segments of a species. The matter of discerning whether populations within a species are indeed discrete entities, and thus deserving of subspecific status, or whether clinal variation exists, is a problem of sampling, as pointed out in Corbet's (1970) examples. Such is not the situation in *Peromyscus*, whose species are among the most widely distributed taxa of mammals in North America, and species of this genus are extremely well-represented in museum collections.

It was a major assumption in our test for congruence of evolutionary subunit boundaries and limits of subspecies that members of the two

chromosomal races each shared a common evolutionary origin after diverging from a parental stock. If this assumption is true, then *Peromyscus leucopus* has at least two subspecies that are delineated by major chromosomal differences.

“It would be highly informative to contrast phenetic and phylogenetic subspecies classifications . . . Such an evolutionary philosophy applied to infraspecific analysis has a number of important advantages, not the least of which is that it focuses attention on the speciation process and not on geographic variation per se . . .” (Lidicker, 1962, page 160). This call for such studies is valid because critical to understanding such processes as evolutionary change and speciation are data that document genetic divergence of evolutionary subunits within a species, and how they are related to one another.

Although chromosomes appear to be an accurate indicator of evolutionary subdivisions in some species such as *Peromyscus leucopus* and *P. melanotis* (Bowers et al., 1973), speciation clearly may be accomplished without any chromosomal rearrangement. The general chromosomal conservatism among bats, order Chiroptera, has been well documented (Bickham and Baker, 1979), and the bat genus *Myotis* is an extreme example (Bickham, 1979). Even within the genus *Peromyscus*, there are several pairs of recognized species that differ by fewer than the three chromosomal rearrangements separating the two cytotypes of *P. leucopus* (Robbins and Baker, 1981). Indeed, at least three species of *Peromyscus* (*P. boylii*, *P. crinitus*, and *P. banderanus*) are karyotypically indistinguishable (Robbins and Baker, 1981; Stangl and Baker, unpub. data). In cases in which chromosomes offer no assistance in resolving evolutionary subunits, then such subunits, if present, may be defined on the basis of morphological or genic (electrophoretic) data alone.

Electrophoresis is a powerful tool in the study of population genetics, but as in *Peromyscus leucopus* (Kilpatrick and Zimmerman, 1975), some species have low genic variability across their total geographic distribution. Here, the determination of subtle differences in allele frequency across zones of contact between populations may establish the genetic integrity of these populations. However, large sample sizes are necessary for such studies, which is reason enough to rule out this approach for most mammalian species.

After evaluating the subspecies concept as applied to mammals, some have proposed a complete abandonment of the trinomen. Burt (1954) was of the opinion that “. . . continental species with more or less continuous ranges would be better understood if we were to discard the subspecific designations, and concentrate on the variations and their behavior geographically.” In light of the current application of the subspecies taxon, this proposal seems to have some merit. But it occurs to us that subspecies can be biologically meaningful subdivisions, and can fill a useful position in the literature, if they should reflect genetically distinct, evolutionary

subunits, as proposed by Lidicker (1962). This obviously is not something that can be easily substantiated. However, our ultimate understanding of speciation and evolutionary processes is to a great extent dependent on the availability of such data.

CONCLUSIONS AND SUMMARY

The current application of the subspecies in mammalian systematics is based, in most cases, on morphological characters that vary geographically, often in a clinal manner. In such cases, particularly where a pattern of clinal variation is involved, confusion and arbitrarily conceived subspecific boundaries may well result. We feel this is the case in *Peromyscus leucopus*, and we have provided data that question the accuracy of the current application of subspecies names in that species.

We stop short of formally assigning the two chromosomal races subspecific status at this time, due to the preliminary nature of our data. However, it is clear to us that the limits of the two chromosomal races impact on any conclusions regarding recognition of subspecies. If the data reported by Kilpatrick and Zimmerman (1975) are at all reflective of genic variation throughout the entire range of *Peromyscus leucopus*, then variation in the species may best be represented by recognition of only two subspecies.

By applying Lidicker's (1962) definition of the subspecies, the trinomen becomes a biologically meaningful part of the mammalian nomenclature. However, extending the implications of our findings in *Peromyscus leucopus* to other taxa should be done with care, and on a case-by-case basis.

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Specimens examined.—All specimens examined are listed in Baker et al., (1983), with the exception of the following 14 animals. OKLAHOMA: Bryan Co., Armstrong (2 males, 2 females); Hughes Co., 4 mi E Wetumka (1 female); Hughes Co., 8 mi W Wetumka (2 males, 1 female). TEXAS: Fannin Co., 3 mi E Bonham (1 male); Grayson Co., 2 mi W Bells (3 males); Montague Co., 2 mi W Nocona (1 female); Wichita Co., 3 mi E Burkburnett (male).

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