CHROMOSOMAL EVIDENCE FOR A MAJOR SUBDIVISION IN PEROMYSCUS LEUCOPUS

Data from G-banded chromosomes of 118 specimens of the white-footed mouse, Peromyscus leucopus, indicate that the taxon consists of at least two well-defined, widely distributed chromosomal races, which divide the species into northeastern and southwestern populations (Fig. 1).

The karyotype of the southwestern form has been described (Arrighi et al., 1976; Robbins and Baker, 1981). Using the numbering system for the standardized karyotype for Peromyscus (Committee, 1977), autosomal pairs for the southwestern cytotype are acrocentric, except for 1, 2, 3, 5, 6, 9, 11, 12, 18, 21, 22, and 23. Pairs 1, 2, 3, 5, 6, and 9 have short arms that are entirely euchromatic, whereas the short arm on pair 12 is entirely heterochromatic. Pairs 11, 18, 21, 22, and 23 have a short arm consisting of a proximal euchromatic and a distal heterochromatic segment. Although interstitial bands of heterochromatin in the long arms of pairs 1, 2, 4, and 7 have been noted (Arrighi et al., 1976; Robbins and Baker, 1981), such bands have been observed consistently only in pair 2. The band on the distal end of the long arm of chromosome 2 (arrow, Fig. 2) distinguishes leucopus from the other 17 species of Peromyscus thus far examined by G-banding (Robbins and Baker, 1981).

The northeastern race has a G-banded karyotype like that described for the southwestern race, except that pairs 5 and 11 are acrocentric and pair 20 is biarmed with the short arm entirely euchromatic. Comparison of G-band positive areas also indicates some minor differences between the two chromosomal races, but at this time we are reluctant to assign them too much significance. Haploid G-banded karyotypes for the two races are shown in Fig. 2. Within the northeastern race (and possibly the southwestern race), there was a widely distributed, distinctive, autosomal polymorphism noted in chromosome 18. This variation appears to be restricted to the heterochromatic portion of the short arm, however. The morphology of 18 varies from biarmed (Fig. 2) to nearly acrocentric. Of the 56 specimens representing the southwestern chromosome race that were examined for chromosome 18, none had the nearly acrocentric condition, but one of the specimens reported by Arrighi et al., (1976) appeared to be heterozygous in 18. Also, in both races there is variation in length of the short arm of the X chromosome (Fig. 2). Finally, in a single individual from Haywood Co., Tennessee, an inversion in the X altered the G-band pattern.

General localities for the two races are shown in Fig. 1; sample sizes, specific localities, and condition of the three marker chromosomes are given in specimens examined. Pure parental types were found at all localities except those listed for intermediate types under specimens examined.

Three points are worthy of note. (1) The two races of P. leucopus are distinguished by three euchromatic pericentric (presumed) inversions. This represents a magnitude of evolution greater than that which distinguishes numerous pairs of species of Peromyscus (Robbins and Baker, 1981). For example, boylii and crinitus, californicus and attuateri, pectoralis and floridanus, and floridanus and ochraventer have respective karyotypes that differ by fewer than three inversions. Furthermore, the northeastern race of P. leucopus is distinguished from P. gossypinus by the G-positive band on the distal end of chromosome 2 and an inversion in chromosome 20. Chromosomally, the northeastern race of leucopus more closely resembles gossypinus than it does the southwestern populations with which it is recognized as being conspecific.

(2) Both chromosomal races of P. leucopus are widely distributed (the only extensive polymorphisms are variation in chromosome pair 18 and in the length of the short arm of the X). Originally, we thought that the boundaries of the chromosomal races might correspond to the north-south subspecific limits based on exomorphology and cranial features. The subspecific limits which most closely match our limited samples (Fig. 1) were first proposed as a northeast-southwest division by Osgood (1909: 115) and later mapped in greater detail by Hall (1981). However, our preliminary samples do not indicate a close agreement between proposed subspecific boundaries (Hall, 1981) and chromosomal types. In the ranges of P. l. n Vulcanensis and P. l. leucopus, as mapped by Hall (1981), we found both chromosomal types.

If chromosomal races identify the limits of populations of common evolutionary origin, then it is important to understand why the classical subspecific boundaries for P. leucopus (Hall, 1981) do not correspond to these limits. There are at least three possible explanations. First, individuals from the two subspecies may be misidentified as to phenotype, and a closer examination of the size and color characteristics of individuals may reveal a concordant distributional pattern. Second, as a result of hybridization, genes controlling the phenotype upon which subspecies are characterized may have introgressed into the different chromosomal races; although the karyotype might still accurately identify the evolutionary origins of the respective populations, the geographic distribution of phenotypes might be incongruent with that of the karyotype.
Finally, it is possible that the phenotypic characteristics used to identify subspecies limits are due either to environmentally controlled variability or, less likely, to genetic convergence. In the first two explanations, the subspecies concept, as applied to *leucopus*, could still have an evolutionary basis (Lidicker, 1962). However, in the third, the implication of subspecies is entirely different because it identifies populations that are similar without regard to evolutionary origin as opposed to evolutionary subunits within a species.

(3) Data from specimens in the samples from Tennessee, Oklahoma, and Mississippi suggest that individuals from the two chromosomal races hybridize over a relatively long zone, producing both F₁ and backcross individuals. Many chromosomal races have been described for mammals, although for a wide variety of reasons, G- and C-banding studies documenting the nature of specific chromosomal rearrangements and that of interaction of chromosomal races have been limited (e.g., see Wahrman and Gourevitz, 1973; Capanna et al., 1976; Baker, 1981).

Several aspects of the biology of *P. leucopus* make it an excellent choice for a study on the role of chromosomal change in evolution: 1) three chromosomal rearrangements distinguish the races, making possible the identification of potential F₁ and backcross individuals; 2) with multiple rearrangements involved, the effects of heterozygosity for one, two, and three rearrangements on viable gamete production can be studied; 3) the two races are widespread and thus may interface at many localities; 4) the species is common and large samples can be obtained from small geographic areas; 5) its high reproductive rate should permit detection of any reductions in fertility of heterozygotes; 6) the species breeds readily in the laboratory, permitting comparison with results from natural populations, as well as studies on environmentally versus genetically controlled variability; and 7) technically, it is relatively easy to prepare G- and C-banded chromosomes from a large number of individuals.
Fig. 2.—Representative haploid genomes from the two chromosomal races of *P. leucopus*. Chromosomes on the left of each pair are representative of the southwestern race (specimen TK 13375 from Garza Co., Texas), whereas chromosomes on the right of each pair are representative of the northeastern race (specimen TK 11735 from Pawnee Co., Kansas). Arrow identifies a dark band in chromosome 2 which distinguishes *leucopus* from the 17 other species of *Peromyscus* thus far studied by G- and C-banding (Robbins and Baker, 1981).

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Specimens examined.—Northeastern race (52). ONTARIO: Leeds Co. (1 δ, 2 ϕ). MINNESOTA: Anoka Co., Blaine (5 δ, 3 ϕ). PENNSYLVANIA: Westmoreland Co., 2.1 mi S, 1.5 mi W Rector (3 δ, 5 ϕ). RHODE ISLAND: Washington Co., 7.9 mi W Kingston (3 δ, 1 ϕ). VIRGINIA: Giles Co., Mountain Lake Biological Station (1 δ, 3 ϕ). NORTH CAROLINA: Jackson Co., Sylva (1 δ, 1 ϕ). KANSAS: Montgomery Co., 3 mi E Liberty (8 δ, 2 ϕ)*; Osage Co., 4 mi E Vassar (1 δ, 1 ϕ); Pawnee Co., 3 mi S Pawnee Rock (3 δ, 2 ϕ); Sumner Co., 1 mi E Oxford (1 δ)*; Thomas Co., 7 mi N, 3 mi E Colby (1 ϕ). OKLAHOMA: McIntosh Co., 19 mi E Henryetta (1 δ, 1 ϕ)*; Tulsa Co., 3 mi NE Collinsville (1 δ, 1 ϕ)*.

Southwestern race (52). KANSAS: Pratt Co., 6 mi S Pratt (2 δ, 2 ϕ). OKLAHOMA: 1.5 mi S, 2 mi E Roman Nose State Park (2 δ)*; Blaine Co., 4 mi NE Hitchcock (1 ϕ)*; Cleveland Co., 2 mi NE Norman (3 δ)*; Grant Co., 2 mi N Pond Creek (3 δ)*; Jackson Co., 13 mi S Altus (1 ϕ)*; Kingfisher Co., 5 mi W Lacey (1 δ)*; 6 mi E Okeene (4 ϕ)*; 7 mi E Okeene (1 δ, 3 ϕ)*; Major Co., 11.5 N Okeene (3 δ, 1 ϕ)*; 1.5 mi S Fairview (3 δ, 4 ϕ)*. TEXAS: Brazos Co., 3 mi SW College Station (1 δ, 2 ϕ); Culberson Co., 6 mi N Kent
(1♀); Garza Co., 14 mi NE Southland (1♂, 1♀); 10 mi S Post (1♂); Jeff Davis Co., 10 mi N Ft. Davis (1♂, 1♀); Jim Wells Co., 4 mi S, 7 mi W Alice on Capito Ranch (3♂, 1♀); Kenedy Co., 12 mi S Sarita (2♀); Wichita Co., 3 mi N Wichita Falls (1♂, 2♀)*. Literature records (11). TEXAS: King Co., 17 mi SSW Paducah (1♀); Palo Pinto Co., 1 mi E Graford (2♂, 3♀). NEW MEXICO: Dona Ana Co., Arroyo, NE Tortugas Mts. (1♂, 2♀); NE Slope Tortugas Mts. (2♀).

Intermediate types (14). Intermediate types from Tennessee and Mississippi were identical to the Northeastern race except as noted. TENNESSEE: Haywood Co., Hatchie National Wildlife Refuge (1♂ heterozygous for chromosome 5, 1♀ heterozygous for 11); Shelby Co., Meeman Biological Field Station (1♂ heterozygous for 11, 1♂ heterozygous for 5, 11, and 20). MISSISSIPPI: Hines Co., 2 mi N, 5 mi W Terry (1♀ heterozygous for 20, 1♀ heterozygous for 11 and 20). Karyotypes of the Oklahoma intermediates for the pairs of the marker chromosomes were as follows. OKLAHOMA: Cleveland Co., 2 mi NE Norman (1♀ biarmed 5 and 11, heterozygous for 20)*, Dewey Co., 3.3 mi W Canton (1♀ heterozygous for 5, biarmed for 11 and acrocentric for 20)*, Pottawatomie Co., 3 mi SE Tecumseh (2♂ heterozygous for 5 and acrocentric for 11 and 20; 2♂ acrocentric for 5 and heterozygous for 11 and 20; 1♀ biarmed for 5, heterozygous for 11 and acrocentric for 20; and 1♂ biarmed for 5, acrocentric for 11 and heterozygous for 20)*.

All specimens examined were G-banded. C-banded specimens are from localities not denoted by an asterisk (*). Method of chromosomal preparation followed Lee and Elder (1980).

**Literature Cited**


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