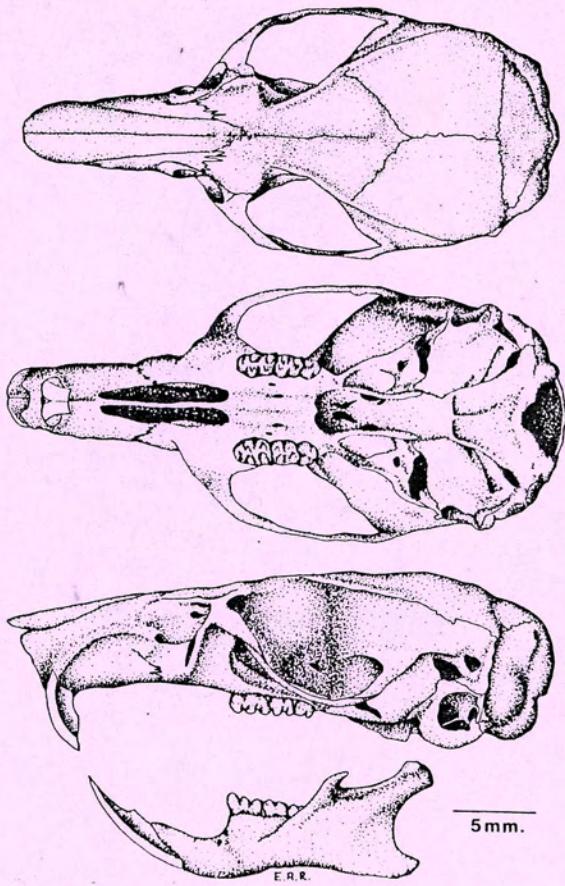


PEROMYSCUS NEWSLETTER

NUMBER EIGHT



SEPTEMBER 1989

Cover: Rendition of skull of *Peromyscus melanocarpus*
by Eric A. Rickart. (Approx. x 2.3)
Based on adult male specimen from Oaxaca, Mexico.
From **Mammalian Species** 241. (1985),
courtesy of American Society of Mammalogists.

In PEROMYSCUS NEWSLETTER Number Eight.....

.....are revised tables and references for biochemical polymorphisms in seven species or species groups. Several changes and additional reports are incorporated. These tables update earlier versions given in PN numbers 2, 4 and 6. Because protein variation in natural populations is not being reported as frequently in recent years, in the future we will update biochemical genetic polymorphism tables at three year intervals.

Also given are tables listing formal genetic loci recognized in *Peromyscus* species other than *P. maniculatus*. Henceforth, these likewise will be published less frequently.

Our featured Peromyscus Pioneer in this issue is T.C. Hsu. Dr. Hsu prepared a personal account of his *Peromyscus* chromosome work which we are reproducing intact, together with an introduction by Oscar Ward (Page 9). Hsu's work with *Peromyscus* cytogenetics, beginning in the mid 1960's, forged the way for two decades of productivity by many others who followed. His 1968 paper with Frances Arrighi, *Chromosomes in Peromyscus. I. Evolutionary trends in 20 species* (Cytogenetics 7:417-446) was a particularly noteworthy landmark and the first in a series of significant papers which appeared over the next decade authored by Hsu and his associates. It was also Hsu who first correctly interpreted the heterochromatic arms of *Peromyscus* chromosomes. T.C. Hsu was a major figure in the growth of the "Texas bunch" - as we in the east perceived them - of peromyscologists who throughout the 1970's were using chromosome morphology and biochemical polymorphism to resolve evolutionary and systematic questions. For many years Hsu edited and nurtured *Mammalian Chromosomes Newsletter*. His memorable "Dear Colleagues" forwards in each issue projected rare cordiality and wit. A wealth of informal information concerning *Peromyscus* cytogenetics, some of it never reported elsewhere, is found in its pages. We are pleased to salute T.C. Hsu.

Please continue to send us the Peromyscus news from your institution. Contributed entries will be published verbatim, except for formatting modifications. Entries are informal, and are not to be cited without specific permission of the contributor. PN is an excellent forum to report tentative or preliminary results, experiments in progress or other information not suitable for a formal article. Graduate or undergraduate research projects may be presented. We are very anxious to learn of any breeding stocks or colonies of *Peromyscus* you may have, whether animals are available for distribution or not.

The next issue is scheduled for March 1990. Please plan to have your entry to us by that date.

Meanwhile, we hope you enjoy Issue Number Eight!

W. D. D.

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South Carolina Institute of Biological Research and Technology
University of South Carolina
Columbia SC 29208

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* * *

- NEWS AND COMMENT -

BRUCE BUTTLER of Canadian Union College is commended by the Deer Mouse Genetic Advisory Committee for the series of comprehensive *Peromyscus* bibliographies he has prepared in recent years. Bruce has established a data base of literature for the genus. The bibliographies are published by his institution and he has made them available upon request. The following compilations are available:

- 1986. Bibliography of *Peromyscus* (Rodentia) Genetics.
- 1987. *Peromyscus* (Rodentia) as Environmental Monitors.
- 1988. *Peromyscus* (Rodentia) 1980 - 1987.
- 1989. Dispersal of *Peromyscus* (Rodentia): A Bibliography.

The commendation was voted at the annual meeting of the Advisory Committee. Thank you, Bruce, for providing a valuable service to peromyscologists!!!

~~~~~

**Elmer Fink** has moved from Kansas State University to Emporia State University, where he has accepted a position as Assistant Professor. He will continue his research on the behavior and population dynamics of *Peromyscus maniculatus* and *P. leucopus* at his new location.

\* \* \* \* \*

Order forms for *ADVANCES IN THE STUDY OF PEROMYSCUS (RODENTIA)* edited by Gordon Kirkland and Jim Layne are available from Texas Tech University Press, Sales Office, Lubbock, TX 79409-1037 Phone: (800) 832-4042.

+++++

Holly Wichman's new address is Department of Biological Science, University of Idaho, Moscow, ID 83843. The *P. leucopus* DNA library which she used earlier is no longer available. She will be constructing new libraries. She has an ongoing collaboration with Robert Baker at Texas Tech.

<><><><><><><><>

**Karl Kranz**, Curator, reports that the Philadelphia Zoo currently holds a small group of *Peromyscus californicus*.

-----

*Don Dewsberry writes that he is scaling back his research with Peromyscus, and will be working primarily with Microtus. However, he anticipates conducting occasional isolated projects with Peromyscus.*

.....

**Xuhua Xia** is completing his Ph.D. degree at the University of Western Ontario with John Millar. He has six publications on *Peromyscus* behavior, reproduction and ecology. Xuhua is seeking a post-doctoral or other appointment related to his experience with *Peromyscus*. He may be contacted at work (519) 679-2111 ext. 6798. If readers know of anything available next year, please contact him.

**Robert Robbins** donated an extensive collection of 2x2 slides documenting physical and behavioral development in three *Peromyscus* species (*P. maniculatus bairdii* and *borealis*, *P. eremicus* and *P. melanophrys*). Slides of each species are bound separately together with the original data sheets containing notations. The set will be added to the Stock Center archives of research materials pertaining to *Peromyscus* which are available for scientific or historical research. We appreciate this worthy addition to the growing collection of materials.

www.aaa

We were saddened to learn of the death of Jan Rood. His work with *Peromyscus* included a study of breeding behavior of seven *Peromyscus* species in captivity (Am. Mid. Nat. 76:496ff).

## *ANNOUNCEMENT*

Dr. Marilyn Scott of McGill University requested that we call attention of our readership to the following postgraduate/postdoctoral positions in parasitology:

Applications are invited from students interested in host-parasite population dynamics and epidemiology. The applicants should have an interest in:

- ## 1. Interaction between malnutrition and population-level aspects of parasitism

- 65 -

- ## **2. The role of drug resistance in design of control programs against gastrointestinal nematodes**

An additional area of research using a mouse model concerns the interface between host population genetics and parasite population dynamics. For this program, some experience in population genetics would be an advantage.

Applicant should send a c.v. as soon as possible, together with copies of transcripts, two letters of reference and a cover letter indicating which research program is of interest. Applicants will be expected to apply for scholarships/fellowships in the Oct.-Nov. '89 competition.

Send materials to: Dr. Marilyn Scott  
Institute of Parasitology of McGill University  
Macdonald College  
21, 111 Lakeshore Road  
Ste-Anne de Bellevue, Qc  
Canada H9X 1C0

## PEROMYSCUS STOCK CENTER

**What is the Stock Center?** The deer mouse colony at the University of South Carolina has been designated a genetic stock center under a grant from the Biological Research Resources Program of the National Science Foundation. The major function of the Stock Center is to provide genetically characterized types of **Peromyscus** in limited quantities to scientific investigators. Continuation of the center is dependent upon significant external utilization, therefore potential users are encouraged to take advantage of this resource. Sufficient animals of the mutant types generally can be provided to initiate a breeding stock. Somewhat larger numbers, up to about 50 animals, can be provided from the wild-type stocks.

A user fee of \$5 per animal is charged and the user assumes the cost of air shipment. Animals lost in transit are replaced without charge. Tissues, blood, skins, etc. can also be supplied at a modest fee. Write or call for details.

### Stocks Available in the Peromyscus Stock Center:

---

| WILD TYPES                                                             | ORIGIN                                                                                                                        |
|------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------|
| <i>P. maniculatus bairdii</i><br>(BW Stock)                            | Closed colony bred in captivity since 1948.<br>Descended from 40 ancestors wild-caught near Ann Arbor MI                      |
| <i>P. polionotus subgriseus</i><br>(PO Stock)                          | Closed colony since 1952.<br>Derived from 21 ancestors wild-caught in Ocala Nat'l.<br>Forest FL. High inbreeding coefficient. |
| <i>P. leucopus</i><br>(LL Stock)                                       | Derived from 38 wild ancestors captured between 1982 and 85 near Linville NC. Fifth to seventh generations in captivity.      |
| <i>P. maniculatus X P. polionotus</i><br><i>F</i> <sub>1</sub> Hybrids | Sometimes available.                                                                                                          |

## MUTATIONS AVAILABLE FROM THE STOCK CENTER

| Coat Colors                                               | ORIGINAL SOURCE                                                   |
|-----------------------------------------------------------|-------------------------------------------------------------------|
| Albino <i>c/c</i>                                         | Sumner's albino deer mice<br>(Sumner, 1922)                       |
| Black (Non-agouti) <i>a/a</i>                             | Horner's black mutant<br>(Horner et al., 1980)                    |
| Blonde <i>bl/bl</i>                                       | Mich. State colony<br>(Pratt and Robbins, 1982)                   |
| Brown <i>b/b</i>                                          | Huestis stocks<br>(Huestis and Barto, 1934)                       |
| Dominant spotting S/-                                     | Wild caught in Illinois<br>(Feldman, 1936)                        |
| Gray <i>g/g</i>                                           | Natural polymorphism.<br>From Dice stocks (Dice, 1933)            |
| Ivory <i>i/i</i>                                          | Wild caught in Oregon.<br>(Huestis, 1938)                         |
| Pink-eyed dilution <i>p/p</i>                             | Sumner's "pallid" deer mice.<br>(Sumner, 1917)                    |
| Platinum <i>pt/pt</i>                                     | Barto stock at U. Mich.<br>(Dodson et al., 1987)                  |
| Silver <i>si/si</i>                                       | Huestis stock.<br>(Huestis and Barto, 1934)                       |
| White-belly non-agouti <i>a<sup>w</sup>/a<sup>w</sup></i> | Egoscue's "non-agouti"<br>(Egoscue, 1971)                         |
| Wide-band agouti <i>A<sup>Nb</sup>/-</i>                  | Natural polymorphism.<br>Univ. Michigan stock<br>(McIntosh, 1954) |
| Yellow <i>y/y</i>                                         | Sumner's original mutant.<br>(Sumner, 1917)                       |

Note: Some of the coat color mutations are immediately available only in combination with others. For example, silver and brown are maintained as a single "silver-brown" double recessive stock. Write the Stock Center or call (803) 777-3107 for details.

MUTATIONS AVAILABLE FROM THE STOCK CENTER (continued)

| Other Mutations and Variants                                             | ORIGIN                                                                    |
|--------------------------------------------------------------------------|---------------------------------------------------------------------------|
| Alcohol dehydrogenase negative<br><i>Adh<sup>0</sup>/Adh<sup>0</sup></i> | South Carolina BW stock.<br>(Felder, 1975)                                |
| Alcohol dehydrogenase positive<br><i>Adh<sup>f</sup>/Adh<sup>f</sup></i> | South Carolina BW stock.<br>(Felder, 1975)                                |
| Epilepsy <i>ep/ep</i>                                                    | U. Michigan <i>artemisiae</i> stock,<br>(Dice, 1935)                      |
| Flexed-tail* <i>f/f</i>                                                  | Probably derived from Huestis<br>flexed-tail (Huestis and<br>Barto, 1936) |
| Hairless-2 <i>hre/hre</i>                                                | Egoscue's hairless<br>(Egoscue, 1962)                                     |
| Juvenile ataxia <i>ja/ja</i>                                             | U. Michigan stock.<br>(VanOoteghem, 1983)                                 |

Enzyme variants. Wild type stocks given above provide a reservoir for several enzyme and other protein variants. See Dawson *et al.* (1983).

\*Available only on pink-eye dilution background.

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Limited numbers of other stocks, species, mutants and variants are on hand, or under development, but are not currently available for distribution. For additional information or details about any of these mutants or stocks contact:

W. D. Dawson  
Peromyscus Stock Center  
Institute of Biological Research and Technology  
University of South Carolina  
Columbia SC 29208  
(803) 777-3107

The Advisory Committee for the Peromyscus Stock Center:

Ira F. Greenbaum (Texas A&M University)  
Rodney C. Honeycutt (Texas A&M University)  
Clement L. Markert (North Carolina State University)  
Joseph H. Nadeau (Jackson Laboratory)  
Suellen Van Ooteghem (Westinghouse Corporation)  
Wallace D. Dawson (University of South Carolina)  
Oscar G. Ward *ex officio* (University of Arizona)

## PEROMYSCUS PIONEER

T. C. HSU

### Introduction by Oscar Ward.

In this issue of PEROMYSCUS NEWSLETTER we honor Dr. Tao-Chiu Hsu as the Pioneer of *Peromyscus* chromosome work. We doubt whether many in North America ever knew Tao-Chiu by his given name. He has always been "T.C." to friends, students and colleagues. An avid interest in "bugs" (*Drosophila*, *Chironomus* and grasshoppers) during his early years in China prepared him for a research assistantship at the University of Texas with Professor J.T. Patterson arranged by his mentor in China, Dr. C.C. Tan. The opportunity to work with tissue cultures in Charles Pomerat's lab in Galveston at the completion of the Ph.D. in 1951 enabled him to make the discovery responsible for the rapid advance in mammalian chromosome study which followed. The event was the serendipitous finding of the marvelous chromosome-spreading effects of hypotonic treatment. Thereafter mammalian chromosomes took on a new interest for him. In 1955 T.C. moved to M.D. Anderson Hospital at Houston. There he established the Section of Cell Biology Lab which, for over two decades, has served as a waypoint and maturing experience for many, if not most, *Peromyscus* cytogeneticists. Beginning in the 60's with the paper by Hsu and Arrighi (Cytogenetics 5:355, 1966), the lab, its post-docs, and visitors produced a continuous stream of new information on karyotypes, polymorphisms, heterochromatin, and evolution in *Peromyscus* which led to the extraordinary richness of cytological knowledge about the genus. A short "visit" to the lab usually led to a return and a prolonged stay to explore a "new" idea hatched during an introductory conversation with "The Chief". Today, "graduates" of the lab and T.C.'s caring mentorship are busy extending this richness of knowledge in studies of the population genetics, behavior and molecular biology of *Peromyscus*. The lab is now busy with cancer genetics but T.C. still prowls about with the ever-present cup of coffee in his hand and the enticing comment... "Say, (throat-clearing sounds) I just thought of a new experiment .....

We asked T.C. to give us some material about himself for this issue with the intent of editing it into an account. He submitted the following - it was too good to be edited (even the photo!):

*Early in the 1960's, I went to one of the annual Somatic Cell Genetics Conferences, held that year at Williamsburg, VA. The organizing committee held a mini-symposium in which Margery Shaw presented her data on *Peromyscus* chromosomes and her husband, Charles, presented the isozyme data on the same animals. Margery used Dr. Lee Dice's *P. maniculatus* for her study and found that all individuals had 48 chromosomes but their karyotypes were highly variable in terms of chromosome morphology. I was fascinated by this observation, and sent word to my mammalogist friends to see if they could help me to procure live specimens of as many species as they could catch. Many positive responses came, including Murray Johnson, Robert Baker, Jim Patton, Ray Lee, Al Gardner, Dean Stock, and others. I particularly appreciated the efforts of Bob Baker, who conducted an eastern field trip for me to collect *P. polionotus* and *P. floridanus*, and Jim Patton, who made several trips for me to Mexico and the West to collect local species, especially members of the *P. eremicus* group. Jim, his wife Carol, and a friend went for me to an uninhabited (except for *Peromyscus*) island in the Gulf of California and were stranded there when a severe storm swept away their boat and all personal belongings except the mouse traps and the bait. For three days they ate the bait and prayed for rescuers. But Jim did collect enough specimens for me. This was not the first time Jim encountered disastrous problems because of me. When he was a graduate student at the University of Arizona, he went to procure for me skin biopsies of *Mephitis*. Carol wouldn't allow him into the bedroom for three weeks.*

At any rate, after analyzing more than 20 species representing all subgenera, we found a weird phenomenon, namely, all species had a diploid number of 48, but the NF varied from 56 (*P. boylei* and *P. crinitus*) to 96 (all species in the *P. eremicus* group). At that time, we had no clear-cut knowledge of heterochromatin in mammals, so that changes in NF were interpreted as the result of either Robertsonian translocations or pericentric inversions. We had no choice but to grudgingly accept the inversion hypothesis since Robertsonian translocations obviously did not apply; but I felt uncomfortable with such an explanation because with so many pericentric inversions, a lot of chromosome arms should be much shorter. When we compared the karyotypes of *P. eremicus* or *P. crinitus* at the same magnification, all long arms seemed comparable in length.

Then came the exciting period of chromosome banding and the realization that highly repetitive DNA sequences form blocks of heterochromatin. The discovery of C-banding, a byproduct of the in situ DNA/RNA hybridization procedure, was made almost simultaneously by Jim Chan and Frank Ruddle, and by us, both with human chromosomes. To human cytogeneticists, C-bands are not as important as G-bands, but to those who had worked on the chromosomes of a variety of animal species, C-banding was indeed a gold mine. It explains many vexing phenomena relating to karyological evolution. We began to realize that inert chromatin can be added to a genome without disturbing the euchromatin. Thus, in *Peromyscus* the addition of heterochromatic short arms to many chromosomes (and in the case of *P. eremicus*, every chromosome) represents an increase of genomic size, not rearrangements. It also answered an argument between cytogeneticists, namely, whether heterochromatin represents a physiological state or a real thing. It is the real thing.

Sen Pathak joined my staff in 1973. We spent considerable time working on *Peromyscus* and found that the G-band patterns of the long arms of practically all species match well. One of the projects Sen did was to measure the length of metaphase chromosomes between *P. eremicus* and *P. crinitus*. He found that the total chromosome length of *eremicus* was approximately 36% over that of *crinitus*. A molecular biologist laughed at this crude approach until he used flow cytometry and confirmed Sen's observation. Upon my urging, Larry Deaven finally did a detailed flow analysis on three species of *Peromyscus* and reached the same conclusion.

Although I have no statistical data to support my claim, I believe most naturalists remain naturalists at heart even though careers have changed, jobs have changed, and environments have changed. Their love for nature was the primary reason for their becoming naturalists. In my own case, I started my college education in China majoring in entomology. By the time I graduated, I knew a lot about bugs but nothing (well, almost nothing) about vertebrates. When I changed my interest to genetics and cytology, I still worked with *Drosophila*, *Chironomus* and grasshoppers. In the era of classic genetics, a variety of organisms, including plants, invertebrates, and vertebrates were used as research materials. It was during that period I first heard of a creature called *Peromyscus*, Dr. Dice's principal research material at Michigan.

Because of my lucky accident from which I found that hypotonic solution could spread chromosomes of cells in tissue culture, I worked for nearly ten years on human and mouse chromosomes. In the early 1960s, I began to work on the chromosomes of zoo animals, especially the big cats, because I love those gorgeous animals. Even now I still think of buying a Jaguar when I have enough money, just for the name's sake.

As more and more mammalogists devoted much of their effort to cytogenetic analyses of various taxa and uncovered a good deal of information, Sen and I decided that it was time to bid adieu to our studies on cytogenetic evolution of mammals and moved to what we were hired to do, the cancer problem. But our love lingers on. I suppose once a naturalist, always a naturalist. Even now, I have occasional dreams finding a beautiful beetle and desperately looking for my cyanide bottle.

Research articles by T.C. Hsu on *Peromyscus* cytogenetics:

1966. Hsu, T.C. and F.E. Arrighi. Chromosomal evolution in the Genus *Peromyscus* (Cricetidae, Rodentia). *Cytogenetics* 5:355-359.
1968. Hsu, T.C. and F.E. Arrighi. Chromosomes of *Peromyscus* (Rodentia, Cricetidae) I. Evolutionary trends in 20 species. *Cytogenetics* 7:417-446.
1971. Hsu, T.C. and F.E. Arrighi. Distribution of constitutive heterochromatin in mammalian chromosomes. *Chromosoma* 34:243-253.
1972. Bradshaw, W.N. and T.C. Hsu. Chromosomes of *Peromyscus* (Rodentia, Cricetidae) III. Polymorphism in *Peromyscus maniculatus*. *Cytogenetics* 11:436-451.
1973. Pathak, S., T.C. Hsu and F.E. Arrighi. Chromosomes of *Peromyscus* (Rodentia, Cricetidae) IV. The role of heterochromatin in karyotype evolution. *Cytogenet. Cell Genet.* 12:315-326.
1974. Jalal, S.M., R.W. Clark, T.C. Hsu and S. Pathak. Cytological differentiation of constitutive heterochromatin. *Chromosoma* 48:391-403.
1977. Deaven, L.L., L. Vidal-Rioja, J.H. Jett and T.C. Hsu. Chromosomes of *Peromyscus* (Rodentia, Cricetidae) VI. The genomic size. *Cytogenet. Cell Genet.* 19:241-249.



T. C. HSU

## FORMAL GENETICS OF *PEROMYSCUS*

Most formal genetic analysis in *Peromyscus* has been conducted in the deer mouse, *P. maniculatus* where more than fifty loci have been described based on traditional genetic crosses. For a tabulation of known genes in the deer mouse (and the oldfield mouse, *P. polionotus*, of the *P. maniculatus* species group) refer to PEROMYSCUS NEWSLETTER Number Seven pp. 12 - 16.

Six loci have been formally identified in the *P. leucopus* species group. These are listed in Table 1. No recombination data has yet been reported for this group.

*P. truei*, *P. eremicus* and *P. californicus* each have a single locus formally designated. These are given in Table 2.

### References for Tables 1 and 2:

- Castle, W.E. 1912. Science 35:346-348.  
Clark, F. H. 1938. J. Hered. 29:79-80.  
Foreman, C.W. 1966. Genetics 54:1007-1012.  
Huestis, R.R. 1925. J. Exp. Zool. 41:429-470.  
Jensen, J.T. 1969. Am. Zool. 9:1129.  
Packchanian, A. and E.E. Louis. 1984. J. Hered. 75:229-230.  
Wilmot, P.L. and D.K. Underhill. 1972. Genetics 71:315-318.  
Wilmot, P.L. and D.K. Underhill. 1973. J. Hered. 64:43-44.  
Zimmerman, E.G. and C. W. Kilpatrick. 1975. Experientia 31:420-421.

**Table 1.**  
**GENETIC LOCI IN THE PEROMYSCUS LEUCOPUS SPECIES GROUP**  
**DEFINED BY FORMAL GENETIC ANALYSIS**

| Name of locus                | Symbol and alleles                                                                                                                                                | Mode of inheritance | Reference                   | Recombination reported |
|------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------|-----------------------------|------------------------|
| Albino                       | c = albino<br>(C = pigmented)                                                                                                                                     | recessive           | Castle (1912)               |                        |
| Carbonic anhydrase           | $Ca^f$ = fast electromorph<br>$Ca^s$ = slow electromorph                                                                                                          | co-dominance        | Wilmot and Underhill (1972) |                        |
| Catalase                     | $Cs^b$ = fast electromorph<br>$Cs^s$ = slow electromorph                                                                                                          | co-dominance        | Jensen (1969)               |                        |
| Esterase-1<br>(erythrocytic) | $Es-1^a$ = null<br>$Es-1^b$ = band present                                                                                                                        | semi-dominant       | Wilmot and Underhill (1973) |                        |
| Esterase-2<br>(serum)        | $Es-2^a$ = null<br>$Es-2^b$ = fast electromorph                                                                                                                   | semi-dominant       | Wilmot and Underhill (1973) |                        |
| Hemoglobin                   | $Hb^A$ = type A in <i>P. gossypinus</i><br>$Hb^B$ = type B in <i>P. gossypinus</i><br>$Hb^C$ = type C in <i>P. gossypinus</i><br>$Hb^D$ = <i>P. leucopus</i> type | co-dominance        | Foreman (1966)              |                        |

**Table 2.**  
**FORMALLY DESCRIBED GENETIC LOCI IN MISCELLANEOUS PEROMYSCUS SPECIES**

| Species                | Locus         | Symbol and alleles                                                  | Mode of inheritance | Reference                       |
|------------------------|---------------|---------------------------------------------------------------------|---------------------|---------------------------------|
| <i>P. truei</i>        | Esterase-1    | $Es-1^{100}$ = fast electromorph<br>$Es-1^{93}$ = slow electromorph | co-dominance        | Zimmerman and Kilpatrick (1975) |
| <i>P. eremicus</i>     | Pectoral spot | $ps$ = spot<br>( $Ps$ = absence)                                    | recessive           | Huestis (1925)<br>Clark (1938)  |
| <i>P. californicus</i> | Hairless      | $hr$ = hairless<br>( $Hr$ = with hair)                              | recessive ?         | Packchanian and Louis (1964)    |

## VARIANT GENETIC LOCI IN NATURAL POPULATIONS OF PEROMYSCUS

Numerous electrophoretic studies of allozymes and other proteins in natural populations of *Peromyscus* have been conducted beginning in the late 1960's. These studies revealed numerous polymorphisms within populations and species, as well as variation among potentially interbreeding species, e.g. *P. maniculatus* and *P. polionotus*. Variants of a protein are generally presumed to identify a genetic "locus", although formal mendelian analysis might not have been accomplished.

PEROMYSCUS NEWSLETTER periodically lists in tabular form the known genetic loci in *Peromyscus* species or species groups. We distinguish between loci which have been formally demonstrated and presumptive loci. The latter are usually protein variants from natural populations identified by electrophoresis. Separate listings for the two categories are published in PN.

In this issue Tables 3. through 9. summarize presumptive variant loci identified in seven species or species groups: *Peromyscus* (=*Megadontomys*) *thomasi*, *P.* (=*Podomys*) *floridanus*, *P. californicus*, *P. eremicus*, *P. boylii* species group, *P. truei* species group and *P. leucopus* species group. A similar table in PN #7, pp. 17-18, lists variant presumptive loci reported in the *P. maniculatus* species group. We plan to update these tables at three year intervals in future issues of PEROMYSCUS NEWSLETTER.

Since limited interbreeding in captivity is frequently possible among different species within a species group, we treat a species group as a single gene pool. Thus while two species may each be monomorphic for alternate alleles, by hybridization heterozygotes can be produced and genetic analysis conducted. Linkage analysis and gene regulation potentially can be investigated using species hybrids. Such systems are currently used in both *Mus* and *Peromyscus*. Thus, the tables serve as a reference to identify reported variants at given loci. Completely monomorphic loci, i.e. loci for which no variation within the species or species group has been reported, are not listed.

Only variants reported in research publications, abstracts excluded, are listed in the tables. References are listed at the foot of each table.

**Table 3. VARIANT PROTEIN LOCI REPORTED FROM  
NATURAL POPULATIONS OF *PEROMYSCUS (MEGADONTOMYS) THOMASI***

| Protein                             | Locus                                        | References                      |
|-------------------------------------|----------------------------------------------|---------------------------------|
| Alcohol dehydrogenase               | <i>Adh-1</i>                                 | Werbitsky and Kilpatrick (1987) |
| Albumin                             | <i>Alb</i>                                   | Werbitsky and Kilpatrick (1987) |
| Amylase                             | <i>Amy-1</i>                                 | Werbitsky and Kilpatrick (1987) |
| Carbonic anhydrase                  | <i>Car-1</i>                                 | Werbitsky and Kilpatrick (1987) |
| Cholinesterase                      | <i>E-2</i>                                   | Werbitsky and Kilpatrick (1987) |
| Glutamate oxaloacetate transaminase | <i>Got-1</i>                                 | Werbitsky and Kilpatrick (1987) |
| Hemoglobin                          | <i>Hba-1</i>                                 | Werbitsky and Kilpatrick (1987) |
| Phosphoglucoisomerase               | <i>Pgi-1</i>                                 | Werbitsky and Kilpatrick (1987) |
| Peptidase                           | <i>Pep-1 (Pep-A)</i><br><i>Pep-4 (Pep-D)</i> | Werbitsky and Kilpatrick (1987) |
| Transferrin                         | <i>Trf</i>                                   | Werbitsky and Kilpatrick (1987) |

**Reference:**

Werbitsky, D. and C.W. Kilpatrick. 1987. J. Mamm. 68:305-312.

**Table 4. VARIANT PROTEIN LOCI REPORTED FROM  
NATURAL POPULATIONS OF *PEROMYSCUS (PODOMYS) FLORIDANUS***

| Protein                                | Locus                                        | Reference                  |
|----------------------------------------|----------------------------------------------|----------------------------|
| Esterase                               | <i>Es-1</i><br><i>Es-2</i><br><i>Es-4</i>    | Smith <i>et al.</i> (1973) |
| Glutamate oxaloacetate<br>transaminase | <i>Got-1</i>                                 | Smith <i>et al.</i> (1973) |
| Hexose-6-phosphate<br>dehydrogenase    | <i>Gpd-1</i>                                 | Smith <i>et al.</i> (1973) |
| Hemoglobin                             | <i>Hb-1</i>                                  | Smith <i>et al.</i> (1973) |
| Isocitrate dehydrogenase               | <i>Idh-1</i>                                 | Smith <i>et al.</i> (1973) |
| Lactate dehydrogenase                  | <i>Ldh-1</i><br><i>Ldh-2</i><br><i>Ldh-3</i> | Smith <i>et al.</i> (1973) |
| Malic enzyme                           | <i>Mod-1</i>                                 | Smith <i>et al.</i> (1973) |
| Phosphoglucomutase                     | <i>Pgm-1</i><br><i>Pgm-3</i>                 | Smith <i>et al.</i> (1973) |
| Pre-albumin                            | <i>Pra</i>                                   | Smith <i>et al.</i> (1973) |
| Transferrin                            | <i>Trf</i>                                   | Smith <i>et al.</i> (1973) |

Smith, M.H., R.K. Selander and W.E. Johnson. 1973. J. Mamm., 54:1-13.

**Table 5. VARIANT PROTEIN LOCI REPORTED  
FROM NATURAL POPULATIONS OF *PEROMYSCUS CALIFORNICUS***

| <b>Protein</b>                           | <b>Locus</b>                                              | <b>References</b>                          |
|------------------------------------------|-----------------------------------------------------------|--------------------------------------------|
| Albumin                                  | <i>Alb</i>                                                | Avise <i>et al.</i> (1974)                 |
| Esterase                                 | <i>Es-3</i><br><i>Es-4</i><br><i>Es-4+</i><br><i>Es-5</i> | Smith (1979)                               |
| $\alpha$ -glycerophosphate dehydrogenase | <i>Gpd-1</i>                                              | Avise <i>et al.</i> (1974)<br>Smith (1979) |
| Isocitrate dehydrogenase                 | <i>Idh-1</i><br><i>Idh-2</i>                              | Avise <i>et al.</i> (1974)<br>Smith (1979) |
| Malate dehydrogenase                     | <i>Mdh-1</i>                                              | Avise <i>et al.</i> (1974)<br>Smith (1979) |
| Malic enzyme                             | <i>Me-1</i><br><i>Me-2</i>                                | Smith (1979)                               |
| Post-albumin                             | <i>Palb</i>                                               | Smith (1979)                               |
| Peptidase                                | <i>Pep-1</i>                                              | Smith (1979)                               |
| 6-Phosphogluconate dehydrogenase         | <i>Pgd-1</i>                                              | Avise <i>et al.</i> (1974)<br>Smith (1979) |
| Phosphoglucoisomerase                    | <i>Pgi-1</i>                                              | Smith (1979)                               |
| Phosphoglucomutase                       | <i>Pgm-1</i><br><i>Pgm-3</i>                              | Avise <i>et al.</i> (1974)<br>Smith (1979) |
| Sorbitol dehydrogenase                   | <i>Sdh-1</i>                                              | Avise <i>et al.</i> (1974)<br>Smith (1979) |
| Transferrin                              | <i>Trf</i>                                                | Avise <i>et al.</i> (1974)                 |

**References:**

- Avise, J.C., M.H. Smith, R.K. Selander, T.E. Lawlor and P.R. Ramsey. 1974. *Syst. Zool.* 23:226-238.  
Smith, M.F. 1979. *J. Mamm.* 60:705-722.

**Table 6. VARIANT PROTEIN LOCI REPORTED  
FROM NATURAL POPULATIONS OF *PEROMYSCUS EREMICUS*  
AND RELATED SPECIES**

| Protein                                  | Locus                        | Species                                                              | References                                                |
|------------------------------------------|------------------------------|----------------------------------------------------------------------|-----------------------------------------------------------|
| Alcohol dehydrogenase                    | <i>Adh-1</i>                 | <i>P. eremicus</i>                                                   | Avise <i>et al.</i> (1974)                                |
| Amylase                                  | <i>Amy-1</i>                 | <i>P. eremicus</i>                                                   | Werbitsky and Kilpatrick (1987)                           |
| Esterase                                 | <i>Es-1</i>                  | <i>P. eremicus</i>                                                   | Rasmussen and Jensen (1971)<br>Avise <i>et al.</i> (1974) |
| Glutamate oxaloacetate transaminase      | <i>Got-1</i>                 | <i>P. eremicus</i>                                                   | Avise <i>et al.</i> (1974)                                |
| $\alpha$ -Glycerophosphate dehydrogenase | <i>Gpd-1</i>                 | <i>P. eremicus</i>                                                   | Avise <i>et al.</i> (1974)                                |
| Isocitrate dehydrogenase                 | <i>Idh-1</i><br><i>Idh-2</i> | <i>P. eremicus</i><br><i>P. guardia</i><br><i>P. interparietalis</i> | Avise <i>et al.</i> (1974)                                |
| Lactate dehydrogenase                    | <i>Ldh-1</i>                 | <i>P. eremicus</i><br><i>P. caniceps</i>                             | Avise <i>et al.</i> (1974)                                |
| Phosphogluconate dehydrogenase           | <i>Pgd-1</i>                 | <i>P. eremicus</i><br><i>P. caniceps</i>                             | Avise <i>et al.</i> (1974)                                |
| Phosphoglucomutase                       | <i>Pgm-1</i>                 | <i>P. eremicus</i>                                                   | Avise <i>et al.</i> (1974)                                |
| Plasma protein B (Macroglobulin)         | <i>Ppb</i>                   | <i>P. eremicus</i><br><i>P. caniceps</i>                             | Avise <i>et al.</i> (1974)                                |
| Transferrin                              | <i>Trf</i>                   | <i>P. eremicus</i><br><i>P. merriami</i><br><i>P. caniceps</i>       | Rasmussen and Koehn (1966)<br>Avise <i>et al.</i> (1974)  |

References:

- Avise, J.C., M.H. Smith, R.K. Selander, T.E. Lawlor and P.R. Ramsey. 1974. *Syst. Zool.*, 23:226-238.  
 Rasmussen, D.I. and J.N. Jensen. 1971. *Comp. Biochem. Physiol.*, 39B:19-24.  
 Rasmussen, D.I. and R.K. Koehn. 1966. *Genetics*, 54:1353-1357.  
 Werbitsky, D. and C.W. Kilpatrick. 1987. *J. Mamm.* 68:305-312.

**Table 7. VARIANT PROTEIN LOCI REPORTED FROM  
NATURAL POPULATIONS OF THE *PEROMYSCUS BOYLII* SPECIES GROUP**

| Protein                                  | Locus                                                    | Species                                                                             | References                                                                                                                                                                                                                                                  |
|------------------------------------------|----------------------------------------------------------|-------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Albumin                                  | <i>Alb</i>                                               | <i>P. boylii</i><br><i>P. pectoralis</i>                                            | Jensen and Rasmussen (1971)<br>Avise <i>et al.</i> (1974)<br>Kilpatrick and Zimmerman (1975)<br>Zimmerman <i>et al.</i> (1975)<br>Kilpatrick and Zimmerman (1976a)<br>Kilpatrick (1984)<br>Rennert and Kilpatrick (1986)<br>Werbitsky and Kilpatrick (1987) |
| Amylase                                  | <i>Amy-1</i>                                             | <i>P. boylii</i>                                                                    | Rennert and Kilpatrick (1986)<br>Rennert and Kilpatrick (1987)                                                                                                                                                                                              |
| Carbonic anhydrase                       | <i>Car-1</i>                                             | <i>P. boylii</i>                                                                    | Rennert and Kilpatrick (1986)<br>Rennert and Kilpatrick (1987)                                                                                                                                                                                              |
| Esterase                                 | <i>Es-1</i><br><i>Es-5</i><br><i>Es-6</i><br><i>Es-7</i> | <i>P. boylii</i><br><i>P. attwateri</i><br><i>P. pectoralis</i><br><i>P. polius</i> | Rasmussen and Jensen (1971)<br>Avise <i>et al.</i> (1974)<br>Kilpatrick and Zimmerman (1975)<br>Zimmerman <i>et al.</i> (1975)<br>Kilpatrick and Zimmerman (1976a)<br>Kilpatrick (1984)<br>Rennert and Kilpatrick (1986)<br>Rennert and Kilpatrick (1987)   |
| Glutamate oxaloacetate transaminase      | <i>Got-1</i>                                             | <i>P. boylii</i><br><i>P. pectoralis</i>                                            | Avise <i>et al.</i> (1974)<br>Kilpatrick and Zimmerman (1975)<br>Zimmerman <i>et al.</i> (1975)<br>Kilpatrick and Zimmerman (1976a)<br>Kilpatrick (1984)<br>Rennert and Kilpatrick (1986)<br>Rennert and Kilpatrick (1987)                                  |
| $\alpha$ -glycerophosphate dehydrogenase | <i>Gpd-1</i><br><i>Gpd-2</i>                             | <i>P. boylii</i><br><i>P. pectoralis</i>                                            | Mascarello and Shaw (1973)<br>Avise <i>et al.</i> (1974)                                                                                                                                                                                                    |
| Glucose-6-phosphate dehydrogenase        | <i>G6pd-1</i><br><i>(H6pd-1)</i>                         | <i>P. pectoralis</i>                                                                | Avise <i>et al.</i> (1974)<br>Kilpatrick (1984)<br>Rennert and Kilpatrick (1986)<br>Rennert and Kilpatrick (1987)                                                                                                                                           |

(Continued)

**Table 7. Protein variants in *P. boylii* group natural populations (Continued)**

| Protein                          | Locus                                        | Species                                                         | References                                                                                                                                                                         |
|----------------------------------|----------------------------------------------|-----------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Hemoglobin                       | <i>Hb-1</i>                                  | <i>P. boylii</i>                                                | Rasmussen <i>et al.</i> (1968)                                                                                                                                                     |
|                                  | <i>Hb-2</i>                                  | <i>P. pectoralis</i>                                            | Avise <i>et al.</i> (1974)                                                                                                                                                         |
|                                  |                                              | <i>P. attwateri</i>                                             | Kilpatrick and Zimmerman (1975)<br>Zimmerman <i>et al.</i> (1975)<br>Kilpatrick and Zimmerman (1976a)<br>Kilpatrick and Zimmerman (1976b)<br>Kilpatrick (1984)                     |
| Hexose-6-Phosphate dehydrogenase | <i>H6pd-1</i>                                | <i>P. boylii</i>                                                | Rennert and Kilpatrick (1986)<br>Rennert and Kilpatrick (1987)                                                                                                                     |
| Isocitrate dehydrogenase         | <i>Idh-1</i>                                 | <i>P. boylii</i><br><i>P. pectoralis</i><br><i>P. attwateri</i> | Mascarelo and Shaw (1973)<br>Avise <i>et al.</i> (1974)<br>Kilpatrick and Zimmerman (1976a)<br>Kilpatrick (1984)<br>Rennert and Kilpatrick (1986)<br>Rennert and Kilpatrick (1987) |
| Lactate dehydrogenase            | <i>Ldh-1</i><br><i>Ldh-2</i><br><i>Ldh-3</i> | <i>P. boylii</i><br><i>P. pectoralis</i><br><i>P. polius</i>    | Mascarelo and Shaw (1973)<br>Avise <i>et al.</i> (1974)<br>Kilpatrick and Zimmerman (1975)<br>Kilpatrick and Zimmerman (1976a)<br>Kilpatrick (1984)                                |
| Leucine aminopeptidase           | <i>Lap-1</i>                                 | <i>P. boylii</i><br><i>P. attwateri</i>                         | Kilpatrick (1984)                                                                                                                                                                  |
| Malate dehydrogenase             | <i>Mdh-1</i>                                 | <i>P. boylii</i><br><i>P. pectoralis</i>                        | Avise <i>et al.</i> (1974)<br>Kilpatrick and Zimmerman (1976a)                                                                                                                     |
| Phosphogluconate dehydrogenase   | <i>Pgd-1</i>                                 | <i>P. boylii</i><br><i>P. pectoralis</i>                        | Avise <i>et al.</i> (1974)<br>Kilpatrick and Zimmerman (1975)<br>Zimmerman <i>et al.</i> (1975)<br>Kilpatrick and Zimmerman (1976a)                                                |
| Phosphoglucose isomerase         | <i>Pgi-1</i>                                 | <i>P. boylii</i><br><i>P. pectoralis</i><br><i>P. attwateri</i> | Avise <i>et al.</i> (1974)<br>Kilpatrick (1984)<br>Rennert and Kilpatrick (1986)<br>Rennert and Kilpatrick (1987)                                                                  |

(Continued)

**Table 7. Protein variants in *P. boylii* group natural populations (Continued)**

| Protein                | Locus        | Species              | References                       |
|------------------------|--------------|----------------------|----------------------------------|
| Phophoglucomutase      | <i>Pgm-1</i> | <i>P. boylii</i>     | Mascarello and Shaw (1973)       |
|                        | <i>Pgm-2</i> | <i>P. pectoralis</i> | Avise <i>et al.</i> (1974)       |
|                        | <i>Pgm-3</i> |                      | Kilpatrick and Zimmerman (1976a) |
|                        |              |                      | Rennert and Kilpatrick (1986)    |
|                        |              |                      | Rennert and Kilpatrick (1987)    |
| Transferrin            | <i>Trf</i>   | <i>P. boylii</i>     | Rasmussen and Koehn (1966)       |
|                        |              | <i>P. pectoralis</i> | Avise <i>et al.</i> (1974)       |
|                        |              | <i>P. attwateri</i>  | Kilpatrick and Zimmerman (1975)  |
|                        |              | <i>P. polius</i>     | Zimmerman <i>et al.</i> (1975)   |
|                        |              |                      | Kilpatrick and Zimmerman (1976a) |
|                        |              |                      | Kilpatrick (1984)                |
|                        |              |                      | Rennert and Kilpatrick (1986)    |
|                        |              |                      | Rennert and Kilpatrick (1987)    |
|                        |              |                      | Werbitsky and Kilpatrick (1987)  |
| Xanthine dehydrogenase | <i>Xdh-1</i> | <i>P. boylii</i>     | Kilpatrick (1984)                |
|                        |              | <i>P. attwateri</i>  |                                  |

**References:**

- Avise, J.C., M.H. Smith and R.K. Selander. 1974. *J. Mamm.* 55:751-763.  
 Jensen, J.N. and D.I. Rasmussen. 1971. *J. Mamm.* 52:508-514.  
 Kilpatrick, C.W. 1984. *Festschrift for W.W. Dalquist*. pp 87-96.  
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 Rennert, P.D. and C.W. Kilpatrick. 1986. *J. Mamm.* 67:481-488.  
 Rennert, P.D. and C.W. Kilpatrick. 1987. *J. Mamm.* 68:799-811.  
 Werbitsky, D. and C.W. Kilpatrick. 1987. *J. Mamm.* 68:305-312.  
 Zimmerman, E.G., B.J. Hart and C.W. Kilpatrick. 1975. *Comp. Biochem. Physiol.* 52B:541-545.

**Table 8. VARIANT PROTEIN LOCI REPORTED FROM  
NATURAL POPULATIONS OF THE *PEROMYSCUS TRUEI* SPECIES GROUP**

| Protein                                  | Locus                                                                                  | Species                                 | References                                                                                                                                           |
|------------------------------------------|----------------------------------------------------------------------------------------|-----------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------|
| Albumin                                  | <i>Alb</i>                                                                             | <i>P. truei</i><br><i>P. difficilis</i> | Brown and Welser (1968)<br>Jensen and Rasmussen (1971)<br>Johnson and Packard (1974)<br>Zimmerman <i>et al.</i> (1975)<br>Avise <i>et al.</i> (1979) |
| Esterase                                 | <i>Es-1</i><br><i>Es-2</i><br><i>Es-3</i><br><i>Es-4</i><br><i>Es-5</i><br><i>Es-6</i> | <i>P. truei</i><br><i>P. difficilis</i> | Rasmussen and Jensen (1971)<br>Johnson and Packard (1974)<br>Zimmerman <i>et al.</i> (1975)                                                          |
| Glutamate oxaloacetate transaminase      | <i>Got-1</i>                                                                           | <i>P. truei</i><br><i>P. difficilis</i> | Zimmerman <i>et al.</i> (1975)<br>Avise <i>et al.</i> (1979)                                                                                         |
| $\alpha$ -glycerophosphate dehydrogenase | <i>Gpd-1</i><br><i>Gpd-2</i>                                                           | <i>P. truei</i><br><i>P. difficilis</i> | Mascarello and Shaw (1973)<br>Johnson and Packard (1974)<br>Avise <i>et al.</i> (1979)                                                               |
| Isocitrate dehydrogenase                 | <i>Idh-1</i>                                                                           | <i>P. truei</i>                         | Mascarello and Shaw (1973)<br>Johnson and Packard (1974)<br>Avise <i>et al.</i> (1979)                                                               |
| Lactate dehydrogenase                    | <i>Ldh-1</i>                                                                           | <i>P. truei</i>                         | Mascarello and Shaw (1973)                                                                                                                           |
| Phosphogluconate dehydrogenase           | <i>Pgd-1</i>                                                                           | <i>P. truei</i><br><i>P. difficilis</i> | Mascarello and Shaw (1973)<br>Johnson and Packard (1974)<br>Zimmerman <i>et al.</i> (1975)<br>Avise <i>et al.</i> (1979)                             |
| Phosphoglucose isomerase                 | <i>Pgi-1</i>                                                                           | <i>P. truei</i><br><i>P. difficilis</i> | Avise <i>et al.</i> (1979)                                                                                                                           |

(Continued)

**Table 8. Variant protein loci in *P. truei* group natural populations (Continued)**

| Protein            | Locus                                        | Species                                  | References                                               |
|--------------------|----------------------------------------------|------------------------------------------|----------------------------------------------------------|
| Phosphoglucomutase | <i>Pgm-1</i><br><i>Pgm-2</i><br><i>Pgm-3</i> | <i>P. truei</i><br><i>P. difficileis</i> | Mascarello and Shaw (1973)<br>Johnson and Packard (1974) |
| Transferrin        | <i>Trf</i>                                   | <i>P. truei</i><br><i>P. difficileis</i> | Avise <i>et al.</i> (1979)<br>Johnson and Packard (1974) |

**References:**

- Avise, J.C., M.H. Smith and R.K. Selander. 1979. J. Mamm. 60:177-192.  
Brown, J.H. and C.F. Welser. 1968. J. Mamm. 49:420-426.  
Jensen, J.N. and D.I. Rasmussen. 1971. J. Mamm. 52:508-514.  
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**Table 9. VARIANT PROTEIN LOCI REPORTED FROM  
NATURAL POPULATIONS OF THE *PEROMYSCUS LEUCOPUS* SPECIES GROUP**

| Protein               | Locus                                                                                  | Species                                    | References                                                                                                                                                                                             |
|-----------------------|----------------------------------------------------------------------------------------|--------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Acid phosphatase      | <i>Acp-1</i>                                                                           | <i>P. leucopus</i>                         | Nelson <i>et al.</i> (1987)                                                                                                                                                                            |
| Adenosine deaminase   | <i>Ada-1</i>                                                                           | <i>P. leucopus</i>                         | Krohne and Baccus (1985)                                                                                                                                                                               |
| Albumin               | <i>Alb</i>                                                                             | <i>P. leucopus</i><br><i>P. gossypinus</i> | Brown and Welser (1968)<br>Jensen and Rasmussen (1971)<br>Browne (1977)<br>Price and Kennedy (1984)<br>Robbins <i>et al.</i> (1985)                                                                    |
| Alcohol dehydrogenase | <i>Adh-1</i>                                                                           | <i>P. leucopus</i>                         | Robbins <i>et al.</i> (1985)<br>Nelson <i>et al.</i> (1987)<br>Tolliver <i>et al.</i> (1987)                                                                                                           |
| Adenylate kinase      | <i>Ak-1</i>                                                                            | <i>P. leucopus</i>                         | Nelson <i>et al.</i> (1987)                                                                                                                                                                            |
| Amylase               | <i>Amy-1</i>                                                                           | <i>P. leucopus</i>                         | Aquadro and Patton (1980)                                                                                                                                                                              |
| Carbonic anhydrase    | <i>Ca-1</i>                                                                            | <i>P. leucopus</i>                         | Wilmot and Underhill (1972)<br>Krohne and Baccus (1985)                                                                                                                                                |
| NADH diaphorase       | <i>Dia-1</i>                                                                           | <i>P. leucopus</i>                         | Nelson <i>et al.</i> (1987)                                                                                                                                                                            |
| Esterase              | <i>Es-1</i><br><i>Es-2</i><br><i>Es-3</i><br><i>Es-4</i><br><i>Es-5</i><br><i>Es-9</i> | <i>P. leucopus</i><br><i>P. gossypinus</i> | Price and Kennedy (1980)<br>Wilmot and Underhill (1973)<br>Browne (1977)<br>Smith <i>et al.</i> (1984)<br>Robbins <i>et al.</i> (1985)<br>Nelson <i>et al.</i> (1987)<br>Tolliver <i>et al.</i> (1987) |
| Fumarate hydratase    | <i>Fh-2</i>                                                                            | <i>P. leucopus</i>                         | Nelson <i>et al.</i> (1987)                                                                                                                                                                            |

(Continued)

**Table 9. Variant protein loci in *P. leucopus* group natural populations (Continued)**

| Protein                                  | Locus                                            | Species                                    | References                                                                              |
|------------------------------------------|--------------------------------------------------|--------------------------------------------|-----------------------------------------------------------------------------------------|
| L-glutamate dehydrogenase                | <i>Gld-1</i>                                     | <i>P. leucopus</i>                         | Nelson <i>et al.</i> (1987)                                                             |
| Glutamate oxaloacetate transaminase      | <i>Got-1</i><br><i>Got-2</i>                     | <i>P. leucopus</i>                         | Price and Kennedy (1980)<br>Nelson <i>et al.</i> (1987)                                 |
| $\alpha$ -Glycerophosphate dehydrogenase | <i>Gpd-1</i><br><i>Gpd-2</i>                     | <i>P. leucopus</i><br><i>P. gossypinus</i> | Mascarelo and Shaw (1973)<br>Browne (1977)<br>Robbins <i>et al.</i> (1985)              |
| Glucose-6-phosphate dehydrogenase        | <i>G6pd-1</i>                                    | <i>P. leucopus</i>                         | Nelson <i>et al.</i> (1987)                                                             |
| Glucose phosphate isomerase              | <i>Gpi-1</i><br>( <i>Pgi-1</i> )                 | <i>P. leucopus</i><br><i>P. gossypinus</i> | Price and Kennedy (1980)<br>Robbins <i>et al.</i> (1985)<br>Nelson <i>et al.</i> (1987) |
| Hemoglobin                               | <i>Hb</i>                                        | <i>P. leucopus</i><br><i>P. gossypinus</i> | Foreman (1966)<br>Price and Kennedy (1980)                                              |
| Isocitrate dehydrogenase                 | <i>Icd-1</i><br>( <i>Idh-1</i> )<br><i>Icd-1</i> | <i>P. gossypinus</i>                       | Robbins <i>et al.</i> (1985)<br>Nelson <i>et al.</i> (1987)                             |
| Lactate dehydrogenase                    | <i>Ldh-1</i>                                     | <i>P. leucopus</i>                         | Robbins <i>et al.</i> (1980)<br>Nelson <i>et al.</i> (1980)                             |
| Malic enzyme                             | <i>Me-1</i>                                      | <i>P. leucopus</i>                         | Nelson <i>et al.</i> (1987)                                                             |
| Nucleoside phosphorylase                 | <i>Np-1</i>                                      | <i>P. gossypinus</i>                       | Smith <i>et al.</i> (1984)<br>Nelson <i>et al.</i> (1987)                               |
| Peptidase                                | <i>Pep-2</i><br>( <i>Pep-B</i> )                 | <i>P. leucopus</i>                         | Nelson <i>et al.</i> (1987)                                                             |
| Phosphogluconate dehydrogenase           | <i>Pgd-1</i>                                     | <i>P. leucopus</i>                         | Robbins <i>et al.</i> (1985)<br>Nelson <i>et al.</i> (1987)                             |

(Continued)

**Table 9. Variant protein loci in *P. leucopus* group natural populations (Continued)**

| Protein                | Locus                                                     | Species                                    | References                                                                                                                                                              |
|------------------------|-----------------------------------------------------------|--------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Phosphoglucose mutase  | <i>Pgm-1</i><br><i>Pgm-3</i>                              | <i>P. leucopus</i><br><i>P. gossypinus</i> | Mascarello and Shaw (1973)<br>Browne (1977)<br>Price and Kennedy (1980)<br>Robbins <i>et al.</i> (1985)<br>Nelson <i>et al.</i> (1987)                                  |
| Plasma protein         | <i>Pprt-1</i>                                             | <i>P. leucopus</i>                         | Krohne and Baccus (1985)                                                                                                                                                |
| Sorbitol dehydrogenase | <i>Sdh-1</i>                                              | <i>P. leucopus</i>                         | Nelson <i>et al.</i> (1987)                                                                                                                                             |
| Superoxide dismutase   | <i>Sod-1</i><br>( <i>Ipo-1, Tetra-1</i> )<br><i>Sod-2</i> | <i>P. leucopus</i><br><i>P. gossypinus</i> | Mascarello and Shaw (1973)<br>Browne (1977)<br>Price and Kennedy (1980)<br>Robbins <i>et al.</i> (1985)<br>Tolliver <i>et al.</i> (1987)<br>Nelson <i>et al.</i> (1987) |
| Transferrin            | <i>Trf</i>                                                | <i>P. leucopus</i><br><i>P. gossypinus</i> | Price and Kennedy (1980)<br>Robbins <i>et al.</i> (1985)<br>Krohne and Baccus (1985)                                                                                    |
| Xanthine dehydrogenase | <i>Xdh-1</i>                                              | <i>P. leucopus</i>                         | Nelson <i>et al.</i> (1987)                                                                                                                                             |

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WITHOUT PERMISSION OF THE CONTRIBUTOR.***

**THANK YOU!**

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## C O N T R I B U T I O N S

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I am preparing a couple of manuscripts on my long-term project on the ecology of tropical and temperate species of *Peromyscus* in Mexico. The project includes aspects on life-history, habitat selection, food habits, home range dynamics and interspecific relationships with other small mammal species. It is my intention to include long-term data to unequivocally demonstrate ecological patterns. My research had also included the ecology of tropical heteromyids which occur sympatrically with *Peromyscus*. Ted Fleming and myself have elaborated a review to be published in a special publication of the ASM on the Biology of the Family Heteromyidae.

\* \* \*

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Our interest in *Peromyscus* primarily regards the *P. leucopus* major histocompatibility complex (MHC). At the molecular level we have examined restriction length polymorphisms in class II genes and defined a genetic complex comparable to the H-2 and HLA in mice and humans, respectively. We have termed the MHC of *P. leucopus*, the P1LA (Crew et al, 1989, Immunogenetics in press).

We have constructed a genomic DNA library from an  $F_5$  individual (from line 12) in the vector EMBL3 and have isolated a number of MHC encoded genes including single copy genes. The library has approximately  $2 \times 10^6$  unique clones with an average size insert of about 16 kilobasepairs. We wish to make this library (now amplified) available to those interested in any molecular genetic aspects of *Peromyscus*.

\* \* \*

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Work begun with a local population of *Peromyscus polionotus* was suspended due to disappearance of the mice from the study site. A limited number were available for breeding in the lab and a series of matings with *P. p. subgriesus* were established. In addition, a small number of *P. p. leucocephalus* were obtained from Bob Lacy, Chicago Zoological Park, and a few matings were established with these mice. Offspring from both these matings will be backcrossed to *P. p. lucubrans* or *P. p. leucocephalus*. This will establish a population with several genetic markers including a restriction fragment length polymorphism we have identified in these three subspecies. I hope to release mice next spring at the study site and follow the new artificially constructed population through several generations to identify forces controlling gene frequencies in these mice. Also, to the best of our knowledge, the offspring from the *lucubrans* X *leucocephalus* matings are the first known for such an inter-subspecific cross. (Renee Flinchum)

Recombination analysis of the markers *platinum* (*pt*), *blonde* (*bl*), *albumin* (*Alb*), *transferrin* (*Trf*), *erythrocytic esterase* (*Es-1*), *liver esterases* (*Es-3*, *Es-5*, *Es-6*), *alcohol dehydrogenase* (*Adh-1*), an *ADH* pseudogene (*Adh-ps*) and *ornithine decarboxylase* (*Odc-1*) are in progress. The analysis employs a combination of coat color, protein electrophoretic and restriction fragment length polymorphism markers. Coat color double mutant platinum-blonde female *P. maniculatus* are hybridized to wild-type male *P. polionotus* to obtain an *F<sub>1</sub>* interspecific hybrid which is fertile when backcrossed to the platinum-blonde *P. maniculatus*. Because of protein and RFLP differences between the species, a multiple point linkage test can be performed using the backcross progeny. No close linkage has been detected thus far, and additional animals are being sampled to detect loose linkage. The *pt* and *bl* loci are independent. The *Trf* and *Alb* loci were previously known to be independent. (Dawson, Covington, Crossland and Felder)

\* \* \*

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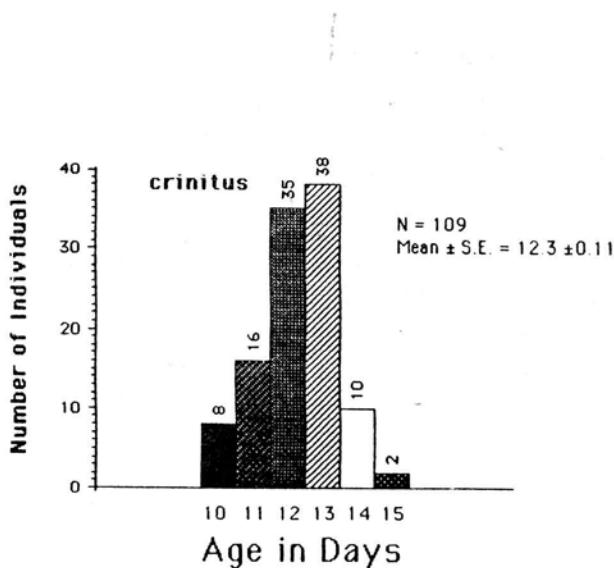
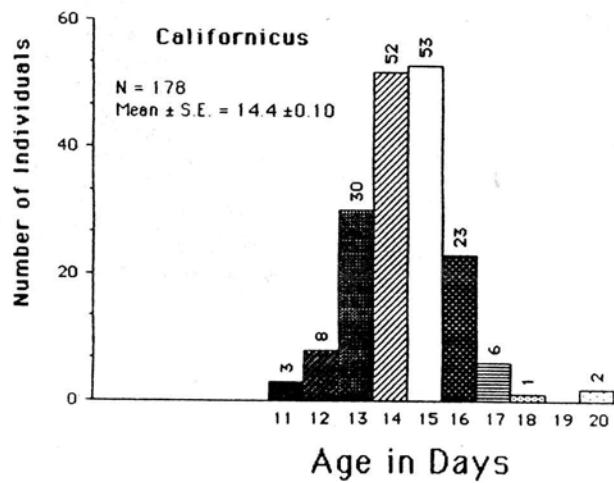
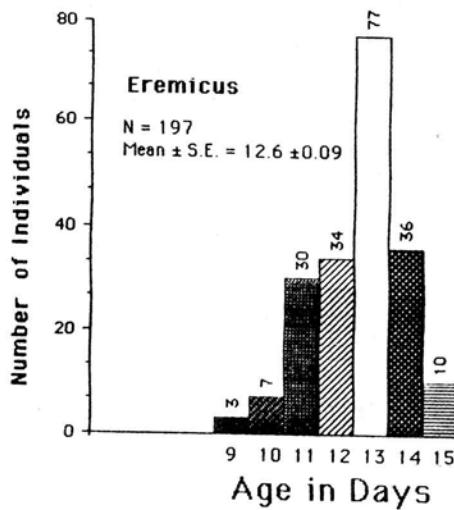
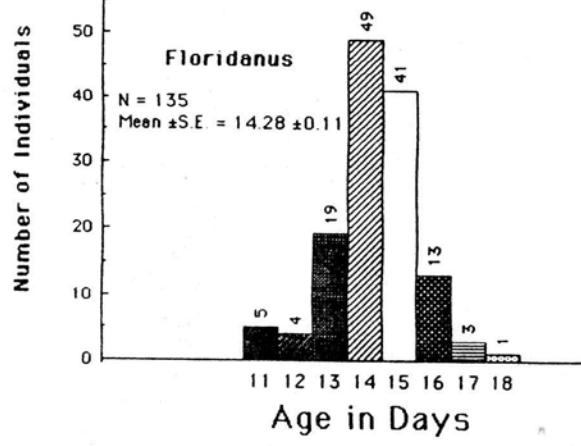
As of August, 1989, we have begun a study of the effects of prolonged low-level exposure to tritium in *Peromyscus polionotus*. Animals will be given tritium in the food and water at a level calculated to achieve a wholebody concentration of 0.1uCi/g. Tissue burdens of tritium will be analyzed to ascertain if there is preferential concentration. Enzymes of the thymus, small intestine and other organs will be compared with those of unexposed controls to assess variation in the activity or electrophoretic pattern. Over several generations of exposure, a number of parameters of reproductive success including fertility, birth weight, litter size, growth and survival will be measured.

\* \* \*

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### AGE OF EYELID SEPARATION IN FOUR SPECIES OF *PEROMYSCUS*

These old and unused data on eyelid separation (eye opening) in my retired files belong to the public domain because they were obtained with federal grants. Although Layne published some of these data in the *Biology of Peromyscus* (1968), the frequency distributions enable a more precise examination. These data can be used by anyone. I have the raw data and will try to send copies to anyone who promises to analyze them further. From time to time, I will try to provide more eye opening data.



[King, J.A. Continued]

Eye opening is a critical maturational stage, which is accompanied by vision (Vestal & King, 1968) and juvenile behavior. It varies within and between species. Each population exhibits variation as revealed by the histograms. Some of the variation is genetically influenced, although nutrition and body temperature also contribute to the maturation rate. Eye opening is responsive to artificial selection (to appear later) and can be partially isolated from other physical and behavioral stages in maturation.

Eye opening was checked daily, usually between 9:00 AM and 3:00 PM. the day of birth was assigned an age of zero, thus, a one day old mouse was about 24 hours old. The eyes were considered open when a slight pressure applied by the forefinger and thumb above and below the eye separated the lids. This pressure was sufficient to open behaviorally closed eyes, but not sufficient to separate the crease in the skin membrane when the eyes were still sealed. Individuals in which one eye opened a day or two before the other were given a mean score between the days of eye opening (e.g. left eye open at 14 days, right eye at 15 days, score = 14.5 days). The sexes are combined in the graphs. The numbers of mothers contributing offspring to these data are: *P. floridanus* = 27 (from Palm Beach Co., FL); *P. crinitus* = 15 (from San Bernardino Co., CA); *P. eremicus* = 25 (from San Diego Co., CA); *P. californicus* = 24 (from Alameda Co., CA).

\* \* \*

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We have begun a project that investigates the population dynamics and dispersal of *Peromyscus leucopus* on isolated forest fragments in west-central Indiana. This part of the state contains two large unbroken tracts of forest along the Wabash River and Sugar Creek. At varying distances from these large tracts are many forest remnants isolated by agricultural fields. We have been surveying a number of these forest islands for population density and structure and comparing them with several control sites in large tracts. We are examining the influence of standard biogeographical variables (island size, distance, shape, etc.) as well as vegetation structure on populations on the islands. In addition, we are attempting to assess the rate of dispersal to islands compared with mainland forest with the antibody technique developed by Glass et al. for determining maternity. Antibodies to an unusual antigen (limpet hemocyanin) are elicited in pregnant females. They are passed to the offspring where they are detectable thus allowing us to measure the fraction of animals on a grid that was born there.

\* \* \*

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We continue to maintain our colony of *Peromyscus maniculatus bairdii*. We use *P. maniculatus* and *P. leucopus* as a model animals to further our general lab goal of developing models to predict animal metabolic rates based on first principles such as fur properties and heat transfer relationships. Work outlining the effects of meteorological variables on metabolic rates forms the basis for exploring the effects of other environmental variables biotic and abiotic. Our metabolic rate studies are facilitated by an automated monitoring system which allows us to measure metabolic parameters continuously for several weeks. We are extending our modeling to the population level, and this will require the basic reproductive parameters that our animal colony is providing. Work in progress includes:

Studies on the effect of *Bourelia burgdorferi* (the spirochaete causing Lyme disease in humans) on oxygen production, carbon dioxide production, metabolic rate, and activity of mice *P. leucopus* obtained from the Peromyscus Stock Center and from other researchers contacted through the newsletter have been used in some of our experiments.

We are monitoring the geographic distribution of infected *P. leucopus* in southern Wisconsin along with the distribution of *Ixodes dammini*, the tick that is the vector for the spirochaete among mammals.

Studies on the effect of daylength and temperature on oxygen production, carbon dioxide production, and metabolic rate.

Studies on the effects of female mating age on reproductive parameters such as juvenile birth weight, number of juveniles born, and percent of females breeding.

Studies on the effect of toxicant exposure on digestive processes and behavior.

We would like to hear from anyone studying these aspects of *Peromyscus* biology.

\* \* \*

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The current status of the efforts to inbreed *P. leucopus* continue: Three lines are at F11 (10, 12, 16), two lines at F10 (13, 752), three lines at F9 (14, 18, 754), and four are at F8 (7, 8, 109, 753). Some lines are doing quite well with good sized litters (4-6). Others sputter along, as is no surprise.

The hairless line (18) continues at F9. The original pattern was development of normal hair then loss beginning at about 10 weeks of age on the face and spreading caudal, to complete loss. In later generations there are animals exhibiting various degrees and peculiar patterns of loss. Data on the multiple generations involved is being pulled together for analysis. More on this later.

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We are doing research involving habitat selection, food habits, population dynamics, and relocation of *Peromyscus floridanus* from several sites in Florida. Sampling is ongoing on the University of Central Florida campus to determine population sizes and habitat selection in scrub and scrub-sandhill habitat mixtures. Both live-trapping and fluorescent powder-tracking have been used to assess habitat selection. Encroaching development has prompted the relocation study, which will be correlated with earlier published studies I have conducted.

\* \* \*

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Our interests lie in long-term ecological studies of *Ixodes dammini*, the tick vector of Lyme disease and human babesiosis. Current research emphasises aspects of tick population dynamics and how these dynamics affect the maintenance of transmission of the Lyme disease spirochaete, *Borrelia burgdorferi*, and the protozoan agent of babesiosis, *Babesia microti*. Ultimately, we seek to describe the ecological effects (if any) of these and other parasites on their small mammal hosts. We currently trap 16 7X7 permanent grids at monthly intervals from April through September, 2 nights monthly at each of 5 distinct coastal Massachusetts sites. Seven of these grids have been so monitored since 1981, and the remaining 9 since 1984. Data is in the form of a mark-release-recapture study, with blood smears, weight, reproductive data, and ectoparasite samples taken from virtually all animals. Most of our captures consist of *Peromyscus leucopus*, the reservoir of both *B. burgdorferi* and *B. microti*.

We maintain a laboratory colony of *P. leucopus*, now in its 5th generation from an Ipswich, MA stock, for experiments on the biology of the Lyme disease spirochaete. Our studies are supported by NIH grant AI 19693 to A. Spielman.

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We continue to investigate seasonal adaptation in *Peromyscus leucopus*. We have undertaken a laboratory investigation of the influence of nest-sharing (huddling) on the expression of spontaneous daily torpor. Nest-sharing, like daily torpor, is an energy-conserving adjustment employed by free-ranging mice during winter. Of particular interest is that torpor occurs in huddles of mice in the field (Lynch, Vogt, and Smith, 1978). Of addition interest is that not all *P. leucopus* in northeastern populations undergo bouts of spontaneous daily torpor. Laboratory and field estimates of the percent incidence of this trait have not rigorously explored the interaction of nest-sharing and torpor.

We hypothesize that: 1) Huddling may facilitate an increased occurrence of torpor (more mice in a population become torpid at least once), and 2) Huddling may increase the frequency of torpor (mice known to enter torpor will do so more often). We surmise that the energy-conserving benefit of nest-sharing may reduce the physiological "risk" encountered during a bout of torpor at low ambient temperature ( $T_A$ ). The energetic benefit of nest-sharing could also lower the minimum  $T_A$  at which mice endure torpor.

We are now monitoring winter-acclimated mice housed alone and in huddles of three. Preliminary data suggest that nest-sharing does not appreciably increase the occurrence or frequency of torpor. Of interest is the observation that mice known to enter torpor when alone tend to all become torpid or all remain euthermic when huddled. "Mixed" huddles of torpid and euthermic mice are less common. We are continuing this research. (Continued next page)

We are also investigating the body temperature profiles of torpid mice in huddles using intraperitoneal implants of radio transmitters. Preliminary research has suggested that grouped animals undergo bouts of torpor in unison and thermoregulate at similar minimum body temperatures during deep torpor in a huddle.

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DEADLINE FOR ENTRIES IN PEROMYSCUS NEWSLETTER #9 IS FEB. 28 1990

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