

# PEROMYSCUS NEWSLETTER

NUMBER THIRTY-ONE



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MARCH 2001

Cover: *Peromyscus maniculatus bairdi* (BW Stock)  
with nursing litter. Superimposed:  
Portion of coding DNA sequence of  
Alcohol Dehydrogenase-1 gene (top)  
and Major Histocompatibility  
Class I gene (below).  
Photo by Clint Cook.

## ISSUE NUMBER 31.

This issue of *PEROMYSCUS NEWSLETTER* is devoted primarily to the **genetics** and **genomics** of *Peromyscus* and other peromyscines. As was announced in *PN#26*, rather than summarize genetic information in each issue as we had done previously, henceforth this would be done in a single dedicated issue at periodic intervals. Originally we had considered every fourth issue. But, after further consideration every sixth issue, or once each third year, was deemed a more realistic interval. A focused topic issue is typically larger and, hence, more costly to produce. Hence the reduced frequency of publication. Issue #25 was largely devoted to genetics, and that was six issues ago. So here we are!

The categories of information we have presented in previous issues are: (1) **Formally described genetic characters**, e.g. coat colors, neurological conditions and protein electrophoretic variants. Most of these were described from *Peromyscus maniculatus*. (2) **Linkage and mapping**, including an updated traditional linkage map. Thus far relatively few genes had been localized to a linkage group, but some *Peromyscus* linkage groups have specific **chromosomal assignments**. (3) A large body of information exists about **electrophoretic variants (allozymes) in natural populations** across a broad spectrum of peromyscine species. That information was heretofore summarized in *PN* periodically in table format. In this issue we continue that tradition, although mitochondrial DNA sequence analysis is largely supplanting allozyme analysis for taxonomic and population genetic studies.

In *PN#25* we initiated a tabulation of entries in GenBank for both **nuclear and mitochondrial genomic sequences**. This table serves as an index of peromyscine sequences in GenBank, but does not contain the actual sequences. These can be accessed by logging onto GenBank. Since *PN #25* was issued the number of *Peromyscus* sequences in GenBank has more than doubled. By far, the great majority of these sequences are mitochondrial, especially D-loop, loci used in phylogenetic reconstruction. There are also a significant number of nuclear repeat element sequences in GenBank, but relatively few *Peromyscus* sequences relate to transcribed nuclear genes. Inasmuch as the mitochondrial gene sequences from a particular study for a particular gene or segment are largely repetitious,

in our tables the locus designations and GenBank accession numbers are consolidated where a series of consecutively listed sequences represent the same mtDNA gene. In our table all consecutive sequences included between the first and last GenBank accession numbers are listed as one entry for that locus. An analogous approach is used for nuclear repeated elements. All coding nuclear ("gene") sequences are listed individually. Of course, more detailed information, including the sequence itself can be had by accessing GenBank and clicking on the desired accession number. For many loci the GenBank sequence can be accessed directly from *PeroBase* by going to "Genetics" and clicking on the GenBank accession number for the gene or element of interest.

WDawson

**NEXT ISSUE:** The deadline for entries or other material for inclusion in the next (September 2001) issue is **September 15, 2001**.

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## News, Comment and Announcements

We recently heard from **Alwynelle (Nell) Ahl**. She tells us that she has a USDA Fellow position with the Center for the Integrated Study of Food, animal and Plant Systems at Tuskegee University. Nell was among the first to recognize hemoglobin polymorphism in deer mice. She also maintained a number of genetic coat color variants. It was good to hear from her again.

\* \* \* \* \*

We received an e-mail from **Charles Calisher** of Colorado State University commenting on our summary of "Mouse in the House" project (PN#30). We received an abbreviated newspaper version that we further shortened for our News and Comment section. As Dr. Calisher correctly notes, our generalized use of the term "hantavirus" should have been more specific. Of course, there are many hantaviruses. It is specifically the Sin Nombre hantavirus that is the causative agent of hantaviral pulmonary syndrome (HPS) in North America. Also, the antibody in the mice is in response to the disease agent organism. In an attempt to abbreviate the informal report, we were less specific.

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We recently heard from **Dr. David Gubernick**. He has numerous used polypropylene mouse cages available for purchase. They are in two sizes: (1) 5X7x11.5 and (2) 6.2X10.5X19 in. He also has bar-style steel lids to fit these cages. Water bottles, stoppers and stainless drinking tubes are also available. Dr. Gubernick may be contacted at [www.rainbowspirit.com](http://www.rainbowspirit.com) for prices and other information. Dr. Gubernick is offering these items at a **significant discount when compared with the purchase prices of new cages and lids**.

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Several recently published papers are of special interest. A paper by **Paul Vrana et al.** of Princeton University (2000. *Nature Genetics* 25:120ff) reports that genetic and epigenetic incompatibilities underlie hybrid dysgenesis in *Peromyscus maniculatus* X *P. polionotus* experimental hybrids. The role of genomic imprinting in reproductive isolation between these species may represent a common mechanism for speciation in mammals. Three recent papers by **Brett Riddle of UNLV** and others (*Molecular Phylogenetics and Evolution* 2000. 17:145-160; 161:161-172 and *PNAS* 2000. 97:14438-14443) discuss the phylogeography and systematics of the *Peromyscus eremicus* species group and other peromyscines in the North American desert southwest, providing interesting new insights into speciation in *Peromyscus*. **Robert Bradley et al.** recently reported a study mitochondrial cytochrome B sequence data to resolve phylsystematics in the *P. boylii* species group. Their data indicates that *P. boylii sacarensis* is more likely a subspecies of *P. beatae* within the *P. boylii* species group.





## PEROMYSCUS GENETIC 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 Living Stocks Collection Program of the National Science Foundation. It also receives significant funding through the NIH Animal Biomedical Models program. The major function of the Stock Center is to provide genetically characterized types of *Peromyscus* 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. Animals requested in greater numbers frequently require a "breed-up" charge and some delay in shipment.

A user fee of **\$17.50 per wild-type animal** and **\$ 25 per mutant or special stock animal** is charged. 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. Arrangements for special orders will be negotiated. Write or call for details.

The Peromyscus Stock Center also publishes *PEROMYSCUS NEWSLETTER* and sponsors *PeroBase*, a comprehensive database for peromyscine rodents.

See our website at <http://stkctr.biol.sc.edu/>

## Stocks Available in the Peromyscus Stock Center

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WILD TYPE STOCKS	ORIGIN
<i>P. maniculatus bairdii</i> (BW Stock)	Closed colony bred in captivity since 1948. Descended from 40 ancestors wild-caught near Ann Arbor MI
<i>P. maniculatus sonoriensis</i> (SM2 Stock)	Closed colony since 1997. Derived from Descended from animals wild caught at White Mtn., CA by J. Hayes
<i>P. polionotus subgriseus</i> (PO Stock)	Closed colony since 1952. Derived from 21 ancestors wild-caught in Ocala Nat'l. Forest FL. High inbreeding coefficient.
<i>P. polionotus leucocephalus</i> (LS Stock)	Derived from beachmice wild-caught on Santa Rosa I., FL. and bred by R. Lacy. Approximately 15 generations in captivity.
<i>P. leucopus</i> (LL Stock)	Derived from 38 wild ancestors captured between 1982 and 85 near Linville NC. Approximately 25 generations in captivity.
<i>P. californicus insignis</i> (IS Stock)	Derived from about 60 ancestors collected between 1979 and 87 in Santa Monica Mts. CA. Approximately 16 generations in captivity.
<i>P. aztecus hylocetes</i> (AM Stock)	Derived from animals collected on Sierra Chincua, Michoacan, Mexico in 1986 Approximately 15 generations in captivity.
<i>P. melanophrys xenerus</i> (XZ Stock)	Originated from a group of animals collected at Zacatecas Mexico in 1977. Formerly maintained by R.W. Hill at Mich. State Univ.
<i>P. eremicus</i>	Originated from 10-12 animals collected at Tucson AZ in 1993. Approx. seven generations in captivity.
<i>P. maniculatus</i> X <i>P. polionotus</i> F <sub>1</sub> Hybrids	Bred to order. Inquire.

## MUTATIONS AVAILABLE FROM THE STOCK CENTER<sup>1</sup>

### Coat Colors

Albino *c/c*  
Ashy *ahy/ahy*  
Black (Non-agouti) *a/a*  
Blonde *bln/bln*  
<sup>2</sup>Brown *b/b*  
California blonde *cfb/cfb*  
Dominant spotting *S/+*  
Golden nugget *b<sup>gn</sup>/b<sup>gn</sup>* [in *P. leucopus*]  
Gray *g/g*  
Ivory *i/i*  
<sup>3</sup>Pink-eyed dilution *p/p*  
Platinum *plt/plt*  
<sup>2,4</sup>Silver *sil/sil*  
Tan streak *tns/tns*  
Variable white *Vw/+*  
White-belly non-agouti *a<sup>w</sup>/a<sup>w</sup>*  
Wide-band agouti *A<sup>Nb</sup>/a*  
Yellowish *yel/yel*

### Other Mutations and Variants

Alcohol dehydrogenase negative *Adh<sup>o</sup>/Adh<sup>o</sup>*  
Alcohol dehydrogenase positive *Adh<sup>f</sup>/Adh<sup>f</sup>*  
Boggler *bg/bg*  
Cataract-webbed *cwb/cwb*  
Epilepsy *ep/ep*  
<sup>3</sup>Flexed-tail *f/f*  
Hairless-1 *hr-1/hr-1*  
Hairless-2 *hr-2/hr-2*  
Juvenile ataxia *ja/ja*  
  
Enzyme variants.

### ORIGINAL SOURCE

Sumner's albino deer mice (Sumner, 1922)  
Wild-caught in Oregon ~ 1960 (Teed *et al.*, 1990)  
Homer's black mutant (Homer *et al.*, 1980)  
Mich. State U. colony (Pratt and Robbins, 1982)  
Huestis stocks (Huestis and Barto, 1934)  
Santa Cruz I., Calif., stock (Roth and Dawson, 1996)  
Wild caught in Illinois (Feldman, 1936)  
Wild caught in Mass. (Homer and Dawson, 1993)  
Natural polymorphism. From Dice stocks (Dice, 1933)  
Wild caught in Oregon (Huestis, 1938)  
Sumner's "pallid" deer mice (Sumner, 1917)  
Barto stock at U. Mich. (Dodson *et al.*, 1987)  
Huestis stock (Huestis and Barto, 1934)  
Clemson U. stock from N.C. (Wang *et al.*, 1993)  
Michigan State U. colony (Cowling *et al.*, 1994)  
Egoscue's "non-agouti" (Egoscue, 1971)  
Natural polymorphism. U. Mich. (McIntosh, 1954)  
Sumner's original mutant (Sumner, 1917)

### ORIGIN

South Carolina BW stock (Felder, 1975)  
South Carolina BW stock (Felder, 1975)  
Blair's *P. m. blandus* stock (Barto, 1955)  
From Huestis stocks (Anderson and Burns, 1979)  
U. Michigan *artemisiae* stock (Dice, 1935)  
Probably derived from Huestis flexed-tail (Huestis and Barto, 1936)  
Sumner's hairless mutant (Sumner, 1924)  
Egoscue's hairless mutant (Egoscue, 1962)  
U. Michigan stock (Van Ooteghem, 1983)

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

<sup>1</sup>Unless otherwise noted, mutations are in *P. maniculatus*.

<sup>2</sup>Available only as silver/brown double recessive.

<sup>3</sup>Available only as pink-eye dilution/flexed-tail double recessive.

<sup>4</sup>Not currently available.

**OTHER RESOURCES OF THE *PEROMYSCUS* GENETIC STOCK CENTER:**

Highly inbred *P. leucopus* ( $I_{20+}$ ) are available as live animals or as frozen tissues.

Several lines developed by George Smith (UCLA) are currently maintained by the Stock Center.

Limited numbers of other stocks, species, mutants, inbreds and variants are on hand, or under development, but are not available for distribution. Currently we can supply up to 10 each of the species *P. eremicus* and *P. melanophrys*.

Preserved or frozen specimens of types given in tables above.

Tissues, whole blood or serum of types given in tables above.

Flat skins of mutant coat colors or wild-type any of the species above.

Reference library of more than 2400 reprints of research articles and reports on *Peromyscus*.

Copies of individual articles can be photocopied and mailed. Please limit requests to five articles at any given time. There will be a charge of 5 cents per photocopied page after the initial 20 pages.

Materials are available through the *Peromyscus* Molecular Bank of the Stock Center. Allow two weeks for delivery. Included is purified DNA or frozen tissues from any of the stocks listed above. Several genomic libraries and a variety of molecular probes are available. (Inquire for more information)

*For additional information or details about any of these mutants, stocks or other materials contact: Janet Crossland, Colony Manager, Peromyscus Stock Center, (803) 777-3107.*

**PLEASE CALL WITH INQUIRIES.**

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## PEROMYSCINE GENETICS AND GENOMICS 2001 UPDATE

As with many research organisms, *Peromyscus* genetic and genomic information is increasing dramatically as the result of developments in technology. A major function of *PEROMYSCUS NEWSLETTER* is to keep abreast of these advances. For many years relatively little was known about the genetics of peromyscine rodents. A handful of coat color and other visible genetic traits were known. There was also a literature of morphological differences among subspecies of a species that were assumed to have a genetic basis, as well as a few instances of interspecific hybridization with predictable genetic consequences. With the development of electrophoresis additional genetic polymorphisms were discovered within species. Variation in electrophoretic mobility of various protein markers was generally attributed individual gene allelism. The formal genetics of about twenty-five such loci are on record, but the existence of many other loci was presumed, even in the absence of formal Mendelian analysis, based on detectible variation in natural populations and probable homology with known loci in other mammalian species. Peromyscine cytogenetics parallels the history of allozymes. Giemsa staining was refined to show detailed banding patterns within the chromosomes, revealing extensive inversion polymorphism and the existence of heterochromatic arm variation within species. This was essentially the status of *Peromyscus* genetics.

Beginning in the mid-1980s, more fundamental variation came to light as newer molecular techniques were rapidly developed. Initially with southern hybridization and subsequently with PCR-based technologies and efficient genomic sequencing methodology variation in DNA at the genomic or gene level became accessible. Concurrently, statistical advances in analysis of Mendelian crosses allowed measurable (quantitative) traits (QTLs) to be localized within the chromosome with respect to discrete traits, that are analyzed with computer-based gene mapping programs. The process of fluorescence in-situ hybridization (FISH) permits genes (or chromosomes) of one species to be localized with respect to another related species. FISH has wide application and promise for development of the *Peromyscus* gene map, and is used in a limited fashion already.

After initial progress between 1935 and 1960 the formal genetic map for the deer mouse remained rudimentary. The addition of several allozyme and other protein markers since the 1970s essentially brings the formal *Peromyscus* linkage map to its current state.

The addition of DNA sequence information greatly expands the total genomic database for peromyscine rodents. While a few nuclear genes, notably those of the major histocompatibility complex, beta globin and alcohol dehydrogenase loci, have been sequenced, most genomic information for peromyscines relates to either mitochondrial genome markers or nuclear repetitive elements. The mitochondrial genomic markers in *Peromyscus* are used predominantly for phylogenetic studies.

For our purposes, we use “**genomic**” to describe nucleic acid-based information, including FISH, and “**genetic**” for the detectible manifestations of the genome, whether discrete or quantitative, observable at the protein level or above, including allozyme and immunogenetic variation, visible traits, including behaviors.

## GENETIC LOCI IN *PEROMYSCUS*

(Deer mice and allied species)

Table I. lists recognized genetic loci described in *Peromyscus maniculatus* or other species of the *maniculatus*-group. Table II. lists loci formally described in the *P. leucopus* species group, and Table III. those of other species of *Peromyscus*. These lists are limited to loci for which formal Mendelian analysis has been conducted and appropriately reported in the published scientific literature, and/or for functional genes for which nucleic acid sequences have been published. Additional genetic traits are known, some of which have been cited in abstracts, casual reports, newsletters, grant proposals, papers presented at meetings *etc.* The latter are not included, since the descriptions and genetics are generally insufficient to formally define the loci. Presumptive loci described from natural polymorphisms in the absence of formal genetic analysis are not listed here. Protein electrophoretic and other biochemical or immunological variants known in natural populations are listed elsewhere. This list is limited to nuclear genes.

Standardization of genetic nomenclature for *Peromyscus* is a function of the Genetic Advisory Committee for the genus. The following guidelines currently are applied:

1. To the maximum extent feasible, *Peromyscus* genetic nomenclature and conventions will be consistent with those used for other mammalian species, particularly mouse (*Mus*). Where homology is evident or very likely, the same locus name and symbol is employed. Because homology among alleles is more difficult to ascertain, allelic symbols (superscripts) do not necessarily correspond to those of other species.

2. Dominant and incompletely dominant variant or mutant genes are designated with the first letter of the symbol capitalized. Recessive variant or mutant genes are indicated in lower case letters. The wild-type (normal or standard) allele for morphological, pelage color and behavioral traits, when recognized, is symbolized with a "+" sign. Electrophoretic allelic variants of proteins or subunits are indicated by superscripts in alphabetical sequence, except for null alleles which are designated, with an "o" superscript; or, in some cases, by relative mobility with reference to a standard mobility "100". Restriction fragment length variant alleles are designated by a numerical sequence or size in kilobases. Distinct loci with similar phenotypic effects may be indicated in a hyphenated numerical or alphabetical series.

3. Symbols published by the original investigator are given priority, unless there is clear homology with *Mus* loci, except for certain loci for which the original symbol was retained under the "grandfather" principle and because of prior use in the literature. If an original symbol is in conflict with an established one for *Mus*, the equivalent *Mus* symbol is given preference. In cases where the original symbols have been superseded by subsequent common usage, the latter has been adopted. If a variant is shown to be allelic with a previously reported gene, the locus symbol is reduced to an allelic symbol. Where two authors have used the identical symbol for different loci in *Peromyscus*, priority is given to the first reported, and an alternate designation is devised for the other. (In Table 1 previously published obsolete names and symbols are listed in parentheses.)

4. Presumed loci described solely on the basis of variation observed among individuals in the absence of convincing Mendelian or molecular analysis are not considered to be formally established and are not included in these tables, but may be listed as polymorphisms in natural populations.

5. Linkage assignments are subject to updates of the *Peromyscus* linkage map.

**Table 1**  
**Genetic Loci Formally Described in the *Peromyscus maniculatus* Species Group:**  
**A. Coat and Eye Pigmentation and Pattern Variants.**

Name of locus and allelic variants	Symbol	Mode of inheritance	Linkage group	Definitive description and analysis	Collateral descriptions, interactions and recurrences	Recombination reported
AGOUTI			III			
Wide-band agouti	$A^{Nb}$	dominant		McIntosh (1956a)	Blair (1947) as "buff"	Clark (1938) as "buff"
White-belly non-agouti	$a^w$	recessive		Egoscue (1971)		
Non-agouti (Black)	$a$	recessive		Homer <i>et al.</i> (1980)		
ASHINESS	$ahy$	recessive		Teed <i>et al.</i> (1990)		
BROWN	$b = bm$	recessive	II	Huestis and Barto (1934)	Blair (1947), McIntosh (1956a), Dawson <i>et al.</i> (1969)	Huestis and Barto (1934) Blair (1947), Barto (1955, 1956), McIntosh (1956a)
Orange-tan	$b^{ot}$	recessive		Egoscue and Day (1958)		
BLONDE <sup>2</sup>	$bln$ ( $bl$ )	recessive		Pratt and Robbins (1982)		
ALBINO	$c$	recessive	I	Sumner (1922)	Clark (1938)	Sumner (1922), Clark (1936, 1938), Feldman (1937), Barto (1942a), Huestis and Lindstedt (1946), Huestis (1946)
CALIFORNIA BLONDE	$ctb$	recessive		Roth and Dawson (1996)		Roth and Dawson (1996)
COLORLESS HAIR TIP*	$ctp$	recessive		Bowen and Dawson (1969)	Bowen (1968)	
DILUTE*	$d = dit$	recessive	II	Dice (1933)		Clark (1938), Barto (1942a, 1956), McIntosh (1956a)
GRAY	$g$	recessive		Dice (1933)	Clark (1938), Blair (1947), McIntosh (1956a)	Blair (1944, 1947)
IVORY	$i$	recessive		Huestis (1938)	Clark (1938)	Barto (1942a, 1956), McIntosh (1956a)
PINK-EYED DILUTION	$p$	recessive	I	Sumner (1917) as "pallid"	Clark (1938), Barto (1942b)	Sumner (1922), Clark (1936, 1938), Feldman (1937), Snyder (1980a)
PLATINUM <sup>2</sup>	$pIt$ ( $pt$ )	recessive		Dodson <i>et al.</i> (1987)		Dodson <i>et al.</i> (1987)
RED EYE <sup>2</sup> (Heterochromia)	$rde$ ( $r$ )	recessive		Huestis and Willoughby (1950)		
DOMINANT SPOT (Whiteface)	$S$	dominant		Feldman (1936)		Feldman (1937)

(Table Continued)

Table 1A. Coat and Eye Color Variants (Continued)

Name of locus and allelic variants	Symbol	Mode of inheritance <sup>1</sup>	Linkage group	Definitive description and analysis	Collateral descriptions, interactions and recurrences	Recombination reported
SILVER	<i>sl</i> ( <i>sl</i> , <i>sl</i> )	recessive	I	Huestis and Barto (1934)		Huestis and Barto (1934), Huestis and Plestrak (1942), Huestis and Lindstedt (1946), Barto (1956)
TAN STREAK	<i>tns</i>	recessive		Wang <i>et al.</i> (1993)		
VARIABLE WHITE	<i>Vw</i>	semi-dominant lethal		Cowling <i>et al.</i> (1994)		Cowling <i>et al.</i> (1994)
WHITE CHEEK <sup>2</sup>	<i>Wck</i> ( <i>Wc</i> )	dominant		Blair (1944)	Bowen and Dawson (1977)	Blair (1944)
WHITESIDE <sup>2</sup>	<i>ws</i> ( <i>wh</i> )	recessive		McIntosh (1956b)		
YELLOWING <sup>2</sup> (Yellow)	<i>y = yel</i>	recessive		Sumner (1917)	Sumner and Collins (1922), Clark (1938), McIntosh (1956a)	Sumner (1922), Feldman (1937), Barto (1956), McIntosh (1956a)
<b>Complexly inherited coat pattern traits:</b>						
Minor white spotting (Star, splash, etc.)	<i>p-1, p-2</i>	recessive incompletely penetrant		Feldman (1936)	Sumner (1932), Barto and Huestis (1933)	
Grizzled <sup>2</sup>	* <i>Gr</i> ( <i>G</i> )	*complex dominant*		Sumner (1928, 1932)		
Coat pattern in <i>P. pollonotus</i>				Bowen and Dawson (1977)	Bowen (1968)	Bowen and Dawson (1977)
Pointed A <sub>2</sub> <sup>2</sup>	<i>Pt-A (P<sub>A</sub>)</i>	dominant	VII			
Pointed B <sup>2</sup>	<i>Pt-B (P<sub>B</sub><sup>A</sup>)</i>	dominant	VII			
Tapered <sup>2</sup>	<i>Tpt (Tp)</i>	dominant				
Coat pattern modifiers				Bowen and Dawson (1977)		
Squared modifier <sup>2</sup>	<i>Msq (Rs)</i>	incompletely dominant				
Tapered modifier <sup>2</sup>	<i>Mtp (Rt)</i>	dominant				

<sup>1</sup>Autosomal unless otherwise stated.

<sup>2</sup>Symbol or name changed to avoid confusion with designations in *Mus*. Obsolete published names and symbols in parentheses.

\*No longer known to be in existence



## B. Integumentary, Skeletal and Pathological Variants.

Name of locus and allelic variants	Symbol	Mode of inheritance <sup>1</sup>	Linkage group	Definitive description and analysis	Collateral descriptions, interactions and recurrences	Recombination reported
CATARACT-WEBBED <sup>2</sup> (Syndactyly)	<i>cwb</i> ( <i>cw</i> )	recessive		Anderson and Burns (1979)	Burns and Feeney (1975)	
FLEXED TAIL	<i>f</i>	recessive	I	Huestis and Barto (1936a)		Huestis and Barto (1936a), Huestis and Piestrak (1942), Huestis and Lindstedt (1946), Huestis <i>et al.</i> (1956), Barto (1956)
HAIRLESS-1	<i>hr-1</i>	recessive		Sumner (1924)		Sumner (1924, 1932), Feldman (1937), Clark (1938), Barto (1942a, 1955, 1956), McIntosh (1956a)
HAIRLESS-2	<i>hr-2</i>	recessive		Egoscue (1962)	Knapp and Dawson (1991)	
NUDE* <sup>2</sup> (Post-juvenile nude)	<i>nd</i> ( <i>n</i> )	recessive		Clark (1938)	Barto (1942a)	
SPHEROCYTOSIS (Inherited jaundice)	<i>sph</i>	recessive		Huestis and Anderson (1954)	Huestis <i>et al.</i> (1956), Motulsky <i>et al.</i> (1956)	Huestis <i>et al.</i> (1956)

<sup>1</sup>Autosomal unless otherwise stated.

<sup>2</sup>Name or symbol changed to avoid confusion with designations in *Mus*. Obsolete published names and symbols in parentheses.

\*No longer known to be in existence.

## C. Behavior and Neurological Variants.

Name of locus and allelic variants	Symbol	Mode of inheritance <sup>1</sup>	Linkage group	Definitive description and analysis	Collateral descriptions, interactions and recurrences	Recombination reported
BOGGLER <sup>2</sup>	<i>bgl</i> ( <i>bg</i> )	recessive		Barto (1955)	Vandermeer and Barto (1969)	Barto (1955)
EPILEPSY <sup>2</sup> (EP; waltzing in <i>artemisiae</i> )	<i>epf</i> (* <i>e</i> *, <i>ep</i> , <i>v</i> <sub>2</sub> )	recessive		Dice (1935)	Clark (1938), Watson (1939), Chance and Yaxley (1950), Barto (1954, 1956)	Watson (1939), Barto (1956)
JUVENILE ATAXIA <sup>2</sup>	<i>jax</i> ( <i>ja</i> )	recessive		Van Ooteghem (1983)		
SPINNER* <sup>2</sup> (Waltzing in <i>rhoadsi</i> )	<i>spn</i> ( <i>sp</i> , <i>v</i> <sub>3</sub> )	recessive		Watson (1939)	Barto (1954)	
TREMOR*	<i>tr</i>	recessive		Huestis and Barto (1936b)		
WALTZER* (Waltzing in <i>bairdii</i> )	<i>v</i> ( <i>w</i> )	recessive	III	Dice (1935)	Clark (1938), Watson (1939), Dice <i>et al.</i> (1963)	Barto (1942a, 1954, 1956), McIntosh (1956a)

<sup>1</sup>Autosomal unless otherwise stated.

<sup>2</sup>Name or symbol changed to avoid confusion with designations in *Mus*. Obsolete published names and symbols in parentheses.

\*No longer known to be in existence.

## D. Biochemical and Immunological Variants.

Name of locus <sup>1</sup>	Allelic designation	Linkage group	Definitive description and formal analysis	Recombination reported
ALCOHOL DEHYDROGENASE-1 (liver)	<i>Adh-1</i> <sup>f</sup> <i>Adh-1</i> <sup>a</sup> <i>Adh-1</i> <sup>o</sup>	VI	Felder (1975), Burnett and Felder (1978a, 1978b)	Dawson <i>et al.</i> (1983) Cowling <i>et al.</i> (1994)
ALCOHOL DEHYDROGENASE-2	<i>Adh-2</i>		Zheng <i>et al.</i> (1993) Haseba <i>et al.</i> (1995)	
ALBUMIN (serum)	<i>Alb</i> <sup>100</sup> <i>Alb</i> <sub>98</sub> <i>Alb</i> <sub>88</sub> <i>Alb</i>	VI	Brown and Weiser (1968), Jensen and Rasmussen (1971)	Dawson (1982), Dawson <i>et al.</i> (1983) Cowling <i>et al.</i> (1994) Roth and Dawson (1996)
AMYLASE (salivary)	<i>Amy-1</i> <sup>a</sup> <i>Amy-1</i> <sub>b</sub> <i>Amy-1</i> <sub>c</sub> <i>Amy-1</i> <sup>c</sup>	VI	Evans <i>et al.</i> (1977)	Dawson <i>et al.</i> (1983)
DELTA-LIKE HOMOLOG (Drosophila)	<i>Dlk1</i>		Schmidt <i>et al.</i> (2001)	
ERYTHROCYTIC ANTIGEN	<i>Ea</i> <sub>B</sub> <sup>A</sup> = ( <i>Pm</i> <sub>B</sub> ) <sup>A</sup> <i>Ea</i> <sub>C</sub> = ( <i>Pm</i> <sub>C</sub> ) <i>Ea</i> = ( <i>Pm</i> )	IV	Rasmussen (1961), Savage and Cameron (1971)	Randerson (1973)
ENDOTHELIAL-B RECEPTOR	<i>ENDRB</i>		Vrana <i>et al.</i> (2000)	
ESTERASE (erythrocytic) <sup>2</sup>	<i>Es-3</i> <sup>o</sup> ( <i>Es-1</i> ) <i>Es-3</i> <sub>a</sub> <i>Es-3</i> <sub>b</sub> <i>Es-3</i> etc.	IV	Randerson (1965), Van Deusen and Kaufman (1978)	Randerson (1973)
ESTERASES (tissue and serum)	<i>Es-1</i> through <i>Es-7</i> (Symbols not standardized)	VIII	Rasmussen and Jensen (1971), Dawson (1982), Gill (1976), Baccus <i>et al.</i> (1980)	Dawson (1982)
FETAL LIVER mRNA	<i>H19</i>		Vrana <i>et al.</i> (2000)	
GLYCEROL-3-PHOSPHATE DEHYDROGENASE <sup>2</sup> (tissue)	<i>Gdc-1</i> <sup>a</sup> <i>Gdc-1</i> <sub>b</sub> ( <i>Gpd-1</i> )		Gill (1976)	
GLUTAMATE OXALOACETATE TRANSAMINASE (soluble) (ASPARTATE AMINO TRANSFERASE)	<i>Gat-1</i> <sup>a</sup> <i>Gat-1</i> <sub>b</sub> = <i>Aat-1</i> <i>Gat-1</i> <sub>c</sub> <i>Gat-1</i> <sup>c</sup>		Gill (1976)	Dawson <i>et al.</i> (1983)
GLUCOSE-6-PHOSPHATE (AUTOSOMAL HEXOSE-6-P) DEHYDROGENASE <sup>2</sup> (soluble)	<i>Gpd-1</i> <sup>a</sup> <i>Gpd-1</i> <sub>b</sub> ( <i>G6pd-1</i> ) <i>Gpd-1</i>		Shaw and Barto (1965), Shaw (1966)	
HEMOGLOBIN - ALPHA TYPE GLOBINS (Duplicated locus)	<i>Hba</i> <sub>2</sub> <sup>1</sup> = ( <i>Hb</i> <sup>f</sup> ) = ( <i>Hb</i> <sup>a</sup> ) <i>Hba</i> <sub>o</sub> <i>Hbc</i> <sub>1</sub> = ( <i>Hb</i> <sup>o</sup> ) = ( <i>Hb</i> <sup>o</sup> ) <i>Hbc</i> <sub>2</sub> <i>Hbc</i> = ( <i>Hb</i> <sup>f</sup> )		Thompson <i>et al.</i> (1966), Rasmussen <i>et al.</i> (1968), Jensen <i>et al.</i> (1976), Maybank and Dawson (1976), Snyder (1978, 1980b)	
HEMOGLOBIN - BETA TYPE GLOBINS (triplicated locus)	<i>Hbb</i> <sub>1</sub> <sup>1</sup> <i>Hbb</i> <sub>1</sub> <sup>o</sup> <i>Hbb</i> <sub>1</sub> or <i>Hbb-b1</i> <i>Hbb</i> <sub>2</sub> <i>Hbb</i> <sub>3</sub> <i>Hbb</i> <sub>1</sub> or <i>Hbb-b3</i> <i>Hbb</i> <sub>1</sub> <i>Hbb</i> <sub>1</sub>	I	Snyder (1978, 1980b), Padgett <i>et al.</i> (1987)	Snyder (1980a)
HAPTOGLOBIN (serum) <sup>2</sup>	<i>Hp</i> <sub>2</sub> <sup>1</sup> ( <i>Hpf</i> ) <i>Hp</i>		Rasmussen (1968), Griswold and Dawson (1971)	

(Table continued)

Table 1D. Biochemical and Immunological Variants. (Continued)

Name of locus	Allelic designation	Linkage group	Definitive description and formal analysis	Recombination reported
IMMUNOGLOBIN (7Sy <sub>1</sub> )	$Ig_s^f$ $Ig$		Coe (1972)	
INTERFERON GAMMA	<i>IFG</i>		Herbst and Schontz (2001)	
LECITHINCHOLESTEROL ACYL TRANSFERASE	<i>LCAT</i>		Robinson <i>et al.</i> (1997)	
LEUCINE AMINOPEPTIDASE (serum)	$Lap-1^a$ $Lap-1^b$	V	Dawson (1982)	Dawson (1982), Dawson <i>et al.</i> (1983)
LEPTIN	<i>ob</i>		Vrana <i>et al.</i> (2000)	
LACTATE DEHYDROGENASE <sup>2</sup> A SUBUNIT (tissue)	$Ldh-1^a$ ( <i>Ldh-A</i> ) $Ldh-1^b$		Cattanach and Perz (1969)	
LACTATE DEHYDROGENASE <sup>2</sup> B SUBUNIT (tissue)	$Ldh-2^f$ ( <i>Ldh-B</i> ) $Ldh-2^s$		Shaw and Barto (1963)	
MAJOR HISTOCOMPATIBILITY COMPLEX	<i>Mhc</i> (Class I)		Crew <i>et al.</i> (1994, 1996)	
MYOGENIC REGULATORY FACTOR	<i>MyoD</i>		Vrana <i>et al.</i> (2000)	
snRNA	<i>BC1RNA</i>		Kass <i>et al.</i> (1996)	
6-PHOSPHOGLUCONATE DEHYDROGENASE (tissue)	$Pgd-1^a$ $Pgd-1^b$		Gill (1976)	Dawson <i>et al.</i> (1983)
PHOSPHOGLUCOMUTASE-1 (tissue)	$Pgm-1^a$ $Pgm-1^b$		Gill (1976)	
PHOSPHOGLUCOMUTASE-4 (tissue)	$Pgm-4^a$ $Pgm-4^b$ $Pgm-4^c$		Gill (1976)	
SUPEROXIDE DISMUTASE	$Sod-1^j = (Ng)$ $Sod-1^p$ $Sod-1^m$		Birdsall <i>et al.</i> (1970)	
TRANSFERRIN (serum)	$Trf^a = (Trf^j)$ $Trf^c$ $Trf^p$ $Trf^m = (Trf^M)$	V	Rasmussen and Koehn (1966), Biggers and Dawson (1971), Griswold and Dawson (1971), Canham <i>et al.</i> (1970)	Dawson (1982), Dawson <i>et al.</i> (1983) Roth and Dawson (1996)
TUMOR NECROSIS FACTOR ALPHA	<i>TNFa</i>		Herbst and Schontz (2001)	

<sup>2</sup>Symbols changed to avoid confusion with those in laboratory mouse (*Mus*). Obsolete published symbols shown in parentheses.

Table 2

Genetic Loci Formally Described in the *Peromyscus leucopus* Species Group

Name of locus and allelic variants	Symbol	Mode of inheritance <sup>1</sup>	Definitive description and analysis	Collateral descriptions, interactions and recurrences	Recombination reported
GOLDEN NUGGET	$b^{gn}$	recessive	Horner and Dawson (1993)		
ALBINO	$c$	recessive	Castle (1912)		
CARBONIC ANHYDRASE	$Ca_1^f$ $Ca_2^f$	co-dominance	Wilmot and Underhill (1972)		
CATALASE	$Cs_a^a$ $Cs_b^a$	co-dominance	Jensen (1969)		
ESTERASE-3 (Esterase-1) <sup>2</sup> (erythrocytic)	$Es-3_b^0$ ( $Es-1^a$ ) $Es-3^b$	semi-dominant	Wilmot and Underhill (1973)		
ESTERASE-2 (serum)	$Es-2_b^0$ ( $Es-2^a$ ) $Es-2^b$	semi-dominant	Wilmot and Underhill (1973)		
HEMOGLOBIN	$Hb_A^A$ (in <i>P. gossypinus</i> ) $Hb_B^A$ (in <i>P. gossypinus</i> ) $Hb_C^A$ (in <i>P. gossypinus</i> ) $Hb_D^A$ (in <i>P. leucopus</i> )	co-dominance	Foreman (1966)		
MAJOR HISTOCOMPATIBILITY COMPLEX	<i>Mhc</i> (Classes I, II; multiple haplotypes)			Crew <i>et al.</i> (1989, 1990)	
PANCREATIC RIBONUCLEASE	<i>MyoD</i>				
TUMOR NECOSIS FACTOR	<i>Tnf</i>			Crew <i>et al.</i>	

<sup>1</sup> All are autosomal.<sup>2</sup> Name and symbol changed to correspond to *Mus*. Obsolete names and symbols in parentheses.

**Table 3**  
**Formally Described Genetic Loci in Miscellaneous *Peromyscus* Species**

Species	Locus	Symbol and alleles	Mode of inheritance	Reference
<i>P. truei</i>	ESTERASE-1	<i>Es-1</i> <sup>100</sup> <i>Es-1</i> <sup>93</sup>	co-dominance	Zimmerman and Kilpatrick (1975)
<i>P. eremicus</i>	PECTORAL SPOT	<i>psp</i>	recessive	Huestis (1925) Clark (1938)
<i>P. californicus</i>	HAIRLESSNESS	<i>hm</i>	recessive ?	Packchianian and Louts (1984)
<i>P. californicus</i>	snRNA	<i>snRNA</i>		

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## GENETIC LINKAGE IN *PEROMYSCUS*. 2001 UPDATE.

Most linkage data for *Peromyscus* to date has been generated by formal recombination genetics. However, partial banding homology between Chromosome 1 of *Rattus* and Chromosome 1 of *Peromyscus* (14) suggests that Linkage Group (LG) I is probably located on Chromosome 1 in deer mouse, as is the homologous group in rat (7). Two loci, *Tk-1* and *Tp53*, have been assigned to Chromosome 13 by fluorescence in situ hybridization (FISH) (21). The diploid chromosome number of all *Peromyscus* species is  $2N = 48$  (6). The standard karyotype was recently revised (11).

Linkage data for the deer mouse (*P. maniculatus*) collected before 1972 are summarized by Robinson (17, 18). The system of assigning linkage groups on the basis of a single marker employed during the 1940s and 50s (2, 15) is no longer used. "Group IV" in the earlier system is now Group II, and old Groups "II" and "III" have been abandoned. In the interim since Robinson's review several additional linkages have been added (3, 8, 10, 19). The current status of the linkage map for the deer mouse and its sibling species, *P. polionotus*, is represented in the accompanying figure. Eight linkage groups are now established by formal genetics and another is tentative.

The order of loci in LG I, reported informally by R.R. Huestis and K. Silliman in an unpublished communication (17, 9), has been recently revised from previously unpublished data of W.B. McIntosh and K. Dodson. Linkage of *Tf* and *Lap* is tentative (8), but is homologous with a similar linkage in *Mus*. The *Pep-2* locus is provisionally assigned to LG VI proximal to *Alb*, but has not been mapped further (10).

Positive, but not significant, lod scores suggesting possible linkage between the gene pairs *Adh* - *Pgd*, *Adh* - *Got-1*, *Adh* - *Idh*, *Alb* - *Pept-1*, *Alb* - *Sdh* and *Est-4* - *Sdh*, respectively, were reported by Baccus *et al.* (1). Subsequent information indicates that *Adh-1* and *Got-1* are independent, as are the *Alb* and *Sdh-1* loci (10).

The *Hbe* locus is part of the triplicated beta globin site (*Hbb*), according to Snyder (19). Unpublished data from Snyder maps the position of the *Gpi-1* and *Hbe* loci relative to the albino (*c*) and pink-eyed dilution (*p*) loci. Silliman (unpub.) proposed that there is a duplication, *f'*, closely linked to the *f* locus. The Pm blood group locus, formerly designated "*Pm*", is redesignated *Ea<sub>Pm</sub>*. Linkage of the agouti locus to waltzing (*v*) was tested using the dominant wide-band agouti allele *A<sup>Nb</sup>* (15).

Two significant markers on the *Peromyscus* linkage map, *d* and *v*, are now extinct in laboratory stocks of deermice. The "flexed tail" trait which occurs in a laboratory stock may not be identical by descent with the original trait used in early linkage studies, but it maps to the same location in LG I.

The *c*, *p*, *a* and *b* coat color loci are phenotypically essentially identical to their counterparts in *Mus* and *Rattus*, and are assumed to be homologous. Enzyme and other protein loci are assumed to be homologous to counterparts in *Mus*, human and other mammals. Specific homologies between esterases and peptidases are not firm, but two clusters of common esterases in *Peromyscus* LG VIII are probably homologous to the esterase clusters on *Mus* Chromosome 8 and *Rattus* LG V. Erythrocytic esterase (*Es-3*, formerly "*Es-1*") of *Peromyscus* is very likely homologous with *Es-3* of *Mus* and is now known to be independent of the esterase loci in LG 8 (D.L. Covington *et al.*, unpub.)

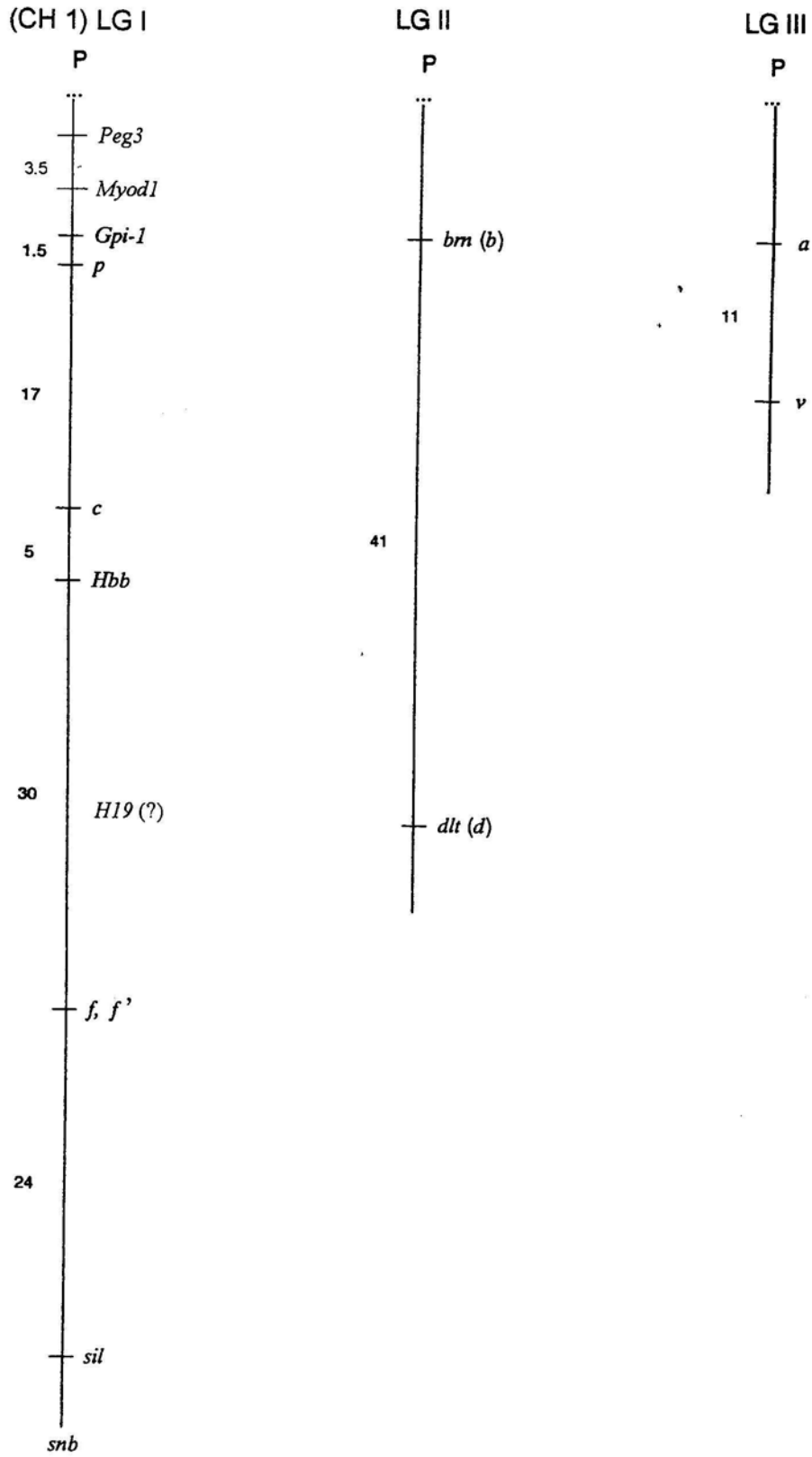
Several non-specific DNA markers (RAPDs and microsatellites) have been provisionally mapped by McClellan and collaborators (unpub.)

## References

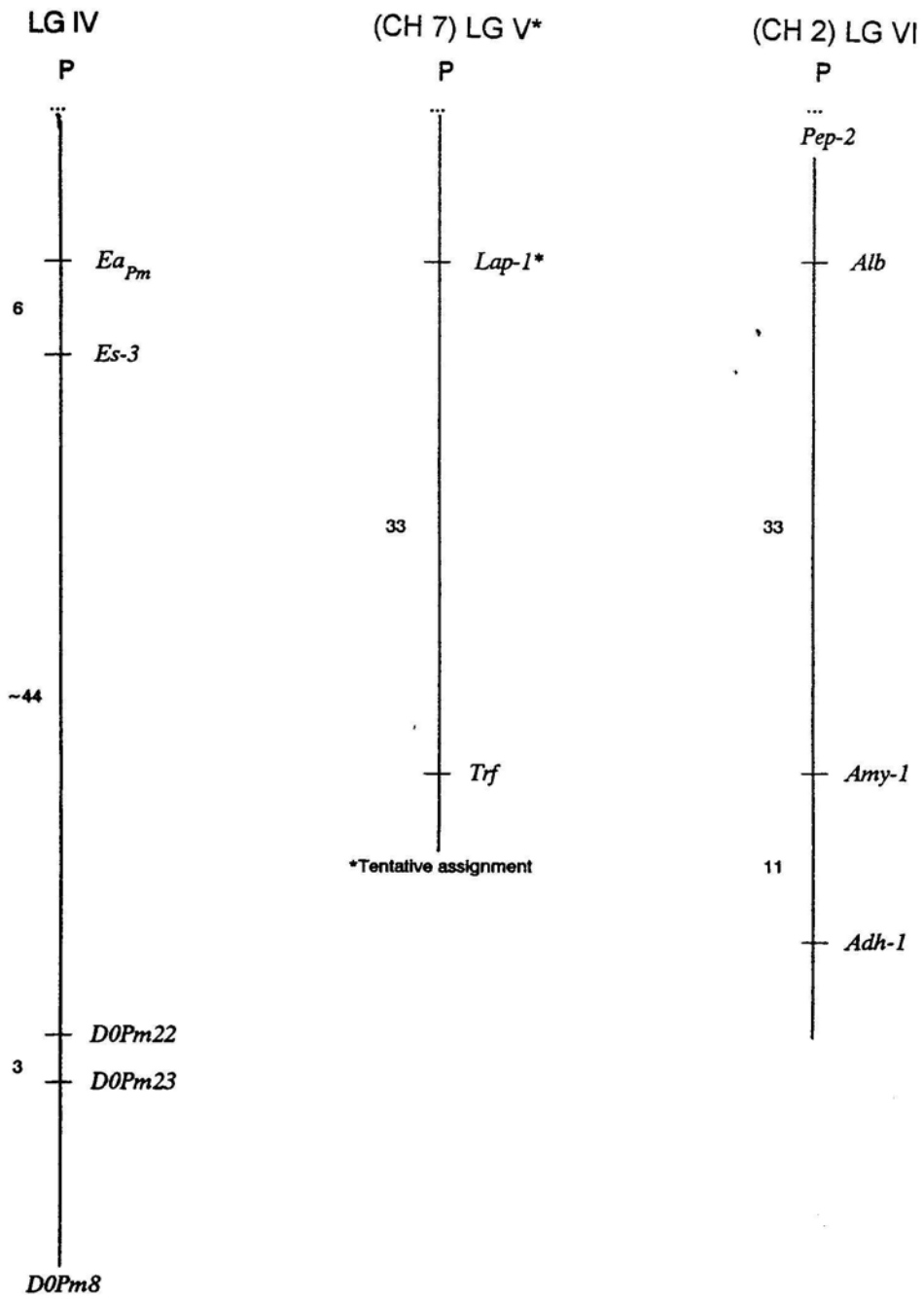
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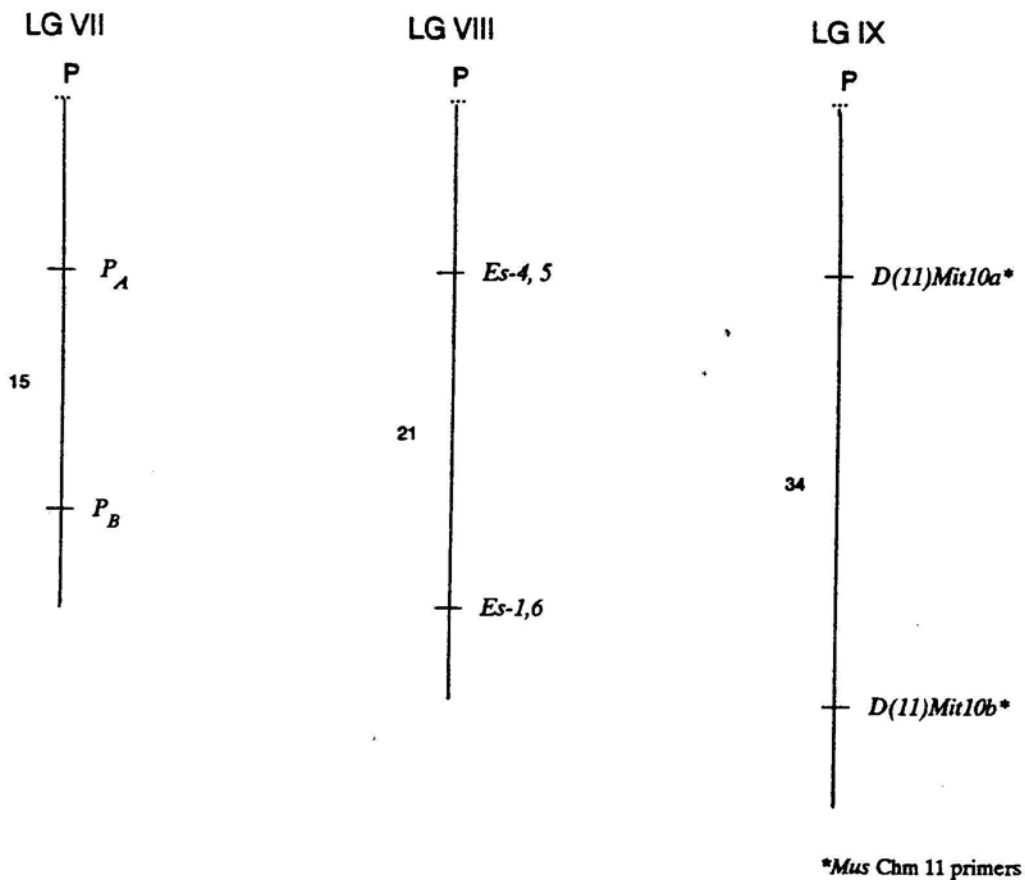
PEROMYSCUS LINKAGE MAP 2001



Peromyscus Linkage Map (Continued).



Peromyscus Linkage Map (Continued).



CHM 13



## PEROMYSCUS CYTOGENETICS

The study of chromosomes of peromyscine rodents has advanced through several stages, beginning in the 1930s with simple drawings of metaphase configurations accompanied by counts (Cross, 1938). By the 1960s improved methods employing induced cell division of bone marrow or other tissues using colchicine, followed by hypotonic treatment and Giemsa staining gave reliable counts of individual chromosome arm numbers, and revealed extensive polymorphism in arm number within and among species of *Peromyscus*, and also demonstrated that chromosome number was remarkably conserved within the genus, all having a normal diploid number = 48 (Hsu and Arrighi, 1966; 1968). Furthermore, much of the variation within species in arm number, as revealed by C-banding, was due to heterochromatic additions, rather than to inversions, whereas euchromatic changes were attributable to inversions.

Further advances in Giemsa-band methodology permitted recognition of individual chromosome bands within arms. Based on banding patterns, evolutionary changes in *Peromyscus* chromosome morphology were amenable to analysis and a phylogenetic model was constructed (Greenbaum and Baker, 1978). G-banding technology also made possible comparisons of the *Peromyscus* karyotype with those of other rodent genera (Koop *et al.* 1984). Stangl and Baker (1984) and Rogers *et al.* (1984) demonstrated that phylogenies derived from karyotypes were consistent with those based on allozymes and morphology. The cytogenetic nomenclature and the karyotype for *Peromyscus* was standardized by Greenbaum *et al.* (1994)<sup>1</sup>. The ideogram on the facing page is based on this standard. Translocation polymorphism has not been observed within or among *Peromyscus* species.

More recently fluorescence *in situ* hybridization (FISH) of specific gene probes or whole chromosome probes to specific chromosomes allows assignment of genes or groups of genes to specific chromosomes or chromosome arms (Wang *et al.* 1995; Dawson *et al.* 1999). FISH has the potential to demonstrate homologous chromosome regions among species of different taxa, *e.g.* house mouse (*Mus*) and *Peromyscus*. Based on FISH methodology all loci on *Mus* Chr 7 are located on the *ad*-centromeric two thirds of *Peromyscus* Chr 1q. About 90% of *Mus* Chr 3 genes are located in two disjunct regions of *Peromyscus* Chr 2q. All *Mus* Chr 9 genes are located on *Peromyscus* Chr 7.

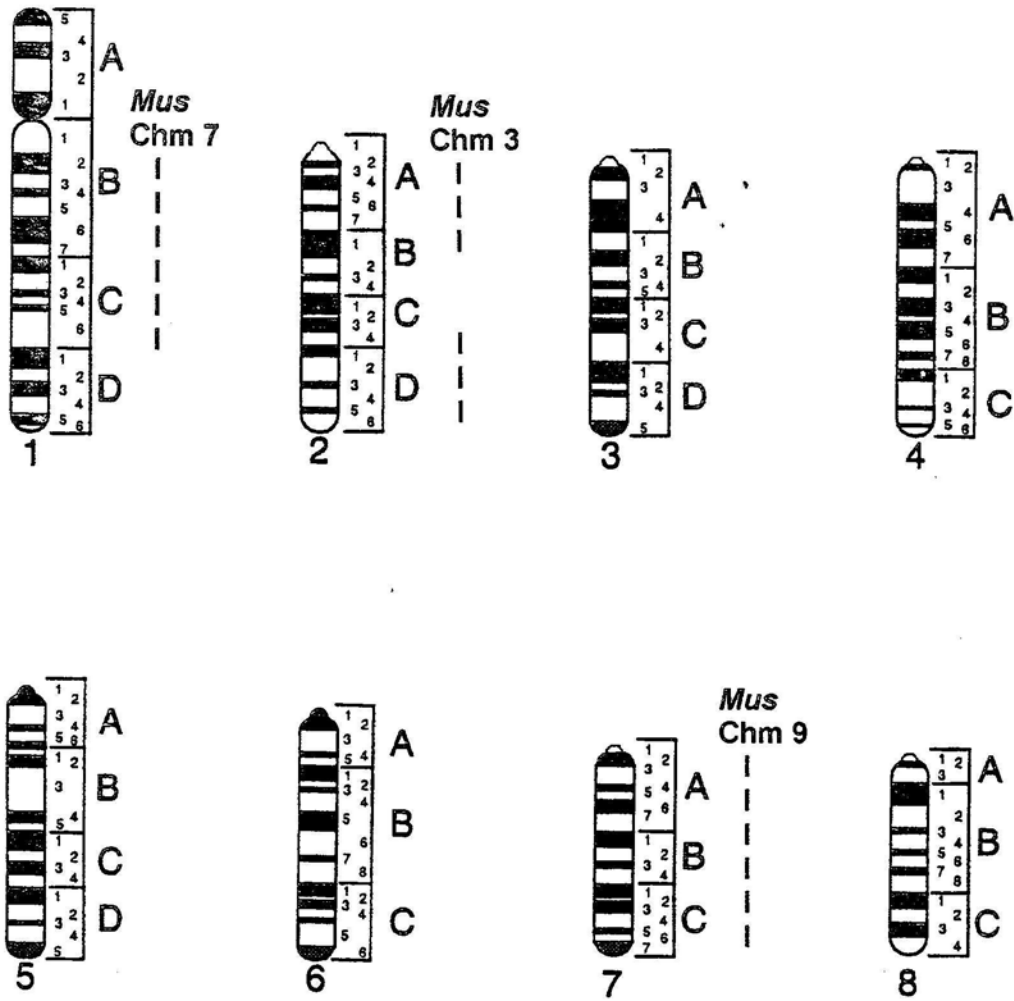
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Wang Z. *et al.* 1995. *Cytogenet Cell Genet* 69:97-100.

<sup>1</sup> Available in limited number, upon request, from the *Peromyscus* Genetic Stock Center.

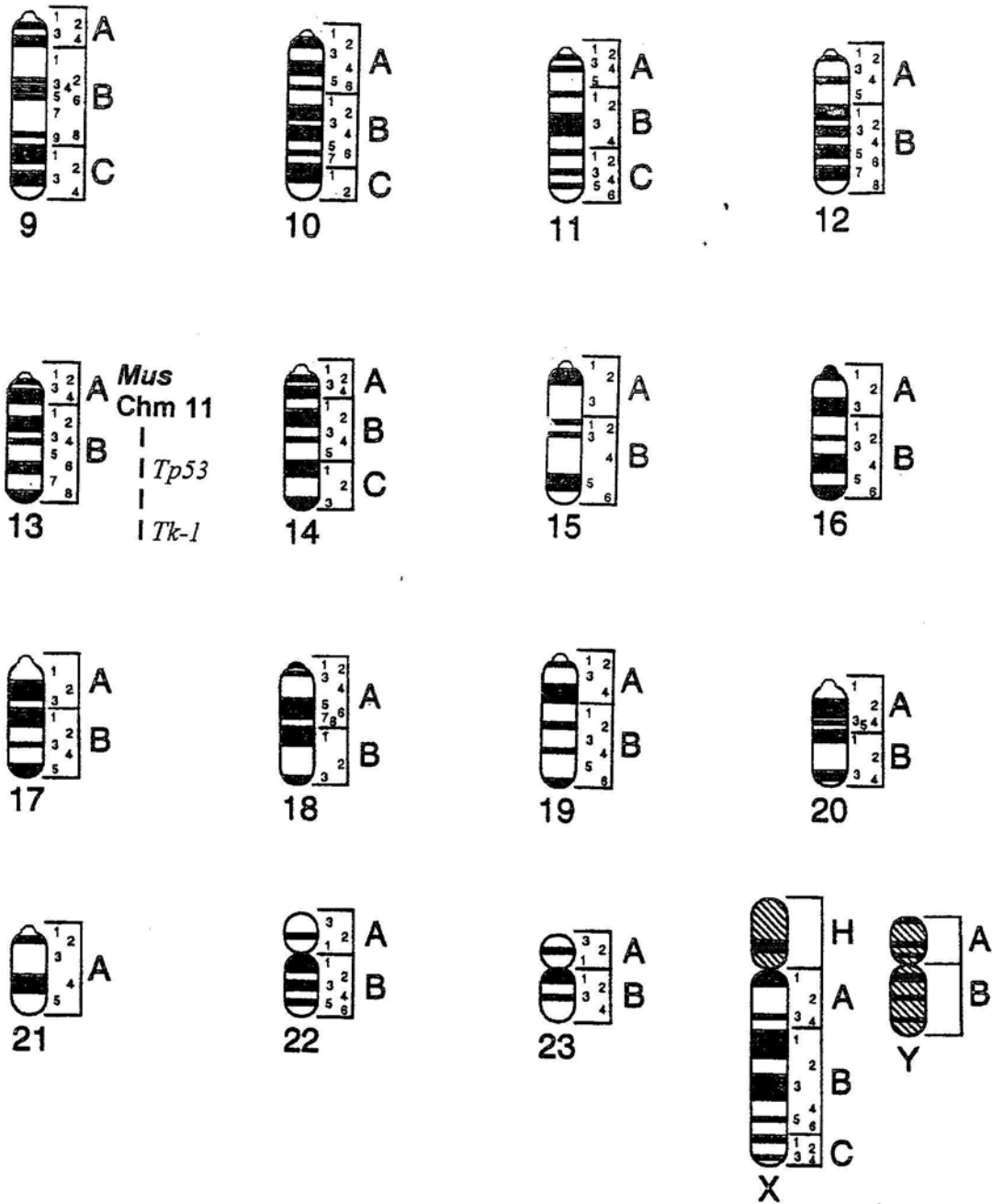
PEROMYSCUS STANDARD IDEOGRAM



*Peromyscus* Ideogram\* showing regions of homology with *Mus* chromosomes as demonstrated with FISH. (Wang *et al.* 1995; Dawson *et al.* 1999). A substantial portion of *Mus* whole Chr 11 probe hybridizes to *Peromyscus* Chr 13, consistent with Wang *et al.* 1995. (Jane Scalzi. Unpublished). The ideogram is based on the presumed "primitive" *Peromyscus* karyotype as exhibited in *P. boylii*. Other peromyscine species typically show inversion variation from the standard, changing the centromeric position and/or the number of acrocentric vs. bi-armed autosomes.

\*Modified from Greenbaum *et al.* (1994). *Cytogenet. Cell Genet.* p.184

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*Peromyscus* Ideogram showing regions of homology with *Mus* chromosomes.  
 (Continued)

## 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 (See PN #18 and #20). 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. Presumptive loci are not listed in the *Peromyscus* Gene Catalog.

In this issue the Tables summarize presumptive variant loci identified in the *Peromyscus* species groups to date. Similar tables in PN #16 list variant presumptive loci reported in other *Peromyscus* species and species groups.

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 might 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*. Therefore, the tables serve as a reference to locate 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 refereed research publications, abstracts excluded, are listed in the tables. References are listed at the foot of each table. Please call our attention to omissions, corrections or newly published additions.

**Table 1. VARIANT PROTEIN LOCI REPORTED FROM  
NATURAL POPULATIONS OF THE *PEROMYSCUS LEUCOPUS* SPECIES GROUP**

<b>Protein</b>	<b>Locus</b>	<b>Species</b>	<b>References</b>
Acid phosphatase	<i>Acp-1</i>	<i>P. leucopus</i>	Nelson <i>et al.</i> (1987)
Aconitase	<i>Acon</i>	<i>P. leucopus</i>	Schnake-Greene <i>et al.</i> (1990)
Adenosine deaminase	<i>Ada-1</i>	<i>P. leucopus</i>	Krohne and Baccus (1985)
Albumin	<i>Alb</i>	<i>P. leucopus</i> <i>P. gossypinus</i>	Brown and Welser (1968) Jensen and Rasmussen (1971) Browne (1977) Price and Kennedy (1984) Robbins <i>et al.</i> (1985)
Alcohol dehydrogenase	<i>Adh-1</i>	<i>P. leucopus</i>	Robbins <i>et al.</i> (1985) Nelson <i>et al.</i> (1987) 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) Merriam <i>et al.</i> (1989) Palas <i>et al.</i> (1992)
Carbonic anhydrase	<i>Ca-1</i>	<i>P. leucopus</i>	Wilmot and Underhill (1972) Krohne and Baccus (1985)
Creatine kinase-1	<i>Ck-1</i>	<i>P. leucopus</i>	Schnake-Greene <i>et al.</i> (1990)
NADH diaphorase	<i>Dia-1</i>	<i>P. leucopus</i>	Nelson <i>et al.</i> (1987)

(Continued)



Table 1. Variant protein loci in *P. leucopus* group natural populations (Continued)

Protein	Locus	Species	References
Esterase	<i>Es-1</i>	<i>P. leucopus</i>	Price and Kennedy (1980)
	<i>Es-2</i>	<i>P. gossypinus</i>	Wilmot and Underhill (1973)
	<i>Es-3</i>		Browne (1977)
	<i>Es-4</i>		Smith <i>et al.</i> (1984)
	<i>Es-5</i>		Robbins <i>et al.</i> (1985)
	<i>Es-9</i>		Nelson <i>et al.</i> (1987) Tolliver <i>et al.</i> (1987) Schnake-Greene <i>et al.</i> (1990)
Fumarate hydratase	<i>Fh-2</i>	<i>P. leucopus</i>	Nelson <i>et al.</i> (1987)
L-glutamate dehydrogenase	<i>Gld-1</i>	<i>P. leucopus</i>	Nelson <i>et al.</i> (1987)
Glutamate oxaloacetate transaminase	<i>Got-1</i>	<i>P. leucopus</i>	Price and Kennedy (1980) Nelson <i>et al.</i> (1987)
	<i>Got-2</i>		
α-Glycerophosphate dehydrogenase	<i>Gpd-1</i>	<i>P. leucopus</i>	Mascarello and Shaw (1973) Browne (1977) Robbins <i>et al.</i> (1985)
	<i>Gpd-2</i>	<i>P. gossypinus</i>	
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>	<i>P. leucopus</i>	Price and Kennedy (1980) Robbins <i>et al.</i> (1985) Nelson <i>et al.</i> (1987) Rogers and Engstrom (1992)
	( <i>Pgi-1</i> )	<i>P. gossypinus</i>	
Hemoglobin	<i>Hb</i>	<i>P. leucopus</i>	Foreman (1960)
		<i>P. gossypinus</i>	Foreman (1966) Price and Kennedy (1980)
Isocitrate dehydrogenase	<i>Icd-1</i>	<i>P. gossypinus</i>	Robbins <i>et al.</i> (1985) Nelson <i>et al.</i> (1987) Schnake-Green <i>et al.</i> (1990)
	( <i>Idh-1</i> )		
	<i>Icd-2</i>		
Lactate dehydrogenase	<i>Ldh-1</i>	<i>P. leucopus</i>	Robbins <i>et al.</i> (1980) Nelson <i>et al.</i> (1980)

(Continued)

**Table 1. Variant protein loci in *P. leucopus* group natural populations (Continued)**

<b>Protein</b>	<b>Locus</b>	<b>Species</b>	<b>References</b>
Malate dehydrogenase-2	<i>Mdh-2</i>	<i>P. leucopus</i>	Schnake-Greene <i>et al.</i> (1990)
Malic enzyme	<i>Me-1</i>	<i>P. leucopus</i>	Nelson <i>et al.</i> (1987) Schnake-Greene <i>et al.</i> (1990)
Mannose phosphoisomerase	<i>Mpi-1</i>	<i>P. leucopus</i>	Rogers and Engstrom (1992)
Major urinary protein	<i>Mup-1</i>	<i>P. leucopus</i> <i>P. gossypinus</i>	Cain <i>et al.</i> (1992)
Nucleoside phosphorylase	<i>Np-1</i>	<i>P. gossypinus</i>	Smith <i>et al.</i> (1984) Nelson <i>et al.</i> (1987) Schnake-Greene <i>et al.</i> (1990)
Peptidase	<i>Pep-2</i> ( <i>Pep-B</i> )	<i>P. leucopus</i>	Nelson <i>et al.</i> (1987) Schnake-Greene <i>et al.</i> (1990)
Phosphogluconate dehydrogenase	<i>Pgd-1</i>	<i>P. leucopus</i>	Robbins <i>et al.</i> (1985) Nelson <i>et al.</i> (1987)
Phosphoglucose mutase	<i>Pgm-1</i> <i>Pgm-3</i>	<i>P. leucopus</i> <i>P. gossypinus</i>	Mascarello and Shaw (1973) Browne (1977) Price and Kennedy (1980) Robbins <i>et al.</i> (1985) Nelson <i>et al.</i> (1987)
Sorbitol dehydrogenase	<i>Sdh-1</i>	<i>P. leucopus</i>	Nelson <i>et al.</i> (1987)
Superoxide dismutase	<i>Sod-1</i> ( <i>Ipo-1, Tetra-1</i> ) <i>Sod-2</i>	<i>P. leucopus</i> <i>P. gossypinus</i>	Mascarello and Shaw (1973) Browne (1977) Price and Kennedy (1980) Robbins <i>et al.</i> (1985) Tolliver <i>et al.</i> (1987) Nelson <i>et al.</i> (1987)

(Continued)

Table 1. Variant protein loci in *P. leucopus* group natural populations (Continued)

Protein	Locus	Species	References
Transferrin	<i>Trf</i>	<i>P. leucopus</i> <i>P. gossypinus</i>	Price and Kennedy (1980) Robbins <i>et al.</i> (1985) Krohne and Baccus (1985)
Xanthine dehydrogenase	<i>Xdh-1</i>	<i>P. leucopus</i>	Nelson <i>et al.</i> (1987)
Non-specific proteins			
Plasma protein	<i>Pprt-1</i>	<i>P. leucopus</i>	Krohne and Baccus (1985)
General protein	<i>Gp</i>		Schnake-Greene <i>et al.</i> (1990)

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Table 2. VARIANT PROTEIN LOCI REPORTED FROM  
NATURAL POPULATIONS OF THE *PEROMYSCUS MANICULATUS* SPECIES GROUP

Protein	Locus	Species <sup>1</sup>	Reference
Aconitase	<i>Acon-1</i>	<i>P. maniculatus</i>	Meagher (1999)
Acid phosphatase	<i>Acp-1</i>	<i>P. maniculatus</i>	Baccus and Wolff (1989)
Adenosine deaminase	<i>Ada-1</i>	<i>P. maniculatus</i>	Baccus and Wolff (1989)
Alcohol dehydrogenase	<i>Adh-1</i>	<i>P. maniculatus</i> <i>P. melanotis</i>	Avise <i>et al.</i> (1979) Baccus <i>et al.</i> (1980) Massey and Joule (1981) Calhoun <i>et al.</i> (1988) Baccus and Wolff (1989) Meagher (1999)
Albumin	<i>Alb</i>	<i>P. maniculatus</i> <i>P. polionotus</i>	Rasmussen (1970) Jensen and Rasmussen (1971) Selander <i>et al.</i> (1971) Avise <i>et al.</i> (1974) Biggers and Dawson (1971) Loudenslager (1978) Baccus <i>et al.</i> (1980) Calhoun <i>et al.</i> (1988)
Aldolase	<i>Aldo-1</i>	<i>P. maniculatus</i>	Baccus and Wolff (1989)
Alkaline phosphatase	<i>Ak-2</i>	<i>P. maniculatus</i>	Meagher (1999)
Amylase	<i>Amy-1</i>	<i>P. maniculatus</i>	Aquadro and Patton (1980) Palas <i>et al.</i> (1992)
Carbonic anhydrase	<i>Ca-1</i>	<i>P. maniculatus</i>	Baccus and Wolff (1989)
Catalase	<i>Cat-1</i>	<i>P. maniculatus</i>	Baccus and Wolff (1989)

(Continued)

Table 2. Variant protein loci from *P. maniculatus* group populations (Continued).

Protein	Locus	Species <sup>1</sup>	Reference
Esterase	<i>Es-1</i>	<i>P. maniculatus</i>	Rasmussen and Jensen (1971)
	<i>Es-2</i>	<i>P. polionotus</i>	Selander <i>et al.</i> (1971)
	<i>Es-3</i>		Peck and Biggers (1975)
	<i>Es-4</i>		Gill (1976)
	<i>Es-5</i>		Loudenslager (1978)
	<i>Es-6</i>		Massey and Joule (1981)
	<i>Es-7</i>		Foltz (1981)
	<i>Es-8</i>		Aquadro and Kilpatrick (1981) Mewaldt and Jenkins (1986)
Glucose dehydrogenase	<i>Gdh-1</i>	<i>P. maniculatus</i>	Mewaldt and Jenkins (1986) Baccus and Wolff (1989)
Glutamate oxaloacetate transaminase (Aspartate aminotransferase)	<i>Got-1</i>	<i>P. maniculatus</i>	Selander <i>et al.</i> (1971)
	<i>Got-2</i>	<i>P. polionotus</i>	Gill (1976)
	<i>(Aat)</i>	<i>P. melanotis</i>	Loudenslager (1978)
			Avisé <i>et al.</i> (1979)
			Baccus <i>et al.</i> (1980)
			Massey and Joule (1981)
			Aquadro and Kilpatrick (1981) Calhoun <i>et al.</i> (1988) Baccus and Wolff (1989) Mewaldt and Jenkins (1986) Meagher (1999)
Glucose-6-phosphate dehydrogenase	<i>G6pd-1</i> ( <i>H6pd-1</i> )	<i>P. maniculatus</i>	Shaw and Barto (1965) Loudenslager (1978) Aquadro and Kilpatrick (1981)
$\alpha$ -Glycerophosphate dehydrogenase	<i>Gpd-1</i>	<i>P. maniculatus</i> <i>P. polionotus</i> <i>P. oreas</i>	Selander <i>et al.</i> (1971) Mascarello and Shaw (1973) Gill (1976) Avisé <i>et al.</i> (1979) Calhoun <i>et al.</i> (1988) Baccus and Wolff (1989)
Glucose phosphate isomerase	<i>Gpi-1</i> ( <i>Pgi-1</i> )	<i>P. polionotus</i> <i>P. melanotis</i> <i>P. maniculatus</i>	Selander <i>et al.</i> (1971) Avisé <i>et al.</i> (1974) Avisé <i>et al.</i> (1979) Massey and Joule (1981) Foltz (1981) Baccus and Wolff (1989)

Table 2. Variant protein loci from *P. maniculatus* group populations (Continued).

Protein	Locus	Species <sup>1</sup>	Reference
Glutamate pyruvate transaminase	<i>Gpt-1</i>	<i>P. maniculatus</i>	Baccus and Wolff (1989)
Hemoglobin	<i>Hba</i> <i>Hbb</i>	<i>P. maniculatus</i> <i>P. polionotus</i> <i>P. melanotis</i>	Thompson <i>et al.</i> (1966) Ahl (1968) Foreman (1968) Rasmussen <i>et al.</i> (1968) Rasmussen (1970) Selander <i>et al.</i> (1971) Snyder (1978, 1980) Loudenslager (1978) Avisé <i>et al.</i> (1979) Massey and Joule (1981) Aquadro and Kilpatrick (1981) Chappell and Snyder (1984)
Haptoglobin	<i>Hpt</i>	<i>P. polionotus</i>	Peck and Biggers (1975)
Immunoglobulin (7S $\gamma$ )	<i>IgG</i>	<i>P. maniculatus</i>	Coe (1972)
Isocitrate dehydrogenase	<i>Idh-1</i> ( <i>Icd-1</i> )	<i>P. maniculatus</i> <i>P. oreas</i> <i>P. polionotus</i> <i>P. sejugis</i>	Mascarello and Shaw (1973) Baccus <i>et al.</i> (1980) Avisé <i>et al.</i> (1974) Massey and Joule (1981) Aquadro and Kilpatrick (1981) Calhoun <i>et al.</i> (1988) Baccus and Wolff (1989) Meagher (1999)
Lactate dehydrogenase	<i>Ldh-1</i> <i>Ldh-2</i>	<i>P. maniculatus</i> <i>P. polionotus</i> <i>P. melanotis</i>	Selander <i>et al.</i> (1971) Avisé <i>et al.</i> (1979) Massey and Joule (1981) Mewaldt and Jenkins (1986) Calhoun <i>et al.</i> (1988)
Malate dehydrogenase	<i>Mdh-1</i> <i>Mdh-2</i>	<i>P. maniculatus</i> <i>P. polionotus</i>	Selander <i>et al.</i> (1971) Massey and Joule (1981)

(Continued)

**Table 2. Variant protein loci from *P. maniculatus* group populations (Continued).**

<b>Protein</b>	<b>Locus</b>	<b>Species<sup>1</sup></b>	<b>Reference</b>
Malic enzyme	<i>Me-1</i>	<i>P. maniculatus</i>	Baccus and Wolff (1989)
Nucleoside phosphorylase	<i>Np-1</i>	<i>P. maniculatus</i>	Baccus and Wolff (1989) Meagher (1999)
Peptidase	<i>Pep-1</i> ( <i>Pep-B</i> ) <i>Pep-2</i>	<i>P. maniculatus</i> <i>P. melanotis</i>	Avise <i>et al.</i> (1979) Baccus <i>et al.</i> (1980) Massey and Joule (1981) Calhoun <i>et al.</i> (1988) Baccus and Wolff (1989)
6-Phosphogluconate dehydrogenase	<i>Pgd-1</i>	<i>P. maniculatus</i> <i>P. polionotus</i> <i>P. oreas</i>	Selander <i>et al.</i> (1971) Mascarello and Shaw (1973) Gill (1976) Avise <i>et al.</i> (1979) Baccus <i>et al.</i> (1980) Massey and Joule (1981) Foltz (1981) Mewaldt and Jenkins (1986) Baccus and Wolff (1989)
Phosphoglucomutase	<i>Pgm-1</i> <i>Pgm-2</i> <i>Pgm-3</i> <i>Pgm-4</i>	<i>P. maniculatus</i> <i>P. polionotus</i> <i>P. melanotis</i>	Selander <i>et al.</i> (1971) Mascarello and Shaw (1973) Gill (1976) Avise <i>et al.</i> (1979) Massey and Joule (1981) Aquadro and Kilpatrick (1981) Baccus and Wolff (1989)
Sorbitol dehydrogenase	<i>Sdh-1</i>	<i>P. maniculatus</i>	Baccus <i>et al.</i> (1980) Massey and Joule (1981)
Superoxide dismutase	<i>Sod-1</i>	<i>P. maniculatus</i>	Baccus and Wolff (1989) Meagher (1999)

(Continued)

Table 2. Variant protein loci from *P. maniculatus* group populations (Continued).

Protein	Locus	Species <sup>1</sup>	Reference
Transferrin	<i>Trf</i>	<i>P. maniculatus</i> <i>P. polionotus</i>	Rasmussen (1970) Biggers and Dawson (1971) Selander <i>et al.</i> (1971) Avisé <i>et al.</i> (1974) Gill (1976) Redfield (1976) Loudenslager (1978) Avisé <i>et al.</i> (1979) Baccus <i>et al.</i> (1980) Massey and Joule (1981) Foltz (1981)
Urinary proteins		<i>P. maniculatus</i>	Cain <i>et al.</i> (1992)
Miscellaneous non-specific proteins (pre- and postalbumins <i>etc.</i> )		<i>P. maniculatus</i>	Mascarello and Shaw (1973) Gill (1976) Baccus and Wolff (1989)

<sup>1</sup>Species from which protein variants were obtained.

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**Table 3. VARIANT PROTEIN LOCI REPORTED FROM  
NATURAL POPULATIONS OF THE *PEROMYSCUS BOYLII* SPECIES GROUP**

<b>Protein</b>	<b>Locus</b>	<b>Species</b>	<b>References</b>
Alcohol dehydrogenase	<i>Adh</i>	<i>P. attwateri</i>	Sugg <i>et al.</i> (1990)
Albumin	<i>Alb</i>	<i>P. boylii</i> <i>P. pectoralis</i>	Jensen and Rasmussen (1971) Avise <i>et al.</i> (1974) Kilpatrick and Zimmerman (1975) Zimmerman <i>et al.</i> (1975) Kilpatrick and Zimmerman (1976a) Kilpatrick (1984) Rennert and Kilpatrick (1986) Werbitsky and Kilpatrick (1987)
Amylase	<i>Amy-1</i>	<i>P. boylii</i>	Rennert and Kilpatrick (1986) Rennert and Kilpatrick (1987)
Carbonic anhydrase	<i>Car-1</i> <i>Car-3</i>	<i>P. boylii</i> <i>P. beatae</i>	Rennert and Kilpatrick (1986) Rennert and Kilpatrick (1987) Sullivan and Kilpatrick (1991)
Catalase	<i>Cas-1</i>	<i>P. attwateri</i>	Sugg <i>et al.</i> (1990)
Creatine kinase	<i>Ck-1</i>	<i>P. attwateri</i>	Schnake-Greene <i>et al.</i> (1990)
Esterase	<i>Es-1</i> <i>Es-3</i> <i>Es-4</i> <i>Es-5</i> <i>Es-6</i> <i>Es-7</i>	<i>P. boylii</i> <i>P. attwateri</i> <i>P. pectoralis</i> <i>P. polius</i> <i>P. beatae</i>	Rasmussen and Jensen (1971) Avise <i>et al.</i> (1974) Kilpatrick and Zimmerman (1975) Zimmerman <i>et al.</i> (1975) Kilpatrick and Zimmerman (1976a) Kilpatrick (1984) Rennert and Kilpatrick (1986) Rennert and Kilpatrick (1987) Sugg <i>et al.</i> (1990) Sullivan and Kilpatrick (1991)
Glucose dehydrogenase	<i>Gdh-1</i>	<i>P. attwateri</i>	Sullivan <i>et al.</i> (1991)

(Continued)

Table 3. Protein variants in *P. boyllii* group natural populations (Continued)

Protein	Locus	Species	References
Glutamate dehydrogenase	<i>Gdh-1</i>	<i>P. attwateri</i>	Sugg <i>et al.</i> (1990)
Glutamate oxaloacetate transaminase	<i>Got-1</i>	<i>P. boyllii</i> <i>P. pectoralis</i> <i>P. attwateri</i> <i>P. simulans</i>	Awise <i>et al.</i> (1974) Kilpatrick and Zimmerman (1975) Zimmerman <i>et al.</i> (1975) Kilpatrick and Zimmerman (1976a) Kilpatrick (1984) Rennert and Kilpatrick (1986) Rennert and Kilpatrick (1987) Sullivan <i>et al.</i> (1991)
a-glycerophosphate dehydrogenase	<i>Gpd-1</i> <i>Gpd-2</i>	<i>P. boyllii</i> <i>P. pectoralis</i>	Mascarello and Shaw (1973) Awise <i>et al.</i> (1974) Janecek (1990)
Glucose-6-phosphate dehydrogenase	<i>G6pd-1</i> ( <i>H6pd-1</i> )	<i>P. pectoralis</i> <i>P. boyllii</i>	Awise <i>et al.</i> (1974) Kilpatrick (1984) Rennert and Kilpatrick (1986) Rennert and Kilpatrick (1987) Sullivan <i>et al.</i> (1991) Rogers and Engstrom (1992)
Hemoglobin	<i>Hb-1</i> <i>Hb-2</i>	<i>P. boyllii</i> <i>P. pectoralis</i> <i>P. attwateri</i> <i>P. simulans</i>	Rasmussen <i>et al.</i> (1968) Awise <i>et al.</i> (1974) Kilpatrick and Zimmerman (1975) Zimmerman <i>et al.</i> (1975) Kilpatrick and Zimmerman (1976a) Kilpatrick and Zimmerman (1976b) Kilpatrick (1984) Sullivan <i>et al.</i> (1991)
Hexose-6-Phosphate dehydrogenase	<i>H6pd-1</i>	<i>P. boyllii</i>	Rennert and Kilpatrick (1986) Rennert and Kilpatrick (1987)

(Continued)

**Table 3. Protein variants in *P. boyllii* group natural populations (Continued)**

Protein	Locus	Species	References
Isocitrate dehydrogenase	<i>Idh-1</i> ( <i>Icd-1</i> ) <i>Icd-2</i>	<i>P. boyllii</i> <i>P. pectoralis</i> <i>P. attwateri</i> <i>P. simulus</i>	Mascarello and Shaw (1973) Avise <i>et al.</i> (1974) Kilpatrick and Zimmerman (1976a) Kilpatrick (1984) Rennert and Kilpatrick (1986) Rennert and Kilpatrick (1987) Schnake-Greene <i>et al.</i> (1990) Sugg <i>et al.</i> (1990) Janecek (1990) Sullivan <i>et al.</i> (1991)
Lactate dehydrogenase	<i>Ldh-1</i> <i>Ldh-2</i> <i>Ldh-3</i>	<i>P. boyllii</i> <i>P. pectoralis</i> <i>P. polius</i> <i>P. attwateri</i>	Mascarello and Shaw (1973) Avise <i>et al.</i> (1974) Kilpatrick and Zimmerman (1975) Kilpatrick and Zimmerman (1976a) Kilpatrick (1984) Schnake-Greene <i>et al.</i> (1990) Sugg <i>et al.</i> (1990) Janecek (1990)
Leucine aminopeptidase	<i>Lap-1</i>	<i>P. boyllii</i> <i>P. attwateri</i>	Kilpatrick (1984) Janecek (1990)
Malate dehydrogenase	<i>Mdh-1</i> <i>Mdh-2</i>	<i>P. boyllii</i> <i>P. pectoralis</i> <i>P. attwateri</i>	Avise <i>et al.</i> (1974) Kilpatrick and Zimmerman (1976a) Schnake-Greene <i>et al.</i> (1990) Sugg <i>et al.</i> (1990) Janecek (1990)
Mannose phosphate isomerase	<i>Mpi-1</i>	<i>P. attwateri</i>	Sugg <i>et al.</i> (1990)
Nucleoside phosphorylase	<i>Np</i>	<i>P. attwateri</i>	Schnake-Greene <i>et al.</i> (1990) Sugg <i>et al.</i> (1990) Rogers and Engstrom (1992)
Peptidase	<i>Pep-1</i> <i>Pep-2</i>	<i>P. attwateri</i>	Schnake-Greene <i>et al.</i> (1990) Sugg <i>et al.</i> (1990) Janecek (1990)

(Continued)

Table 3. Protein variants in *P. boylei* group natural populations (Continued)

Protein	Locus	Species	References
Phosphogluconate dehydrogenase	<i>Pgd-1</i>	<i>P. boylei</i> <i>P. pectoralis</i> <i>P. attwateri</i>	Awise <i>et al.</i> (1974) Kilpatrick and Zimmerman (1975) Zimmerman <i>et al.</i> (1975) Kilpatrick and Zimmerman (1976a) Sugg <i>et al.</i> (1990) Janecek (1990)
Phosphoglucose isomerase	<i>Pgi-1</i>	<i>P. boylei</i> <i>P. pectoralis</i> <i>P. attwateri</i> <i>P. simulus</i>	Awise <i>et al.</i> (1974) Kilpatrick (1984) Rennert and Kilpatrick (1986) Rennert and Kilpatrick (1987) Sullivan <i>et al.</i> (1991) Rogers and Engstrom (1992)
Phosphoglucomutase	<i>Pgm-1</i> <i>Pgm-2</i> <i>Pgm-3</i>	<i>P. boylei</i> <i>P. pectoralis</i> <i>P. attwateri</i>	Mascarello and Shaw (1973) Awise <i>et al.</i> (1974) Kilpatrick and Zimmerman (1976a) Rennert and Kilpatrick (1986) Rennert and Kilpatrick (1987) Sugg <i>et al.</i> (1990) Janecek (1990)
Sorbitol dehydrogenase	<i>Sdh-1</i>	<i>P. boylei</i>	Janecek (1990)
Superoxide dismutase	<i>Sod-2</i>	<i>P. boylei</i>	Janecek (1990)
Transferrin	<i>Trf</i>	<i>P. boylei</i> <i>P. pectoralis</i> <i>P. attwateri</i> <i>P. polius</i>	Rasmussen and Koehn (1966) Awise <i>et al.</i> (1974) Kilpatrick and Zimmerman (1975) Zimmerman <i>et al.</i> (1975) Kilpatrick and Zimmerman (1976a) Kilpatrick (1984) Rennert and Kilpatrick (1986) Rennert and Kilpatrick (1987) Werbitsky and Kilpatrick (1987) Sullivan <i>et al.</i> (1991)

(Continued)

**Table 3. Protein variants in *P. boylii* group natural populations (Continued)**

Protein	Locus	Species	References
Xanthine dehydrogenase	<i>Xdh-1</i>	<i>P. boylii</i> <i>P. attwateri</i>	Kilpatrick (1984)
Unspecified protein	"Gp"	<i>P. boylii</i>	Janecek (1990)

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Table 4. 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> <i>P. difficilis</i>	Brown and Welser (1968) Jensen and Rasmussen (1971) Johnson and Packard (1974) Zimmerman <i>et al.</i> (1975) Avise <i>et al.</i> (1979)
Esterase	<i>Es-1</i> <i>Es-2</i> <i>Es-3</i> <i>Es-4</i> <i>Es-5</i> <i>Es-6</i>	<i>P. truei</i> <i>P. difficilis</i>	Rasmussen and Jensen (1971) Johnson and Packard (1974) Zimmerman <i>et al.</i> (1975)
Glutamate oxaloacetate transaminase	<i>Got-1</i> ( <i>Aat-1</i> ) <i>Got-2</i>	<i>P. truei</i> <i>P. difficilis</i> <i>P. gratus</i>	Zimmerman <i>et al.</i> (1975) Avise <i>et al.</i> (1979) Janecek (1990) Sullivan <i>et al.</i> (1991)
$\alpha$ -glycerophosphate dehydrogenase	<i>Gpd-1</i> <i>Gpd-2</i>	<i>P. truei</i> <i>P. difficilis</i> <i>P. gratus</i>	Mascarello and Shaw (1973) Johnson and Packard (1974) Avise <i>et al.</i> (1979) Janecek (1990)
Isocitrate dehydrogenase	<i>Icd-1</i> ( <i>Idh-1</i> ) <i>Icd-2</i>	<i>P. truei</i> <i>P. difficilis</i> <i>P. gratus</i>	Mascarello and Shaw (1973) Johnson and Packard (1974) Avise <i>et al.</i> (1979) Rogers and Engstrom (1992) Janecek (1990)
Lactate dehydrogenase	<i>Ldh-1</i> <i>Ldh-2</i>	<i>P. truei</i> <i>P. gratus</i>	Mascarello and Shaw (1973) Janecek (1990)
Malate dehydrogenase	<i>Mdh-2</i>	<i>P. difficilis</i> <i>P. gratus</i>	Janecek (1990)

(Continued)

**Table 4. Variant protein loci in *P. truei* group natural populations (Continued)**

Protein	Locus	Species	References
Nucleoside phosphorylase	<i>Np-1</i>	<i>P. truei</i> <i>P. difficilis</i> <i>P. gratus</i>	Janecek (1990)
Peptidase	<i>Pep-1</i> <i>Pep-2</i> <i>Pep-3</i>	<i>P. difficilis</i> <i>P. gratus</i> <i>P. truei</i>	Janecek (1990)
6-Phosphogluconate dehydrogenase	<i>Pgd-1</i>	<i>P. truei</i> <i>P. difficilis</i> <i>P. gratus</i>	Mascarello and Shaw (1973) Johnson and Packard (1974) Zimmerman <i>et al.</i> (1975) Avisé <i>et al.</i> (1979) Janecek (1990) Sullivan <i>et al.</i> (1991)
Phosphoglucose isomerase	<i>Pgi-1</i>	<i>P. truei</i> <i>P. difficilis</i> <i>P. gratus</i>	Avisé <i>et al.</i> (1979) Sullivan <i>et al.</i> (1991)
Phosphoglucomutase	<i>Pgm-1</i> <i>Pgm-2</i> <i>Pgm-3</i>	<i>P. truei</i> <i>P. difficilis</i> <i>P. gratus</i>	Mascarello and Shaw (1973) Johnson and Packard (1974) Janecek (1990)
Sorbitol dehydrogenase	<i>Sdh-1</i>	<i>P. difficilis</i>	Janecek (1990)
Transferrin	<i>Trf</i>	<i>P. truei</i> <i>P. difficilis</i>	Avisé <i>et al.</i> (1979) Johnson and Packard (1974) Sullivan <i>et al.</i> (1991)

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**Table 5. 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) 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> <i>Idh-2</i>	<i>P. eremicus</i> <i>P. guardia</i> <i>P. interparietalis</i>	Avise <i>et al.</i> (1974)
Lactate dehydrogenase	<i>Ldh-1</i>	<i>P. eremicus</i> <i>P. caniceps</i>	Avise <i>et al.</i> (1974)
Phosphogluconate dehydrogenase	<i>Pgd-1</i>	<i>P. eremicus</i> <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> <i>P. caniceps</i>	Avise <i>et al.</i> (1974)
Transferrin	<i>Tf</i>	<i>P. eremicus</i> <i>P. merriami</i> <i>P. caniceps</i>	Rasmussen and Koehn (1966) Avise <i>et al.</i> (1974)

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

**Table 6. VARIANT PROTEIN LOCI REPORTED FROM NATURAL POPULATIONS  
OF THE *PEROMYSCUS MEXICANUS* SPECIES GROUP (*Sensu* Carleton, 1989)**

Protein	Locus	Species	References
Esterase (NADA)	<i>Es-3</i>	<i>P. mexicanus</i> <i>P. gymnotis</i>	Rogers and Engstrom (1992)
Glutamate oxaloacetate transaminase	<i>Got-1</i>	<i>P. mexicanus</i>	Rogers and Engstrom (1992)
6-Glycerophosphate dehydrogenase	<i>Gpd-1</i>	<i>P. mexicanus</i>	Rogers and Engstrom (1992)
Glucose phosphate isomerase	<i>Gpi-1</i>	<i>P. mexicanus</i> <i>P. gymnotis</i>	Rogers and Engstrom (1992)
Isocitrate dehydrogenase	<i>Icd-2</i> ( <i>Idh-2</i> )	<i>P. mexicanus</i>	Rogers and Engstrom (1992)
Malate dehydrogenase	<i>Mdh-1</i> <i>Mdh-2</i>	<i>P. yucatanicus</i> <i>P. mexicanus</i>	Rogers and Engstrom (1992)
Malic enzyme	<i>Me</i>	<i>P. mexicanus</i> <i>P. gymnotis</i>	Rogers and Engstrom (1992)
Mannose phosphoisomerase	<i>Mpi-1</i>	<i>P. mexicanus</i> <i>P. zarhynchus</i>	Rogers and Engstrom (1992)
Nucleoside phosphorylase	<i>Np-1</i>	<i>P. zarhynchus</i>	Rogers and Engstrom (1992)
Peptidase	<i>Pep-1</i> (B) <i>Pep-2</i> (D)	<i>P. mexicanus</i>	Rogers and Engstrom (1992)
Phosphoglucomutase	<i>Pgm-1</i> <i>Pgm-2</i>	<i>P. mexicanus</i> <i>P. zarhynchus</i>	Rogers and Engstrom (1992)

Reference:

Rogers, D.S. and M.D. Engstrom. 1992. *J. Mamm.* 73:55-69.

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

<b>Protein</b>	<b>Locus</b>	<b>Species</b>	<b>References</b>
Amylase	<i>Amy-1</i>	<i>P. aztecus</i> <i>P. spicilegus</i> <i>P. winkelmani</i>	Sullivan and Kilpatrick (1991)
Carbonic anhydrase	<i>Car-3</i>	<i>P. aztecus</i> <i>P. spicilegus</i> <i>P. winkelmani</i>	Sullivan and Kilpatrick (1991)
Esterase	<i>Es-1</i> <i>Es-2</i> <i>Es-5</i>	<i>P. aztecus</i> <i>P. spicilegus</i> <i>P. winkelmani</i>	Sullivan and Kilpatrick (1991)
Glutamate oxaloacetate transaminase	<i>Got-1</i>	<i>P. aztecus</i> <i>P. winkelmani</i>	Sullivan and Kilpatrick (1991)
Hemoglobin	<i>Hba-1</i>	<i>P. aztecus</i>	Sullivan and Kilpatrick (1991)
Isocitrate dehydrogenase	<i>Idh-1</i> ( <i>Icd-1</i> ) <i>Icd-2</i>	<i>P. aztecus</i> <i>P. spicilegus</i> <i>P. winkelmani</i>	Sullivan and Kilpatrick (1991)
Lactate dehydrogenase	<i>Ldh-2</i>	<i>P. spicilegus</i>	Sullivan and Kilpatrick (1991)
Malate dehydrogenase	<i>Mdh-1</i>	<i>P. winkelmani</i>	Sullivan and Kilpatrick (1991)
Malic enzyme	<i>Me-1</i> ( <i>Mod-1</i> )	<i>P. winkelmani</i>	Sullivan and Kilpatrick (1991)
Peptidase	<i>Pep-1</i> (A) <i>Pep-4</i> (D)	<i>P. aztecus</i> <i>P. winkelmani</i>	Sullivan and Kilpatrick (1991)
Phosphogluconate dehydrogenase	<i>Pgd-1</i>	<i>P. spicilegus</i> <i>P. winkelmani</i>	Sullivan and Kilpatrick (1991)

(Continued)

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

<b>Protein</b>	<b>Locus</b>	<b>Species</b>	<b>References</b>
Phosphoglucomutase	<i>Pgm-2</i> <i>Pgm-3</i>	<i>P. aztecus</i> <i>P. spicilegus</i> <i>P. winkelmanni</i>	Sullivan and Kilpatrick (1991)
Sorbitol dehydrogenase	<i>Sdh-1</i>	<i>P. aztecus</i> <i>P. winkelmanni</i>	Sullivan and Kilpatrick (1991)
Transferrin	<i>Trf</i>	<i>P. aztecus</i> <i>P. winkelmanni</i>	Sullivan and Kilpatrick (1991)

**Reference**

Sullivan, J.M. and C. W. Kilpatrick. 1991. *J. Mamm.* 72:681-696.

**Table 8. VARIANT PROTEIN LOCI REPORTED FROM  
NATURAL POPULATIONS OF *PEROMYSCUS FURVUS***

<b>Protein</b>	<b>Locus</b>	<b>Reference</b>
Acid phosphatase	<i>Acp</i>	Harris and Rogers (1999)
Adenosine deaminase	<i>Ada</i>	Harris and Rogers (1999)
Alopine dehydrogenase	<i>Alpdh</i>	Harris and Rogers (1999)
Albumin	<i>Alb</i>	Harris and Rogers (1999)
Arabinofuranosidase	<i>Arab</i>	Harris and Rogers (1999)
Glucose phosphate isomerase	<i>Gpi</i>	Harris and Rogers (1999)
Glyceraldehyde-3-phosphate dehydrogenase	<i>Gapdh</i>	Harris and Rogers (1999)
Iditol dehydrogenase	<i>Iddh</i>	Harris and Rogers (1999)
Isocitrate dehydrogenase	<i>IdhM</i> <i>IdhS</i>	Harris and Rogers (1999)
Lactate dehydrogenase-A	<i>LdhA</i>	Harris and Rogers (1999)
Malate dehydrogenase	<i>MdhM</i> <i>MdhS</i> <i>Mdhp</i>	Harris and Rogers (1999)

Table continued next page

**Table 8. Protein variants in *P. furvus* natural populations (Continued)**

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Mannose phosphate isomerase	<i>Mpi</i>	Harris and Rogers (1999)
Peptidase	<i>PepA</i> <i>PepB</i> <i>PepC</i> <i>PepF</i>	Harris and Rogers (1999)
Phosphoglucomutase	<i>Pgm</i>	Harris and Rogers (1999)
Purine-nucleoside phosphorylase	<i>Pnp</i>	Harris and Rogers (1999)
Sorbitol dehydrogenase	<i>Sod</i>	Harris and Rogers (1999)
Thiosulphate-sulfur transferase	<i>Tst</i>	Harris and Rogers (1999)

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Ref: Harris, D. and D.S. Rogers. J. Mamm. 80:530-544

**Table 9. VARIANT PROTEIN LOCI REPORTED FROM  
NATURAL POPULATIONS OF PEROMYSCUS (PODOMYS) FLORIDANUS**

<b>Protein</b>	<b>Locus</b>	<b>Reference</b>
Esterase	<i>Es-1</i> <i>Es-2</i> <i>Es-4</i>	Smith <i>et al.</i> (1973)
Glutamate oxaloacetate transaminase	<i>Got-1</i>	Smith <i>et al.</i> (1973)
Hexose-6-phosphate 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> ( <i>Icd-1</i> )	Smith <i>et al.</i> (1973) Rogers and Engstrom (1992)
Lactate dehydrogenase	<i>Ldh-1</i> <i>Ldh-2</i> <i>Ldh-3</i>	Smith <i>et al.</i> (1973) Rogers and Engstrom (1992)
Malic enzyme	<i>Mod-1</i>	Smith <i>et al.</i> (1973)
Phosphoglucomutase	<i>Pgm-1</i> <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)

**Reference:**

Rogers, D.S. and M.D. Engstrom. 1992. *J. Mamm.* 73:55-69.  
Smith, M.H., R.K. Selander and W.E. Johnson. 1973. *J. Mamm.* 54:1-13.

**Table 10. VARIANT PROTEIN LOCI REPORTED FROM  
NATURAL POPULATIONS OF *PEROMYSCUS (MEGADONTOMYS) THOMASI***

<b>Protein</b>	<b>Locus</b>	<b>References</b>
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> <i>Pep-4 (Pep-D)</i> <i>Pep-B1</i>	Werbitsky and Kilpatrick (1987) Rogers and Engstrom (1992)
Transferrin	<i>Trf</i>	Werbitsky and Kilpatrick (1987)

**Reference:**

Rogers, D.S. and M.D. Engstrom. 1992. *J. Mamm.* 73:55-69.  
Werbitsky, D. and C.W. Kilpatrick. 1987. *J. Mamm.* 68:305-312.



## ***Peromyscus* Nucleic Acid Sequences**

Numerous nucleic acid sequences from *Peromyscus* species are registered in GenBank. The sequences are periodically indexed in *PEROMYSCUS NEWSLETTER*. As a service, the *Peromyscus* Genetic Stock Center will furnish a printout of the full GenBank sequence, citations *etc.* Please request by GenBank accession number given in parentheses in this listing. Limit requests to no more than five at any given time. Include a FAX number and it will be transmitted by FAX if less than 8 pages. A hardcopy by mail will also be furnished, if requested. Call (803) 777-3107 or e-mail [peromyscus@stkctr.biol.sc.edu](mailto:peromyscus@stkctr.biol.sc.edu)

Sequences in this index are listed under major categories: (1) Nuclear genes, (2) Nuclear elements and repeats, and (3) Mitochondrial genes. Formal locus designations are abbreviated and italicized, *e.g.* *Adh1* (alcohol dehydrogenase-1). Sequences are arranged alphabetically within these categories by (a) gene, (b) species and (c) alphabetic/numeric successive GenBank accession numbers, in that order. An appended index lists GenBank entries for non-*Peromyscus* peromyscine genera.

### **Section 1. NUCLEAR GENES**

#### **Alcohol dehydrogenase (*Adh1*, *Adh2*)**

[ADH1B] *P. maniculatus* alcohol dehydrogenase 1 (*Adh1*) mRNA, complete cds. (L15703)

[ADH2A] *P. maniculatus* alcohol dehydrogenase 2 (*Adh2*) mRNA, complete cds. (L15704)

#### **Delta-like homolog *Drosophila* (*Dlk1*)**

[DLK1] *P. maniculatus* delta-like *Drosophila* homolog protein (*Dlk1*) mRNA, partial cds. (AF272850)

#### **Endothelin-B receptor (*EndrB*)**

[EDNRB] *P. maniculatus* endothelin-B receptor (*EndrB*) gene, partial cds. (AF212999)

[EDNRB] *P. polionotus* endothelin-B receptor (*EndrB*) gene, partial cds. (AF213000)

#### **Fetal liver mRNA (*H19*)**

[H19] *P. maniculatus* fetal liver mRNA (*H19*) complete cds. (AF214115)

#### **Hemoglobin beta chain (*Hbb*)**

[HBB1BB] *P. maniculatus* (deer mouse) beta-1-globin (*Hbb-b1*) DNA, 5' region. (M15289)

[HBB2BB] *P. maniculatus* (deer mouse) beta-2-globin (*Hbb-b2*) DNA, 5' region. (M15290)

[HBB3BA] *P. maniculatus* (deer mouse) beta-3-globin (*Hbb-b3*) DNA, 5' region. (M15291)

Continued next page

### **Hemoglobin beta chain (*Hbb*) - Continued**

- [HBB1BA] *P. maniculatus* (deer mouse) beta-1-globin (*Hbb-b1*) DNA, 5' region. (M15292)
- [HBB2BA] *P. maniculatus* (deer mouse) beta-2-globin (*Hbb-b2*) DNA, 5' region. (M15293)
- [HBB1BC] *P. maniculatus* (deer mouse) beta-1-globin (*Hbb-b1*) DNA, second coding-block region, partial cds. (M15294)
- [HBB2BC] *P. maniculatus* (deer mouse) beta-2-globin (*Hbb-b2*) DNA, second coding-block region, partial cds. (M15295)
- [HBB3BB] *P. maniculatus* (deer mouse) beta-3-globin (*Hbb-b3*) DNA, second coding-block region, partial cds. (M15296)
- [HBB1BD] *P. maniculatus* (deer mouse) beta-1-globin (*Hbb-b1*) DNA, 3' region. (M15297)
- [HBB2BD] *P. maniculatus* (deer mouse) beta-2-globin (*Hbb-b2*) DNA, 3' region. (M15298)
- [HBB3BC] *P. maniculatus* (deer mouse) beta-3-globin (*Hbb-b3*) DNA, 3' region. (M15299)

### **Interferon gamma (*InfG*)**

- [IFG] *P. maniculatus* interferon gamma (*InfG*) mRNA, partial cds. (AF307011)

### **Interleukin-10 (*Il10*)**

- [IL10] *P. maniculatus* interleukin-10 (*Il10*) mRNA, partial cds. (AF307012)

### **Lecithin cholesterol acyl transferase (*Lcat*)**

- [PMLCAT01] *P. maniculatus* lecithin:cholesterol acyl transferase (*Lcat*) exons 2 – 5 and partial cds. (U72307)
- [PMLCAT02] *P. maniculatus* lecithin:cholesterol acyl transferase (*Lcat*) exon 6 and partial cds. (U72308)

### **Leptin (*ob*)**

- [OB] *P. maniculatus* leptin (*ob*) gene, partial cds. (AF213001)
- [OB] *P. polionotus* leptin (*ob*) gene, partial cds. (AF213002)

### **Lymphotoxin alpha (*Lta*)**

- [LTA] *P. maniculatus* lymphotoxin alpha (*Lta*) mRNA, partial cds. (AF348259)

### **Major Histocompatibility Complex – CLASS I (*MHCI*)**

- [MHCIBM4] *P. leucopus* MHC class Ib precursor (*PeleM4*), partial cds. (AF006618)
- [MHCIA11B] (*P. leucopus* group) Mouse MHC class I antigen (*Pele-A11b*) gene, exon 5. (M59218)
- [MHCIA6B] (*P. leucopus* group) Mouse MHC class I antigen (*Pele-A6b*) gene, exon 5. (M59219)
- [MHCIA24A] (*P. leucopus* group) Mouse MHC class I antigen (*Pele-A24a*) gene, exon 5. (M59220)

Continued next page

### Major Histocompatibility Complex – CLASS I (*MHCI*) - Continued

- [MHCIA34C] (*P. leucopus* group) Mouse MHC class I antigen (*Pele-A34c*) gene, exon 5. (M59221)
- [MHCIA37A] (*P. leucopus* group) Mouse MHC class I antigen (*Pele-A37a*) gene, exon 5. (M59222)
- [MHCIA38B] (*P. leucopus* group) Mouse MHC class I antigen (*Pele-A38b*) gene, exon 5. (M59223)
- [MHCIA42B] (*P. leucopus* group) Mouse MHC class I antigen (*Pele-A42b*) gene, exon 5. (M59224)
- [MHCIA42C] (*P. leucopus* group) Mouse MHC class I antigen (*Pele-A42c*) gene, exon 5. (M59225)
- [MHCIA48C] (*P. leucopus* group) Mouse MHC class I antigen (*Pele-A48c*) gene, exon 5. (M59226)
- [MHCIA5] *P. leucopus* MHC class I gene, exon 5. (M60611 = M33983)
- [MHCIA4] *P. leucopus* MHC class I gene, exon 5. (M60612 = M33984)
- [MHCIAA] *P. leucopus* MHC class I gene, exon 5. (M60613 = M33985)
- [MHCIM42] *P. leucopus* MHC class I *PeleM4* gene, exons 4 and 5 and partial cds. (U21212)
- [MHCIM4] *P. leucopus* MHC class I *PeleM4* gene, exons 1, 2 and 3. (U21213)
- [MHCCIA3] *P. leucopus* MHC class I antigen *alpha 3* domain gene, partial cds. (U37435)
- [MHCIT24A] *P. maniculatus* nonclassical class I antigen (*PemaT24*) mRNA, complete cds. (U03104)
- [MHCIA13A] *P. maniculatus* major histocompatibility complex class I antigen mRNA, complete cds. (U12822)
- [MHCII1A] *P. maniculatus* major histocompatibility complex class I antigen mRNA, clone *Pema11*, partial cds. (U16846)
- [MHCIA53A] *P. maniculatus* major histocompatibility complex class I antigen mRNA, clone *Pema53*, complete cds. (U16847)
- [MHCIA41A] *P. maniculatus* clone *Pema41* major histocompatibility complex class I antigen mRNA, complete cds. (U12885)
- [MHCIA52A] *P. maniculatus* clone *Pema52* major histocompatibility complex class I antigen mRNA, complete cds. (U12886)
- [MHCIA62A] *P. maniculatus* clone *Pema62* major histocompatibility complex class I antigen mRNA, complete cds. (U12887)

### Major Histocompatibility Complex – CLASS II (*MHCII*)

- [MHCIIAa] *P. leucopus* MHC class II protein alpha-chain *PeleAa* (*MhcPeleAa*) gene, partial cds. (U34805)

### Myogenic regulatory factor (*MyoD*)

- [MYOD] *P. maniculatus* myogenic regulatory factor (*MyoD*) gene, partial cds. (AF213003)
- [MYOD] *P. polionotus* myogenic regulatory factor (*MyoD*) gene, partial cds. (AF213004)

### Pancreatic ribonuclease (*Prnase*)

- [PLPRN] *P. leucopus* pancreatic ribonuclease (*Prnase*). Complete cds. (AJ005770)

### **RAS guanine nucleotide releasing factor 1 (*Rasgr1*)**

[RASGRF1] *P. maniculatus* RAS guanine nucleotide-releasing factor 1 (*Rasgrf1*) mRNA, partial cds. (AF045648)

[RASGRF1] *P. polionotus* RAS guanine nucleotide-releasing factor 1 (*Rasgrf1*) mRNA, partial cds. (AF045647)

### **Tumor Necrosis Factor (*Tnf*)**

[TNF] *P. leucopus* tumor necrosis factor (*Tnf*) gene sequence, cds 5' end. (M59233)

[TNF] *P. maniculatus* tumor necrosis factor (*Tnf*) alpha mRNA, partial cds. (AF307013)

### **Von Willebrand factor (*Vwf*)**

[VWF] *P. maniculatus* partial gene (*Vwf*) for von Willebrand factor. (AJ402697)

## **Section II. NUCLEAR ELEMENTS and REPEATS**

### **LINE-1 (*L1*)**

[L1RT-ps] *P. californicus* LINE-1 repetitive element reverse transcriptase pseudogenes, partial cds.

13 consecutive GenBank entries: (U70828 - U70840)

[L1RT-ps] *P. leucopus* LINE-1 repetitive element reverse transcriptase pseudogenes, partial cds.

4 consecutive GenBank entries: (U70925 - U70928)

[L11RT-ps] *P. leucopus* LINE-1 repetitive element reverse transcriptase gene, partial cds. (U43365=U70932)

[L1PM62X] (*P. maniculatus* group) Deer mouse (*L1Pm62*) gene. (M97517)

[L1PM55X] (*P. maniculatus* group) Deer mouse (*L1Pm55*) gene. (M97518)

[L1RT] *P. maniculatus* LINE-1 repetitive element reverse transcriptase gene, partial cds. (U43360)

[L1RT-ps] *P. maniculatus* LINE-1 repetitive element reverse transcriptase gene, partial cds. Three consecutive GenBank entries representing distinct specimens: (U43362 - U43364. Duplication of U70924, U70934 and U70935)

### **MYS-1, MYS-2 (*Mys*)**

[MYSPER] Mouse (*P. leucopus*) retrovirus-like transposable element *mys-2*, left flank. (AH002117)

[MYS21PER] Mouse (*P. leucopus*) retrovirus-like transposable element *mys-2*, left flank. (M13343)

[MYS22PER] Mouse (*P. leucopus*) retrovirus-like transposable element *mys-2*, right flank. (M13344)

[MYS1PL] *P. leucopus* retrovirus-like transposable element *mys-1*. (X02855)

### **B2 Repeat (*B2*)**

[PMB2] *P. maniculatus* B2 repetitive elements. Three consecutive GenBank entries for distinct samples: (U93039 - U93041)

### **ID Repeat (ID)**

- [IDPMA2] *P. maniculatus* clone *Pma2* ID repeat element. (U33854)  
[IDPMA3] *P. maniculatus* clone *Pma3* ID repeat element. (U33855)  
[IDPMF0] *P. maniculatus* clone *Pmf0* ID repeat element. (U33856)  
[IDPMG1] *P. maniculatus* clone *Pmg1* ID repeat element. (U33857)  
[IDPMG2] *P. maniculatus* clone *Pga2* ID repeat element. (U33858)  
[IDPMG3] *P. maniculatus* clone *Pmg3* ID repeat element. (U33859)  
[IDPMG4] *P. maniculatus* clone *Pmg4* ID repeat element (U33860)  
[IDPMG5] *P. maniculatus* clone *Pmg5* ID repeat element. (U33861)  
[IDPMH1] *P. maniculatus* clone *Pmh1* ID repeat element. (U33862)  
[IDPMH3] *P. maniculatus* clone *Pmh3* ID repeat element. (U33863)  
[IDPMH5] *P. maniculatus* clone *Pmh5* ID repeat element. (U33865)

### **Ppa55 Repeat (Ppa55)**

- [PPA55] *P. polionotus* microsatellite *Ppa55* repeat. Eight consecutive GenBank sequences representing distinct individuals of two subspecies: (AF016855 - AF016862)

## **Section 3. Mitochondrial Genes**

### **Cytochrome B (mtCytB)**

- [MTCYTB] *P. attwateri* mitochondrial cytochrome *cytB* gene, partial cds. Two consecutive GenBank entries for distinct specimens: (AF155384 - AF155385)  
[MTCYTB] *P. aztecus* mitochondrial DNA *cytB* gene, partial cds. Eight consecutive Gen Bank entries representing distinct specimens: (U89966 - U89973)  
[MTCYTB] *P. beatae* mitochondrial *cytB* gene, partial cds. Eight consecutive GenBank entries representing distinct specimens: (AF13194 - AF131923)  
[MTCYTB] *P. beatae (sacarensis)* mitochondrial *cytB* gene, partial cds. (AF131914)  
[MTCYTB] *P. boylii* cytochrome B (*cytB*) gene, partial cds. (AF131915)  
[MTCYTB] *P. boylii* mitochondrial cytochrome B (*cytB*) gene, partial cds. Two consecutive GenBank entries: (AF131924 - AF131925)  
[MTCYTB] *P. boylii* cytochrome B (*cytB*) gene, partial cds. Seven consecutive GenBank entries representing distinct subspecies and individuals: (AF155386 - AF155392)  
[MTCYTB] *P. (boylii species group)* cytochrome B (*cytB*) gene, partial cds. Six consecutive GenBank entries representing distinct populations of uncertain specific status: (AF155405 - AF155410)  
[MTCYTB] *P. boylii* cytochrome B (*cytB*) gene, partial cds. (AF155413)

Continued next page

## Cytochrome B (mtCytB) - Continued

- [MTCYTB] *P. boylii* cytochrome B (*cytB*) gene, partial cds. (U89965)
- [MTCYTB] *P. californicus* cytochrome B (*cytB*) gene., partial cds. (AF155393)
- [MTCYTB] *P. difficilis* cytochrome B (*cytB*) gene, partial cds. (AF155394)
- [MTCYTB] *P. eremicus* mitochondrial DNA *cytB* gene. (X89799)
- [MTCYTB] *P. furvus* cytochrome B (*cytB*) gene partial cds. Fifty-three consecutive GenBank entries representing distinct specimens from various localities: (AF270980 - AF271032)
- [MTCYTB] *P. gossypinus* (*P. leucopus* group) mitochondrial DNA *cytB* gene. (X89786)
- [MTCYTB] *P. gratus* cytochrome B (*cytB*) gene partial cds. (AF155395)
- [MTCYTB] *P. hylocetes* cytochrome B (*cytB*) gene partial cds. Five consecutive GenBank entries representing distinct specimens: (U89974 - U89978)
- [MTCYTB] *P. keeni* (*P. maniculatus* group) mitochondrial DNA *cytB* gene. (X89787)
- [MTCYTB] *P. leucopus* mitochondrial DNA *cytB* gene (AF131926)
- [MTCYTB] *P. leucopus* mitochondrial DNA *cytB* gene. (X89790)
- [MTCYTB] *P. leviceps* cytochrome B (*cytB*) gene, partial cds. Two consecutive GenBank entries representing distinct specimens: (AF131928 - AF131929)
- [MTCYTB] *P. leviceps* cytochrome B (*cytB*) gene, partial cds. (AF155396)
- [MTCYTB] *P. madrensis* cytochrome B (*cytB*) gene, partial cds. (AF155397)
- [MTCYTB] *P. maniculatus* cytochrome B (*cytB*) gene, for mitochondrial product. (AF119261)
- [MTCYTB] *P. melanotis* cytochrome B (*cytB*) gene., partial cds. (AF155398)
- [MTCYTB] *P. melanotis* (*P. maniculatus* group) mitochondrial DNA *cytB* gene. (X89791)
- [MTCYTB] *P. nasutus* cytochrome B (*cytB*) gene, partial cds. (AF155399)
- [MTCYTB] *P. pectoralis* cytochrome B (*cytB*) gene, partial cds. Three consecutive GenBank entries representing two subspecies: (AF155400 - AF155402)
- [MTCYTB] *P. polionotus* (*P. maniculatus* group) mitochondrial DNA *cytB* gene. (X89792)
- [MTCYTB] *P. polius* cytochrome B (*cytB*) gene., partial cds. (AF15403)
- [MTCYTB] *P. sagax* cytochrome B (*cytB*) gene., partial cds. (AF15404)
- [MTCYTB] *P. simulus* cytochrome B (*cytB*) gene, partial cds. (AF131927)
- [MTCYTB] *P. spicilegus* cytochrome B (*cytB*) gene, partial cds. Two consecutive GenBank entries representing distinct samples: (U89979 - U89980)
- [MTCYTB] *P. stephani* cytochrome B (*cytB*) gene, partial cds. (AF155411)
- [MTCYTB] *P. truei* cytochrome B gene (*cytB*) gene, partial cds. (AF108703)
- [MTCYTB] *P. truei* cytochrome B (*cytB*) gene, partial cds. (AF155412)
- [MTCYTB] *P. winkelmanni* cytochrome B (*cytB*) gene, partial cds. (AF131930)
- [MTCYTB] *P. winkelmanni* cytochrome B (*cytB*) gene, partial cds. Three consecutive GenBank entries representing distinct samples: (U89981 - U89983)

## Cytochrome oxidase (mtCOIII)

- [MTCOIII] *P. boylii* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. (AY0099175)
- [MTCOIII] *P. californicus* cytochrome oxidase subunit III. (*COIII*) gene, partial cds. (AY009176)
- [MTCOIII] *P. caniceps* cytochrome oxidase subunit III. (*COIII*) gene, partial cds. (AF343761)
- [MTCOIII] *P. collatus* cytochrome oxidase subunit III. (*COIII*) gene, partial cds. (AF343768)
- [MTCOIII] *P. crinitus* cytochrome oxidase subunit III. (*COIII*) gene, partial cds. (AY009177)
- [MTCOIII] *P. dickeyi* cytochrome oxidase subunit III. (*COIII*) gene, partial cds. (AF343759)
- [MTCOIII] *P. dickeyi* cytochrome oxidase subunit III. (*COIII*) gene, partial cds. Two consecutive GenBank entries: for distinct samples: (AF343772 - AF343773)
- [MTCOIII] *P. eremicus* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. (AF343756)
- [MTCOIII] *P. eremicus* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. (AF343760)
- [MTCOIII] *P. eremicus* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. Three consecutive GenBank entries representing distinct specimens: (AF343763 - AF343765)
- [MTCOIII] *P. eremicus* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. Thirty-five consecutive GenBank entries representing distinct specimens: (AY009186 - AY009220)
- [MTCOIII] *P. eva* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. (AY009223)
- [MTCOIII] *P. eva* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. Five consecutive GenBank entries representing distinct specimens: (AY009226 - AY009230)
- [MTCOIII] *P. eva* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. (AY009237)
- [MTCOIII] *P. fraterculus* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. Two consecutive GenBank entries representing distinct specimens: (AY009221 - AY009221)
- [MTCOIII] *P. fraterculus* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. Two consecutive GenBank entries representing distinct specimens: (AY009224 - AY009225)
- [MTCOIII] *P. fraterculus* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. Six consecutive GenBank entries representing distinct specimens: (AY009231 - AY009236)
- [MTCOIII] *P. interparietalis* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. Two consecutive entries in GenBank representing distinct specimens: (AF343757 - AF343758)
- [MTCOIII] *P. interparietalis* mitochondrial cytochrome oxidase subunit III (*COIII*) gene, partial cds. Two consecutive entries in GenBank representing distinct specimens: (AF343762 - AF343763)
- [MTCOIII] *P. leucopus* cytochrome oxidase subunit III (*COIII*) gene partial cds. (AY009173)
- [MTCOIII] *P. maniculatus* cytochrome oxidase subunit III. (*COIII*) gene, partial cds. (AY009174)
- [MTCOIII] *P. sejugis* cytochrome oxidase subunit III. (*COIII*) gene, partial cds. Two consecutive GenBank entries: for distinct samples: (AF343772 - AF343773)
- [MTCOIII] *P. slevini* cytochrome oxidase subunit III. (*COIII*) gene, partial cds. (AF343755)
- [MTCOIII] *P. slevini* cytochrome oxidase subunit III. (*COIII*) gene, partial cds. Two consecutive GenBank entries: for distinct samples: (AF343774 - AF343775)
- [MTCOIII] *P. stephani* cytochrome oxidase subunit III. (*COIII*) gene, partial cds. (AF343767)

**NADH dehydrogenase and transfer RNAs (mtNADHDH and tRNAs)**

- [MTNADHDH/tRNA-Arg] *P. boylii* ND3 and ND4 genes complete cds., tRNA-Arg complete seq., ND4 partial cds. (U83864)
- [MTNADHDH/tRNA-Arg] *P. eremicus* ND3 and ND4 genes complete cds., tRNA-Arg complete seq., cds. (U83861)
- [MTNADHDH/tRNA-Arg, gly] *P. gossypinus* ND3 and ND4 genes complete cds., tRNA-Arg complete seq., tRNA-Gly gene partial seq. and ND4 gene partial cds. (U40246)
- [MTtRNA-Phe] *P. gossypinus* mt D-loop, partial seqs., and tRNA-Pro gene, partial seqs. encoding Mt RNA . Two consecutive GenBank entries: (AF031757 - AF031758)
- [MTtRNA-Pro] *P. gossypinus* mt D-loop, partial seqs., tRNA-Pro gene, partial seqs. encoding mtRNA. Two consecutive GenBank entries: (AF031806 - AF031807)
- [MTtRNA-Phe] *P. leucopus* mt D-loop, partial seqs., and tRNA-Phe gene, partial seqs. encoding mt tRNA. Forty-six consecutive GenBank entries representing samples from throughout the range of the species: (AF031710 - AF031756)
- [MTtRNA-Pro] *P. leucopus* mt D-loop, partial seqs., and tRNA-Pro gene, partial seqs. encoding mt tRNA. Forty-seven consecutive GenBank entries representing samples from throughout the range of the species: (AF031759 - AF031805)
- [MTNADHDH/tRNAs] *P. leucopus* ND3 and ND4L genes, complete cds., tRNA(arg) gene, complete seq., tRNA(gly) gene, partial seq., and ND4 gene partial cds.; mt DNA gene products. (U40252)
- [MTNADHDH/tRNAs] *P. keeni* ND3 and ND4L genes, complete cds., tRNA(arg) gene, complete seq., tRNA(gly) gene, partial seq., and ND4 gene partial cds.; mt DNA gene products. Two consecutive entries in GenBank for distinct ssp.: (U40062 - U40063)
- [MTNADHDH/tRNAs] *P. maniculatus* ND3 and ND4L genes, complete cds., tRNA(arg) gene, complete seq., tRNA(gly) gene, partial seq., and ND4 gene partial cds.; mt DNA gene products. Three consecutive entries in GenBank for distinct ssp.: (U40249 - U40251)
- [MTNADHDH/tRNAs] *P. maniculatus* ND3 and ND4L genes, complete cds., tRNA(arg) gene, complete seq., tRNA(gly) gene, partial seq., and ND4 gene partial cds.; mt DNA gene products. Two consecutive entries in GenBank for distinct ssp.: (U40062 - U40063)
- [MTNADHDH/tRNAs] *P. melanotis* ND3 and ND4L genes, complete cds., tRNA(arg) gene, complete seq., tRNA(gly) gene, partial seq., and ND4 gene partial cds.; mt DNA gene products. (U40247)
- [MTNADHDH/tRNAs] *P. mexicanus* ND3 and ND4L genes, complete cds., tRNA-Arg complete seq., ND4 partial cds. (U83862)
- [MTNADHDH/tRNAs] *P. polionotus* ND3 and ND4L genes, complete cds., tRNA(arg) gene, complete seq., tRNA(gly) gene partial seq., and ND4 partial cds.; mtDNA products. (U40254)
- [MTNADHDH/tRNAs] *P. sejugis* ND3 and ND4L genes, complete cds., tRNA(arg) gene, complete seq., tRNA(gly) gene partial seq., and ND4 partial cds.; mtDNA products. Two entries in GenBank for different specimens: (U40253, U40255)
- [MTNADHDH/tRNAs] *P. slevini* ND3 and ND4L genes, complete cds., tRNA(arg) gene, complete seq., tRNA(gly) gene partial seq., and ND4 partial cds.; mtDNA products. (U40248)



***mtSSU* ribosomal RNA (*mtssrRNA*)**

- [MT12SrRNA] *P. eremicus* mitochondrial DNA for SSU ribosomal RNA gene. (X89784)
- [MT12SrRNA] *P. leucopus* mitochondrial DNA for 12S ribosomal RNA gene. (X89797)
- [MT12SrRNA] (*P. leucopus* group) *P. gossypinus* mitochondrial DNA for SSU ribosomal RNA gene. (X89795)
- [MT12SrRNA] *P. leucopus* mitochondrial 12S rRNA gene. (X99463)
- [MT12SrRNA] *P. melanotis* mitochondrial DNA for 12S ribosomal RNA gene. (X89785)
- [MT12SrRNA] (*P. maniculatus* group) *P. keeni* mitochondrial DNA for SSU ribosomal RNA gene. (X89796)
- [MT12SrRNA] *P. leucopus* mitochondrial DNA for 12S ribosomal RNA gene. (X89797)
- [MT12SrRNA] (*P. maniculatus* group) *P. polionotus* DNA for 12S ribosomal RNA gene. (X89888)
- [MTsnRNA] *P. maniculatus* snRNA (*Bci RNA*) gene, partial sequence. (U33851)
- [MTsnRNA] *P. californicus* snRNA (*Bci RNA*) gene, partial sequence. (U33850)

**D-loop undefined sequences**

- [MTDloop] *P. atterwateri* mitochondrial D-loop region sequence, complete. (AF081492)
- [MTDloop] *P. beatae* D-loop region sequence, complete. (AF081487)
- [MTDloop] *P. boyliii* D-loop region sequence, complete. (AF081486)
- [MTDloop] *P. leucopus* D-loop region sequence, complete. (AF081490)
- [MTDloop] *P. leviceps* D-loop region sequence, complete. Two consecutive GenBank entries for distinct ssp.  
(AF081488 - AF081489)
- [MTDloop] *P. simulus* D-loop region sequence, complete. (AF081491)

## Nucleic Acid Sequences in GenBank for other Peromyscine Genera

### MITOCHONDRIAL GENES

#### *ONYCHOMYS* sp.:

[MTCYTB] *O. arenicola* cytochrome oxidase subunit III (*COIII*) gene. Three isolates from different specimens: (U21648 - U21650)

[MTCYTB] *O. leucogaster* cytochrome oxidase subunit III (*COIII*) gene. Three isolates from different specimens: (U21614 - U21616)

[MTCYTB] *O. torridus* cytochrome oxidase subunit III (*COIII*) gene. Three isolates from different specimens: (U21633 - U21635)

[MTCYTB] *O. arenicola* mitochondrial DNA for cyt B (*cytB*) gene. (X89793)

[MTCYTB] *O. leucogaster* mitochondrial DNA for cyt B (*cytB*) gene. (X89794)

[MTCYTB] *O. torridus* mitochondrial DNA for cyt B (*cytB*) gene. (X89798)

[MT12SrRNA] *O. arenicola* mitochondrial DNA for SSU ribosomal RNA (*ssuRNA*) gene. (X89782)

[MT12SrRNA] *O. leucogaster* mitochondrial DNA for 12S ribosomal RNA (*ssuRNA*) gene. (X89889)

[MT12SrRNA] *O. arenicola* mitochondrial DNA for SSU ribosomal RNA (*ssuRNA*) gene. (X89783)

#### *OSGOODOMYS* [*PEROMYSCUS*] *BANDERANUS*:

[MTCYTB] *O. [P.] bandeanus* cytochrome b gene (*cytB*) gene, partial cds. (AF155383)

[MTCOIII] *O. [P.] banderanus* cytochrome c oxidase II (*COII*) gene, partial cds. (U18836)

[MTCOIII] *O. [P.] banderanus* cytochrome c oxidase II gene, mitochondrial gene product, partial cds. (U62572)

[MT12SrRNA] *O. [P.] banderanus* 12s ribosomals RNA gene, partial sequence. (U67295)

[MTNADHDH/tRNA-Arg] *O. [P.] banderanus* NADH dehydrogenase subunits ND3, ND4L and tRNA-Arg complete seqs., ND4 partial cds. (U83860)

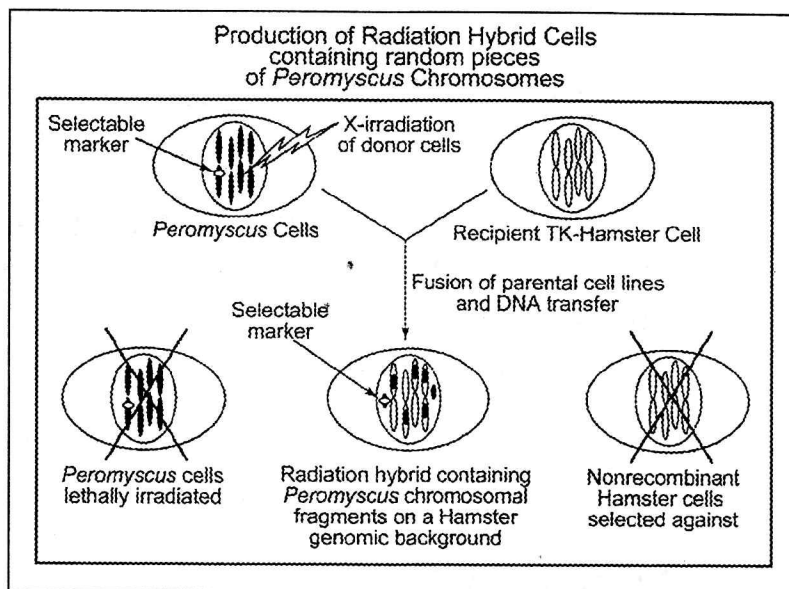
#### *PODOMYS* [*PEROMYSCUS*] *FLORIDANUS*:

[NADHDH/tRNA-Arg] *P. floridanus* NADH dehydrogenase subunits ND#, ND4 and tRNA-Arg complete sequence, ND4 oartial cds. (U83865)



DEWEY (continued)

Figure. Construction of radiation hybrids. The cell line (*Peromyscus*) donating DNA of interest is lethally irradiated (5000 R for whole genome hybrids) and fused with a recipient line, immortalized Chinese hamster ovary (CHO) cells. The CHO cell line rescues chromosomal fragments from the irradiated cell line, which contains a selectable marker (thymidine kinase) allowing selection against non-recombinant CHO cells. Individual hybrids so derived contain *random* groups chromosomal fragments. Thus, each hybrid will contain a *unique* mixture of fragments.



Primary fibroblasts were harvested from midgestation *P maniculatus* embryos and expanded a few days in culture. Subsequently the cells were irradiated with 5000 rad and were fused with a thymidine kinase-deficient Chinese hamster cell line, A23, provided by WJ Murphy (NCI). Cell fusion was induced by polyethylene glycol and subsequent selection was in HAT medium. Colonies appearing after two weeks were picked and subcultured in larger flasks. One aliquot of each was frozen for future expansion, and another aliquot subjected to DNA extraction for further characterization. At this point we have 108 hybrid clones frozen on liquid nitrogen. A panel of this size is the norm for providing an adequate statistical foundation for linkage analyses of whole genome radiation hybrid panels. In a preliminary characterization of 14-24 hybrid clones DNA PCR characterization with 5 randomly cloned *Peromyscus* microsatellites (Prince, 2001) as well as primers that selectively amplify *Peromyscus* PL1 and PL5 (placental lactogen). The overall retention frequency of these seven was determined to be 44%, thereby establishing the legitimacy of these clones for future linkage analysis.

We are in the process of developing a set of microsatellites (Type II markers) to supplement ones we already have on hand and that are already published. Microsatellite location will be anchored with Type I loci. We'd appreciate getting any unpublished *Peromyscus* Type I or Type II sequence information anyone may have on hand. The linkage map of *P maniculatus* microsatellites will likely be very useful for genetic studies of other peromyscines. In a recent survey of microsatellites isolated from *P polionotus* we found that the majority of them gave comparable signals with other species including *P maniculatus*, *P leucopus*, *P eremicus*, *P melanophrys*, *P aztecus*, and *P californicus*.

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### **Peg3/Pw1 as a candidate locus for overgrowth effects in *P. maniculatus* / *P. polionotus* Hybrids**

We have been investigating the genetic/epigenetic causes of the parent-of-origin dependent growth phenotypes seen in *Peromyscus* hybrids. It has been known for over 35 years that when a *P. polionotus* (PO or LS) female is mated to a *P. maniculatus* (BW) male, the offspring were oversized. However, in the reciprocal cross, the offspring are smaller than the parents. [1] Genomic imprinting, parent-of-origin dependent gene expression, is perturbed in these hybrids suggesting a possible mechanism for the phenotypes.

Genetic analyses point to at least two candidate regions involved in this phenomenon. Both of these regions are subject to imprinting- one autosomally and one on the X chromosome. *Peg3* is a large (9kb) paternally expressed zinc finger region of phenotypic linkage (The *plt* mutation may also be linked- Dawson and Rice unpublished). [2] The homologous gene is found on proximal chromosome 7 of *Mus* and chromosome 19q13.1 of human [3], and likely located on *Peromyscus* chromosome 1. This gene has been implicated in growth, behavior and apoptosis. [4] Loss of *Peg3* imprinting is seen in the oversized F1 offspring and is associated with more severe phenotypes in backcross embryos. There is also an indication that the *Peg3* linked locus and the X chromosomal locus may interact, suggesting there may be differences between the PO and BW alleles.

We isolated the *Peg3* gene in *Peromyscus* in order to determine any differences between the two species that would lead to allelic interactions and loss of imprinting. Gene isolation was accomplished by screening a complete cDNA *Peromyscus* library of both species and using PCR techniques to fill in missing areas between cDNA clones. This work is being completed presently. We will then analyze the nucleic acid sequence, amino acid sequence, protein structure, and expression. We are looking for deviations between the two species that would account for the phenotype if the gene from one species is placed in the context of the others alleles. Such changes might include frame shifts, splicing variants, changes in protein configuration, loss or gain of a zinc finger, or different expression levels.

We have also cloned the promoter region of the locus and are isolating the first intron, which we believe also harbors regulatory elements. We have undertaken methylation analysis in this region. This shows that the maternal (silenced) allele is normally methylated, but that this is mostly lost in the oversized hybrids. We will undertake a more refined analysis (bisulfite sequencing) to see which residues must be unmethylated for expression.

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### **A Differential Display Screen Using *Peromyscus* Hybrids To Identify Novel Imprinted Genes**

Genomic imprinting is the non-equivalent expression of the parental alleles of a gene based on parent-of-origin. By rendering all imprinted loci functionally hemizygous, the evolution of imprinting in mammals imposes a survival cost to the organism. For this reason there has been intense debate about the function of imprinting. Identified imprinted genes to date have shown that a disproportionate number appear to involve growth. The placenta and CNS seem to be particularly affected.

To test these generalities (as well as species-specific imprinting), we utilized an allelic differential display similar to that of Hagiwara, 1997 to identify genes subject to genomic imprinting. In this procedure RNA is isolated from the same tissue of age matched parental, F1 and backcross (BC) animals. We utilized the PO and BW strains from the *Peromyscus* Stock Center, their reciprocal F1's (BW x PO and PO x BW; female shown first and the backcross (BW x PO) x BW). cDNA is then made from the RNA, and subjected to PCR with individual pairs of random primers. These PCR products are then run out on acrylamide gels. In this case banding differences between strains are likely due to polymorphisms at the sites of primer annealing, or due to a size polymorphism in the PCR product. By having the F1 animals one can ascertain the allelic expression status of a given gene. Figure 1 illustrates this both schematically as well as showing an example from an actual gel.

The back cross animals were our addition in order to rule out mitochondrial transcripts. As mitochondrial transcripts are maternally inherited, all alleles in the BS animals will be BW. As imprinted genes are re-set every generation, an F1 mother will pass on both PO and BW alleles. Thus by utilizing a number of the above BC animals, one can essentially rule out mitochondrial genes.

Our initial experimental gels were performed on whole brain cDNA. These gels showed the promise of the system in that the PO and BW strains showed a comparable level of polymorphism to that seen between inbred strains of *Mus domesticus* and *Mus spretus*. Of the bands we characterized from this mini-screen, a phospholipase known to be upregulated at parturition was among the more interesting. Two bands corresponded to this gene.

A more thorough screen was performed on mature placentas. This screen yielded known as well as novel imprinted genes. The *Dlk* locus was first shown to be imprinted from this screen (Schmidt et al, 2000). The first imprinting of a placental lactogen (Vrana

VRANA (continued)

et al., submitted) gene, predicted to be target of imprinting by Haig, was also shown. A number of bands await characterization. The screen also yielded X linked loci, and showed that they are imprinted in the placenta of *Peromyscus* females. This also revealed the non-random X – inactivation seen in the somatic tissues of the hybrids (Vrana et al., 2000). Further screens in other tissues/times might reveal other imprinted loci, and any tissue specific tendencies they exhibit.

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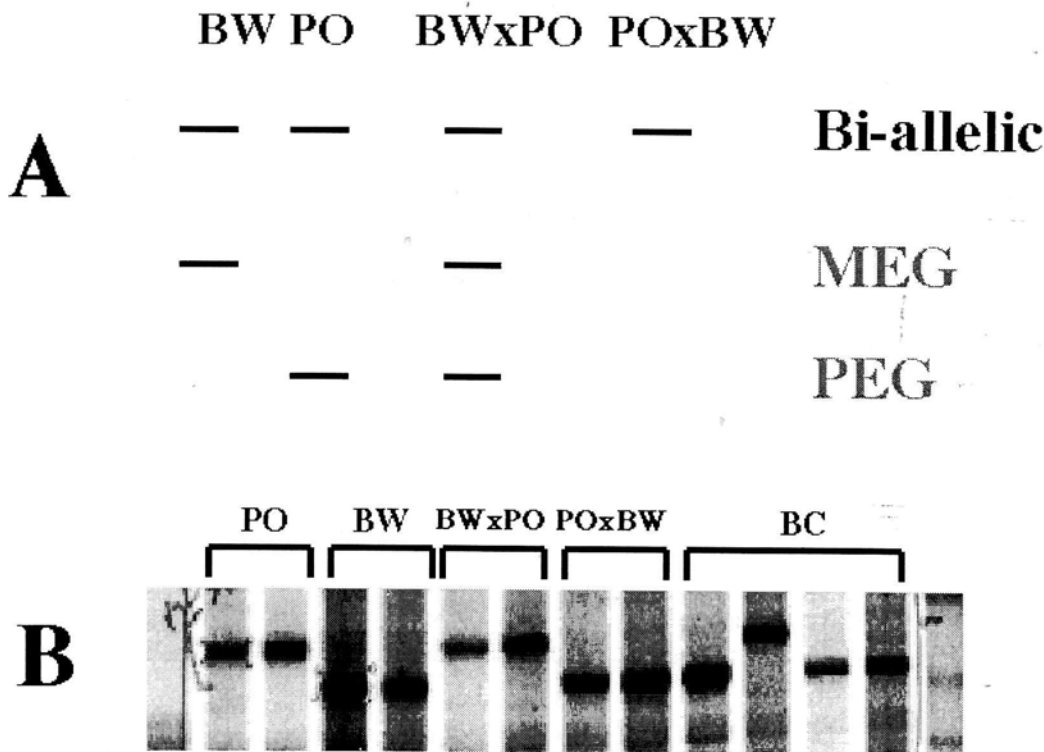


Figure Legend:

A: Schematic of bands on a differential display gel representing bi-allelic expression, a maternally –expressed gene (MEG) and a paternally –expressed gene (PEG).

B: Actual picture of one set of bands on a gel. Besides parentals and F1 animals, Backcross (BS) animals are also included to rule out mitochondrial genes.

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