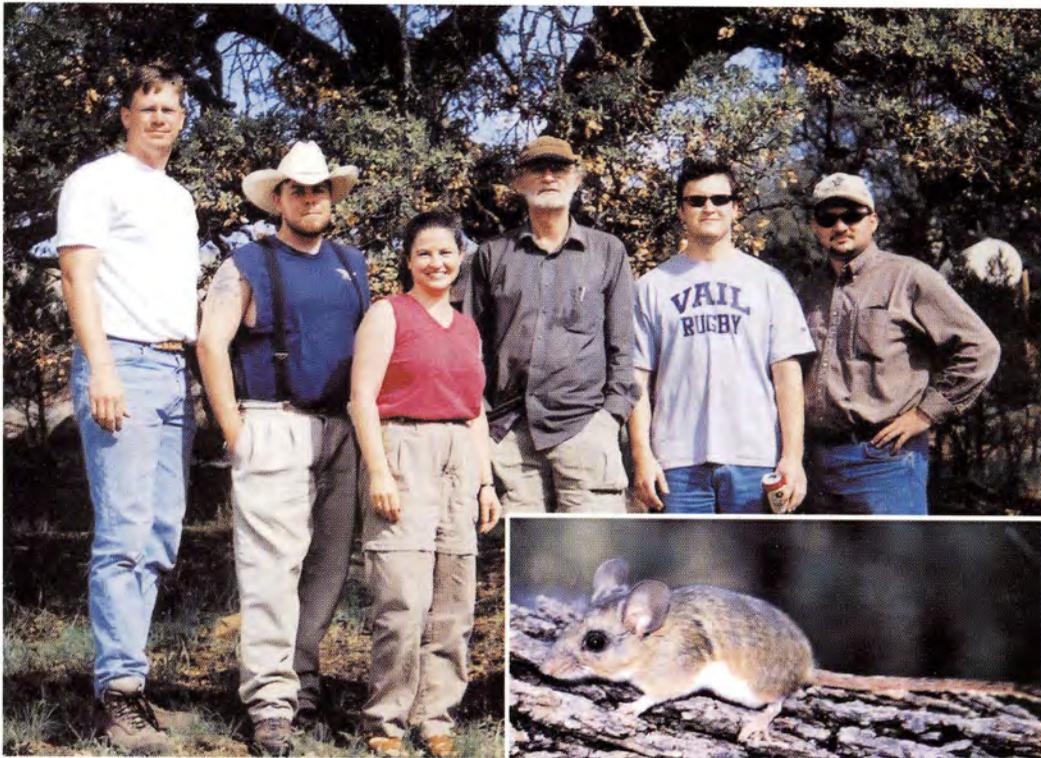


# PEROMYSCUS NEWSLETTER

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NUMBER THIRTY-SIX

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SEPTEMBER 2003

Cover: Group that collected *Peromyscus boylii* (inset) for founding a stock of this species at the Peromyscus Genetic Stock Center. Left to right: Rex McAliley, Jay Vacca, Julie Weston, Mike Dewey, Cliff Ramsdell and Joel Brant. (Mouse photo by L. Rex McAliley)

## ***PEROMYSCUS NEWSLETTER 36***

*Peromyscus Newsletter* is produced by the *Peromyscus* Genetic Stock Center at the University of South Carolina and is published semi-annually. The primary function of *PN* is to communicate informally the results of recent research projects and other information concerning peromyscine rodents. *PN* is not a formal research publication and information published in the "Contributions" section should not be cited without permission of the contributor. *PN* also includes a comprehensive list of research articles published during the previous 18 months that treat *Peromyscus* and closely allied taxa. A third function of the *Newsletter* is to inform the readership of the resources and research opportunities available through the *Peromyscus* Genetic Stock Center.

Research and other entries for inclusion in *PN* are invited. These should be limited to two single-spaced pages, and should include no more than one figure or graph. Occasional exceptions may be made by arrangement with the editor. Color photographs are acceptable only when pertinent to the subject, although particularly interesting color photos may be considered for the cover. Acceptable entries are published without review and are edited only for format and obvious typographical errors.

*PN* particularly invites submissions of preliminary research results, graduate or undergrad student projects of merit, theoretical concepts and other information relevant to peromyscine biology. Expanded abstracts of recently presented papers are also encouraged.

**ENTRIES FOR *PEROMYSCUS NEWSLETTER* #37 ARE DUE 26 MAR 04.**

Submit entries to:

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The Stock Center sponsors **PeroBase**, a comprehensive database for peromyscine rodents.

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## *News, Comment and Announcements*

The American Society of Mammalogists held its 83<sup>rd</sup> annual meeting at Texas Tech University in Lubbock June 21-25, 2003. Peromyscine rodents were the focus of twenty-two of the posters and oral presentations. .

+ + + +

We received a letter recently from **John A. (Jack) King**. Jack is moving back to the Lansing MI area where he enjoyed a long career on the faculty of Michigan State University until his retirement about 15 years ago. Jack is best known among peromyscologists as the editor of *Biology of Peromyscus*, a vital reference for all of us working with these rodents. Jack was also one of the original members of the Peromyscus Genetic Stock Center Advisory Committee.



**Barbara Blake** (University of North Carolina Greensboro), Editor of the *Journal of Mammalogy*, and **Hopi Hoekstra** (University of California San Diego) are conducting research projects utilizing the facilities and resources of the Peromyscus Stock Center. They have made recent visits to the Stock Center in connection with their respective projects.

The **Stock Center invites collaboration** with investigators interested in utilizing our stocks and other resources. Please call Mike Dewey (803-777-4132) or e-mail ([dewey@biol.sc.edu](mailto:dewey@biol.sc.edu)) for additional information.



IN THIS ISSUE **HANAVIRUS UPDATE** : See pages 23 - 27  
ENTRY BY **Emily Jentes** and **Jim Mills**.

\* \* \* \* \*

Re: "**Perobase Needs a Tree**" (See recent issues). A tentative consensus phylogenetic tree is projected for the next issue of *PN*. Initially the tree will be in "draft" form until a reasonable consensus version is agreed upon by various individuals in the field. **Anyone desiring to have input is invited to contact the editor (W. Dawson) as soon as possible.** The "best" tree will be posted in *PeroBase*, hopefully, by July 04. It may be desirable to post reasonable alternative trees, as well.

## NEUROSCIENCE POSTERS

Several posters are scheduled for presentation at the Society for Neuroscience meeting November 9 -11 that address projects using *Peromyscus*:

L.M. Pyter, A.K. Hotchkiss and R.J. Nelson: "Photoperiod affects brain mass and expression of genes regulating angiogenesis in brains of adult *Peromyscus leucopus*"

D.A. Geddes and C.A. Marler: "Interactions between vasopressin-manipulated fathers and their mates and pups in California mice (*Peromyscus californicus*)"

E.S. Davis, C. Auger, A.P. Auger, B.C. Trainor and C.A. Marler: "The role of progesterone and progesterone receptor isoforms A and B in paternal behavior and Aggression"

B.C. Trainor, C.R.M. Frazier, C.J. Cravens and C.A. Marler: "Paternal retrieving increases aggression and vasopressin (AVP) in the biparental California Mouse.

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**Smithsonian Holiday Card Categories** is featuring a card with a deer mouse peeking from beneath a Santa cap. See: [www.holidaycardcenter.org/2003/SM/main.asp](http://www.holidaycardcenter.org/2003/SM/main.asp)

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THE *PEROMYSCUS* STOCK CENTER IS DEVELOPING A NEW STOCK (*P. boylii rowleyi*) FOR FUTURE DISTRIBUTION AND RESEARCH UTILIZATION. In June, Mike Dewey and associates trapped 30 *P. boylii rowleyi* from Davis Mountains Nature Conservancy Preserve TX and transported them to the Stock Center in Columbia SC where they are currently in quarantined paired matings. Lab born individuals will be used to found a new stock to produce captive-born wild-type *P. boylii* that are expected be available from the Stock Center by summer 2004. The founders have been screened for hantaviruses and other pathogens.

~~~~~

### ***MAMMALIAN SPECIES UPDATE ON PEROMYSCINES:* \* \* \* \* \***

A list of peromyscine (*sensu strictu*) species accessible on-line is found in *PN* #35, p. 6. Omitted was *Podomys floridana* Mammalian Species #427. Species accounts available through the American Society of Mammalogists in print form for a charge, but not yet on-line, are *Peromyscus aztecus* (649) *P. dickeyi* (659), *P. hooperi* (709), *P. sejugis* (658), *P. simulus* (669), and *P. slevini* (705).

# THE PEROMYSCUS GENETIC STOCK CENTER

## General

The University of South Carolina has maintained a genetic stock center for *Peromyscus* (deer mice and congeneric species) since 1985. The center was established under a grant from the Living Stocks Collection Program of the National Science Foundation and continues to be supported by NSF and the NIH Biological Models and Materials Research Program. It also receives support from the University and from user fees.

The major function of the Stock Center is to provide genetically characterized types of *Peromyscus* in limited quantities to scientific investigators and educators. Continuation of the center is dependent upon significant external utilization, therefore potential **users are encouraged to take advantage of this resource.**

## Policies and Procedures.

The Stock Center currently maintains several categories of stocks of living animals: 1.) Closed colony random-bred<sup>1</sup> "wild-type" stocks of seven species of *Peromyscus*. 2.) Two highly inbred<sup>2</sup> stocks of "wild-type" *P. leucopus*. 3.) Stocks of eighteen coat color mutations, mostly in *P. maniculatus*. 4.) Stocks of nine other monogenic traits. The Stock Center operates in strict compliance with the Animal Welfare Act and is located in an AAALAC approved facility. All animal care is performed by certified technicians. Stocks are monitored regularly for presence of disease and parasites and are free of hantavirus and 15 murine viruses.

The Stock Center also provides blood, organs, tissues, fetuses, skins and other biological materials from *Peromyscus*. The Stock Center operates a Molecular Bank where selected genomic libraries and probes are available. Other resources include a reference collection of more than 2,500 reprints of articles on peromyscine rodents copies of which may be provided. The Stock Center is the primary sponsor of **PeroBase**, an on-line database dedicated to information regarding *Peromyscus* and closely related species.

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.

## Orders and Pricing.

A user fee of **\$17.50 is charged per wild-type stock animal. (\$22.50 for corporate users). Coat color and other mutants, as well as special stock animals are currently available for \$25 per animal.** User assumes the cost of air shipment. Animals lost in transit are replaced without charge. Tissues, blood, skins, *etc.* are supplied at a modest fee that includes technician time. Arrangements for special orders will be negotiated. Billing will be submitted upon satisfactory delivery. **Write or call for details.**

## Stocks Available

### WILD TYPE STOCKS

### ORIGIN

|                                                                        |                                                                                                                         |
|------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------|
| <i>P. maniculatus bairdii</i><br>(BW Stock)<br>Deer Mouse              | Closed colony bred in captivity since 1948.<br>Descended from 40 ancestors wild-caught near Ann Arbor MI.               |
| <i>P. maniculatus sonoriensis</i><br>(SM2 Stock)<br>Sonoran Deer Mouse | Derived from about 50 animals wild-caught by Jack Hayes in 1995 near White Mountain Research Station, CA                |
| <i>P. polionotus subgriseus</i><br>(PO Stock)<br>Oldfield Mouse        | Closed colony since 1952. Derived from 21 ancestors wild-caught in Ocala Nat'l. Forest FL. High inbreeding coefficient. |
| <i>P. polionotus leucocephalus</i><br>(LS Stock)<br>Beach Mouse        | Derived from beach mice wild-caught on Santa Rosa Island FL and bred by R. Lacy.                                        |
| <i>P. leucopus</i><br>(LL Stock)<br>White-footed Mouse                 | Derived from 38 wild ancestors captured between 1982 and 1985 near Linville NC                                          |
| <i>P. californicus insignis</i><br>(IS Stock)<br>California Mouse      | Derived from about 60 ancestors collected between 1979 and 1987 in Santa Monica Mts. CA                                 |
| <i>P. aztecus</i><br>(AM Stock)<br>Aztec Mouse                         | Derived from animals collected on Sierra Chincua Michoacan, Mexico in 1986.                                             |
| <i>P. melanophrys</i><br>(XZ Stock)<br>Plateau Mouse                   | Derived from animals collected between 1970 and 1978 from Zacatecas, Mexico and bred by R. Hill.                        |
| <i>P. eremicus</i><br>(EP Stock)<br>Cactus Mouse                       | Originated from 10-12 animals collected at Tucson, AZ in 1993.                                                          |

### INTERSPECIFIC HYBRIDS

|                                                                        |                                 |
|------------------------------------------------------------------------|---------------------------------|
| <i>P. maniculatus</i> X <i>P. polionotus</i><br>F <sub>1</sub> Hybrids | Bred by special order.          |
| <i>P. leucopus</i> X <i>P. gossypinus</i><br>F <sub>1</sub> Hybrids    | Sometimes available by request. |

### MUTATIONS AVAILABLE FROM THE STOCK CENTER<sup>3</sup>

| COAT COLORS                                                                    | ORIGINAL SOURCE                                      |
|--------------------------------------------------------------------------------|------------------------------------------------------|
| Albino <i>c/c</i>                                                              | Sumner's albino deer mice (Sumner, 1922)             |
| Ashy <i>ahy/ahy</i>                                                            | Wild-caught in Oregon ~ 1960 (Teed et al., 1990)     |
| Black (Non-agouti) <i>a/a</i>                                                  | Horner's black mutant (Horner et al., 1980)          |
| Blonde <i>bln/bln</i>                                                          | Mich. State U. colony (Pratt and Robbins, 1982)      |
| <sup>4</sup> Brown <i>b/b</i>                                                  | Huestis stocks (Huestis and Barto, 1934)             |
| California blonde <i>cfb/cfb</i>                                               | Santa Cruz I., Calif., stock (Roth and Dawson, 1996) |
| Dominant spotting <i>S/+</i>                                                   | Wild caught in Illinois (Feldman, 1936)              |
| Golden nugget <i>b<sup>gn</sup>/b<sup>gn</sup></i><br>[in <i>P. leucopus</i> ] | Wild caught in Mass. (Horner and Dawson, 1993)       |
| Gray <i>g/g</i>                                                                | Natural polymorphism. From Dice stocks (Dice, 1933)  |
| Ivory <i>i/i</i>                                                               | Wild caught in Oregon (Huestis, 1938)                |
| <sup>5</sup> Pink-eyed dilution <i>p/p</i>                                     | Sumner's "pallid" deer mice (Sumner, 1917)           |
| Platinum <i>plt/plt</i>                                                        | Barto stock at U. Mich. (Dodson et al., 1987)        |
| <sup>4</sup> Silver <i>sil/sil</i>                                             | Huestis stock (Huestis and Barto, 1934)              |
| Tan streak <i>tns/tns</i>                                                      | Clemson U. stock from N.C. (Wang et al., 1993)       |
| Variable white <i>Vw/+</i>                                                     | Michigan State U. colony (Cowling et al., 1994)      |
| White-belly non-agouti <i>a<sup>w</sup>/a<sup>w</sup></i>                      | Egoscue's "non-agouti" (Egoscue, 1971)               |
| Wide-band agouti <i>A<sup>Nb</sup>/a</i>                                       | Natural polymorphism. U. Mich. (McIntosh, 1954)      |
| Yellowish <i>y/y</i>                                                           | Sumner's original mutant (Sumner, 1917)              |

## OTHER MUTATIONS AND VARIANTS

|                                                                          |                                                                                                                               |
|--------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------|
| Alcohol dehydrogenase negative<br><i>Adh<sup>o</sup>/Adh<sup>o</sup></i> | South Carolina BW stock (Felder, 1975)                                                                                        |
| Alcohol dehydrogenase positive<br><i>Adh<sup>f</sup>/Adh<sup>f</sup></i> | South Carolina BW stock (Felder, 1975)                                                                                        |
| Boggler <i>bg/bg</i>                                                     | Blair's <i>P. m. blandus</i> stock (Barto, 1955)                                                                              |
| Cataract-webbed <i>cwb/cwb</i><br>(1979)                                 | From Huestis stocks (Anderson and Burns, 1979)                                                                                |
| Epilepsy <i>ep/ep</i>                                                    | U. Michigan <i>artemisiae</i> stock (Dice, 1935)                                                                              |
| <sup>5</sup> Flexed-tail <i>fff</i>                                      | Probably derived from Huestis flexed-tail (Huestis and Barto, 1936)                                                           |
| Hairless-1 <i>hr-1/hr-1</i>                                              | Sumner's hairless mutant (Sumner, 1924)                                                                                       |
| Hairless-2 <i>hr-2/hr-2</i>                                              | Egoscue's hairless mutant (Egoscue, 1962)                                                                                     |
| Juvenile ataxia <i>ja/ja</i>                                             | U. Michigan stock (Van Ooteghem, 1983)                                                                                        |
| Enzyme variants                                                          | Wild type stocks given above provide a reservoir for several enzyme and other protein variants. (Dawson <i>et al.</i> , 1983) |

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<sup>1</sup>"Random-bred" stocks are mated without deliberate selection, and sib-sib mating is avoided.

<sup>2</sup>Inbred lines are bred by sib-sib (or parent-offspring equivalent) mating for 21 generations or more.

<sup>3</sup>Unless otherwise noted, mutations are in *P. maniculatus*

<sup>4</sup>Available only as silver/brown double recessive

<sup>5</sup>Available only as pink-eye dilution/flexed-tail double recessive

## Other Resources of the Peromyscus Stock Center

Highly inbred *P. leucopus* (I<sub>30+</sub>) are available as live animals or as frozen tissues.  
Two lines developed by George Smith (UCLA) are currently maintained by the Stock Center.

Limited numbers of other stocks are on hand, but not currently available. Inquire.

Preserved or frozen specimens of types given in the above tables.

Flat skins of mutant or wild-type coat colors or wild-types of any of the stocks listed above.

Reference library of more than 2500 reprints of research papers, articles and reports on *Peromyscus*. Single 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 10 cents per photocopied page after the initial 20 pages.

Photocopies of back issues of Peromyscus Newsletter (\$5 ea.) or original back copies, when still available, without charge.

Materials are available through the *Peromyscus* Molecular Bank of the Stock Center. Allow two weeks for delivery. Included is purified DNA or frozen tissues of 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, e-mail [crosslan@biol.sc.edu](mailto:crosslan@biol.sc.edu)***

PLEASE CALL WITH INQUIRIES

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<http://stkctr.biol.sc.edu>***

## **AHY (Ashy) Stock of *Peromyscus maniculatus* (Deer Mouse) – A Model for Reversing Hair Color Loss?**

(This is the second in a series a particular stock of *Peromyscus* maintained by the Peromyscus Genetic Stock Center. These accounts describe the origin and history of the various stocks and research projects for which they may prove useful. Basic references are cited. To obtain more information contact the Stock Center by phone or e-mail. The purpose of these accounts is to promote the utilization of the resources of the Stock Center.)

Ashy deer mice (officially “ashiness” to emphasize that the gene is not homologous with a the ash mutant gene in house mouse) were first collected about 1960 by the late Ralph R. Huestis from a wild deer mouse population (*P. m. rubidus*) inhabiting sand dunes near Alsea Bay, Oregon. Although Huestis believed that the trait was attributable to a recessive gene, this was not confirmed until the trait was formally described by Teed *et al.* (1990). The animals in the Stock Center were derived directly from the six pairs of ash deer mice obtained from Huestis in the 1960s. Over a number of years the trait was bred into a *P. m. bairdii* (BW Stock) background.

Ashy *Peromyscus* appear normal as juveniles. By two months of age, some animals destined to become ash develop paler than normal ankles above the white foot typical of this genus, and in some instances partial de-pigmentation on the rostrum leaves a pigmented spot. Progression of graying follows a typical pattern (Figure): Between 80 and 120 days, the first appearance of gray hairs on the rostrum occurs and gray begins to extend upward on the limbs, but some animals are still not distinguishable. By 120 to 180 days more than 90% of homozygotes show some graying on the muzzle and base of the tail. At six to nine months virtually all homozygotes express the trait, at least to some degree. After six months most animals are gray on the head, legs and rump and most remain at this stage. About 10% of the animals in our Ashy stock continue to lose pigment and eventually the coat becomes all white. Pigment in the skin is not affected, and the eyes, tail and ears remain fully pigmented. For a more detailed account of this trait and its development see Teed *et al.* (1990). No linkage or gene interaction data have been developed for this trait.

When melanocyte stimulating hormone (MSH) pellets were implanted beneath the skin on the heads of advance-stage ash deer mice, pigment was restored, although the restored hairs lacked the normal agouti band. Dummy implants did not restore pigmentation. These experiments were done with a very small number of animals, but additional studies might reveal more effective means of restoring hair color in graying mice using MSH implants or topical treatments. The potential for application to humans might be explored and funding by the cosmetic industry or health agencies pursued.

The Peromyscus Genetic Stock Center can supply small numbers of Ashy deer mice sufficient to establish a breeding stock to interested investigators. Contact the Stock Center for details.

### Reference:

Teed, S.K., J.P. Crossland and W.D. Dawson. Coat color genetics of *Peromyscus*: I. Ashiness, an age-dependent coat color mutation in the deer mouse. *J. Heredity* 1990, 81:309-313. (Available by request from the Peromyscus Stock Center)

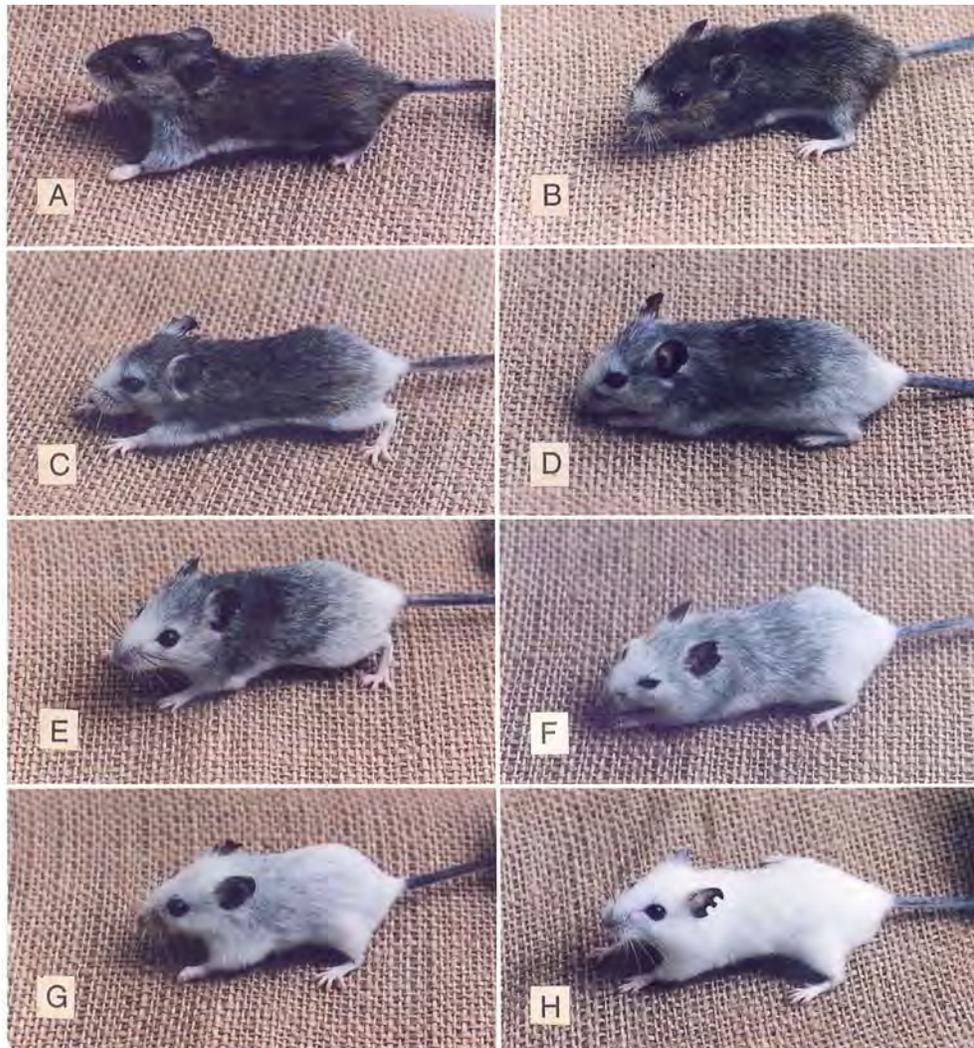


Figure: (A) Wild-type adult deer mouse. (B-F) Typical development of the ashy phenotype. (G and H) Extreme depigmentation observed in some animals.

Figure Source: S. K. Teed, J. P. Crossland and W. D. Dawson. Coat color genetics of *Peromyscus*. I. Ashiness and age-dependent coat color Mutation in the Deer Mouse. *Journal of Heredity*, 1990. 81:311. by permission of Oxford University Press.

## ***Peromyscus* Species and Speciation: A Commentary. I.**

Peromyscine rodents as experimental animals - what is their most valuable asset? In my view, I think that among mammals no group is so ideally suited to the study of speciation as is *Peromyscus*. I relate this to my personal odyssey with these creatures. Permit me to interject a bit of my experience and history. Thanks to reading Ernest Thompson Seton books as a boy, by age 12 I had developed a fascination with mammals and read whatever I could find. One summer morning I found a live mouse (*P. leucopus* as it turned out) that could not escape from an empty ornamental fishpond. My sister had recently bought me a birthday gift of H.E. Anthony's *Field Book of North American Mammals*. With mouse in a jar, I immediately grabbed my field guide for identification. It was very clear that it was a *Peromyscus*, but what one? What I found were color illustrations of numerous species of "Peromyscus", most of which were not helpful. By eliminating all of the forms that occurred west of the Mississippi, I eventually eliminated all but a few and finally, with more detail, identified the specimen as "white-footed mouse", *i.e.* THE "white-footed mouse", since the guide had other "white-footed mice" with various prefatory descriptors. The question arose in my mind: "Can there really be this many different species that look so much alike?" That led me to try to find out more about what constituted a "species" and trips to the school library encyclopedia and to my neighbor's set of nature books she had just bought from a door-to-door salesman. I became vaguely aware that different species could not successfully breed with one another and this was the biological distinction. I still wasn't convinced that there were that many different species of *Peromyscus* in North America. I developed a grand dream - I would build a large "brooder" house with many cages and I would attempt to cross all of the many combinations of *Peromyscus* "species", and thereby show, I hypothesized, that there were not nearly as many species ("good" species, we sometimes say) as Anthony's guide showed. But then came high school, college, work, Air Force and other priorities, but the idea was still vaguely in the back of my mind.

Meanwhile, my biological interests had expanded to genetics and evolution in a broader sense. In 1957 I started grad school at the University of Kentucky working under the direction of John Carpenter, who had done his doctoral work at the University of Texas with J. T. Patterson and W. S. Stone, the highly regarded *Drosophila* biologists. Carpenter's particular interest was food (yeast species) preferences in larval drosophilids as a speciating mechanism. Thus, I worked on native *Drosophila* species for my MS thesis, but during the second semester Carpenter taught an Evolution course with a required term paper. Thinking back to my earlier speculation about *Peromyscus*, I titled the paper "Speciation in *Peromyscus*". My literature search immediately introduced me to the studies of Lee Dice at Michigan during the 1930's, '40s and '50s. Essentially, he had already done the "Big brooder house" experiment many years previously. I was also introduced about this time to the paradigm-shifting works of Dobzhansky, Huxley, Mayr, Rensch, Simpson, and Stebbins and to the population genetic concepts of Fisher, Haldane and Wright. I had become a convinced proponent of neodarwinism and the Biological Species Concept. Hence, I pursued a life-long commitment to understanding the nature of species and speciation as applied to peromyscine rodents.

*Peromyscus* had many advantages for speciation studies, as I saw it. There were many species and subspecies. There were varying degrees of interfertility or sterility in laboratory crosses among them. There was a significant literature base dating to Osgood's 1909 taxonomic revision that served as a starting point and continued with the early studies by F. B. Sumner, R.R. Huestis, L.R. Dice, W.F. Blair and their associates. *Peromyscus* was the most common small mammal, or nearly so, in most natural environments in temperate North America. They could be maintained easily and bred in captivity. Some species were known to hybridize to some extent, making possible genetic detection of genes responsible for reduced fertility among species. There was also the potential for comparison with the laboratory mouse, the biology of which was becoming well known. All of these things are still true.

Initially, as a dissertation subject, I followed up on some earlier studies at Michigan done by T. T. Liu in Dice's lab on fetal loss of embryos in *P. maniculatus* X *P. polionotus* crosses. In the process I found that reciprocal F<sub>1</sub> hybrids differed significantly in size (Dawson, 1965) with hybrids born to *P. polionotus* mothers averaging significantly larger in weight and other size parameters than either parent form and the hybrids born to *P. maniculatus* mothers were significantly smaller. Subsequent studies showed that parallel differences also occurred in the placentas and fetuses (Rogers and Dawson, 1970). These differences were eventually accounted for by parental imprinting (Vrana *et. al.*, 1998, 2000). Some of our studies in the intervening years eliminated several alternative explanations based on immunogenetic and endocrinological differences between *Peromyscus* species.

Over my academic career most of my research effort was devoted to a better understanding of the genetics of peromyscine rodents, but in addition to teaching major and non-major courses in genetics, I taught upper-level courses in "Biology of Mammals" and "Evolutionary Genetics". My view of "species" was modified somewhat by a talk by Alan Templeton I heard in 1988 at a symposium on "Speciation and Its Consequences" in Philadelphia, and was further expanded with other discourses on speciation, *e.g.* Gabriel Dover's "molecular drive" hypothesis. The increasing application of molecular sequence data to analyze phylogeny and the application of cladistic models to these data have done much to clarify larger scale phylogeny, but, at least at present, are not the panacea originally envisioned for resolving the "species question". At some point around 1990 I further refined my thinking about "species" and "speciation" as I initiated a graduate level course in "Speciation".

In the next issue of *Peromyscus Newsletter*, I will elaborate on my view of "species". What I will maintain is that there are four fundamental ways ("concepts") of defining species with numerous variations on each theme, and, at least for *Peromyscus*, that no single approach is always the most useful, or most realistic or most "correct".

W. DAWSON

See Buttler Bibliography in **PeroBase** for full citation of references.



***NOTICE***

**PEROMYSCUS NEWSLETTER IS NOT A FORMAL SCIENTIFIC PUBLICATION.**

**Therefore ...**

**INFORMATION AND DATA IN THE CONTRIBUTIONS SECTION MUST NOT BE CITED OR  
USED WITHOUT PERMISSION OF THE CONTRIBUTOR.**

**THANK YOU!**



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### Various aspects of activity metabolism in *Peromyscus maniculatus*

Kim Hammond, Enrico Rezende, and I have been studying various aspects of activity metabolism in *Peromyscus maniculatus* (these animals are derived from *P. m. sonoriensis* collected at 3,800 m in the White Mountains of California). Recently we have examined the energetics and behavior of voluntary locomotor exercise. A running wheel (circumference 1.12 m) and a modified standard mouse cage were enclosed in a Plexiglas housing equipped with fans to circulate air and input and output ports for air flow, so that metabolism could be continuously measured as oxygen consumption ( $O_2$ ) while animals exercised. We monitored  $O_2$  and exercise performance (as wheel velocity) over periods of 24-48 h under a 14L:10D photoperiod, with sampling every 1.5 seconds. We tested mice at near-thermoneutral temperatures (25-26 °C) and in cold conditions (3 and 10 °C). As far as we know, these may be the first measurements of voluntary exercise costs in small mammals – our current understanding of locomotor energetics is based on forced exercise.

Results to date (about 40 animals) show huge between-individual variation in voluntary running behavior, with some mice running just a few hundred meters while others covered distances of over 20 km/night at speeds of up to 4.7 km/h. There was a wide range in preferred running speeds as well as the distance covered. Similar to findings with selected lines of laboratory *Mus* by Ted Garland and his colleagues, all of our deer mice ran intermittently, with frequent entries and exits from the wheel and many reversals in the direction of wheel rotation.

There was considerably less variance in metabolism than in running performance. All mice (including the most vigorous runners) did not attain the maximal rate of oxygen consumption elicited by forced treadmill exercise ( $O_{2max}$ ); the highest  $O_2$  in voluntary running was about 80-90% of  $O_{2max}$ . We used a spaced sequential sampling protocol to find the relationship between voluntarily-attained speed and  $O_2$  for each mouse as an estimate of the energy cost of running. Preliminary results suggest this relationship may differ from what is obtained during forced treadmill exercise.

When voluntarily running at low ambient temperatures, deer mice appear to be able to partially substitute the heat produced as a by-product of exercise for thermostatic heat that would otherwise need to be produced by shivering or NST. This saves energy and maintains a scope for sub-maximal activity that would be severely compromised if substitution did not occur. However, other studies (*currently in press*) show that exercise  $O_{2max}$  attained during cold exposure (zero to -16°C) is the same or lower than that attained at 20-22°C, for both warm-and cold-acclimated animals. Taken together, these findings suggest that the duration of intense activity (*i.e.*, exercise endurance) for deer mice is curtailed at low ambient temperatures.

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### **Embryonic Phenotypes associated with Loss-of-Imprinting in *Peromyscus* hybrids**

*Peromyscus*, like other mammals, has a method of inheritance termed genomic imprinting. Genomic Imprinting refers to differences in allelic expression that depend on the parental origin of the allele. The maternal and paternal genes must be marked or “imprinted” before the two parental genomes fuse in the zygote, thus causing the two genomes to be uniquely modified. These modifications in the oocyte, before fusion of the two genomes, are thought to be largely controlled by the maternally inherited factors present in the cytoplasm of the egg (Latham and Sapienza 1998). Many of the genes subject to imprinting regulate growth.

It has been shown that when female *Peromyscus polionotus* (PO strain) are crossed with male *Peromyscus maniculatus* (BW strain), overgrown nonviable offspring is produced when compared to parental pups. The reciprocal cross between a female BW and a male PO produces small but viable offspring when compared to the parental strains. These phenomena are thought to be largely controlled by differential control of imprinted genes between the two species (Vrana et al., 2000). Many genes show loss-of- imprinting (LOI) in the hybrids.

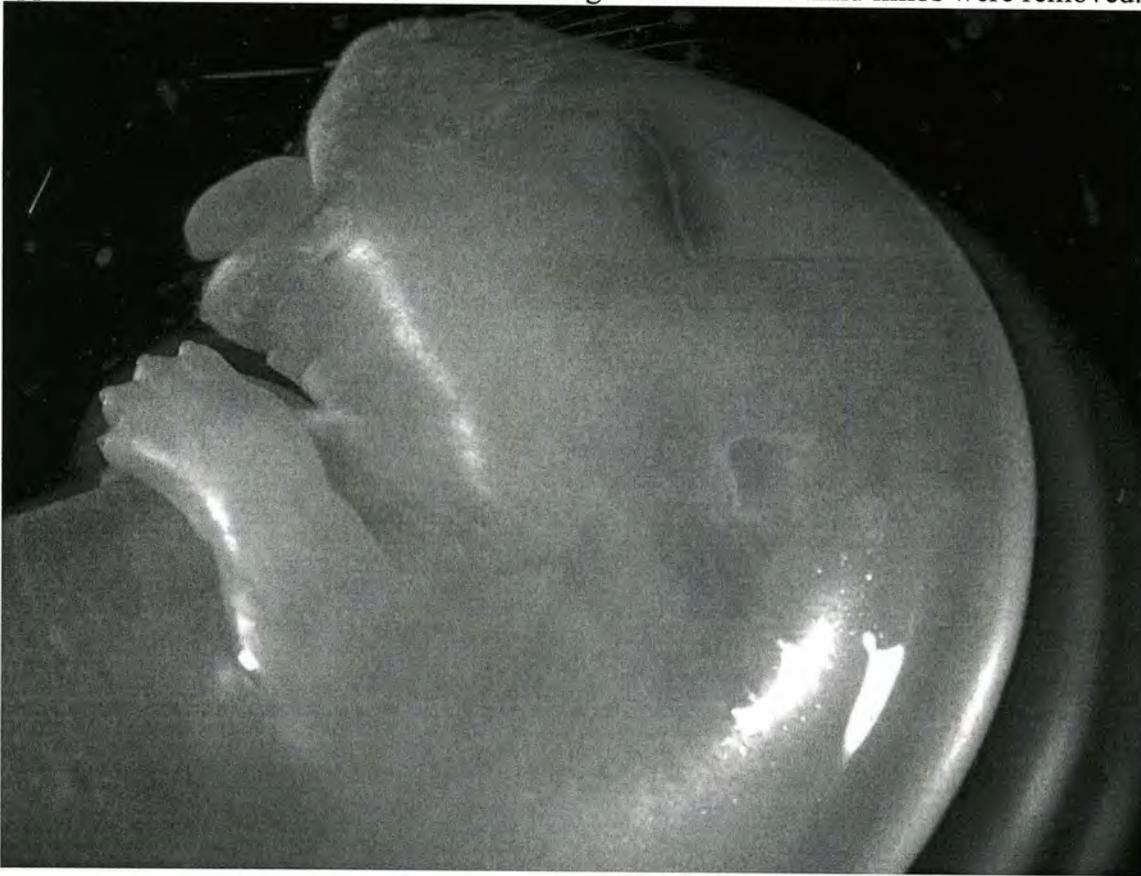
Our studies have focused on the large offspring (PO x BW) and identifying the gene(s) that are responsible for the LOI. One gene of interest that may have an affect on the loss of imprinting is the maternally inherited factors that are present in the cytoplasm of the egg. To investigate this we have developed advanced intercross lines between PO x BW. At generation 10 we backcrossed these mixed PO/BW interbred females to BW and examined the embryos.

We have found some interesting phenotypes that are very similar in appearance to human diseases such as Beckwith-Wiedemann syndrome, Simpson’s syndrome, as well as other overgrowth diseases. These phenotypes include omphalocele (failure of gut to close), macroglossia (tongue overgrowth), visceromegaly (disproportionately large organs), internal hemorrhaging, shortened limbs, loose folds of skin, no to little bleeding, excessive bleeding and a “jellybean”- like appearance due to overgrowth (see Figure 1). Table 1 shows the amounts of each found in the advanced backcross and the picture gives an example to the severe overgrowth that is seen. Enlarged placentas are seen in all overgrown hybrids and backcross animals, and are not tallied here. With this method we are hoping to narrow down the region in which this maternal effect locus could be on the genome by identifying the phenotypes of the embryos thought to carry the loss of imprinting. We also hope to correlate over/under expression of particular genes with the phenotypes.

Table 1: Overview of embryonic phenotypes seen in advanced backcross

| Phenotype               | Number of Embryos |
|-------------------------|-------------------|
| “Jellybean”             | 6                 |
| Macroglossia            | 2                 |
| Shortened Limbs         | 8                 |
| Wrinkly Skin Appearance | 17                |
| Internal Hemorrhaging   | 2                 |
| Excessive Bleeding      | 1                 |
| No External Bleeding    | 2                 |
| Omphalocele             | 13                |
| Total                   | 51                |

Figure 1. Close up of an overgrowth embryo (18.5 d.p.c.) that has macroglossia, ‘jellybean’ appearance, shortened limbs and little bleeding when head and hind limbs were removed.



Latham, K. E. and Sapienza, C. (1998) Localization of genes encoding egg modifiers of paternal genome function to mouse chromosomes one and two. *Development* 125, 929-935.

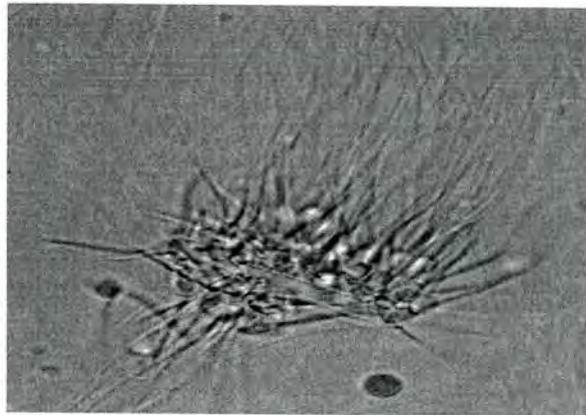
Vrana, P.B., Fossella, J.A., Matteson, P., del Rio, T., O’Neill, M.J., and Tilghman, S.M. 2000. Genetic and epigenetic incompatibilities underlie hybrid dysgenesis in *Peromyscus*. *Nature Genetics* 25:120-124

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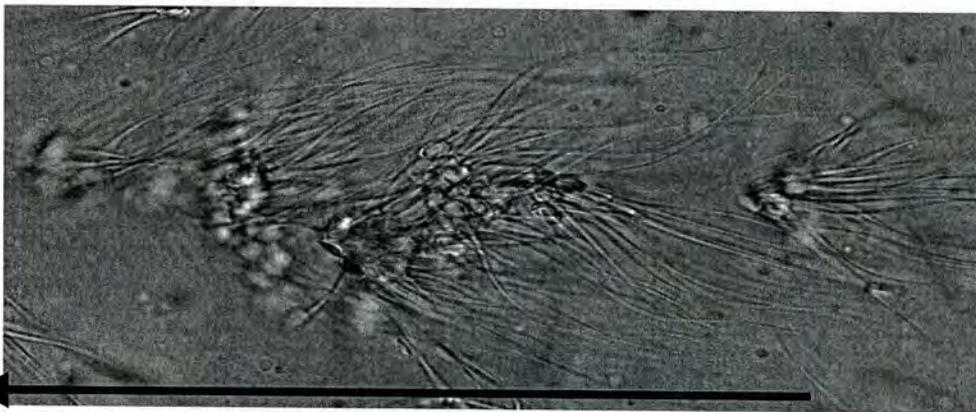
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### Sperm Aggregation in the *Peromyscus* Species: a Mutualistic Act?

While developing the technology for cryopreservation of *Peromyscus* sperm, we found that sperm from certain species of *Peromyscus* undergo extensive head-to-head aggregation (Figs.1 & 2). The aggregates tend to swim in a single organized direction, have greater motility, and appear healthier than the sperm unassociated with aggregates.



**Figure 1. An aggregate formation composed of *P maniculatus sonoriensis* spermatozoa.**

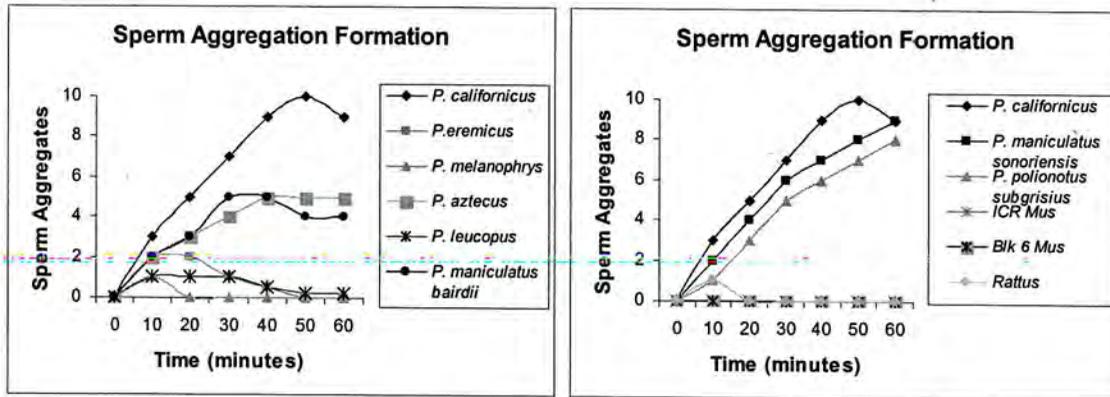


**Figure 2. A *P californicus* sperm chain. All groups in this figure are attached to each other and all were moving in the same direction (indicated by the arrow).**

Similar, but more dramatic, sperm aggregates have recently been reported for *Apodemus* (Moore et al, 2002). The suggestions were made that such aggregates are a manifestation of sperm cooperation (Moore et al, 2002) and that they are more likely to be associated with polygamous species (Short, 2002). We tested this latter notion by surveying sperm aggregation in species maintained at the Stock Center, making comparisons of monogamous species such as *P polionotus* and *P californicus* with polygamous ones such as *P maniculatus* and *P leucopus* (Dewsbury, 1981). Epididymides were removed aseptically and incubated in Petri dishes

containing HTF medium (Human Tubal Fluid with Gentamicin, Irvine Scientific, catalogue #90125). The sperm and HTF solution were aerated with 5% CO<sub>2</sub> at 37 °C.

We observed considerable variation among the *Peromyscus* species both in the degree as well as the timing of sperm aggregation (Figs 3 and 4). *P. californicus* was the most prolific aggregator, and the sperm were seen aggregating into chains similar to ones observed in *Apodemus* (Fig 2). *P. melanophrys* was the only species that did not aggregate.



Figures 3 & 4. Comparative kinetics of sperm aggregate formation among several peromyscines, *Mus*, and *Rattus*.

If aggregate formation were associated with sperm competition in polygamous mice then we would have witnessed reduced aggregation in monogamous mice. *P. californicus* and *P. polionotus* are both models for monogamy and they were among the greatest sperm aggregators. The polygamous *P. maniculatus* also showed high sperm aggregation; *P. leucopus*, another polygamous species showed much less. Thus, among these peromyscines there is no correlation of partner fidelity with sperm aggregation. Perhaps species differences in sperm aggregation reflect species-specific differences in the interaction of sperm with the female reproductive tract.

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### Three species of *Peromyscus* from the late Pleistocene of Zacatecas, México

The Calera Site is located approximately to 50 km to the northeastern of the city of Zacatecas, within the municipality of Pánuco, at 23°05'15 "N, 102°31'20 "W and 2,150 m in altitude in the State of Zacatecas, México. The sediments are characterized by calcareous rocks, Upper Cretaceous in age, in which cracks are formed that are padded with a silty sandy clayish sediment, with oxides and iron hydroxides. The studied material was found in one of these cracks.

Recent specimen skeletons were used for the identification of the material along with identification manuals and specialized bibliography (Dalquest and Stangl, 1983; Hooper, 1957). Based exclusively on dental remains, three species from the genus *Peromyscus* were identified: (1) *Peromyscus difficilis* (J. A. Allen, 1891). Its molars are characterized by the presence of stylids and lophids in the labial and lingual sides of m1 (Dalquest and Stangl, 1983), as well as the accessory cusps on M1 and M2 (Hooper, 1957). From measurements taken on the fossil specimens (lengths), in general the fossil material slightly exceeds the measurement range for both comparative Mexican specimens and those from New Mexico (Dalquest and Stangl, 1983) (Table 1). (2) *Peromyscus eremicus* (Baird, 1858). The upper molars are simple, do not have accessory cusps, but sometimes small cusps are developed only for the mesoloph and mesostyle, originating from the wall (Hooper, 1957). The lower molars are also simple, without accessory cusps. In general, the fossil molars are similar to the size of the reference materials, except in the length of M2 that surpasses the recent specimens (Table 2). The m1 is almost similar in size to the Mexican comparative materials, but smaller than the sample from New Mexico, while m2 is smaller than any comparative material. (3) *Peromyscus pectoralis* Osgood, 1904 (Table 3). Fossil specimens are of the same size as the recent Mexican samples. The fossil m1 are within the size interval of recent Mexican material, but they are smaller than those from New Mexico.

Other taxa, include the desert shrew *Notiosorex crawfordi*, Mexican extinct rabbit *Aztlanolagus agilis* (Jau-Mexía et al., 2002), desert cottontail *Sylvilagus audubonii*, Mexican cottontail *S. cunicularius*, eastern cottontail *S. floridanus*, jack rabbit *Lepus californicus*, ground squirrel *Spermophilus* sp., chipmunk *Tamias* sp., gopher *Thomomys umbrinus*, grasshopper mouse *Onychomys* cf. *O. torridus*, southern pygmy mouse *Baiomys taylori*, cotton rat *Sigmodon* sp., white-throated woodrat *Neotoma albigula*, hog-nosed skunk *Conepatus leuconotus*, and Pleistocene camel *Camelops* cf. *C. hesternus*. Their presence could support the consideration that the fauna is representative of the late Pleistocene (Jau-Mexía, 2002). This faunal complex represents a grassland habitat with a nearby deciduous forest. The present environs is a shrubland.

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Table 1. Measurements for M1, M2, m1, and m2 from *Peromyscus difficilis*.

|                                          | M1          | M2          | m1          | m2          |
|------------------------------------------|-------------|-------------|-------------|-------------|
|                                          | length      | length      | length      | length      |
| Comparative Mexican specimens (N=5)      | 1.87 (0.04) | 1.54 (0.02) | 1.87 (0.04) | 1.54 (0.02) |
|                                          | 1.81-1.94   | 1.5-1.56    | 1.81-1.94   | 1.5-1.56    |
| New Mexico specimens (N=28) <sup>1</sup> |             |             | 1.94 (0.06) |             |
|                                          |             |             | 1.85-2.05   |             |
| Fossil specimens, N=                     | 6           | 11          | 12          | 7           |
|                                          | 1.85 (0.05) | 1.55 (0.05) | 1.84 (0.06) | 1.48 (0.11) |
|                                          | 1.75-1.88   | 1.5-1.69    | 1.75-1.94   | 1.25-1.56   |

<sup>1</sup>Dalquest and Stangl (1983).

Table 2. Measurements for M1, M2, m1, and m2 from *Peromyscus eremicus*.

|                                          | M1          | M2          | m1          | m2          |
|------------------------------------------|-------------|-------------|-------------|-------------|
|                                          | length      | length      | length      | length      |
| Comparative Mexican specimens (N=5)      | 1.42 (0.05) | 1.17 (0.02) | 1.45 (0.02) | 1.18 (0.04) |
|                                          | 1.38-1.5    | 1.13-1.19   | 1.44-1.5    | 1.13-1.25   |
| New Mexico specimens (N=28) <sup>1</sup> |             |             | 1.61 (0.07) |             |
|                                          |             |             | 1.50-1.75   |             |
| Fossil specimens, N=                     | 2           | 3           | 7           | 3           |
|                                          |             | 1.25 (0.20) | 1.42 (0.04) | 1.06 (0.11) |
|                                          | 1.5-1.5     | 1.1-1.5     | 1.4-1.5     | 1.0-1.2     |

<sup>1</sup>Dalquest and Stangl (1983).

Table 3. Measurements for M2, m1, and m2 from *Peromyscus pectoralis*.

|                                          | M2          | m1          | m2          |
|------------------------------------------|-------------|-------------|-------------|
|                                          | length      | length      | length      |
| Comparative Mexican specimens (N=5)      | 1.18 (0.01) | 1.45 (0.08) | 1.19 (0.08) |
|                                          | 1.18-1.2    | 1.31-1.5    | 1.06-1.25   |
| New Mexico specimens (N=28) <sup>1</sup> |             | 1.71 (0.05) |             |
|                                          |             | 1.65-1.85   |             |
| Fossil specimens, N=                     | 4           | 1           | 2           |
|                                          | 1.18 (0.05) |             |             |
|                                          | 1.12-1.25   | 1.5         | 1.18-1.18   |

<sup>1</sup>Dalquest and Stangl (1983).

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### **Hantaviruses – An Update, with Emphasis on the Genus *Peromyscus***

Hantavirus pulmonary syndrome (HPS) is a serious cardiopulmonary disease that may be contracted by humans following exposure to infected rodents. Since the discovery of HPS following a disease outbreak in the southwestern United States in 1993, there have been 344 confirmed cases in the U.S. (including 32 confirmed retrospectively with onset prior to 1993), with an overall case fatality of 38%.

Horizontal transmission, via biting, is believed to be an important route of transmission between rodents. Human infection occurs after inhalation of virus particles from rodent urine, feces, and saliva, from contact of broken skin or mucous membranes with infectious virus, or by rodent bite. Exposures frequently occur within closed structures, such as homes or outbuildings that contain active infestations of infected rodents. Rodents are most infectious to humans and other rodents during the early stages of infection when host antibodies are absent or at low titers and virus titers are highest.

Early symptoms of HPS include an influenza-like prodrome with fever, myalgia, headaches, and fatigue. Disease progresses quickly and patients enter a cardiopulmonary stage with dry cough, shortness of breath, and tachycardia. Cardiac arrhythmias and severe hypotension with pulmonary edema occur in patients with severe disease.

With a single possible exception, all known hantaviruses are hosted by rodents in three subfamilies of the family Muridae (Murinae, Arvicolinae, and Sigmodontinae). Those associated with the Murinae (e.g., Hantaan, Dobrava, and Seoul viruses) cause hemorrhagic fever with renal syndrome (HFRS) in Europe and Asia; Puumala virus, associated with the Arvicolinae, causes mild HFRS in Europe; hantaviruses causing HPS are strictly associated with the subfamily Sigmodontinae, the so-called New World rats and mice. Although several hantaviruses are associated with arvicoline species in North America, none is associated with human disease. Seoul virus occurs nearly worldwide with its cosmopolitan host, the Norway rat, but only rarely is associated with disease in the Americas. Each hantavirus is usually associated with a single species or subspecies of rodent host (Table 1) and there is close phylogenetic concordance between the two. This concordance suggests that the viruses have co-evolved with their rodent hosts since the divergence of the three subfamilial lineages of the Muridae some 40 million years ago.

At least 11 hantaviruses, with about as many rodent hosts, have been recognized in North America. All pathogenic New World hantaviruses are hosted by sigmodontine rodents. The most important pathogenic hantavirus in North America is Sin Nombre virus (SNV), which is hosted by the deer mouse, *Peromyscus maniculatus*. The genus *Peromyscus* is especially “rich” when considering its association with hantaviruses. Besides the association of *P. maniculatus* with SNV in the western and central U.S., *P. m. nubiterrae* has been associated with Monongahela virus in the eastern U.S., *P. leucopus* with New York virus in the eastern U.S. and Blue River virus in the central U.S., and *P. boylii* with Limestone Canyon virus in the southwestern U.S. Of the other common *Peromyscus* species in the U.S., *P. truei* also is often found to be antibody positive for hantavirus. This may represent “spillover” from sympatric host species, but a thorough characterization of the virus associated with the pinyon mouse is needed. Several other *Peromyscus* species are relatively rarely found with hantavirus antibody. These include *P. californicus*, *P. difficilis*, *P. eremicus*, and *P. mexicanus*.

Mexico is a center of diversity for *Peromyscus*, with 46 species. Although HPS has not been reported in Mexico, this may be more related to the failure to recognize cases than to the scarcity of disease. Antibody to

hantaviruses have been found in several Mexican species of *Peromyscus* – *P. maniculatus*, *P. hylocetes*, and *P. melanotis* – and in *Reithrodontomys sumichrasti* and *R. megalotis*.

Research suggests that mammalogists and wildlife biologists (i.e., those who handle wild rodents on a regular basis) are at greater risk for infection with hantaviruses. Prevalence of antibody to SNV in mammalogists is positively associated with the number of *Peromyscus* rodents these researchers had handled in their careers. However, this risk may be reduced greatly by following relatively simple, established safety guidelines when trapping and handling potentially infected animals. In brief, persons collecting trapped mice should wear protective clothing including, long-sleeved shirts, long pants, laced shoes, and rubber gloves, and they should avoid inhalation of or other exposures to rodent excreta and secretions. Traps with captured mice should be placed in airtight plastic bags for transportation to rodent-processing sites and they should be placed away from the passenger compartment of the transport vehicle. Handling and sampling of rodents should be done by trained personnel wearing personal protective equipment, including latex gloves, gowns or overalls, fitted respirators with high-efficiency particulate air filters (N-100 or P-100), and eye protection. The optimum location for rodent-processing sites is an isolated, open, outside area that is well ventilated and exposed to ultraviolet light of the sun, which can act as a natural disinfectant. Three-percent hospital-strength Lysol or 10% household bleach in water should be used to disinfect instruments, traps, and other items used during processing. Contaminated gloves, gowns, and wastes should be autoclaved or burned, and clothes should be washed at the end of each trapping expedition. Rodent carcasses should be decontaminated in 10% formalin for 48 hours if they are to be used for museum specimens. Refer to selected references 7 and 8 for details or visit the Centers for Disease Control and Prevention web site at <<http://www.cdc.gov/ncidod/diseases/hanta/hps/index.htm>> for safety guidelines and other updated information.

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Table One: Recognized Hantaviruses in the World, their Hosts, Diseases Caused, and the Recognized Geographic Occurrence of the Virus

| Virus                                                   | Host Species (subspecies) <sup>a</sup>          | Distribution of Virus                    | Disease            | Reference |
|---------------------------------------------------------|-------------------------------------------------|------------------------------------------|--------------------|-----------|
| Order Rodentia, Family Muridae, Subfamily Murinae       |                                                 |                                          |                    |           |
| Hantaan <sup>b</sup> (HTNV)                             | <i>Apodemus agrarius (mantchuricus)</i>         | Eastern Russia, Northern Asia, Balkans   | Severe HFRS        | 1         |
| Seoul <sup>b</sup> (SEOV)                               | <i>Rattus norvegicus</i>                        | Nearly Worldwide                         | Mild/Moderate HFRS | 2         |
| Dobrava <sup>b</sup> (DOBV)                             | <i>Apodemus flavicollis</i>                     | Balkans                                  | Severe HFRS        | 3         |
| Thai <sup>b</sup> (THAIV)                               | <i>Bandicota indica</i>                         | India                                    | NR                 | 4         |
| Saaremaa <sup>b</sup> (SAAV)                            | <i>Apodemus agrarius (agrarius)</i>             | Europe                                   | Mild HFRS          | 5         |
| Amur (AMRV)                                             | <i>Apodemus peninsulae</i>                      | Far Eastern Russia                       | HFRS               | 6         |
| Order Rodentia, Family Muridae, Subfamily Arvicolinae   |                                                 |                                          |                    |           |
| Puumala <sup>b</sup> (PUUV)                             | <i>Clethrionomys glareolus</i>                  | Europe, Scandinavia, Russia, Balkans     | Mild HFRS          | 7         |
| Prospect Hill <sup>b</sup> (PHV)                        | <i>Microtus pennsylvanicus</i>                  | North America                            | NR                 | 8         |
| Bloodland Lake (BLLV)                                   | <i>Microtus ochrogaster</i>                     | North America                            | NR                 | 9         |
| Isla Vista (ISLAV)                                      | <i>Microtus californicus</i>                    | North America                            | NR                 | 10        |
| Tula (TULV)                                             | <i>Microtus arvalis/ M. rossiaemeridionalis</i> | Russia, Slovakia                         | NR                 | 11        |
| Khabarovsk (KBRV)                                       | <i>Microtus fortis</i>                          | Eastern Russia                           | NR                 | 12        |
| Topografov (TOPV)                                       | <i>Lemmus sibiricus</i>                         | Siberia                                  | NR                 | 13        |
| Order Rodentia, Family Muridae, Subfamily Sigmodontinae |                                                 |                                          |                    |           |
| Sin Nombre <sup>b</sup> (SNV)                           | <i>Peromyscus maniculatus</i>                   | North America                            | HPS                | 14        |
| New York <sup>b</sup> (NYV)                             | <i>Peromyscus leucopus</i>                      | Eastern USA and Central USA              | HPS                | 15        |
| Black Creek Canal <sup>b</sup> (BCCV)                   | <i>Sigmodon hispidus</i>                        | Southeastern USA                         | HPS                | 16        |
| Bayou <sup>b</sup> (BAYV)                               | <i>Oryzomys palustris</i>                       | Southeastern USA                         | HPS                | 17        |
| Muleshoe (MULEV)                                        | <i>Sigmodon hispidus (textanus)</i>             | Southern USA                             | HPS                | 18        |
| Monongahela (MONV)                                      | <i>Peromyscus maniculatus (nubiterrae)</i>      | Eastern USA and Canada                   | HPS                | 19        |
| Limestone Canyon (LSCV)                                 | <i>Peromyscus boylii</i>                        | Southwestern USA                         | NR                 | 20        |
| Blue River (BRV)                                        | <i>Peromyscus leucopus</i>                      | Central USA                              | NR                 | 21        |
| El Moro Canyon <sup>b</sup> (ELMCV)                     | <i>Reithrodontomys megalotis</i>                | Western USA and Mexico                   | NR                 | 22        |
| Río Segundo (RIOSV)                                     | <i>Reithrodontomys mexicanus</i>                | Costa Rica                               | NR                 | 23        |
| Caño Delgado <sup>b</sup> (CDGV)                        | <i>Sigmodon alstoni</i>                         | Venezuela                                | NR                 | 24        |
| Juquitiba (JUQV)                                        | Unknown                                         | Southeastern Brazil                      | HPS                | 25        |
| Araraquara (ARAV)                                       | Unknown                                         | Southeastern Brazil                      | HPS                | 25        |
| Castelo dos Sonhos (CASV)                               | Unknown                                         | Central Brazil                           | HPS                | 25        |
| Río Mamoré (RIOMV)                                      | <i>Oligoryzomys microtus</i>                    | Bolivia, Peru                            | NR                 | 26        |
| Laguna Negra <sup>b</sup> (LNV)                         | <i>Calomys laucha</i>                           | Western Paraguay and Bolivia             | HPS                | 27        |
| Andes <sup>b</sup> (ANDV)                               | <i>Oligoryzomys longicaudatus</i>               | Southern Argentina and Chile             | HPS                | 28        |
| Lechiguana <sup>b</sup> (LECV)                          | <i>Oligoryzomys flavescens</i>                  | Central Argentina                        | HPS                | 28        |
| Bermejo (BMJV)                                          | <i>Oligoryzomys chacoensis</i>                  | Northwestern Argentina, Southern Bolivia | HPS                | 28,31     |
| Orán (ORNV)                                             | <i>Oligoryzomys longicaudatus<sup>e</sup></i>   | Northwestern Argentina, Southern Bolivia | HPS                | 28        |
| Maciel (MACV)                                           | <i>Bolomys obscurus</i>                         | Central Argentina                        | NR                 | 28        |
| Hu39694                                                 | Unknown                                         | Central Argentina                        | HPS                | 28        |
| Pergamino                                               | <i>Akodon azarae</i>                            | Central Argentina                        | NR                 | 28        |
| Choclo                                                  | <i>Oligoryzomys fulvescens (costaricensis)</i>  | Central Argentina                        | HPS                | 28        |
| Calabazo                                                | <i>Zygodontomys brevicauda (cherriei)</i>       | Southwestern Panama                      | HPS                | 29        |
| Maporal                                                 | <i>Oecomys bicolor</i>                          | Southwestern Panama                      | NR                 | 29        |
| Order Insectivora, Family Soricidae                     |                                                 |                                          |                    |           |
| Thottapalayam <sup>b</sup>                              | <i>Suncus murinus</i>                           | Central Venezuela                        | NR                 | 32        |
|                                                         |                                                 | India                                    | NR                 | 30        |

NR=None Recognized; <sup>a</sup> Taxonomy follows Wilson, D.E. and D.M. Reeder. Eds. 1992. Mammal Species of the World: A Taxonomic and Geographic Reference 2<sup>nd</sup> ed. Smithsonian Institution Press, Washington; <sup>b</sup> Virus isolated in cell culture; others identified from genetic sequence; <sup>e</sup> May be different species or subspecies of *Oligoryzomys longicaudatus*.

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