Sustainable Ecosystems Institute

EVALUATION OF SCIENTIFIC INFORMATION REGARDING PREBLE'S MEADOW JUMPING MOUSE

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EXECUTIVE SUMMARY

This scientific panel was charged with evaluating existing data and analyses on the taxonomic status of Preble's jumping mouse (*Zapus hudsonius preblei*). In particular, the panel was asked to determine why two research groups--Ramey et al. (2005; hereafter REA) and King et al. (in press, Mol. Ecol.; hereafter KEA)-- came to opposite conclusions regarding the validity of *Z. h. preblei* as a distinct subspecies. In doing so, the panel considered a wide variety of information, including the reports and recently-published papers of REA and KEA, and a number of third-party critiques of the two studies. We also had opportunities to discuss a variety of questions and concerns with the principle investigators for each study and other scientists during the public panel meeting in Ft. Collins, Colorado, July 6-7, 2006. The panel also re-examined and reanalyzed portions of the original datasets of REA and KEA.

The panel concluded that two of the lines of evidence presented by REA (their analyses of cranial morphometrics and ecological exchangeability) are based on insufficient data to support their suggestions for taxonomic change. Specifically, REA's cranial morphometric analysis did not adequately test the original characters, or specimens, on which the taxonomic description of *Z. h. preblei* was based. Similarly, the panel found that the criterion of ecological exchangeability had not been adequately tested by REA or others. At this point in time, there are no data that are sufficient to address either Krutzsch's (1954) original description of *Z. h. preblei* or whether this taxon is ecologically exchangeable with other subspecies of *Z. hudsonius*.

Both REA and KEA analyzed mitochondrial DNA (mtDNA) sequence data and microsatellites in an attempt to determine whether *Z. h. preblei* is genetically distinct from other subspecies of *Z. hudsonius;* however, the two studies varied in the amount of data and sampling strategies employed. The most significant difference between the two studies in terms of data was whether *Z. h. preblei* shared any mtDNA haplotypes with other subspecies of *Z. hudsonius* examined. REA found that there was evidence for a low level of haplotype sharing (i.e., ~11% between *Z. h. preblei* and *Z. h. campestris*). KEA found no evidence for haplotype sharing among any of the subspecies of *Z. hudsonius* examined. The source of this disagreement is the different mtDNA sequences obtained by REA and KEA for several museum specimens from the University of Kansas, Museum of Natural History (KUMNH). Our re-analysis (detailed in the report) of the original chromatograms provided to the panel by the first authors indicates that there is evidence of contamination in some of the samples (i.e., there is clear evidence of multiple, different haplotypes in a single chromatogram), and that many of the sequences found to differ between the two studies were based on poor chromatogram quality (i.e., chromatograms with many ambiguous base calls) and/or quantity (i.e., based on only a single sequencing read, rather than multiple overlapping reads that allow for corroboration of sequence accuracy and purity). Based on our inspection and re-analysis of the data, the panel has determined that there is no definitive evidence for any sharing of mtDNA control region haplotypes between *Z. h. preblei* and any of the other subspecies of *Z. hudsonius* examined.

In terms of the microsatellite data, the two studies largely agree. Both REA and KEA recover the same three primary clusters in STRUCTURE analyses (including a *Z. h. preblei* cluster), they estimate similar N_em and similar F_{ST} values (which also documents statistically-significant subdivision), and they both find a lesser degree of subdivision within *Z. h. preblei*. The panel believes that some of the most significant differences between REA and KEA with regard to their interpretations of the microsatellite data in particular, and the status of *Z. h. preblei* in general, are philosophical, and stem from issues relating to the definition of subspecies, determination of biological vs. statistical significance, and choice of null vs. alternative hypotheses in scientific inquiry.

Overall, the panel concludes that the available data are broadly consistent with the current taxonomic status of *Z. h. preblei* and that no evidence has been presented that critically challenges that status. However, we also note that *Z. h. preblei* appears to be at a stage in its evolution in which clearly determining taxonomic rank will not be easy to do, and that large groups of scientists are unlikely to reach a unanimous consensus concerning its status. The panel believes that there are additional data that could be collected that may help to further clarify this issue. First, a thorough analysis of the original characters and specimens used by Krutzsch (1954) to describe *Z. h. preblei* is required. Second, the KUMNH specimens found to have conflicting mtDNA control region sequences by REA and KEA should be re-analyzed by multiple, independent labs that specialize in obtaining sequence data from "ancient DNA." This should provide unequivocal evidence for the true mtDNA sequences for these specimens. Finally, the geographic and taxonomic scope used to evaluate *Z. h. preblei* should be expanded. Both REA and KEA examined only five of the 12 recognized subspecies of *Z. hudsonius*. The evolutionary and biogeographic history, as well as the taxonomic status of *Z. h. preblei* could be evaluated more critically within this broader framework.

BRIEF OVERVIEW OF THE REPORT

We summarize our findings here regarding why the two sets of studies (those of Ramey et. al. and King et al.) came to different conclusions regarding the validity of *Z. h. preblei* as a distinct subspecies. We organize our findings into 6 sections:

1. an overview of the studies for the data collected, analysis, key results, and conclusions
2. a discussion of what we conclude are the sources of disagreement between the studies
3. a summary of our conclusions regarding the types of evidence and resolution of the disagreements
4. a final summary of the available evidence
5. our evaluation of how the data conform to several common subspecies conventions or concepts
6. comments on information needed to resolve any outstanding questions.

Where applicable, most of these sections are further divided into 4 areas based on REA's 4 lines of evidence; morphology, ecological exchangeability, mitochondrial DNA, and microsatellites. Within Section 2, we include a reexamination and reanalysis of the pivotal 15 KUMNH DNA samples that are a major source of disagreement between the two sets of studies (because most of them had different DNA sequences estimated by the 2 studies).

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THE PEER REVIEW PROCESS

Sustainable Ecosystems Institute (SEI) is a public-benefit non-profit organization dedicated to scientific resolution of issues. The institute had carried out numerous peer review processes on endangered species and related resource management concerns. SEI was contracted by the US Fish and Wildlife Service (USFWS) to evaluate scientific materials on the Preble's Meadow Jumping Mouse. The basic charge of the review process was to 'analyze, assess, and weight the reasons why the data, finding, and conclusions of King *et al*. differ from the data, finding, and conclusions of Ramey *et al*.'

The terms of the contract are set out in the contractual document. They include the following:

- Selection of reviewers
- Organizing, structuring, leading and managing the scientific review panel
- Managing and producing a final report
- Maintaining an official record for this process

SEI administers a standing group of reviewers of conservation science (the Conservation Science Network). In addition we maintain strong contacts with numerous other scientists active in this area of research. In selecting scientists for this peer review panel, we followed our normal procedure of consulting our database for potential reviewers, and also consulting with SEI board members (e.g. Prof. W. Watt of Stanford University) and previous SEI panelists (e.g. Dr. J. Dumbacher of Cal. Academy of Science). In this instance we were somewhat restricted in our choice of our reviewers in that we were prohibited from employing any scientists who had previously participated in any significant manner in discussions of PMJM. This effectively eliminated a large proportion of US scientists concerned with application of genetics techniques to taxonomic issues in small mammals. Following the dictates of the contract we sought a panel that was 'balanced, independent, and objective ...with the appropriate expertise' including panelists that were 'established, [with] high-caliber scientific credentials (based on peer reviewed publications) in genetics and systematics, with preference given to those experienced with mammalian genetics and systematics'.

We identified some 12 individuals that appeared to meet the criteria of scientific excellence, appropriate experience, and lack of conflicts of interest. Given the extremely constrained timeframe of this project (essentially 4 weeks) we approached all potentially qualified individuals about their willingness to serve on the panel. Not all scientists responded, and some were unable to meet the timelines of the project due to impending field seasons etc. One potential panelist agreed to serve but identified a potential conflict and SEI decided not to employ him. Five qualified scientists agreed to serve and were constituted as the panel. Later (after the panel had been constituted) a sixth scientist (Dr. George Barrowclough of AMNH) expressed willingness to serve (he was not included in the panel which was already active).

The five panelists selected were:

Dr. Brian Arbogast (Humboldt State University)
Dr. Jack Dumbacher (Cal Academy of Sciences)
Dr. Eric Routman (San Francisco State University)
Dr. Scott Steppan (Florida State University)
Dr. Ron Van Den Bussche (Oklahoma State University)

All panelists were well qualified to serve on the panel, and brought a wealth of expertise to the issue. All were interviewed by Dr. Courtney of SEI about their abilities, expertise and any potential conflicts. No serious problems were identified. All 5 panelists completed a conflict of interest statement derived from that used by the National Academies of Sciences. SEI was confident in the ability of all the panelists to reach fair and objective evaluations of the materials. However, early in the review process, representations were made by the National Geological Survey that one of the panelists selected by SEI (Dr. Routman) had trained in the same laboratory as one of the potential protagonists to the PMJM debate. Dr. Routman had himself raised this issue with Dr. Courtney during the selection interview but neither considered it significant (following standard practice in selecting e.g. NSF review panels). However given the extreme sensitivity of the PMJM debate, Dr. Routman offered to recuse himself, in an effort to ensure that the process was seen to be fair. The panel was then reduced to four scientists. Unfortunately another panelist (Dr. Van Den Bussche) was unable for personal reasons to attend the panel meeting. Although he participated in initial discussions of materials, he did not hear testimony or other information at the meeting, and SEI decided that it would be unfair to all concerned to ask him to continue to participate. Hence the panel was eventually reduced to just three scientists - Drs. Arbogast, Dumbacher and Steppan. Their vitae are attached as Appendix 1.

The panel discussed the available materials (including all primary sources, and other materials suggested by interested parties such as previous peer reviews, unpublished theses, etc.). In addition the panel (through SEI) contacted the primary scientists and other interested parties, to explain the process, and to solicit any additional scientific materials or scientific opinions that the parties wished to present. Several parties elected to develop materials (mostly emailed comments) to submit to the panel.

The panel also asked to see some of the primary data collected by the two research groups (Ramey et al. and King et al.), in an effort to evaluate data quality.

After initial discussions to set the scope of the project, the panel met on July 6 and 7 in Fort Collins Colorado, in a public meeting. Drs. King and Ramey were present and responded to questions posed by the panelists. Other scientists also attended, and they also participated in discussions led by the panel. Two scientists (Dr. Vignieri (currently of Sussex University) and Dr. Patton (UC Berkeley)) did not attend but were able to telephone into the meeting, and to make comments to the panel, and to respond to questions from them. Full transcripts of this meeting are in preparation, and will be appended to this report.

At the outset of this project, SEI instructed the panelists that all decision-making authority rests with USFWS and that the panelists were charged solely with a scientific evaluation of one part of the scientific record regarding PMJM (but not for instance issues of rarity, management, or status under ESA). The panelists rigorously adhered to this guideline. In addition, SEI made clear to the panelists that they were in no way obligated to reach a consensus and that they should each express their separate opinions as necessary. In this case, the panel did not disagree on any substantive or stylistic issue. Hence this report, although it reflects a strong consensus of all three panelists, also mirrors the individual opinion of each panelist.

SECTION 1. OVERVIEW OF THE STUDIES

MORPHOLOGY

Of the two sets of studies, only REA examined morphological data to test Krutzsch's (1954) original definition. Krutzsch gave a differential diagnosis by comparing *preblei* to *campestris* and *pallidus*, noting that it most closely resembled *campestris*. Krutzsch listed the following 7 traits that distinguished *preblei* from the topotypes of *campestris*:

1. upper parts generally dull, averaging lighter, less black-tipped hair
2. dorsal band less distinct, sides duller
3. averaging smaller in most cranial measurements taken
4. least interorbital constriction narrower
5. auditory bullae smaller, less inflated
6. incisive foramina narrower, not truncate posteriorly
7. frontal region usually more inflated.

OVERVIEW OF RAMEY ET AL. (2005)

Data and Sampling — REA examined 40 *preblei*, 41 *campestris*, and 37 *intermedius*. Neither type nor topotype specimens of these 3 taxa were examined. None of the other 8 other subspecies in *Z. hudsonius* were examined (Krutzsch only compared *preblei* to *Z. h. campestris* and *Z. h. pallidus*). Of the 7 discriminating traits cited by Krutzsch (1954), REA tested 2; skull size (using 9 cranial distances) and interorbital constriction, citing their inability to quantify the other traits.

Analyses — REA tested for the distinctiveness of *preblei* in 2 ways; they tabulated the number of cranial traits that were significantly smaller in *preblei* than in their sample of *campestris*, and they used linear discriminant analysis (LDA) with the criterion that taxa were distinguishable if ≥90% of specimens could be correctly classified to subspecies with jackknifed posterior probabilities ≥95% (after removal of outliers). The 90% assignment probability is one proposed by REA and in Wehausen and Ramey (2000). This is a relatively conservative standard and has not been widely followed as yet.

Key Results — Interorbital breadth was smaller in *preblei* than *campestris* ($P<0.05$) but the degree of separation, 0.54 standard deviations, was small. Several other univariate measures were larger in *preblei* and principal components analysis (PCA) of the cranial data indicated that *preblei* variation was almost entirely contained within *campestris* variation, although on average having larger size (not smaller, as Krutzsch stated). In LDA, only 42% of samples could be correctly classified at high confidence, although it was not reported what percentage were correctly classified in the non-bootstrapped analysis (the 95% confidence standard will necessarily reduce the percent considered correctly classified relative to a single analysis). Although the authors did not highlight it, the PCA did suggest that *preblei* is distinguishable from *intermedius*; 82% of *intermedius* fall outside the shape-space (convex polygon) of *preblei* and 35% of *preblei* fall outside the polygon of *intermedius*.

Key Conclusion — REA's analyses did not support *preblei* as morphologically distinguishable from the other subspecies. They asserted that distinguishability is best addressed with multivariate data, not single characters. Based on these results, REA recommended synonymy with *campestris* and *intermedius*.

OVERVIEW OF KING ET AL. (IN PRESS, MOLECULAR ECOLOGY)

KEA did not examine morphology.

ECOLOGICAL EXCHANGEABILITY

OVERVIEW OF RAMEY ET AL. (2005)

Data and Sampling — REA tested ecological exchangeability (Crandall et al. 2000) by exploring the literature for evidence of adaptive differences such as life history or (functional) morphology. The extent of the literature survey was not presented, but in a commentary, Vignieri et al., (2006) stated that they could find only a handful of relevant papers.

Analyses — The criterion for recognizing ecological differences appears to be "major habitat and/or climatic differences" (REA, p. 340).

Key Results — REA found no "major" published differences in morphology, life history, or habitat.

Key Conclusion — Unable to reject a null hypothesis of ecological exchangeability between *preblei* and other subspecies. However, REA noted that "the absence of evidence" is not the same as "the evidence of absence".

MITOCHONDRIAL DNA

Both REA and KEA examined portions of the mitochondrial genome in their respective studies. These two data sets, and conclusions drawn from them, are one source of substantial disagreement between the two studies. Below we provide an overview of the mitochondrial DNA (mtDNA) data examined in each study. We conclude this section by describing how the mtDNA data, and conclusions based on these data, differ between the two studies.

OVERVIEW OF RAMEY ET AL. (2005)

Data and Sampling — REA analyzed a 346 base pair (bp) segment of the mitochondrial DNA (mtDNA) control region (CR) for 205 individuals (sequences were deposited in Genbank with the accession numbers AY598142-AY598316). These included 58 *Z. hudsonius preblei*, 33 *Z. h. campestris*, 32 *Z. h. luteus*, 35 *Z. h. pallidus* and 47 *Z. h.*

intermedius. This represents 5 of the 12 recognized subspecies of *Z. hudsonius* (see Fig. 1, REA). Some samples (such as those of *Z. h. preblei*) came from modern, high-quality tissues, whereas others (such as those from other subspecies) consisted of tissue snips removed from museum study skins ("ancient" DNA). For outgroups, data from a homologous region of the mtDNA control region were obtained from 17 western jumping mice (*Z. princeps*). Details of laboratory techniques used to extract, amplify and sequence the mtDNA control region are provided in REA. Geographic sampling for each of the five subspecies of *Z. hudsonius* consisted of a relatively wide range of localities, with a small number of individuals sampled per locality (see REA, Fig. 3, Appendix 2).

Analyses — REA used several approaches to evaluate the phylogenetic position and population structure of the mtDNA control region haplotypes found in *Z. h. preblei* relative to those found in the other subspecies of *Z. hudsonius.* They also used these data to evaluate whether recent gene flow between *Z. h. preblei* and other subspecies of *Z. hudsonius* has occurred. Although not exhaustive, below is a summary of the major analyses they performed.

1. Phylogenetic analysis (based on distance, likelihood and parsimony criteria) of the mtDNA control region haplotypes. REA presented a neighbor-joining tree based on a best-fit model of nucleotide evolution (REA, Fig. 3). The tree is rooted with representative haplotypes from *Zapus princeps* and bootstrap values greater than 50 are shown at each node. Results of the likelihood and parsimony analyses are not shown, but were stated to be congruent with the neighbor-joining tree except with regard to the positioning of terminal taxa. Tree inference and nodal support was computed using the computer program PAUP* 4.0b10 (Swofford, 2002).

2. A molecular analysis of variance (AMOVA) was performed using the computer program Arlequin 2.0 (Excoffier et al. 1992) to determine the proportion of genetic variance within and between subspecies and populations.

3. A coalescent likelihood approach was used to estimate recent gene flow using the computer program MDIV (Nielson and Wakeley 2001).

Key Results— The key results of the mtDNA analysis of REA are:

1. *Z. h. preblei* was not reciprocally monophyletic relative to any other subspecies of *Z. hudsonius* based on phylogenetic analysis of the 346 bp of mtDNA control region examined (see REA, Fig. 3).

2. Seven specimens of *Z. h. campestris* had mtDNA control region haplotypes identical to those of *Z. h. preblei.*

3. Analysis of molecular variance between *Z. h. preblei* and *Z. h. campestris* revealed that most of the genetic variation was within (63%) rather than between (37%) these putative subspecies.

4. MDIV analysis of the mtDNA control region data showed low, but non-zero estimated levels of very recent gene flow between *Z. h. preblei* and *Z. h. campestris.* No recent gene flow was detected between *Z. h. preblei* and the other subspecies examined.

Key Conclusion — *Z. h. preblei* is not a distinct subspecies; rather, they conclude that *Z. h. preblei* is a subpopulation of *Z. h. campestris.*

OVERVIEW OF KING ET AL. (IN PRESS, MOLECULAR ECOLOGY)

Data and Sampling —— For the mtDNA portion of their study, KEA examined a total of 1,380 bp representing portions of both the non-coding control region (374 bp) and the protein-coding cytochrome-b gene (1,006 bp). These sequences have been deposited in Genbank under accession numbers DQ664546-DQ664900 (control region) and DQ664901-DQ665221 (cytochrome b). Like REA, 5 of the 12 recognized subspecies of *Z. hudsonius* were examined, representing 13 geographic locations. The number of specimens examined was 322 for the control region and 320 for the cytochrome-b gene. There were 25 and 56 haplotypes present in these 2 data sets, respectively. These samples all came from modern tissues (typically ear punches or frozen tissues). In addition to these samples, KEA also obtained mtDNA control region data for 15 specimens from the University of Kansas Natural History Museum (KUNHM) that were also examined in the REA study (see KEA, Table 1B). These samples represented 7 of the 10 haplotypes reported as being shared among subspecies by REA. Details of laboratory techniques used to extract, amplify and sequence the mtDNA control region and cytochrome b gene are provided in KEA. Geographic sampling for each of the 5 subspecies of *Z. hudsonius* differed from that of REA in that KEA sampled fewer localities with a larger number of individuals sampled per locality. Also, the geographic sampling strategy of KEA focused on areas that were not at or near the contact zones between subspecies.

Analyses — KEA used a variety of approaches to evaluate the phylogenetic position and population structure of *Z. h. preblei* relative to those found in the other subspecies of *Z. hudsonius.* They combined their control region and cytochrome b data based on the results of an ILD test (Farris et al. 1994). They also used these data to evaluate whether recent gene flow between *Z. h. preblei* and other subspecies of *Z. hudsonius* has occurred. Although not exhaustive, below is a summary of the major analyses they performed.

1. Phylogenetic analysis (based on parsimony and partitioned Bayesian analysis) of the mtDNA control region and cytochrome b data. Like REA, KEA used *Z. princeps* as an outgroup in phylogenetic analyses. For parsimony analysis, KEA used the program PAUP* 4.0b10 (Swofford 2002). Nodal support for parsimony trees was assessed using non-parametric bootstrapping. Partitioned Bayesian analysis of the combined data set was performed using the computer program MrBayes 3.0 (Huelsenbeck and Ronquist 2001). The parsimony and Bayesian trees are presented in KEA, Fig. 5.

2. Intraspecific haplotype networks for the control region and cytochrome b data were

inferred using the program TCS (Clement et al. 2000). The haplotype network for the cytochrome b data is shown in KEA, Fig. 3. This analysis implemented the statistical parsimony approach of Templeton et al. (1992) and Crandall et al. (1994).

3. A molecular analysis of variance (AMOVA) was performed using the computer program Arlequin 2.0 (Excoffier et al. 1992) to determine the proportion of genetic variance within and between subspecies and populations. Both F_{st} and Φ_{st} were estimated.

Key Results — The key results of the mtDNA analysis of KEA are:

1. KEA's analysis of the control region data produced different sequences than those reported by REA for 13 of the 15 KUMNH specimens examined in both studies (see KEA, Table 1B). All 7 specimens of *Z. h. campestris* reported to have *Z. h. preblei* haplotypes by REA were found by KEA to have common *Z. h. campestris* haplotypes.

2. For the combined control region and cytochrome b data sets, *Z. h. preblei* did not share any haplotypes with any other subspecies of *Z. hudsonius*. No haplotypes were shared by any 2 subspecies examined. No haplotypes of *Z. h. preblei* occurred within a clade containing haplotypes of other subspecies of *Z. hudsonius*. However, in the rooted parsimony and Bayesian analyses (KEA, Fig. 5), *Z. h. preblei* was not reciprocally monophyletic with respect to the other subspecies (this part of the tree did not have a high degree of resolution in the rooted analyses).

3. Statistical parsimony analysis of the sequence data from each mitochondrial gene region produced similar haplotype networks. The cytochrome b haplotype network (KEA, Fig. 3) indicated that within the (*Z. h. preblei-intermedius-campestris*) networks, haplotypes made up of individuals from each subspecies clustered together.

4. Analysis of molecular variance from each gene region indicated strong, significant genetic differentiation among the 5 subspecies of *Z. hudsonius* examined. The global Φ_{st} was 0.96, indicating that nearly all (96%) of the haplotypic variance was distributed between subspecies.

Key Conclusion — KEA concluded that *Z. h. preblei* is a genetically distinct subspecies, not sharing any haplotypes with *Z. h. campestris* or any other subspecies of *Z. hudsonius.*

MICROSATELLITE DATA

Microsatellites or STRs ("short tandem repeats") are segments of tandemly-repeated DNA, found primarily in the nuclear genome of vertebrate animals. The repeat regions typically consist of 2-4 bases repeated over and over, often hundreds of times. For example, a microsatellite containing an AC repeat may contain a lead-in sequence of DNA followed by dozens or even hundreds of ACs repeated, and then followed again by another sequence. The normal sequences flanking the repeat can be used to PCR amplify the microsatellite.

The number of tandem repeats in microsatellites can evolve quickly, and so many natural populations can have dozens of alleles at each variable microsatellite locus. Each allele will differ in the number of repeats that causes differences in the length of the region. Variation is assessed by PCR amplifying across the repeat array and evaluating the size of the resultant fragments, usually on an acrylamide gel or an automated capillary DNA sequencer. Individuals can be scored for which alleles they carry.

Populations can differ in which alleles are present, the frequencies of alleles at each locus, and the variance-covariance structure of alleles across multiple loci. These differences at microsatellite loci afford incredible power to detect and resolve differences among populations. Geneticists have derived several techniques for estimating parameters associated with population isolation, population size fluctuations, migration rates among populations, and geneticists can use these properties to assign individuals to candidate populations.

Microsatellite markers have several advantages: they are fast evolving, usually autosomally inherited (ie. they are rarely sex linked), relatively easy to score, have many alleles at each locus, and tend to be useful for diagnosis at the subspecies or even population level. Microsatellites are often used to infer patterns of nuclear gene flow and geographic subdivision in order to compliment mitochondrial studies, and are additionally useful for analyses of parentage, genetic census, and other fine-resolution issues.

Both REA and KEA include analyses of microsatellite data, but there are several differences in their sampling and analyses. In addition, Crandall and Marshall (2005) re-examine some of these data to evaluate potential differences between the datasets and conclusions, and they attempt to ask further questions. Here we evaluate the different datasets and different analytical approaches, and we offer our summary interpretation of these microsatellite data.

OVERVIEW OF RAMEY ET AL. 2005

Data and sampling — The study performed by REA included an analysis of 5 microsatellite loci. All were bi-nucleotide CA or AC repeats, as is consistent with the magnetic-bead technique for developing microsatellites. They sampled 195 individuals (sum of N, table 3, REA) from five of the 12 *Zapus hudsonius* subspecies (*Z. h. preblei* [N=54], *Z. h. campestris* [N=29], *Z. h. intermedius* [N=46], *Z. h. pallidus* [N=34], *and Z. h. luteus* [N=32].) This represents relatively smaller sample sizes, but even sampling of individuals across subspecies and geographic space. These numbers differed slightly from those examined in their mitochondrial study (N=198, table 2). Like the mitochondrial DNA study, many of the samples studied were fresh high-quality DNA, but many samples were taken from museum specimens or other sub-standard (or "ancient") DNA sources. In ancient DNA, microsatellites are often more difficult to accurately and repeatedly recover because nuclear DNA is found in fewer copy numbers and it is relatively less protected than mtDNA. Thus, it is especially important to

consider measures taken to prevent contamination and to ensure accurate and repeatable scoring of microsatellite loci.

Analyses — The authors examined a number of microsatellite statistics, including population pairwise F_{st} and Nei's D, they used analysis of molecular variance (AMOVA), and examined population structure using the computer programs BAPS and STRUCTURE. These were used to infer a variety of population parameters and to infer population histories. Overall, most of these demonstrated some degree of population differentiation; the key interpretation hinges on whether these differences represent "historic" vs. "recent" genetic exchangeability (sensu Crandall et al. (2000)).

Key results —

1. F_{IS} was positive across populations, with a signature of heterozygote deficiency. This is interpreted as being caused by the Wahlund effect, caused by a certain degree of local isolation (either fine-degree population subdivision, isolation by distance, or local inbreeding). REA interpret this as a result of their sampling scheme, as they sampled only one or a few individuals per local population. Depending upon how F_{ST} is calculated, this sampling can affect how overall variance is partitioned to among vs. within population genetic variance. This is important to the analysis and interpretation of "key result # 4" below.

2. REA report a low rate of "missing data" of 2%. This is unusually low for studies that include ancient DNA sources such as museum skins, which typically report lower success rates. Given the lack of reported controls and replication, we cannot rule out some unknown level of allelic dropout (ie. alleles that are erroneously not detected or scored). It is unknown what effect this may have on overall results and interpretation.

3. Allelic richness was relatively low in Preble's jumping mouse. This was interpreted as being caused by a bottleneck, founder event, or low effective population size, although explicit tests for these hypotheses were not performed. Because the geographic range (and population size) is smaller in *Z. h. preblei*, this is not surprising, and should have no bearing on the question of evolutionary significance or value of the putative taxon.

4. REA tested for genetic exchangeability a) by testing whether the variance within populations exceeded the variance among populations using AMOVA and F_{ST}, b) by testing whether multiple private alleles be at higher frequency than shared alleles at the majority of loci, and c) by calculating N_em from F_{ST} values.

a. AMOVA of the five putative subspecies showed that 7.5% of the variance partitioned among populations, and the remaining 92.5% partitioned within populations. This was considered by REA to be a critical test for the validity of the subspecies: if the variance within populations exceeded the variance among populations, then they rejected the validity of the subspecies. We feel that this does not explicitly test the validity of Preble's mouse for two reasons: first, if *Z. h. preblei* is a good subspecies but is UNDERSPLIT (i.e., there are multiple hidden groups within *Z. h. preblei*) this will drive up the within-population variance. Second, if

other subspecies (not *Z. h. preblei*) are OVERSPLIT (i.e., should not be split into subspecies) then this drives the among-population variance down. Both REA's and KEA's microsatellite datasets suggest that both of these factors are contributing to the low among-species variance and higher within species variance. Thus, it is not clear what exactly is being tested, but this may not be an explicit or appropriate test for the validity of *Z. h. preblei*.

b. Three unique alleles were found in *Z. h. preblei* in three loci, and all of these were found at low frequencies (< 0.05). One locus that was dropped from the study because of a low heterozygote deficiency had a single unique allele at frequency 0.55 in the southern population of *Z. h. preblei* and 0.048 in the northern population.

c. F_{ST} values were reportedly significant for <u>all</u> pairwise comparisons, including all comparisons that involved *Z. h. preblei*. This suggests statistically-significant subdivision. One key question, however, is how much subdivision is biologically significant. The authors utilize a benchmark of $N_em < 1$ as being biologically significant (Crandall etal. 2000). N_e is the genetic effective population size and m is the per individual migration rate, so N_em is the scaled effective migration rate (genetically averaged over many generations.) The authors used F_{ST} values calculated from GENEPOP and estimated N_em using the formula, $N_em = [(1/ F_{ST})-1]/4$. This can be a relatively robust estimate of N_em, given the assumptions that the populations meet the island model of population subdivision and are in migration-drift equilibrium, but there can be errors when assumptions are not met (Whitlock and McCauley 1999). Using this technique, N_em values varied from 1.3125 (southern *Z. h. preblei – Z. h. luteus*) to 3.321428571 (northern *Z. h. preblei – Z. h. pallidus*). No confidence interval around N_em is generated or presented, so it is difficult to tell whether a confidence interval or plausible range excludes values of $N_em < 1$.

5. The authors examined population clustering using BAPS and STRUCTURE software packages. In REA's analyses, BAPS gave strong support (posterior probability > 0.95) of different allele frequencies in both north and south populations of *Z. h. preblei* and *Z. h. luteus*, but showed less structure in the north-eastern populations that encompassed *Z. h. campestris, Z. h. intermedius*, and *Z. h. pallidus*. Their STRUCTURE analysis also recovered *Z. h. preblei* and *Z. h. luteus* groupings, despite STRUCTURE lacking power to resolve groups when using fewer than seven microsatellite loci (Pritchard et al. 2000). Crandall and Marshall (2005) reanalyzed their data in STRUCTURE using a more conservative estimate for *K* (the number of estimated subdivisions). Using the same data, they estimated *K*=3 significant populations, but one of these three groups consisted of a *Z. h. preblei* group, which suggests that *Z. h. preblei* is significantly different from other *Z. hudsonius* subspecies.

Key conclusions — Microsatellite analyses of REA support a statistically-significant division in the data corresponding to *Z. h. preblei*. The data does suggest that there is some level of gene flow between *Z. h. preblei* and other named subspecies, but this gene flow is relatively restricted.

OVERVIEW OF KING ET AL. (IN PRESS, MOLECULAR ECOLOGY)

Data and sampling — KEA scored genotypes at a total of 21 microsatellite loci developed in three different laboratories. Genotypes were scored for a total of 348 *Zapus hudsonius* individuals sampled from 14 geographical localities within the same five named subspecies (*Z. h. preblei* [N=170], *Z. h. campestris* [N=61], *Z. h. intermedius* [N=49], *Z. h. pallidus* [N=48], *and Z. h. luteus* [N=20].) This represents greater sampling in terms of individuals per population (and most subspecies), greater genomic sampling in terms of more microsatellites scored per individual, but fewer geographic localities than REA.

Analyses — The authors examined a number of microsatellite statistics, including population pairwise F_{ST} and R_{ST}. While F_{ST} assumes that allelic differences result from migration and drift, R_{ST} additionally considers mutational differences among loci. KEA used AMOVA and examined population structure using the computer program STRUCTURE. Genetic distances among populations were also mapped onto a distance dendrogram using geometric based D_a distances calculated with DISPAN. Overall, most of these demonstrated population differentiation and the distinctness of *Z. h. preblei*; again, the key interpretation hinges on whether these differences represent "historic" vs. "recent" genetic exchangeability (sensu Crandall et al. (2000)) and biologically (or genetically or evolutionarily) significant clusters.

Key Results —

1. Population samples were generally in Hardy-Weinberg equilibrium. When populations were combined, heterozygote deficiencies were detected. As in REA, this is attributed to the Wahlund effect and suggests population substructure.

2. Results from STRUCTURE analyses suggested that *K*=3 was the appropriate number of recognizable clusters. One of these clusters corresponded to *Z. h. preblei*. The other clusters corresponded to a *Z. h.campestris + Z. h.intermedius* cluster and to a *Z. h. pallidus+ Z. h.luteus* cluster. Structure was confirmed by 100% assignment of individuals to their cluster of origin, with *q*-values greater than 0.93. The analyses detected some subclustering within *Z. h. preblei* corresponding to northern and southern Colorado and southern Wyoming groups.

3. Pairwise genetic distances (D_a) were calculated among all pairs of geographic collections to investigate similarities among localities. Underlying genetic structure was depicted in a neighbor-joining unrooted dendrogram. Bootstrap support was calculated for each branch. The resulting tree supported the same clusters as recovered by the STRUCTURE analysis. Strong bootstrap support (98%) supported the separation of *Z. h. preblei* from all other subspecies.

4. All pairwise F_{ST} estimates were significant ($p < 0.001$) and supported the subdivision of the groups investigated in STRUCTURE. Pairwise F_{ST} values between *Z. h. preblei* and other subspecies were either similar to the values presented in REA (ie. *Z. h. preblei - Z. h. campestris*, $F_{ST} \approx 0.1$) or higher than those presented in REA (ie. *Z. h. preblei - Z. h.*

intermedius, $F_{ST} \approx 0.18$; *Z. h. preblei - Z. h. pallidus*, $F_{ST} \approx 0.21$; *Z. h. preblei - Z. h. luteus*, $F_{ST} \approx 0.33$.) KEA additionally investigated R_{ST} values for comparison to F_{ST}. Ratios of $R_{ST} : F_{ST}$ values ranged from 1.0 (between *Z. h. pallidus* and *Z. h. lucidus*) to 2.9 (between *Z. h. preblei* and *Z. h. pallidus*). This suggests that, in addition to drift, mutational process have acted over longer time periods to increase differentiation.

5. AMOVA found significant variation at the subspecies level ($p<0.001$) and at the collections within subspecies level ($p<0.001$). This is consistent with other inferences suggesting the Wahlund effect and significant metapopulation structure.

6. The variation and partitions found in the data correspond to mitochondrial DNA partitions in unrooted parsimony haplotype networks, and thus are corroborating evidence of other independent differences.

Key Conclusions — Microsatellite analyses of KEA support a division in the data corresponding to *Z. h. preblei*. The data does suggest that *Z. h. preblei* is most similar to *Z. h. campestris* perhaps due to historic or recent gene flow between *Z. h. preblei* and *Z. h. campestris.*

SECTION 2. SOURCES OF DISAGREEMENT BETWEEN THE TWO STUDIES

MORPHOLOGY

Only one of the 2 studies examined morphology (REA). They failed to find a strong pattern of separation among subspecies in cranial measurements, contributing to their conclusion of synonymy. REA considered it sufficient to examine a subset of characters used by Krutzsch (1954) and that use of multivariate statistics should have detected any biologically significant differences should they exist. By not considering the relatively undifferentiating morphological data, the analyses by KEA placed proportionately greater weight on the discriminating ability of the molecular data.

ECOLOGICAL EXCHANGEABILITY

Similarly, only REA of the 2 studies considered ecological exchangeability. Their survey of the literature did not indicate to them that there were "major" difference in habitat, life history, or morphology (presumably, of a sort that would indicate functionally significant differences in feeding or other important attributes). REA did caution that absence of evidence did not mean evidence of absence. As with morphology, the absence of clear differences supported the conclusion of REA that *preblei* was not distinct whereas KEA, by not considering this line of evidence, emphasized the distinctiveness indicated by their molecular data.

MITOCHONDRIAL DNA

REA and KEA came to the opposite conclusion regarding the genetic uniqueness and subspecific status of *Z. h. preblei* based on their respective analyses of mtDNA sequence data. Our goal was to determine why these two studies came to such different conclusions. In terms of mtDNA data, we have identified three potential sources that may have lead to the apparently conflicting results of the studies by REA and KEA. They are: (1) geographic sampling design, (2) quantity of mtDNA data and, (3) quality of mtDNA data. In this section, we describe how the two studies differed in these three areas.

1. Sampling Design. The different sampling approaches of REA and KEA could influence the probability of detecting reciprocal monophyly, gene flow and significant population structuring (see Crandall's peer-review of KEA). REA examined a relatively large number of geographic areas, with the number of samples examined per locality being relatively small. In contrast KEA examined fewer geographic locales, but a larger number of individuals per locale. REA also examined many specimens from areas close to subspecies boundaries and KEA did not (although this latter difference may have been mitigated by KEA's recent addition of all specimens reported by REA to have haplotypes that were shared between subspecies).

2. Quantity of Data. The mtDNA data sets examined in the two studies varied in quantity. Whereas REA examined a 346 bp of the non-coding control region, KEA examined data from both the control region and the protein-coding cytochrome-b gene. The total number of bp examined by KEA was 1,380 bp.

3. Quality of Data. Although geographic sampling scheme and amount of mtDNA data examined are important differences between the studies of REA and KEA, the most striking difference between the mtDNA results of the two studies is the conflicting control region sequences reported for the 15 KUNHM specimens of *Z. h. campestris* (see KEA, Table 1B). Using samples from the same museum specimens, REA and KEA obtained different mtDNA control region sequences for 13 of the 15 specimens. This point is especially relevant because REA found that these particular samples of *Z. h. campestris* contained the same mtDNA control region sequences (haplotypes) as those found in *Z. h. preblei* (in other words, REA found evidence that *Z. h. preblei* and *Z. h. campestris* shared some of the same haplotypes). In contrast, KEA found no evidence of shared haplotypes between these two subspecies. Overall, seven of the *Z. h. campestris* that were reported as having *Z. h. preblei* haplotypes by REA were reported by KEA to have common *Z. h. campestris* haplotypes. Thus, the two studies have a major and fundamental difference in their mtDNA control region results, with REA reporting *Z. h. preblei* and *Z. h. campestris* to have shared haplotypes, and KEA reporting the opposite. This is perhaps the single most influential difference between the two studies in terms of data.

In an effort to evaluate potential sources of the observed disagreement in these data, the panel obtained the original mtDNA control region sequence files from each research group (these were provided by the first-authors to the panel at the meeting in Ft. Collins, CO, July 6-7, 2006). In both cases, the data were supplied in the form of Sequencher (Gene Codes Corp., Ann Arbor, MI) project files comprised of chromatograms for each sequencing run performed for each sample. For each position in each chromatogram, there is a peak(s) corresponding to which nucleotide(s) occurs at that position (A, C, T or G). In the haploid mtDNA data, there should be only a single peak at each position (i.e., there are no heterozygotes in haploid data). In cases where there is ambiguity at a given position, either because of low signal or conflicting signal (i.e., the presence of multiple peaks that are similar enough in amplitude that the program can not assign an A, C, T, or G to that position with confidence), the position is assigned a value of "N". Thus, Sequencher will provide a haplotype, consisting of a string of letters (A, C, T, G or N) for each specimen. The user then has the choice of either (1) accepting the value assigned by the computer program for each position, or (2) overriding the value assigned by the computer program and assigning that position a different value. Such changes are highlighted, allowing one to easily observe at which positions "user-overrides" have occurred in each DNA sequence.

Normally, multiple sequencing runs using different primers will be assembled for each individual specimen. This results in sequences being assembled into one longer sequence. It also provides an opportunity for overlap between different sequence runs for a given sample. This is important because the overlapping portions provide an

opportunity to: (1) cross-validate results, and (2) to potentially reduce the proportion of ambiguous nucleotides (the "N's") in a sequence. In addition, this type of approach can help identify certain positions that consistently exhibit multiple chromatogram peaks. For mtDNA data, multiple peaks at a given position can be due to contamination (i.e., the presence of DNA from more than one individual in the sample), the presence of nuclear copies of the mtDNA (referred to as "numts"; Sorenson and Quinn 1998), heteroplasmy (see Tully et al. 2000), or simply poor quality of PCR product, all of which can lead to errors in determining the actual DNA sequence of the individual in question.

USE OF MUSEUM SPECIMEN DNA

Although researchers do regularly succeed in amplifying DNA from ancient or substandard DNA sources (including DNA extracted from dried museum specimens), this work is quite challenging. The DNA from such substandard sources is usually scarce and degraded, and researchers find it difficult to reliably amplify DNA segments greater than about 500bp; most target PCR regions are less than 300 bases. The control region target amplified by REA was approximately 460 bases. KEA typically succeeded with a slightly smaller fragment at 366 bases.

Much has been written concerning standards for documenting valid and accurate ancient DNA work (Cooper and Poinar 2000), and at a minimum, researchers 1) strive for a physically isolated work area for ancient DNA extractions and PCR setup, 2) use numerous controls to check for contamination of extracts and PCR reactions, 3) strive to repeat DNA amplifications and sequence multiple amplicons, 4) have iconoclastic results or those of great import independently repeated in another ancient DNA laboratory, and 5) check sequences for proper behavior in phylogenies and unusual results are repeated to test for reproducibility. A number of other requirements have been suggested (Cooper and Poinar 2000), but are done less often than most would wish. Based on their papers and information presented at the panel hearings (Ft. Collins, CO), REA followed practices 1 and 2 and KEA followed 1, 2, 4, and in part 3. Neither group specifically addressed their approach to item 5.

It is our experience that tissues sampled from museum specimens, even specimens 45 years old or younger (cf. Ramey et al. 2006) are treated by most molecular systematists as “ancient DNA samples.” Many of us regularly use these in our work, so we do not criticize their inclusion, however we have carefully examined the care with which these samples appeared to be handled and to what lengths the principal investigators used controls and methods to detect contamination.

In order to assess the relative quality of the mtDNA data of REA and KEA, we examined the data files provided to us by the authors. In particular, we scrutinized the chromatograms for those specimens reported to have conflicting haplotypes in REA and KEA. This leads us to the following section.

REANALYSIS OF SELECTED SEQUENCES AFTER REEXAMINATION OF ORIGINAL SEQUENCE FILES: CONTROL REGION

Original sequence chromatograms acquired from Ramey and King were examined by the panel. We specifically looked for evidence of quality and possible contamination using the following criteria: 1) Number of overlapping reads (individual sequencing reactions), 2) degree of overlap among reads (if there is minimal overlap, it would be difficult to detect the possibility that 2 different PCRs had amplified different templates, as when one is a contaminant), 3) quality of signal (are peaks clearly separated, is there background noise?), and 4) presence of secondary peaks of sufficient height above background to suggest a second DNA template/haplotype.

All chromatograms were examined individually without reference to outside sequences; those from REA were examined first. In some cases, there was evidence of secondary peaks that rose above normal background. In those cases, when one peak was called decisively by the original authors, and when a plurality of reads showed the same corresponding secondary peaks (e.g., 2 of 3 reads showing a small C peak), a new sequence was generated where the second peak was called instead (e.g., if there was a C peak with half the height of a T peak and the authors had called a T, we called a C). In this way we generated a "residual" sequence, one that contained the residual bases after removing the original calls. If more than one haplotype was present in a PCR reaction, these residuals would be evidence of that. We emphasize that the residual base calls were made *only* in reference to the original sequence and the authors' original base calls — no outside sequences were examined in any way prior to generating the residual sequences. Several sequences from REA indicated residual sequences. There was no clear evidence by these criteria of a residual sequence in any chromatograms supplied by KEA.

If the residual peaks were due to noise (e.g., *Taq* polymerase error early in PCR or changes such as C-T or G-A substitution that are typical of ancient DNA template (Hofreiter et al. 2001)) rather than a second haplotype, then their positions in the sequence should be random and should not carry any phylogenetic signal. As such we would expect this category of residual sequences to cluster cladistically near the original sequences, but to be divergent (i.e., connected by a long branch). In contrast, if the residual signal is due to the presence of a second haplotype, rather than due to "noise", we would expect the residual sequence to cluster closely to other haplotypes on a phylogeny (not near the original) and not have a long branch. To test whether random error in the sequences could masquerade as another haplotype just by chance, we also generated "randomly permuted" sequences at the same time we estimated the residual sequences. In those random sequences, we made the exact same base call differences detected in the residual, but applied those changes to the next downstream location (e.g., if the authors called a T and we detected a small C, we left the original T alone but went to the next T downstream and changed that to a C). That way, if the residual sequence was actually noise, the residual sequence OTU (operational taxonomic units) should behave like the randomly permuted sequence (although not be identical to it because different substitutions were made). We were able to distinguish secondary peaks from

background noise with moderate to high confidence because the overall background noise level among nearly all sequencing reads was relatively low. See an example in Fig.1.

Eleven of the 15 reexamined samples were represented by only single sequencing reads from REA (Table 1). Single reads do not allow the conventional level of corroboration and are particularly problematic at detecting multiple templates. Such concerns are greater when working with ancient DNA as in this case. Even when 2 haplotypes have been amplified by PCR, a given primer may preferentially amplify one and only show a clean read. We excluded 9 of these 11 from the phylogenetic analyses because they were single reads and do not meet conventional standards for sequence corroboration (especially of ancient DNA). The 4 samples from REA with multiple reads and 2 others with single reads were included in the phylogenetic analysis. Together, the residual sequences estimated from REA chromatograms, the original sequences from REA and KEA, and the random sequences we generated from the REA chromatograms yielded 24 OTUs.

TABLE 1

Specimen #	Number of Reads (forward/reverse)		Evidence of Contamination (see Fig. 2 and text)	
	REA	KEA	REA	KEA
KU109972	2/2	6/6	yes: residual sequence grouping with *campestris* detected	no*
KU115700	1/1	2/2	yes: appears to be evidence of a second *campestris*-like haplotype in the REA chromatograms, although it did not affect the reported sequence	no
KU112665	0/1	2/2	yes: partial sequence groups with *campestris*, long stretch of multiple equal-height peaks consistent with the consequences of the length difference (due to insertion or deletion) distinguishing the two recovered sequences.	no*
KU123592	0/3	5/5	no*	Most no, but weak evidence of second haplotype in 2 out of 10 reads*
KU109978	1/1	3/2	no*	no
KU109984	0/1	5/6	no*	no*
KU109985	0/1	2/2	no*	no*
KU109963	0/1	2/2	no*	no*
KU110013	0/1	4/4	no*	no*
KU112661	0/1	2/2	no*	no*
KU112663	0/1	2/2	no*	no*
KU115730	0/1	2/2	no	no*
KU123597	0/1	3/4	no*	no*
KU153706	0/1	1/2	no	no
KU110033	0/1	1/2	no*	no*

*no evidence of contamination, but REA and KEA reported different sequences

The new sequences were combined with the most recent CR sequences from KEA and phylogenetic analyses using MP and NJ were conducted. The results were qualitatively similar between analyses and any relevant differences will be noted. The behaviors of the different sequence types (e.g., original, random) are distinct and insensitive to method of tree construction. The NJ tree using an HKY85 + gamma model of evolution is shown in Figure 2. The results of these analyses are summarized here. Numbering of samples on the figure correspond to the list below.

Key points as numbered on Figure 2:

1) The *campestris* KU109972 sequence reported by REA groups with *preblei* as reported. The random version of the sequence joins nearby but with a long branch, as expected from random noise. However, the residual sequence we detected grouped with *campestris*, close to the sequence acquired by KEA. The only decisive difference between the KEA sequence and the residual sequence was a shallow peak visible on the Ramey chromatogram but that we conservatively treated as noise rather than as a clear secondary peak. There appears to be evidence of 2 haplotypes present in the REA chromatograms.

2) Both REA and KEA reported the same sequence for *intermedius* KU115700. There was evidence of a residual signal in the REA chromatograms. The random sequence again behaves as expected. The residual sequence however was identical to several *campestris* sequences (including KEA's for KU109972). There appears to be evidence of a second haplotype in the REA chromatograms, although it did not affect the reported sequence for KU115700.

3) The original sequence from REA for *campestris* KU112665 falls out in a *luteus* clade. A random sequence was not generated because of difficulty reading approximately 40% of the sequence due to many overlapping peaks of nearly-equal height, a pattern that resembles that produced by a PCR product with 2 haplotypes differing by an insertion/deletion that causes a single-base shift in the position of the peaks for one of the haplotypes. Many pairs of equal-height peaks were called decisively by REA whereas we could not resolve the ambiguity. There was only 1 read from REA for this sample. The partial residual sequence falls out approximately 2/3 of the distance to the *preblei/campestris/intermedius* clade, that with the rooting supplied by *Z. princeps*, places it as the sister group to all *preblei/campestris/intermedius* on the NJ tree. Most equally-parsimonious trees (67%) place the residual sequence in the same *campestris* sub-clade that contains the sequence estimated by KEA and 9 other samples. Outside of the uncertain region where the length polymorphism makes base calling difficult, the residual sequence is nearly identical to the KEA sequence (the residual had one tall peak near the beginning of the sequence not found in either the REA or KEA sequences). The residual sequence differs at 6 positions over the same region from the REA sequence. We view this as strong evidence for the presence of both sequences in the REA data.

4) The *campestris* KU123592 shows no evidence of 2 different haplotypes in either REA or KEA chromatograms, although each lab produced different sequences. The REA sequences consisted of 3 reads, all in the same direction and apparently from the same primer. The KEA sequences consisted of 10 reads (5 in each direction). The residual sequence derived from the REA data behaved like the random sequence, suggesting that the secondary peaks were noise.

5) The *campestris* KU109978 likewise shows only 1 haplotype in each set of chromatograms, although not the same haplotype (*preblei*-like in REA, *campestris*-like in KEA). The REA sequences consist of 1 read in each direction, and KEA consists of 3 forward and 2 reverse reads.

6) The residual sequence for *campestris* KU109984 behaves like the random sequence and the secondary peaks therefore are likely due to noise and not a detected second haplotype. The REA *preblei*-like sequence was based on a single read, the KEA *campestris*-like sequence was based on 5 forward and 6 reverse reads.

In summary we reexamined the chromatograms from the 15 museum specimens that were sequenced by both labs and that were cited by REA as providing evidence for shared haplotypes among subspecies. Eleven of the REA sequences were based on single reads. All KEA sequences were based on at least 1 read in **both** directions (3-13 reads total). None of the KEA data sets show clear evidence of more than one haplotype for any specimen. One of the REA single reads shows evidence of more than one haplotype in the PCR product (KU112665), the others did not. The remaining 4 specimens had 2-4 reads in the REA data set. Two of these show evidence for only one haplotype (KU109978, KU123592) in the REA data. The other 2 (KU109972, KU115700) show clear evidence for 2 haplotypes being amplified. In 2 of the 3 cases of multiple haplotypes being detected in the REA data, the residual sequence is identical or very similar to the sequence acquired by KEA from the same specimens. In the 3rd case of multiple haplotypes, the residual sequence was different from both the KEA and REA sequences but did match a sequence from other specimens.

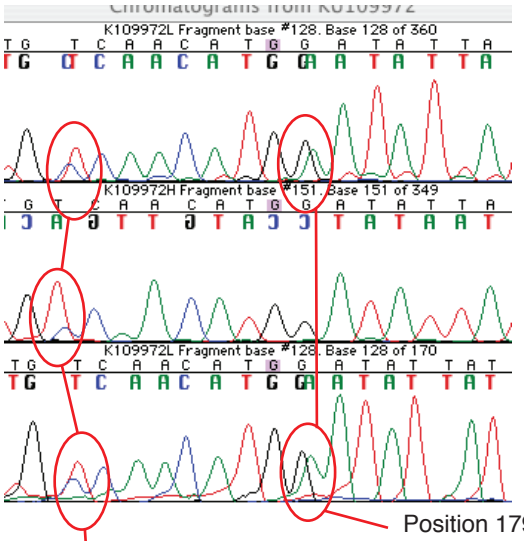
The data from the 2 labs were subjected to the same level of scrutiny with one exception. After initial examination of the KEA data (in which we detected no evidence of residual sequences using the criteria applied to the REA data), we aligned the chromatograms with the corresponding consensus sequence of the same individuals from those REA data. We then looked for secondary peaks missed during the first examination that might correspond to the nucleotide differences in the REA data. Twelve of the samples showed no secondary peak on any read. One specimen (KU109985) showed a secondary peak at 1 of 5 differing sites (that is, sites that differed between the two studies); that peak was 1/4 the height of the primary peak and was seen in 1 read. One specimen (KU123592) showed 3 out of 5 segregating sites with some secondary peaks; the first peak appeared in 1 of 3 reads for that position (1/2 height), the second in 2 of 6 reads (1/2 height), and the third in 2 out of 9 reads (1/4 and 2/3 height). We find this evidence suggestive but not compelling for a residual sequence in that one KEA sequence.

There are several possible explanations for secondary peaks in sequencing reads: 1) random nucleotide incorporation error by the polymerase enzyme during PCR, 2) heteroplasmy, where mitochondria in the sperm are transferred to the egg, producing individuals with haplotypes from both parents, 3) the presence of NUMTs, or nuclear psuedogene copies of mitochondrial DNA, and/or 4) inadvertent contamination of lab samples during extraction or PCR set-up, resulting in amplification of the contaminant in addition to the target sample. Random error, a common occurrence, seems to be the explanation for secondary peaks in 3 REA samples. Heteroplasmy, while a rare phenomenon in nature, can not be definitively ruled out for the other 3 samples with secondary peaks. However, it is unclear why KEA, with their multiple reads, would fail to detect a second heteroplasmic sequence, but preference amplification of multiple templates can be difficult to predict. Contamination of REA reactions does provide a more parsimonious explanation.

1 KU109972 Control Region example

Fig. 1

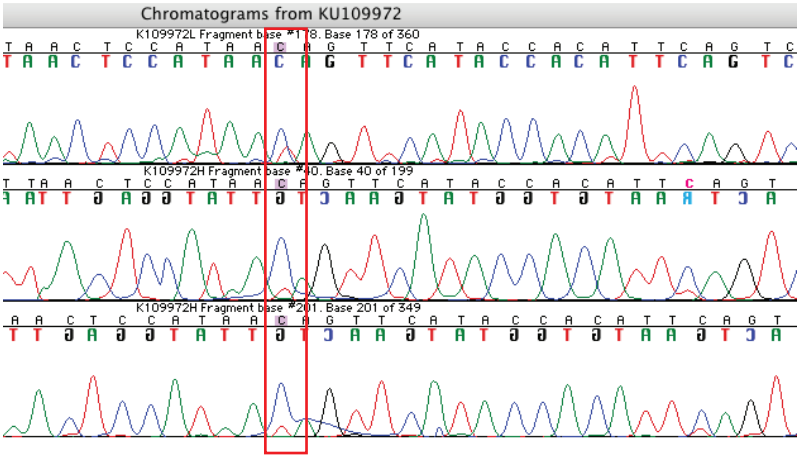
Ramey et al.



Position 171. Residual (secondary) peaks "C" under the higher "T".

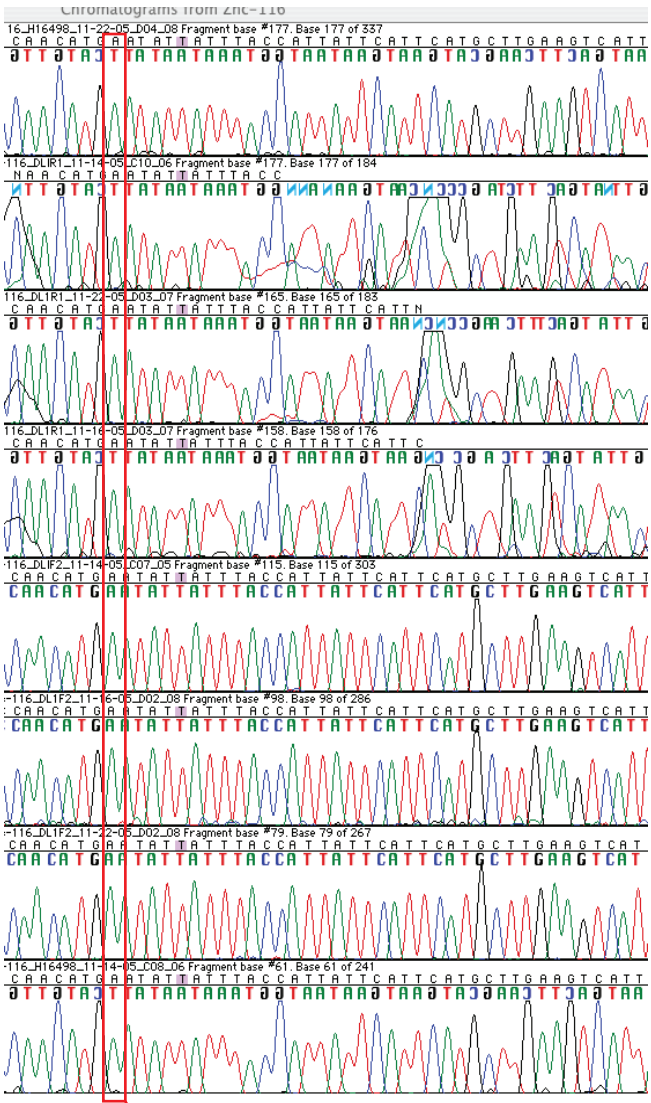
Position 179. Residual "A" in addition to "G".

Both the *preblei*-like and *campestris*-like sequences are visible in chromatograms.



Position 228. Residual "T".

King et al.



Position 179. Only one trace visible ("A").

7/12/06 King new Control Region data plus three resolutions of 6 samples from Ramey et al,
Neighbor Joining tree (HKY85+G model)

Fig. 2a

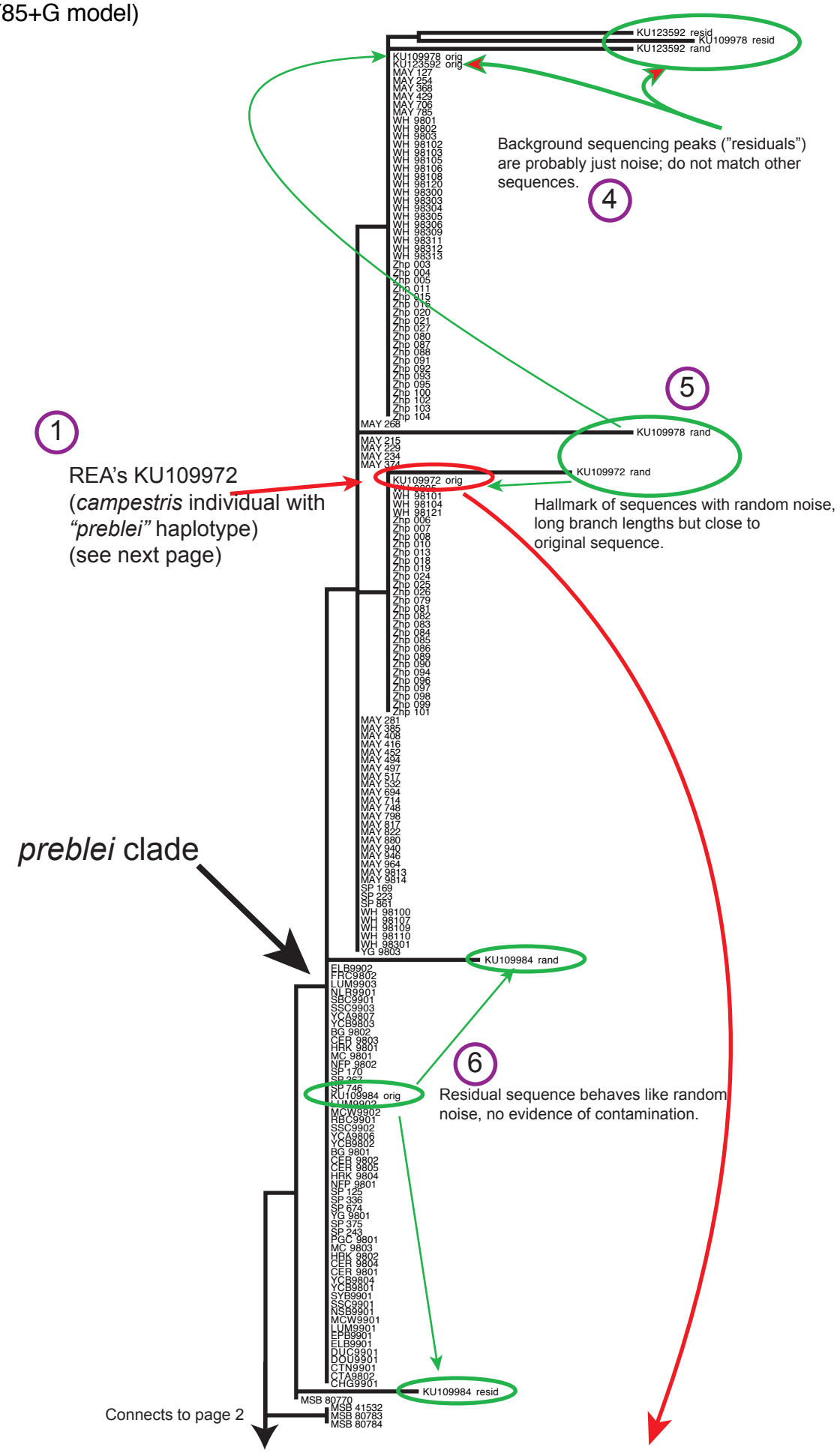
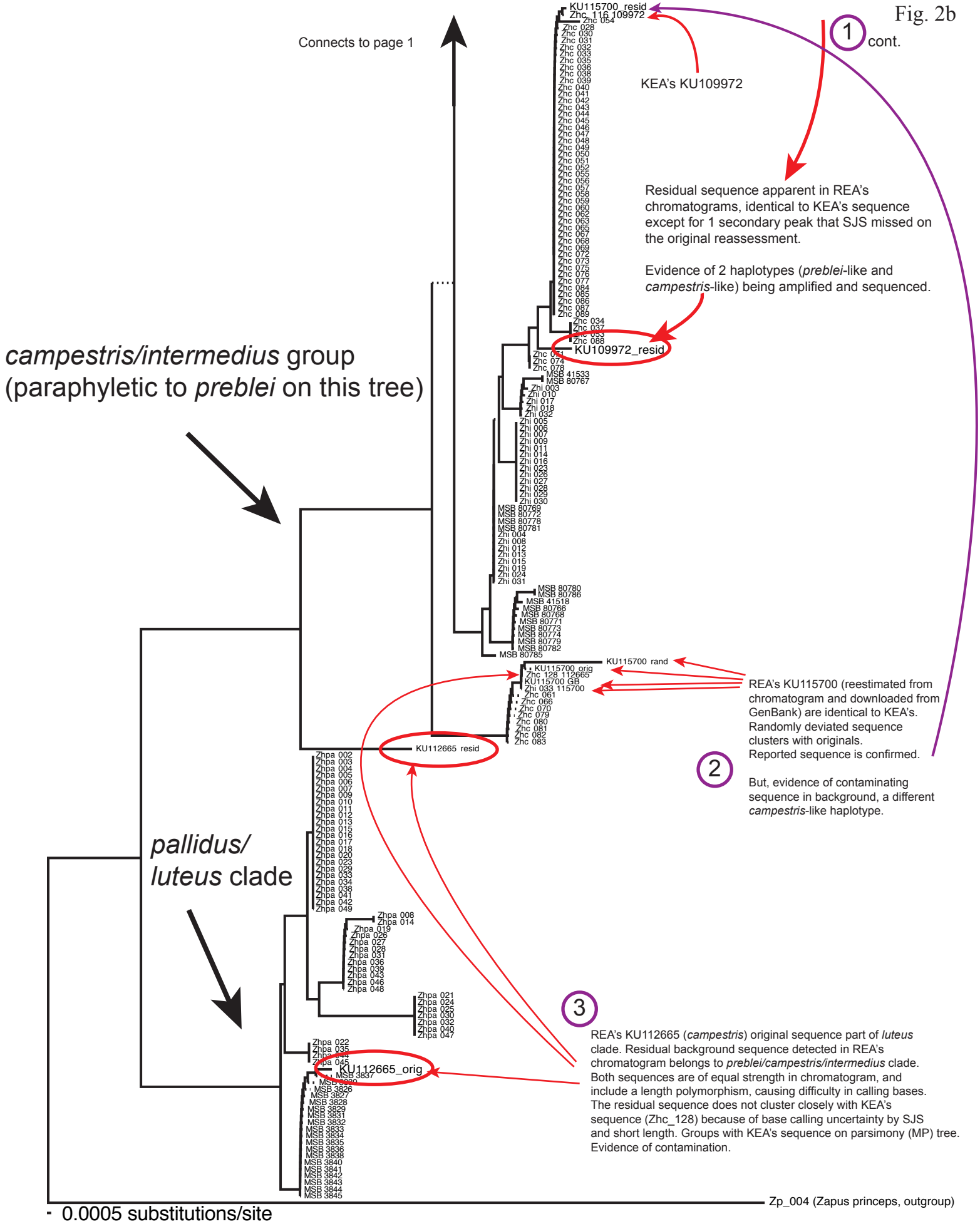


Fig. 2b


Connects to page 1
KU115700_resid
Zhc_116_109972
KEA's KU109972
1 cont.
Residual sequence apparent in REA's chromatograms, identical to KEA's sequence except for 1 secondary peak that SJS missed on the original reassessment.
Evidence of 2 haplotypes (preblei-like and campestris-like) being amplified and sequenced.
KU109972_resid
campestris/intermedius group
(paraphyletic to preblei on this tree)
KU115700_rand
KU115700_orig
REA's KU115700 (reestimated from chromatogram and downloaded from GenBank) are identical to KEA's. Randomly deviated sequence clusters with originals. Reported sequence is confirmed.
2
But, evidence of contaminating sequence in background, a different campestris-like haplotype.
KU112665_resid
pallidus/
luteus clade
3
KU112665_orig
REA's KU112665 (campestris) original sequence part of luteus clade. Residual background sequence detected in REA's chromatogram belongs to preblei/campestris/intermedius clade. Both sequences are of equal strength in chromatogram, and include a length polymorphism, causing difficulty in calling bases. The residual sequence does not cluster closely with KEA's sequence (Zhc_128) because of base calling uncertainty by SJS and short length. Groups with KEA's sequence on parsimony (MP) tree. Evidence of contamination.
Zp_004 (Zapus princeps, outgroup)
0.0005 substitutions/site

SECTION 3. DIFFERENCES IN CONCLUSIONS BETWEEN THE TWO STUDIES

MITOCHONDRIAL DNA DATA

In this section we discuss how the mtDNA sampling, quantity and quality issues outlined above may have lead REA and KEA to come to different conclusions regarding the taxonomic status of *Z. h. preblei*.

Sampling Design and Quantity of Data.
In theory, the difference in sampling strategies, along with the amount of mtDNA sequence data obtained in the two studies, could have acted in concert to lead REA and KEA toward different conclusions. In terms of sampling design, REA's approach of sampling a comparatively high number of localities, including many at or near subspecies boundaries, increased the likelihood that they would be able to detect introgression or migration (that is, they were more likely to find shared haplotypes between subspecies if they existed). Compared to REA, KEA sampled fewer geographic localities, but many more individuals per locality. KEA tended to sample away from, rather than at or near subspecies boundaries. Thus, KEA may have been less likely to find shared haplotypes between subspecies if they occurred primarily near subspecies boundaries. As Crandall (peer review of KEA) points out: "...the optimal sampling strategy for such studies is often a combination of the two approaches, guided by preliminary examination of molecular genetic data (Morando et al. 2003)." In essence, KEA have recently done that by adding to their study all of the specimens reported by REA as having shared haplotypes between subspecies (KEA, Table 1B). In theory, this should have mitigated, at least to some degree, differences between the original sampling strategies of the two studies.

In addition to differences in sampling design, differences in the quantity of mtDNA data may have also lead to apparent disagreement between the two studies. The relatively small number of nucleotides examined by REA may have made it difficult to obtain high resolution in their phylogenetic analyses. As Crandall points out in his peer-review of KEA: "Importantly, King et al. correctly point out that phylogenetic inference is highly dependent upon the length of the sequence data used and the addition of the cytb sequence data coupled with a longer control region allows for more robust inference. King et al. also correctly point out that the cytb locus is a standard for species delimitation studies (as is COI – barcoding) and the control region has difficulties due to evolutionary constraints on this region." Thus, the greater number of nucleotides examined by KEA (~4-fold more than the number examined by REA) may be expected to recover a more resolved mtDNA phylogenetic tree than the approach used by REA.

The main point of this comparison is that the different sampling strategies and amounts of mtDNA data used by REA and KEA could have contributed to their differing results. In particular, REA's approach would tend to find more haplotypes shared among subspecies (if actually present) and would be less likely to find phylogenetic structure corresponding to monophyletic subspecies (if actually present). KEA's approach would tend toward the

opposite (i.e., it would be less likely to find haplotypes shared among subspecies, if actually present, and would be more likely to find phylogenetic structure corresponding to monophyletic subspecies, if present). However, these differences may be less substantial than in earlier versions of the studies given KEA's recent addition of the specimens identified as having shared haplotypes by REA (the KUMNH specimens in KEA, Table 1B) and additional samples from Wyoming.

Data Quality--Influence of Conflicting Haplotypes for KUMNH Museum Specimens
The conflicting mtDNA control region data obtained for some of the museum specimens from KUMNH (summarized in KEA, Table 1B) clearly played an important role in REA and KEA ultimately coming to opposite conclusions regarding the subspecies status and genetic distinctness of *Z. h. preblei*. The haplotype-sharing between *Z. h. preblei* and *Z. h. campestris* reported in REA suggested that the former was not reciprocally monophyletic for mtDNA and that there was very recent gene flow between these two subspecies (i.e., based on the MDIV analysis). Thus, these shared haplotypes provided support for REA's general conclusion that *Z. h. preblei* was not genetically distinct from *Z. h. campestris.* In contrast, KEA obtained different sequences than those reported by REA for some of the KUMNH specimens. In KEA's analyses, there was no evidence for shared haplotypes between *Z. h. preblei* and any other subspecies of *Z. hudsonius* (including *Z. h. campestris).* The lack of any shared haplotypes provided support for KEA's general conclusion that *Z. h. preblei* is indeed genetically distinct from all five of the other subspecies of *Z. hudsonius* examined.

Based on the available data, it is the panel's conclusion that there is no reliable evidence for any shared haplotypes between *Z. h. preblei* and any of the other subspecies at this time. There is evidence for contamination of several key sequences reported by REA, raising concerns about the remaining sequences that have only single reads. If these conflicting mtDNA sequences are simply removed from consideration, the two studies would largely agree (albeit the larger amount of mtDNA data in KEA should, in theory, provide more power for recovering phylogenetic signal in the data).

MICROSATELLITE DNA DATA

REA and KEA came to opposite conclusions regarding the subspecific status of *Z. h. preblei* based upon microsatellite data. In many respects, however, the two microsatellite datasets contain similar information. They recover the same three primary clusters in STRUCTURE analyses (including a *Z. h. preblei* cluster), they estimate similar N_em and similar F_{ST} values (which also documents statistically-significant subdivision), and they both find a lesser degree of subdivision within *Z. h. preblei*. We feel that some of the most significant differences are philosophical, and stem from issues relating to the definition of subspecies, determination biological vs. statistical significance, and choice of null vs. alternative hypotheses in scientific inquiry. These issues will be considered in a later section.

Because both research groups and publications discuss several key scientific differences between the studies, we discuss these below. However, it is the opinion of this panel that

in most key respects the microsatellite data from these two studies are substantially compatible, and that the two studies largely corroborate each other.

1) Number of microsatellites: REA analyzed a total of five microsatellite loci whereas KEA analyzed a total of 21 microsatellite loci. This provides KEA with substantially greater power to detect population differences and accurately measure population parameters. Where REA failed to detect differences and KEA did detect differences (or found greater differences) these may be due to differences in statistical power. For example, this is demonstrated in analyses performed by the computer program STRUCTURE; authors of the STRUCTURE software package warn that the analyses may not have sufficient resolving power for less than seven scored loci (Pritchard et al. 2000). This smaller data set of REA had reduced power to assign individuals to populations. Nonetheless, REA did detect statistically significant F_{ST} and relatively large Nei's D, and even STRUCTURE recovered the same three major groupings (including a *Z. h. preblei* group) although power to assign individuals to groups was lower than KEA.

2) Geographic sampling: REA sampled fewer individuals per population but many more populations; KEA sampled many individuals per population but fewer populations (Fig. 3).

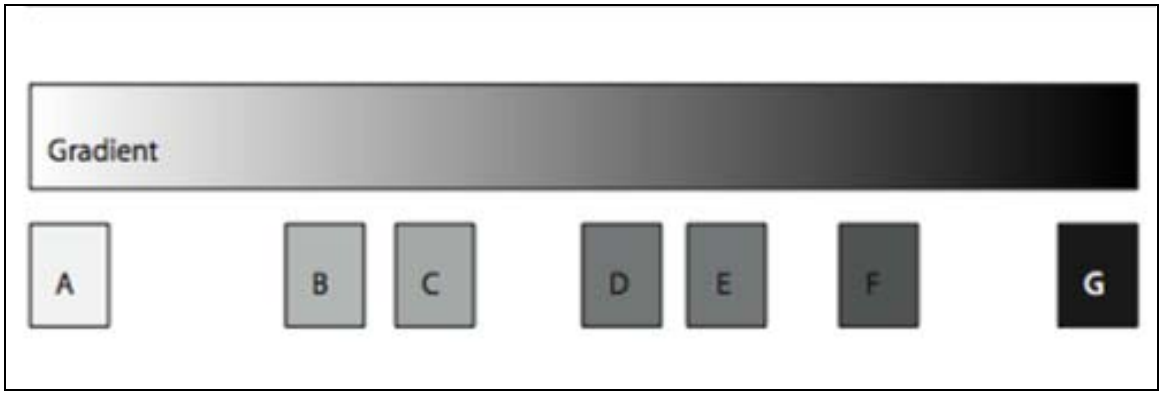


Fig. 3. Illustration of the two different geographic sampling designs.

KEA's sampling allowed them great statistical power, and they detected discrete differences among their sampling groups, much like the boxes above labeled A through G. REA argued that even if the underlying genetic variation was arranged like a gradient (above), KEA's discrete and dense sampling biased them to detecting discrete groups.

> a. This issue cannot be clearly resolved by the present two datasets. REA's data did not have adequate sampling of microsatellites or locations to clearly demonstrate an underlying gradient. KEA's dataset, while having the depth at each locality, did have discrete geographic breaks between collection areas. Ideally, future sampling would have some combination of the two sampling regimes.

b. Crandall and Marshall (2005) critiqued an earlier draft of KEA for not sampling the areas most likely to find hybrids, especially southern Wyoming. The final draft of KEA (2006) included sampling of *Z. h. preblei* in southern Wyoming. Although the population fell genetically between *Z. h. campestris* and Colorado populations of *Z. h. preblei*, it still clustered with *Z. h. preblei* and southern Wyoming individuals were assigned to the *Z. h. preblei* cluster in STRUCTURE analyses.

c. Gaps in geographic sampling also correspond to ACTUAL gaps in the current geographical distribution. For example, in our panel meetings, Drs. Ramey and King both pointed out that there are actual gaps in the distribution of *Z. hudsonius* between *Z. h. preblei* and *Z. h. luteus* in the south and between *Z. h. preblei* and *Z. h. campestris* in the north (~160km gap between the latter two subspecies). Thus, *Z. h. preblei* is geographically isolated from other named subspecies. Furthermore, the gaps between southern and northern populations of *Z. h. preblei* are presently occupied by the Denver metropolitan area. This prevents scientists from sampling in these areas, and creates discrete biological gaps. An important question at issue here is how biologically significant and how recent are these gaps? No independent data were presented that demonstrated whether these splits were historical or recent, so we have had to rely only on genetic data to determine the biological meaning of this split. Ideally, climatological, geological, or historical biological community data on ancient connections of *Z. h. preblei* to other *Z. hudsonius* populations would be valuable in assessing the biological meaning of these genetic and geographical gaps. We do believe that it is biologically important to know whether there once was (but no longer is) a cline, and understanding how long ago this may have occurred.

3) Statistical vs. biological significance: A key difference between the two studies involved the interpretation of whether the differences detected were biologically significant as opposed to just statistically significant. REA espoused using the cutoff of $N_em < 1$ (Crandall et al. 2000). Theoretical work has suggested that populations are essentially evolving independently when migration values of N_em are much less than one, and that the gene pools are essentially mixing when N_em is much greater than one. The dynamic shifts around $N_em = 1$, but this is not a hard-and-fast cutoff. Crandall and Marshall (2005) obtained estimates of N_em from both REA and KEA datasets using the program MIGRATE. Unlike estimates from F_{ST}, MIGRATE can estimate migration between two populations in both directions, and these are believed to be more accurate than estimates using F_{ST} (Beerli and Felsenstein 1999). Estimates of migration from other groups into *Z. h. preblei* was less than 1 ($N_em \leq 0.47$). This suggested that *Z. h. preblei* was substantially isolated from other groups. Interestingly, migration from *Z. h. preblei* to other groups was greater than 1 ($N_em \geq 1.18$) which suggests some movement (albeit minimum) from *Z. h. preblei* to other groups. There are multiple explanations for directional migration, including barriers that are more easily crossed by one genetic group than the other, barriers that only allow directional movement, or one population may be a "source" and the other a "sink." The evidence of directional gene flow, if this is statistically significant, may also argue for the biological significance of *Z. h. preblei*.

Crandall and Marshall (2005) used MIGRATE to estimate N_em from KEA's data. N_em was slightly higher and was more symmetric (N_em values ranged from 1.21 – 2.45.) Regardless of the dataset, the migration values were consistently near the cutoff of 1.0, and confidence intervals (which can sometimes be large) were not presented.

4) Analyses performed: Some analyses performed as "critical tests" by one research group were considered inappropriate by the other. For example, REA used two critical tests of uniqueness for subspecies and historic genetic exchangeability – a) that there be greater variation between *Z. h. preblei* and other subspecies than within subspecies, and b) that multiple private alleles be at higher frequency than shared alleles. These criteria were criticized extensively by KEA as well as by some reviewers. The panel feels that neither of these are critical tests of genetic exchangeability. If these things are present they may argue strongly for historical exchangeability. However, not finding high frequency of private alleles – especially when analyzing only 5 loci – is not terribly unexpected, and not finding higher among group variances is not surprising – especially when there is a high level of structure within the subspecies examines (especially *Z. h. preblei*.)

5) Key Similarities: With regard to microsatellite data, it is also important to point out key similarities. For the most part, both studies detected significant population structure (significant Fst values, high Nei's D, partition analyses in STRUCTURE etc.) with respect to Preble's jumping mouse. Crandall's reanalysis of both REA and KEA's data strongly supports a statistically-significant independent cluster that corresponds to *Z. h. preblei*. Thus both datasets, even the smaller dataset of REA recovered support for a distinct *Z. h. preblei*. Again, the key difference in the conclusion is that REA interpret this as "recent" genetic exchangeability (ie. biologically insignificant) while KEA interpret this as "historic" genetic exchangeability (ie. biologically significant). This panel feels that these data fall very much in the middle, and it is difficult if not impossible to make a strong case either way using these microsatellite data alone. We do, however, feel strongly that these are important "supporting data" in that they do show differences among these groups. If other independent data (ie. morphological, behavioral, mitochondrial DNA, climatic data, presence of a clear geographic split, etc.) suggest similar or identical groupings, then these microsatellite data offer strong support that these groups are evolutionarily significant (sensu Avise and Ball 1990) If other independent data conflict with or offer no additional support to the microsatellite data, then we may conclude that these microsatellite groupings are more recent.

PHILOSOPHICAL DIFFERENCES

There are multiple philosophical differences between KEA and REA that contribute to their difference of opinion regarding the taxonomy of *Z. h. preblei*. These include (but are not limited to) a) their definitions of subspecies or taxon, b) their choice of null and alternative hypotheses and the "burden of proof," and c) the value and significance of different datasets. We discuss these briefly below.

Subspecies Definitions

Preble's meadow jumping mouse (*Z. h. preblei*) was formally designated as threatened under the Endangered Species Act on May 13, 1998. Early forms of the ESA afforded protection only to named species and subspecies. In 1978, the ESA was amended to include "distinct population segments" of vertebrates in order to protect reproductively isolated populations that have unique genetic attributes ["Any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature" (Endangered Species Act, Sec. 3 (15))]. There has been substantial criticism of the subspecies concept (e.g., Wilson and Brown 1953, Selander 1971, Zink 2004), and some response to this criticism (Smith and White 1956, Parkes 1982, Patten and Unitt 2002), but this taxonomic level was included in the U. S. ESA, and Preble's meadow jumping mouse was originally listed as threatened at this taxonomic level. Thus we address whether existing data support designation of Preble's meadow jumping mouse as a distinct subspecies. In Part I, we evaluate evidence pertaining to the validity of the subspecies designation of Preble's meadow jumping mouse (*Z. h. preblei*). We compare the available and relevant morphological, ecological, and genetic data to established criteria for designating subspecies, and where relevant, other categories.

The reader should bear in mind that there is a diversity of opinion among biologists about such definitions and their application. For example, some biologists might advocate that subspecies never need to be defined; if taxa are diagnosable then they should be considered separate phylogenetic species. In addition, while some of these are classical taxonomic units (e.g., subspecies, biological species), others were not initially defined in a taxonomic context and represent a unit that was defined instead for conservation management purposes (e.g., ESU, DPS, MU). Also, these units do not necessarily nest into a hierarchy of levels.

1) Traditional Subspecies definitions:

Subspecies are considered to be recognizably different but interbreeding populations of the same biological species in different geographical areas. A subspecies may be considered "a collection of populations occupying a distinct breeding range and diagnosably distinct from other such populations" (Mayr and Ashlock 1991). There are two critical elements to this definition. First, *populations* are diagnosed, not individuals, so this permits uncertainty regarding the exact determination of individuals and considerable overlap between populations. Second, the critical question is the definition of “diagnosable” or “diagnosably distinct.” This latter point is open to some interpretation itself.

Amadon (1949) derived the "75% rule" for delineation of subspecies, in which 75% of a population must be distinct or diagnosably different from 75% of the individuals of the other population. Patten and Unitt (2002) proposed formalizing the 75% rule, and provided a quantitative method for determining the validity of subspecies. Under their methods, "to be a valid subspecies 75% of a population must lie outside 99% of the range of other populations for a given defining character or set of characters." For characters that occur as separate states, such as presence or absence of a pelage pattern or mtDNA haplotype or clade, the test involves a simple contingency table analysis. For

continuously varying, normally distributed traits, such as measurements of body size, the rule involves comparison of the two distributions via their means, standard deviations and the expectation of 75% non-overlap from a t-distribution. This rule has been applied sporadically, but increasingly, in the literature (e.g., Patten and Unitt 2002, Meijaard and Groves 2004), and it provides a quantitative method to evaluate distinctiveness and in which to make subspecies designations (Patten and Unitt 2002). Relevant morphological, genetic and ecological information about the *Zapus hudsonius* subspecies will be compared to the criteria of these definitions in order to ascertain the support for the subspecies status of *Z. h. preblei*.

An important consideration for understanding status of 'traditional' subspecies is that gene flow is expected. Hence complete genetic differentiation is not predicted. Some level of gene exchange between populations (e.g. shared haplotypes) would be expected.

2) Phylogenetic species definitions:
The Phylogenetic Species Concept defines a species on the basis of phylogenetic history and diagnosability. The argument for using them over subspecies or ESUs (see below) is that "species" are traditional taxonomic entities. Cracraft (1983) defines a species as "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" or later (Cracraft 1989) as "an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent".

3) Evolutionarily significant unit definitions:
Several definitions for "evolutionarily significant units" (ESUs) have been proposed in the scientific conservation literature (Ryder 1986, Waples 1991, Moritz 1994a, b, Vogler and DeSalle 1994, Barrowclough and Flesness 1996, Moritz and Faith 1998, Crandall et al. 2000, Moritz 2002). Perhaps the most stringent definition is that of Vogler and DeSalle (1994), in which an ESU is "delimited by characters that diagnose clusters of individuals to the exclusion of other such clusters" (one that is similar in its criteria to the Phylogenetic Species Concept, see above). An early definition of ESUs required assessment of characters that may be adaptive to local environments (Waples 1991), but evidence of this sort can be very difficult to obtain, and other methods based more on maintenance of evolutionary history over adaptability became more widely accepted. In this vein, Moritz's (1994b) definition was developed, and relies largely on the determination of reciprocal monophyly in mtDNA sequences (each geographically based population coalesces to a common mtDNA haplotype ancestor) and significant differentiation of nuclear gene allele frequencies. This definition has been used widely in conservation biology, (e.g., Fleischer 1998, Lovette et al. 1999, Tarr and Fleischer 1999, Zink et al. 2000). A more recent method for defining ESU's incorporates information from morphological and ecological traits, as well as molecular characters (Crandall et al. 2000). These all agree on two essential points. First, to be defined as a unique unit, an ESU must have diverged sufficiently in diagnosable characteristics to allow identification of one *population* from another. Second, these characteristics should have some heritable or genetic component. This broader ESU concept is in many ways similar to the PSC (Cracraft 1989).

ESUs do not necessarily need to meet the criteria for "biological species" (Mayr 1963), which define actually or potentially interbreeding populations as the same species. Thus, while the biological species concept relates to the future potential for genetic mixing, the ESU (and phylogenetic species) concept is related to the past evolutionary relationships and recognizing groups that have broadly significant genetic differences (including differences in adaptation or genetic attributes).

Note that all three concepts (subspecies under the Biological Species Concept, Phylogenetic species, and ESUs) are explicitly evolutionary in philosophy, and recognize the importance of diagnosing distinctiveness as well as any gene flow present.

Criterion used by REA and KEA to assess status of *Z. h. preblei*

REA considered four lines of evidence in their assessment of subspecies status of *Z. h. preblei*: skull morphometrics, ecological exchangeability, and two forms of genetic data (mtDNA and microsatellites). KEA examined genetic evidence exclusively (mtDNA and microsatellites). The skull morphometric data of REA were used to evaluate whether *Z. h. preblei* was significantly differentiated from other selected subspecies of *Z. hudsonius*. This was viewed by REA as a test of the original formal taxonomic description of *Z. h. preblei* by Krutsch (1954), which was based on several cranial and pelage descriptions (see "Summary: Morphology" section for a discussion of REA's morphometric data and comments by Vignieri et al., Patton, and other reviewers). The ecological exchangeability criteria were evaluated by REA primarily based on a literature review. This review revealed no clear evidence for or against ecological exchangeability between *Z. h. preblei* and other subspecies, and we and other reviewers felt that this had not been specifically tested (see "Summary: Ecological Exchangeability" section for a discussion of REA's approach for evaluating ecological exchangeability and comments by Vignieri et al. and reviewers).

In their respective evaluations of the subspecific status of *Z. h. preblei*, REA and KEA utilized similar types of molecular genetic data (mtDNA sequence data and microsatellites). Interestingly, neither REA nor KEA rigorously employed a definition of "subspecies" per se from the literature (e.g., *sensu* Patten and Unitt 2002). Rather, both use a definition of ESU as a proxy for subspecies, even citing some of the same references in doing so (e.g., Avise and Ball 1990, Ball and Avise 1992). However, there are subtle but important differences in the perspectives of REA and KEA in terms of translating definitions of ESUs into a testable definition of subspecies. Whereas REA view this as requiring clear reciprocal monophyly of mtDNA lineages, KEA view subspecies as ESUs as defined by "significant phylogeographic separation of mtDNA alleles between subspecies (or populations), combined with congruent phylogeographic structure for nuclear loci."

Burden of Proof

There is an important difference in the philosophies of REA and KEA in terms of where they consider the burden of proof to lie when assessing the taxonomic status of *Z. h. preblei*. The differences between these two perspectives are illustrated by asking: "what

would each study conclude if their data were too few or lacked power to reject their null hypothesis?" In the case of REA, they would conclude that a formally named taxon is not valid and that the subspecies be eliminated from the nomenclature. In the case of KEA, there would be no foundation upon which to change the nomenclature, so the existing status of *Z. h. preblei* would not change. For example, REA's treatment of ecological exchangeability was to look in the literature for evidence of non-exchangeability, and if none could be found, then they concluded that *Z. h. preblei* was exchangeable with other subspecies.

Because *Z. h. preblei* is a formally described, valid, and commonly recognized taxon, we concluded that the burden of proof should lie in clearly showing that its taxonomic status is not warranted. Thus, a lack of evidence for differentiation of *Z. h. preblei* from other species of *Z. hudsonius* is not equivalent to providing evidence that differentiation is lacking. This is the approach taken by KEA; their null hypotheses view *Z. h. preblei* as a distinct, formally named taxon, and they therefore require clear evidence of genetic interchange to reject that null hypothesis. REA take the opposite approach in their study design: their null hypothesis is that *Z. h. preblei* is *not* distinct from the other species of *Z. hudsonius* that they examined.

SECTION 4. SUMMARY OF THE EVIDENCE

MORPHOLOGY

An argument has been made in several of the critiques of REA (e.g., Vignieri et al., 2006), most forceably by Patton (2006), that REA failed to adequately test the original morphological hypothesis of Krutzsch. In addition, Patton argued that for a recognized taxon, it is incumbent upon the reviser to reject the original basis of the diagnosis by directly testing the characters used in formulating the original hypotheses (in this case, the 7 morphological characters reported by Krutsch that distinguish *preblei* from *campestris* topotypes) in reference to the original specimens examined. Neither REA, nor KEA (nor subsequent commentators) have done so. Not all systematists would require the traditional morphological test of a valid taxon before using additional data to evaluate subspecific boundaries — and there is no formal requirement to do so — but we find compelling the argument that this important (and many would agree, necessary) first test has not been conducted. REA argued that they tested the hypothesis by examining two of the characters (size and interorbital breadth) in combination with a separate multivariate analysis of skull shape. They suggested that even if the cranial characters were not the same as those listed by Krutzsch, that multivariate data should nonetheless distinguish the subspecies if they are real. The panel found that argument to be unconvincing, recognizing instead that adaptive (or even evolutionarily significant non-adaptive) changes can be concentrated in just a few characters. Failure to detect taxon divergence in their chosen characters is not a complete test of the original hypothesis.

REA went on further to state that the other 5 characters of Krutzsch (upper parts dull, averaging lighter; dorsal band less distinct; auditory bullae smaller, less inflated; incisive foramina narrower, not truncate posteriorly; frontal region usually more inflated) were not quantifiable and therefore did not need to be tested. We disagree with that position and suggest that they all can be coded for systematic analysis, and most, if not all, are quantifiable and measurable. In fact, Jones (1981) quantified crudely bullar size, finding that some *preblei* were different from some *intermedius*, and improved measures of bullar size and shape are easy to imagine (note, Jones did not compare *preblei* to *campestris*, nor did he conduct statistical tests of morphology between *preblei* and any other subspecies, leaving his decision to not recognize any subspecies in *Z. hudsonius* difficult to evaluate). One of us (SJS) found bullar size to be the sole distinguishing trait of an isolated population of leaf-eared mice that multiple molecular data sets subsequently confirmed (Steppan, unpubl. data).

REA and Wehausen and Ramey (2000) consider subspecies to be distinguishable if ≥90% of specimens could be correctly classified to subspecies in LDA with jackknifed posterior probabilities ≥95%. As noted earlier, this is a high standard (although we do not claim that it is unjustifiable) without evidence that it has been widely accepted. Wehausen and Ramey (2000) do not cite a source or justification for this standard and their paper has been cited only 2 times by other authors. We question whether it is appropriate to introduce a relatively strict new convention in as contentious a test case as this one.

Finally, none of the type series for any of the taxa in question have been examined by these authors. Examination of the type specimens (because in taxonomy, the name of a species-level taxon is associated with a type, not with populations) is the standard procedure when evaluating the taxonomic standing of a taxon.

In summary, we find that many systematists would consider that the critical test of the subspecific status of *preblei* to have not yet been made, making discussions of molecular data premature. On the other hand, treating the formal morphological test as convention (or recommendation) rather than requirement, we still find that an insufficient test of the morphological definition of *preblei* has been conducted to support the synonymy of *preblei* with other subspecies. The original characters of Krutzsch (1954) should be examined in *preblei* and neighboring subspecies (and preferable more broadly) and the respective type specimens should be included in the analysis.

For those systematists that do not find the traditional and formal test as articulated by Patton as a necessary requirement before revisionary decisions are made, we continue here with evaluation of the non-morphological data.

ECOLOGICAL EXCHANGEABILITY

The panel concluded that there was no persuasive evidence presented regarding ecological exchangeability. Some workers (e.g., Crandall, Ft. Collins panel meeting) have argued that morphological data, especially multivariate analysis of skulls, are reasonable proxies for ecology, life history, or physiology because of expected character correlations. While we agree that cranial data *can* detect differences that suggest taxa are not exchangeable, we note many possible circumstances where we would expect cranial traits not to be significantly correlated with adaptive traits whose differences reduce exchangeability (e.g., behavior, physiology). We therefore agree with the qualification by REA that failure to detect major differences (and “major” remains undefined by REA) does not mean that differences are absent. The ecological exchangeability of the subspecies remains unknown.

MITOCHONDRIAL DNA

The mtDNA data provided by REA and KEA vary in geographic sampling strategy, amount of sequence data examined, aspects of the analyses, and quality. All of these could potentially affect whether or not haplotypes of ***Z. h. preblei*** were found to be "distinct" from those of other subspecies. In terms of sampling design, REA's approach of sampling a comparatively high number of localities, including many at or near subspecies boundaries, increased the likelihood that they would find shared haplotypes between subspecies if they existed. In contrast, KEA tended to sample away from, rather than at or near, subspecies boundaries. In general, KEA sampled fewer geographic localities, but many more individuals per locality. While this approach has some advantages and disadvantages (see Crandall's review of KEA), in theory, it would be less likely to find shared haplotypes between subspecies if they occurred primarily near subspecies boundaries. However, because KEA were recently able to analyze all of the specimens

identified as having shared haplotypes by REA (the KUMNH specimens in KEA, Table 1B) and additional samples from Wyoming, this difference is geographic sampling strategies is less pronounced than before.

In terms simply of amount of data, the combined data of KEA (which included two gene regions vs. one in REA, and ~4-times as many nucleotides) is superior to that of REA. The analyses were similar in that both REA and KEA performed phylogenetic analyses of the mtDNA haplotypes using *Z. princeps* as an outgroup. The details of these approaches differed, but all were valid approaches. There is concern from the panel that in both studies, *Z. princeps* is relatively distantly related to *Z. hudsonius*, and may therefore perform poorly as an outgroup, leading to poor resolution of relationships within *Z. hudsonius*. The unrooted haplotype network of REA (Fig. 3) suggests this might be the case, because it shows much clearer structuring of haplotypes than the rooted phylogenetic analysis of either REA or KEA. The test-statistics used in the AMOVA also differed between the studies, with REA using F_{st} and KEA using both F_{st} and Φ_{st}.

The biggest difference between the mtDNA results of the two studies really comes down to whether *Z. h. preblei* does or does not share haplotypes with other subspecies of *Z. hudsonius*. Based on the data at hand, there is no reliable evidence of any haplotype sharing. Thus, the available data suggests the *Z. h. preblei* is distinct and diagnosable based on the combined control region and cytochrome b haplotypes. It would be worthwhile to have the samples in question sequenced by multiple independent laboratories to further validate the mtDNA sequences in question.

Regardless of the conflicting haplotypes from the KUMNH specimens, the results of REA and KEA both suggest that *Z. h. preblei* shares few, if any, haplotypes with other subspecies of *Z. hudsonius*. If we were to assume that KEA was correct, there would be no sharing of haplotypes among subspecies. If we were to assume that REA was correct, there would still be a relatively small proportion of shared haplotypes between *Z. h. preblei* and *Z. h. campestris* (i.e., 7 out of 61 haplotypes shared, or approximately 11%). The implications of this level of shared haplotypes are discussed in Section 5: "Evaluation of *Z. h. preblei* Status Under Selected Subspecies Concepts".

MICROSATELLITE DNA DATA

In many respects, the two microsatellite datasets contain similar information. They recover the same three primary clusters in STRUCTURE analyses (including a *Z. h. preblei* cluster), they estimate similar N_em and similar F_{ST} values (which also documents statistically-significant subdivision), and they both find a lesser degree of subdivision within *Z. h. preblei*. We feel that some of the most significant differences are philosophical, and stem from issues relating to the definition of subspecies, determination of biological vs. statistical significance, and choice of null vs. alternative hypotheses in scientific inquiry.

Crandall and Marshall's (2005) reanalysis of both REA and KEA's data strongly supports a statistically-significant independent cluster that corresponds to *Z. h. preblei*. Thus both datasets(including the smaller dataset of REA) recovered support for a distinct *Z. h. preblei*. Again, the key difference in the conclusion is that REA interpret this as "recent" genetic exchangeability (ie. biologically insignificant) while KEA interpret this as "historic" genetic exchangeability (ie. biologically significant). This panel feels that these data fall very much in the middle, and it is difficult if not impossible to make a strong case either way using these microsatellite data alone. We do, however, feel strongly that these are important "supporting data" in that they do show differences among these groups. If other independent data (ie. morphological, behavioral, mitochondrial DNA, climatic data, presence of a clear geographic split, etc.) suggest similar or identical groupings, then these microsatellite data offer strong support that these groups are evolutionarily significant (sensu Avise and Ball 1990) If other independent data conflict with or offer no additional support to the microsatellite data, then we may conclude that these microsatellite groupings are more recent. We find that mitochondrial DNA data do support the significant clustering of *Z. h. preblei* groups, and so these two datasets corroborate the distinctness of *Z. h. preblei*.

SECTION 5. EVALUATION OF *Z. H. PREBLEI* STATUS UNDER SELECTED SUBSPECIES CONCEPTS

Traditional Subspecies

a) Mayr and Ashlock (1991) defined subspecies as "a collection of populations occupying a distinct breeding range and diagnosably distinct from other such populations." This places subspecies within the Biological Species Concept, wherein there is expected to be some gene flow among subspecies. *Z. h. preblei* clearly satisfies the "distinct breeding range" criterion with its geographic separation from the other subspecies of 60-160 km. Krutzsch proposed that *preblei* is diagnosably distinct from *campestris*, and that hypothesis has not been refuted. The PCA from REA indicates that populations of *preblei* are probably diagnosable from populations of *intermedius*, but not necessarily from *campestris*. Mitochondrial DNA is diagnostic given that there are no well documented haplotypes that are shared between *preblei* and the other subspecies, making either *preblei* or *campestris/intermedius* monophyletic (the rooting varying at times with different analyses, making one or the other monophyletic, if not both). The genetic divergence for mitochondrial DNA is small and the morphological distinction seems marginal, but the definition does not set magnitude as a criterion. Finally, the microsatellite analyses of both REA and KEA demonstrate that *preblei* is diagnosably distinct from the other subspecies. On balance, we would conclude that *preblei* satisfies this definition of subspecies.

b) Patten and Unitt (2002) formalized the 75%-rule with "to be a valid subspecies 75% of a population must lie outside 99% of the range of other populations for a given defining character or set of characters." Krutzsch's original description is not sufficiently detailed to apply this rule. PCA of cranial data from REA would fail to meet this threshold, although a different selection of characters focusing on more discriminating traits might. The LDA from REA at first glance would also suggest that the threshold is not met (42% of individuals correctly assigned to species with >95% posterior probability), but the definition does not require such a high degree of confidence (>95%) in the assignment of each individual. The definition is not worded in terms of phylogenetic structure (e.g., clades or network bipartitions), but it does not seem unreasonable to equate "range" of a population with distribution on a network. Excluding the questionable CR sequences, 100% of *preblei* sequences form a partition (e.g., clade) distinct from sequences of *intermedius* and *campestris*. Other interpretations are possible, such as equating range of variation with genetic distances, in which case *preblei*-to-*intermedius/campestris* distances may not fall outside the range of genetic distances within the *intermedius/campestris* complex. This definition only requires that separation be made for at least one trait (or combination), so any single line of evidence is sufficient. The microsatellite data provides high discrimination and *preblei* would appear to exceed this threshold given the assignment probabilities.

Phylogenetic Species Concept

Phylogenetic Species Concept of Cracraft (1989) defines species as "an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within

which there is a parental pattern of ancestry and descent." To paraphrase Cracraft, species are defined by the presence of any apomorphy (shared derived character) among a set of populations among which there has been historical gene flow. This definition applies to a higher taxonomic level than subspecies, but some workers would equate phylogenetic species with subspecies under a Biological Species Concept. Both the Cracraft species definition and the Mayr and Ashlock subspecies definition are built on the idea of "diagnosably distinct" populations, although the meaning of "diagnosis" probably differs; for Mayr and Ashlock it probably equates to central tendencies of populations while for Cracraft it explicitly means fixation of derived character states throughout the populations. There is no evidence of fixation of derived morphological traits in *preblei*. Mitochondrial DNA indicate fixation of a derived trait (DNA substitutions) as evidenced by monophyly in phylogenetic and network analyses, but without high confidence. Microsatellite data show strong discrimination when used in combination but no unequivocal fixation of unique alleles. A single apomorphy is sufficient to diagnose a phylogenetic species, even in mtDNA (Cracraft 1989) but the terminal position of *preblei* in the *Z. hudsonius* mitochondrial tree would seem to fall short of the definition (see also Weins and Penkrot 2002, under whose operationalization of phylogenetic concepts *preblei* would not be a species). Current data would not support *preblei* as a phylogenetic species.

Evolutionary Significant Units (ESUs)

Several researchers have defined evolutionarily significant units (ESUs) in a variety of ways. Some of these require reciprocally-monophyletic groups with some corroboration at nuclear loci (Moritz 1994). Mitochondrial data cluster into haplotype networks that are consistent with clades, however statistical confidence in monophyly is lacking, and reciprocal monophyly is especially uncertain because of rooting difficulties within the haplotype network. Microsatellites do corroborate the mitochondrial data, giving some level of added comfort. Several authors argue that reciprocal monophyly is too stringent a criterion, as even significantly different populations are expected to pass through periods of polyphyly to paraphyly while evolving towards reciprocal monophyly (Crandall et al. 2000) and even many widely-recognized species do not meet the criteria of reciprocal monophyly (Funk and Omland 2003). Alternatively, they argue that ecological differences and local adaptation (i.e., the lack of ecological exchangeability) are equally important for recognizing ESUs (Crandall et al. 2000). Unfortunately, we have seen no data that provides solid evidence for or against ecological exchangeability, but ideally some evidence or critical tests should be performed. It has been argued by Ramey and Crandall (Panel meetings, Fort Collins, CO) that morphological differences among populations provide evidence rejecting ecological exchangeability or for local adaptation. While we agree with this statement, we also believe that there are other forms of local adaptation (physiological, biochemical, behavioral, etc.) that are not tested, so lack of gross cranial differences should not be considered evidence for ecological exchangeability. Finally, many of these ESU definitions do not allow gene flow (cf. definition of strict reciprocal monophyly) or may require conditions that are more stringent than traditional subspecies, and thus may be the equivalent to taxonomic category higher than subspecies.

The question of whether *Z. h. preblei* is a distinct ESU largely depends on which of the available definitions are used, and how they are interpreted. If strongly supported reciprocal monophyly of mtDNA haplotypes is viewed as essential, then *Z. h. preblei* would not be an ESU. On the other hand, if a less stringent definition is used, such as one requiring *nearly complete* monophyly or *significant phylogeographic separation* of mtDNA, then *Z. h. preblei* would be appear to qualify as an ESU given that corroborating evidence from the nuclear genome also exists. Owing to a lack of adequate data on ecological exchangeability, it is not possible to determine if other definitions of ESU's that incorporate this parameter (e.g., Crandall et al. 2000) would be met or not. Thus, the status of *Z. h. preblei* as a distinct ESU is debatable, and depends on which of the many available definitions of ESU are employed.

SECTION 6. POTENTIAL ISSUES FOR FUTURE RESEARCH

We include here a discussion of additional information that would be useful in any future evaluation of the status of *Z. h. preblei*. This is not intended as a roadmap for further work, and should not be seen as constituting recommendations for research programs. These are however areas where additional information would be useful in reducing any remaining uncertainties.

MORPHOLOGICAL STUDIES

1. Testing the original taxonomic description of *Z. h. preblei* — A critical first test of the subspecific status of *preblei* would be to evaluate all the characters proposed by Krutzsch (1954) to distinguish *preblei* from *campestris*. Ideally, this would be part of a syntopic survey of the species rather than just one region. This study should include examination of the type specimens and finer scale geographic analysis to best estimate the extent of any phenotypic clusters assignable to subspecies.

ECOLOGICAL EXCHANGEABILITY

1. Investigations into the ecological exchangeability of *Z. h. preblei* with other subspecies — REA and others pointed out the lack of studies that examine the ecological exchangeability of *Z. hudsonius* subspecies. Such tests may be critical for determining the taxonomic status of *Z. h. preblei* under some taxonomic categories (Crandall et al. 2000) and they may be useful for any population management or species recovery planning. Simple tests of climate differences (i.e., BIOCLIM-type analyses) and habitat differences (i.e., floral assemblage differences) may represent a first start, and may help elucidate differences in physiology or diet that could be investigated in greater detail.

MITOCHONDRIAL DNA

1. Further Sampling of *Zapus hudsonius* subspecies — Both current studies (REA and KEA) sampled only five of the 12 described subspecies of *Z. hudsonius*. It would be very beneficial to have data from the remaining subspecies. Ideally, a geographic sampling strategy that combined the approaches of REA and KEA would be used for each subspecies so that each is sampled thoroughly throughout its respective range. This would provide an expanded evolutionary and geographic context within which to evaluate the data for *Z. h. preblei.* In terms of data type and amount, the combined approach of KEA, using both control region and cytochrome b data is preferable to using just control region data alone.

2. Sequence verification for the KUMNH specimens — It would be very useful to have the control region data for the KUMNH specimens repeated by multiple, independent laboratories. Although the panel has provided some potential insights into why REA and KEA reported different sequences for the same specimens, the best way to

confirm the true mtDNA sequences for these is to have them re-extracted and sequenced by two or more laboratories that: (1) are independent and not associated with any of the parties involved in this debate; and (2) have a high level of experience obtaining quality DNA sequences from ancient DNA. Given the relatively small number of samples in disagreement, this should not be overly expensive or time-consuming.

MICROSATELLITE DNA

1. Further sampling of *Z. hudsonius* subspecies — Like mitochondrial DNA studies, future studies of *Z. hudsonius* subspecies should attempt to include all 12 subspecies and the entire breadth of the geographic range. The 21 existing microsatellite loci should be sufficiently powerful for most basic analyses that would be performed. Ideally, the sampling strategy would be a combination of REA and KEA approaches. Realistically, however, researchers may want to begin with a KEA type approach, but then follow up with additional sampling between genetically differentiated populations and potential hybrid zones to examine evidence for mixing, gene flow, and isolation by distance.

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Riddle, B.R. Comment on Ramey, R.R., II, H. Liu, and L. Carpenter. 2004. Testing the taxonomic validity of Preble's meadow jumping mouse (*Zapus hudsonius preblei*).

Riddle, BR. Comments on King, T.L., J.F. Switzer, C.L. Morrison, M.S. Eackles, C.C. Young, B.A. Lubinski and P. Cryan. 2006 Comprehensive genetic analyses reveal evolutionary distinction of a mouse (*Zapus hudsonius preblei*) proposed for delisting from the U.S. Endangered Species Act.

Shenk, T. Forward of the instructions for collecting genetic tissue samples by Larry Riggs. Material offered to SEI review panel

Sites, J.W., Jr. Comment on Ramey, R.R., II, H. Liu, and L. Carpenter. 2004. Testing the taxonomic validity of Preble's meadow jumping mouse (*Zapus hudsonius preblei*). 5 July 2004

Spencer, W.D. Comment on Genoma LLC Report concerning genetic assessment of Preble's Meadow Jumping Mouse (*Zapus hudsonius preblei*) and further

comments on studies by King et al. Material offered to SEI review panel 5 July 2006

Taylor, R. Comment on protocol. Material offered to SEI review panel 15 May 2006

Vignieri, S. Informal comments on Ramey's response to Vignieri et al. Material offered to SEI review panel 6 July 2006

Vignieri, S. Email Statement to the panel. Summary of VEA. Material offered to SEI review panel 6 July 2006

Waits, L.P. Comment on Ramey, R.R., II, H. Liu, and L. Carpenter. 2004. Testing the taxonomic validity of Preble's meadow jumping mouse (*Zapus hudsonius preblei*).

Waits, L.P. Comment on Ramey, R.R., II, H. Liu, L.M. Carpenter, and C.W. Epps. 2004. Testing the uniqueness of *Z. h. intermedius* relative to *Z. h. campestris*.

White, G.C. Comment on Ramey, R.R., II, H. Liu, and L. Carpenter. 2004. Testing the taxonomic validity of Preble's meadow jumping mouse (*Zapus hudsonius preblei*).

White, G.C. Comment on Ramey, R.R., II, H. Liu, L.M. Carpenter, and C.W. Epps. 2004. Testing the uniqueness of *Z. h. intermedius* relative to *Z. h. campestris*. 28 April 2005

* Bibliography also contains documents reviewed by the panel which are not cited in this report.

APPENDIX 1: CURRICULA VITAE

BRIAN S. ARBOGAST

Associate Professor and Curator of Mammals
Department of Biological Science
Humboldt State University
Arcata, CA 95521

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Fax: 707-826-3201
E-mail: bsa2@humboldt.edu
Web: www.humboldt.edu/~bsa2

EDUCATION

PhD Wake Forest University (1999) Advisor: Peter Weigl
MS Louisiana State University (1996) Advisor: Mark Hafner
BS Wake Forest University (1992)

POSITIONS HELD

Associate Professor and Curator of Mammals. Department of Biological Sciences, Humboldt State University, Arcata, California (2006-present)

Assistant Professor and Curator of Mammals. Department of Biological Sciences, Humboldt State University, Arcata, California (2001-2006)

Post-Doctoral Research Associate, Burke Museum and Department of Zoology, University of Washington, Seattle (1999-2001)

PUBLICATIONS

Blois, JL and BS Arbogast (2006) Conservation genetics of the Sonoma Tree Vole (*Arborimus pomo*) based on mitochondrial and AFLP markers. *Journal of Mammalogy* (in press)

Arbogast, BS, SV Drovestski, RL Curry, P Boag, P Grant, R Grant, G Seutin and D. J. Anderson (2006) Origin and diversification of Galápagos mockingbirds. *Evolution* 60:370-382.

Arbogast, BS. (2006) The geography of life. Book Review of Biogeography, by M Lomolino, B Riddle and J Brown. *Trends in Ecology and Evolution* 21:14-15.

Arbogast, BS, RA Browne, PD Weigl and GJ Kenagy (2005) Conservation genetics of endangered flying squirrels from the Appalachian mountains of eastern North America. *Animal Conservation* 8:123-133.

Zheng X, BS Arbogast and GJ Kenagy (2003) Historical demography and genetic structure of sister species: deer mice (*Peromyscus spp*.) in the North American temperate rainforest. Molecular Ecology 12:711-724.

Arbogast BS, SV Edwards, J Wakeley, P Beerli and JB Slowinski (2002) Estimating

Divergence Times from Molecular Data on Phylogenetic and Population Genetic Timescales. *Annual Review of Ecology & Systematics* 33:707-740.

Arbogast, BS, and GJ. Kenagy (2001) Comparative phylogeography as an integrative approach to historical biogeography. *Journal of Biogeography* 28:819-825.

Arbogast, BS (2001) Phylogeography, by JC Avise. Book Review, *American Zoologist* 41:134-135.

Arbogast, BS, RA Browne and PD Weigl (2001) Evolutionary genetics and Pleistocene biogeography of North American tree squirrels (*Tamiasciurus*). *Journal of Mammalogy* 82:302-319.

Arbogast, BS (1999) Mitochondrial DNA phylogeography of the New World flying squirrels (*Glaucomys*): implications for Pleistocene biogeography. *Journal of Mammalogy* 80:42-155.

Slowinski, JB, and BS Arbogast (1999) Is there an inverse relationship between body size and the rate of molecular evolution? *Systematic Biology* 48:396-399.

Arbogast, BS, and JB Slowinski (1998) Pleistocene speciation and the mitochondrial DNA clock. *Science* 282:1955a.

MANUSCRIPTS IN PREPARATION

Arbogast, BS. Whence *Glaucomys*? A review of the evolutionary and biogeographic history of the New World Flying Squirrels. Special Feature of Symposium Papers from the 86th meetings of the American Society of Mammalogists (to be published in *Journal of Mammalogy,* 2007*).*

Kenagy, GJ, K Warheit, BS Arbogast and M Linders. Conservation Genetics of the Western Gray Squirrel (*Sciurus griseus*) in Washington

Arbogast, BS, A. Bidlack, JC Cook, and GJ Kenagy. Paleodemography and post-glacial expansion of the northern flying squirrel, *Glaucomys sabrinus*

Callahan, C and BS Arbogast. Molecular Systematics and Biogeography of whale lice living on gray whale islands.

MUSEM & CURATORIAL EXPERIENCE

2001-present	Curator of Mammals, Vertebrate Museum, Humboldt State University
2003-2005	Board of Directors, HSU Museum of Natural History
1999-2001	Post-doctoral Fellow, Mammalogy Program, Burke Museum, Univ. of Washington
1996-1999	Assistant in the vertebrate collection, Wake Forest University

1994-1996 Curatorial Assistant, Collection of Genetic Resources, LSU Museum of Natural Science

1993-1994 Curatorial Assistant, Mammal Collection, LSU Museum of Natural Science

RECENT GRANT SUPPORT

Genetic and Bioacoustic Studies of Mesoamerican Flying Squirrels. HSU Research Scholarship and Creative Activities Grant. $3,500. PI: Brian Arbogast

Comparative molecular evolution of whale ectoparasites. CSUPERB Faculty Research Grant. $10,000. PI: Brian Arbogast

Systematics and Evolutionary Ecology of New and Old World Avian Sister Radiations [Aves: Mimidae and Sturnidae]. National Science Foundation DEB – Systematic Biology PI Irby Lovette, Cornell University (~$296,071)

I am one of nine researchers included on this NSF-funded project designed to construct molecular phylogenies of two diverse Families of birds (mockingbirds and starlings), and to use these phylogenies to explore the evolution of song mimicry and cooperative breeding.

Origin and diversification of Galapagos mockingbirds. HSU Foundation Small Grant Competition. $1100. PI: Brian Arbogast

Whales as Islands: Biogeography and co-evolution of whales and their ectoparasites. HSU Research and Creative Acctivities Grant. $4,300. PI: Brian Arbogast

Developing a Web-Based Searchable Database for the HSU Mammal Collection. HSU Foundation Small Grant Competition. $1200. PI: Brian Arbogast

The Effects of Habitat Fragmentation on the Demographic and Genetic Structure of a Temperate Rainforest Endemic, the Sonoma Red Tree Vole (Arborimus pomo). HSU Research Scholarship and Creative Activities Grant. $5,000. PI: Brian Arbogast

Articulating the Complete Skeleton of a Beaked Whale. HSU Foundation Small Grant Competition. $1200. PI: Brian Arbogast

Reconstructing the Ice-Age History of Pacific Northwest Mammals. HSU Foundation Small Grant Competition. HSU Foundation Small Grant Competition. $1200. PI: Brian Arbogast

TEACHING EXPERIENCE

Courses: Mammalogy (Lecture and Lab), Advanced Mammalogy (Lecture, Lab and Field Methods), Biogeography, Zoogeography (Humboldt)

Seminars: Phylogeny Ecology & Behavior, Animal Extinctions (Humboldt)

Other teaching experience: Guest lecturer in Biogeography (Univ. of Washington). Teaching Assistant in a variety of courses at LSU and Wake Forest.

AWARDS

President McCrone Promising Faculty Scholar Award. Humboldt State University (2004)

American Society of Mammalogists. First Runner-Up for the Albert R. and Alma Shadle Fellowship in Mammalogy (1998).

American Museum of Natural History, Frank M. Chapman Memorial Fund Grant. Phylogeography of the Galápagos mockingbirds: a test of the prevailing-wind hypothesis of dispersal (1998).

American Museum of Natural History, Theodore Roosevelt Memorial Fund Grant. The evolution of boreal mammal communities in North America: a comparative phylogeographic approach (1998).

Southwestern Association of Naturalists, Wilks Award Finalist. Student Paper Competition: Recalibrating the mitochondrial DNA clock: implications for Pleistocene vicariance biogeography (1998).

American Society of Mammalogists, Grant-in-aid of Research. The evolution of boreal mammal communities in North America: a comparative phylogeographic approach (1997).

American Society of Mammalogists, Elizabeth Horner Award. Outstanding Graduate Student Research Proposal (1997).

Wake Forest University Department of Biology, Graduate Student of the Year (1997).

National Sigma Xi Competition. Phylogeography of the Galápagos mockingbirds (1996).

Marine Biological Lab, Woodshole, MA. Workshop on Molecular Evolution Scholarship (1996).

American Society of Mammalogists, Grant-in-aid of Research. Mitochondrial DNA variation and biogeography of the New World flying squirrels (Glaucomys) (1995).

Louisiana State University (four research and travel grants--1993-1995).

National Sigma Xi Competition. Mitochondrial DNA variation and biogeography of the New World flying squirrels (Glaucomys) (1993)

Wake Forest University, Howard Hughes Undergraduate Travel Grant. Field-course in mainland Ecuador and the Galápagos Islands (1992).

Derieux Award Winner (best student paper), Meeting of the North Carolina Academy of Science (1992).

Wake Forest University, Howard Hughes Undergraduate Summer Research Fellowship (1991).

SELECTED SCHOLARLY PRESENTATIONS

Arbogast, BS. Evolutionary and biogeographic history of the New World flying

squirrels (*Glaucomys*). Invited symposium presentation in " The northern flying squirrel: a biological portrait of a forest specialist in post-European North America." 86th annual meetings of the American Society of Mammalogists, Amherst, MA (2006).

Callahan, CM and BS Arbogast. Phylogeography of whale lice (Cyamidae) living on gray whale islands. 86th annual meetings of the American Society of Mammalogists, Amherst, MA (2006).

Callahan, CM, BS Arbogast, PD Goley, JW Demastes. Biogeography of Whale Lice (Amphipoda: Cyamidae) Living on Gray Whale Islands. 16th Biennial Conference on the Biology of Marine Mammals, San Diego, CA (2005).

Blois, JL and BS Arbogast. Patterns of genetic variation within an endemic arboreal vole, *Arborimus pomo*, in northern California. Meetings of the International Biogeography Society, Shepherdstown, West Virginia (2005).

Blois, JL and BS Arbogast. A multilocus assessment of the genetic structure and diversity within an endemic, arboreal vole, *Arborimus pomo*, in northern California. 7th Annual Bay Area Conservation Biology Symposium, Stanford University (2005).

Arbogast, BS, SV Drovetski, RL Curry, PT Boag, G Seutin, PR. Grant, BR Grant & DJ Anderson. Origin and diversification of Galápagos mockingbirds. Meetings of the Society for the Study of Evolution, University of Alaska, Fairbanks, AK (2005).

Kenagy, GJ, X Zheng, BS Arbogast, J Booth, J Bradley, M Linders and K Warheit. Genetic Structure and Historical Biogeography of Disjunct and Declining Populations of Western Gray Squirrels In Washington. 84th Annual Meeting of the American Society of Mammalogists, Humboldt State University (2004).

Callahan, CM, BS Arbogast, PD Goley and JW. Demastes. Whales as Islands: Biogeography of the Epibiotic Fauna of Gray Whales. 84th Annual Meeting of the American Society of Mammalogists, Humboldt State University (2004).

Browne, RA, BS Arbogast and PD Weigl. Pleistocene Forest Dynamics and the Genetic Diversity of Flying Squirrels. 16th Annual Meeting of the Society for Conservation Biology. Canterbury, UK (2002).

Arbogast, BS. Presentation to Host the 84th Annual Meetings of the American Society of Mammalogists. 82nd Annual Meetings of the ASM. Lake Charles, LA (2002).

Comparative phylogeography of mammals and birds. *Invited Seminar*, Cornell University (2001). .

Using comparative phylogeography to reconstruct the mammalian faunal history of the Pacific Northwest. *Invited Seminar*, University of Washington (2000)

Estimating rates of molecular evolution and dates of divergence using likelihood. *Invited Seminar*, University of Virginia (1999)

Is there an inverse relationship between body size and the rate of molecular evolution in vertebrates? Meetings of the American Society of Mammalogists, Seattle, WA (1999)

Recalibrating the mitochondrial DNA clock: implications for Pleistocene vicariance biogeography. *Invited Presentation*, Wilks Award Competition, Meetings of the Southwestern Association of Naturalists, Albuquerque, NM (1998)

Comparative phylogeography of codistributed boreal mammals. *Invited Presentation*, Euro-American Mammal Congress, Santiago de Compostela, Spain (with B. R. Riddle; 1998)

Pleistocene speciation and the mitochondrial DNA clock. Meetings of the American Society of Mammalogists, Blacksburg, VA (1998)

Comparative phylogeography of codistributed boreal mammals. Meetings of the American Society of Mammalogists, Stillwater, OK (1997)

Zoogeography of the northern flying squirrel (*Glaucomys sabrinus*) based on analysis of mitochondrial DNA. Meetings of the Society for the Study of Evolution and Society of Systematic Biologists, St. Louis, MO (1996)

Have the giant (*Ratufa*) and pigmy (*Exilisciurus*) squirrels of Borneo stopped being squirrels? (with P. D. Weigl and T. K. Knowles). Meetings of the American Society of Mammalogists, Grand Forks, ND (1996)

Pleistocene biogeography of the New World flying squirrels. *Invited Seminar*, University Science Colloquium, Francis Marion University (1996)

Zoogeography of the northern flying squirrel (*Glaucomys sabrinus*) based on analysis of mitochondrial DNA. Meetings of the Southwestern Association of Naturalists, Shreveport, LA (1995)

Zoogeography of the northern flying squirrel (*Glaucomys sabrinus*) based on analysis of mitochondrial DNA. Meetings of the American Society of Mammalogists, Burlington, VT (1995)

HOST OF NATIONAL MEETINGS

84th Annual Meetings of the American Society of Mammalogists, Humboldt State University (2004)

OUTSIDE REVIEWER

Journals: Evolution, Systematic Biology, Molecular Phylogenetics & Evolution, Journal of Mammalogy, Animal Conservation, Australian Journal of Zoology

Grant Programs: NSF Systematic Biology Program; AAAS Women in International Scientific Collaboration Program; National Geographic Society Research & Exploration Program

Books: Frontiers of Biogeography

FIELD EXPERIENCE

Extensive collecting of specimens for use in examining the molecular ecology of small mammals of the Pacific Northwest of North America, including flying squirrels, red squirrels, redback voles, deer mice, ermine, water shrews, pocket gophers, chipmunks, tree voles, ground squirrels, & jumping mice

Fieldwork on birds of the Galápagos Islands, Ecuador

Fieldwork on the Giant (*Ratufa*) and Pigmy (*Exilisciurus*) squirrels in Malaysian Borneo

CURRENT RESEARCH PROJECTS

Comparative Phylogeography of Pacific Northwest Mammals: The main focus of my current research is the molecular systematics and biogeography of Pacific Northwest mammals. I am collaborating with Dr. Jim Kenagy (the Burke Museum, University of Washington) to compare geographic patterns of evolutionary subdivision (or phylogeographic patterns) among a variety of boreal forest mammals. This research will allow us to develop a synthesis of how the members of this particular biotic assemblage responded to the dramatic climatic changes of the Quaternary (which includes the ice ages of the Pleistocene). This project involves extensive field studies throughout the Pacific Northwest of the U.S. and Canada. We currently have samples from over a dozen species/ species pairs from all or nearly all of the major mountain ranges in the Northwest. One important aspect of our research is to measure levels of genetic diversity in mammals inhabiting some of the National Parks of the Pacific Northwest, including North Cascades National Park and Olympic National Park. The information we obtain will be useful in developing conservation plans for a variety of small mammals. Because so many species and localities are involved, this is necessarily a long-term project. However, we anticipate being able to publish manuscripts on the biogeography of individual species or species pairs as we work toward an overall synthesis.

Evolution and Biogeography of Mexican Flying Squirrels. I am in the beginning stages of establishing this research project, which will include scientists from both the U.S. and Mexico. We will attempt to locate isolated and little known populations of

flying squirrels in Mexico and examine their evolution and biogeography via molecular phylogenetic analyses in my lab at HSU.

Whales As Islands: Biogeography of the Epibiotic Fauna of Gray Whales: I am working with Dawn Goley and student Chris Callahan of HSU and Jim Demastes of the University of Northern Iowa to investigate the biogeography of the ectoparasites of Gray whales (*Eschrichtius robustus*). Gray whales are living "islands" to a diverse but little known assemblage of ectoparasites that includes at least three species of whale lice (*Cyamus* spp.) and one species of whale barnacle (*Cryptolepas rhachianecti*). These two types of ectoparasitic crustaceans differ greatly in terms of their dispersal abilities within and among host individuals. Whereas barnacles have a free-living pelagic larval stage (allowing transmission among host individuals even in the absence of direct contact), whale lice do not. Thus, whale lice are thought to be dependent on direct physical contact, such as mating or nursing, to colonize a new host. Following transmission, barnacles become sessile, but lice remain free to move about the body of the host whale. The ectoparasite fauna of gray whales provides a unique and remarkable system for studying island biogeography and host-parasite co-evolution. Using a combination of methods, including population genetic analysis and phylogenetic techniques, this study will provide valuable insights into the colonization dynamics and biogeography of ectoparasties on whale "islands."

Systematics and Evolutionary Ecology of New and Old World Avian Sister Radiations I am collaborating on this project (lead by Irby Lovette of Cornell University) focused on examining the comparative evolution of song mimicry and cooperative breeding in two families of birds, Sturnidae and Mimidae.

Conservation Genetics of Western Gray Squirrels. I am working with a team of investigators to examine the conservation genetics of this species (which, although common in California, is present only in very small numbers in Washington State. I began this project during my post-doc and am continuing to work on it. We presented our results at the Mammal Meetings this summer at Humboldt State and have a manuscript nearing completion on this work.

CURATORIAL ACTIVITIES

One of the most important components of my appointment is to act as the Curator of the Mammal Collection at the HSU Vertebrate Museum. The Mammal Collection is one of the finest in the CSU system, and in terms of teaching collections, it is one of the best in the country. Each year we use the collection to teach over 100 students in Mammalogy; many of these students also receive training in mammal curation at the Museum. The collection-based training in Mammalogy offered at HSU is one of the most influential programs of its kind in the country; for example, HSU alumni previously trained in the Mammal Collection at HSU are now Curators or Collections Managers at many of the largest and finest museums in the country, including The Field Museum, the University of Kansas, the Los Angeles County Museum, and the University of New Mexico's Museum of Southwestern Biology.

A major addition to the Mammal Collection since my arrival has been the development of a Frozen Tissue Collection. Virtually all new mammal specimens added to the collection have corresponding tissue samples (blood, liver, kidney etc.) that are being stored in a dedicated ultracold freezer that was part of my start-up package (housed in the stockroom). We expect this frozen tissue collection to become an increasingly valuable resource for future genetic studies of Northwest mammals. We recently obtained the personal tissue collection of Dr. Tim Lawlor (several hundred specimens).

Major achievements for 2004/2005:

- 40 students were trained in specimen preparation and museum curation (27 independent study and volunteer students and 13 from the Advanced Mammalogy Course). This is by far the largest number since my appointment, and certainly makes the HSU Vertebrate Museum one of the most active student training grounds in the country.

- The accessioning of 220 new specimens. This brings our total to approximately 7, 900. Nearly all of the new specimens have associated frozen tissues.

- Launching of the beta version of the online searchable database for the HSU Vertebrate Museum.

- The Vertebrate Museum received a very positive review and re-accreditation from the Systematics Collection Committee of the American Society of Mammalogists in August of 2004.

John Philip Dumbacher Jr., Assistant Curator and Department Chair
Department of Ornithology and Mammalogy, California Academy of Sciences
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Phone: 415-750-7176; Fax: 415-750-7178; email: jdumbacher@calacademy.org.

Positions held:

Assistant Curator and Department Chair, Ornithology and Mammalogy, California Academy of Sciences, July 2003 to present.

Smithsonian Research Associate, Molecular Genetics Laboratory, and Smithsonian Conservation Research Center, National Zoological Park, Smithsonian Institution, 2001-2003.

Academic Degrees:

Ph.D. Ecology and Evolution, The University of Chicago, June 1997.

M.S. Ecology and Evolution, The University of Chicago, March 1995.

B.S. General Biology, Vanderbilt University, May 1987.

Honors and Awards:

Scientific Advisor, Pinhead Institute's Biodiversity Monitoring Program, Telluride, CO 2002-pres.

Smithsonian Scholarly Studies Fellow, Conservation Research Center, National Zoo, 1999-2000.

Friends of the National Zoo Post-doctoral Fellowship, Genetics Program, National Zoo, 1998-99.

Smithsonian Post-doctoral Fellowship, Genetics Program, National Zoological Park, 1997-98.

US Department of Education GAANN Training Grant Fellow, University of Chicago, 1997.

William Rainey Harper Doctoral Dissertation Fellowship, University of Chicago, 1995-96.

NIH Genetics Training Grant Fellow, Committee on Genetics, University of Chicago, 1993-95.

National Institutes of Health Summer Fellowship, Laboratory of Bioorganic Chemistry, 1994.

AOU Travel Award to International Ornithological Congress in Vienna, Austria 1994.

Quintessence Award, Publication Excellence in Environmental Contamination and Toxicology, 1994.

Christensen Research Institute Fellow, Papua New Guinea, 1993-1994.

Who's Who in Science and Engineering, biographical sketch published, 1993 - 2000.

Centennial Fellowship, University of Chicago, 1991.

Research Grants:

National Science Foundation, 2006, asking $500K, Cabinetry for O&M new building, pending.

National Geographic Society, 2005, $26K, Linking diet, toxicity and defense in New Guinea's poisonous pitohui birds (active through 2006)

WWF and TNC, 2002, $40,000, Assessing the ecological impacts of oil palm development in PNG.

National Science Foundation, 2001, $325K, Lowland phylogeography of New Guinea (active through 2006).

Abbott Fund, National Zoological Park, 2001, $9,900 for captive studies of Hooded Pitohuis

Sisley Fund, National Zoological Park, 2000, $7,000 for field studies of Hooded Pitohuis.

Abbott Fund, National Zoological Park, 2000, $8,000 for field studies and telemetry training course.

Smithsonian Scholarly Studies Grant, 1999-2001, $64,000 for field studies of Hooded Pitohuis.

Sisley Fund, National Zoological Park, 1999, $5,100 for field studies of Hooded Pitohuis.

Pittsburgh Zoo Conservation Grant, 1999, $1,400 for radiotelemetry study of Hooded Pitohuis.

National Geographic Society, 1993, $41,140, Geographical variation in New Guinea's poisonous birds.

Hinds Fund Grant, University of Chicago, 1991, $750, Chemistry of toxin use by *Pitohuis*.

Sigma Xi Grant-in-aid of Research, 1988, $600, Study of lek evolution in Raggiana Birds of Paradise.

Publications:

Original Papers:

1. Dumbacher, J.P., A. Mack. Chapter 4.9: Birds of Papua. In Beehler, B.M. ed., The Ecology of Papua. Volume IX in the Ecology of Indonesia series. Oxford University Press, UK. In Press.

2. Topf, A.L., Gilbert, M.T.P., Dumbacher, J.P. & Hoelzel, A.R. 2005. Tracing the phylogeography of human populations in Britain based on 4th-11th century mtDNA genotypes. Molecular Biology and Evolution. doi:10.1093/molbev/msj013

3. J.P. Dumbacher. 2005. "Batrachotoxin" in Encyclopedia of Toxicology (Wexler P), 2nd edition. Oxford. Elsevier. pp. 215-17.

4. Beadell, J. S., E. Gering, J. Austin, J. P. Dumbacher, M. A. Peirce, T. K. Pratt, C. A. Atkinson, and R. C. Fleischer. 2004. Prevalence and differential host-specificity of two avian blood parasite genera in the Australo-Papuan region. Molecular Ecology 13:3829-3844.

5. J. P. Dumbacher, A. Wako, S. R. Derrickson, A. Samuelson, T. F. Spande, and J. W. Daly. 2004. Melyrid beetles (Choresine): A putative source for the batrachotoxin alkaloids found in poison-dart frogs and toxic passerine birds. PNAS, 101(45): 15857-15860.

6. S. P. Courtney, J. A. Blakesley, R. E. Bigley, M. L. Cody, J. P. Dumbacher, R. C. Fleischer, A. B. Franklin, J. F. Franklin, R. J. Gutiérrez, J. M. Marzluff, L. Sztukowski. 2004. Scientific evaluation of the status of the Northern Spotted Owl. Sustainable Ecosystems Institute, Portland, Oregon.

7. J. P. Dumbacher, T. K. Pratt, and R. C. Fleischer. 2003. Phylogeny of the owlet-nightjars (Aves: Aegothelidae) based on mitochondrial DNA sequence. Molecular Phylogenetics and Evolution 29: 540-549.

8. J. P. Dumbacher and R. C. Fleischer. 2001. Phylogenetic evidence for colour-pattern convergence in toxic pitohuis: Müllerian mimicry in birds? Proceedings of the Royal Society of London: Biology, **268**: 1971-1976.

9. L. Shapiro and J. P. Dumbacher. 2001. Adenylate kinase intron 5: A new nuclear locus for avian systematics. The Auk, 118(1): 248-255.

10. J. P. Dumbacher, T. Spande, and J. W. Daly. 2000. Batrachotoxin alkaloids from passerine birds: A second toxic bird genus (*Ifrita kowaldi*). Proc. Natl. Acad. Sci. USA, 97(24): 12970–12975.

11. J. P. Dumbacher. 1999. The evolution of toxicity in *Pitohuis*: I. Effects of homobatrachotoxin on chewing lice (Order Phthiraptera). The Auk **116**(4): 957-963.

12. R. Visnak and J. P. Dumbacher. 1999. Comparison of four fumigants for removing avian lice. Journal of Field Ornithology, **70**(1): 42-48.

13. J. P. Dumbacher. 1997. The ecology and evolution of chemical defense in the avian genus *Pitohui*. Ph.D. Thesis. University of Chicago.
14. J. P. Dumbacher and S. Pruett-Jones. 1996. Avian chemical defense. Current Ornithology, **13**: 137-174.

15. B. M. Beehler and J. P. Dumbacher. 1996. More examples of fruiting trees visited predominantly by birds of paradise. Emu, **96**: 81-88.

16. J. P. Dumbacher, B. M. Beehler, T. F. Spande, H. M. Garraffo, and J. W. Daly. 1993. Pitohui: How toxic and to whom? Science, **259**: 582-583.

17. J. P. Dumbacher, B. M. Beehler, T. F. Spande, H. M. Garraffo, and J. W. Daly. 1992. Homobatrachotoxin in the genus *Pitohui*: Chemical defense in birds? Science, **258**: 799-801.

Publications (continued):

18. J. P. Dumbacher. 1991. Bird life of Kagi, Central Province. Muruk (Journal of the Papua New Guinea Bird Society), **5**(1): 19-21.

19. B. M. Beehler and J. P. Dumbacher. 1990. Interesting observations of birds at Varirata National Park, June - July 1990. Muruk, **4**(3): 111.

Abstracts:

20. J. P. Dumbacher. 1994. Chemical defense in New Guinean birds. Journal für Ornithologie **135**(3): 407.

21. J. W. Daly and J. P. Dumbacher. 1994. Alkaloids as a chemical defense in birds. Journal für Ornithologie **135**(3): 408.

Book Reviews:

22. J.P Dumbacher. 2004. [review of] My Family Album, by Franz de Waal, and Animal Social Complexity, edited by Franz de Waal and Peter Tyack. California Wild Magazine.

23. J. P. Dumbacher. 2002. [review of] The Birds of Paradise, by Clifford Frith and Bruce M. Beehler. The Auk **119**(3): 880-881.

24. J. P. Dumbacher. 1991. [review of] The Ruff, by Johan G. Van Rhijn. The Auk **108**(4): 1007.

25. J. P. Dumbacher. 1991. [review of] Social, Sexual, and Pseudosexual Behavior of the Blue-bellied Roller, *Coracias cyanogaster*: The Consequences of Crowding or Concentration, by Martin Moynihan. Auk **108**(2): 457.

Museum Curatorial Experience:

Curator, Ornithology and Mammalogy, California Academy of Sciences, 2003 to present.

Organized and co-led ornithological collecting trips to Purari River, PNG, May 2002.

Organized and co-taught museum biology course, August 2001, University of Papua New Guinea

Ornithological collection technician, North Carolina Museum of Natural History, 1988.

Ornithological collection technician, Cincinnati Museum of Natural History, 1988 (volunteer).

Teaching Experience:

Vertebrate Natural History, UC Berkeley, Co-taught IB104 with Jim McGuire and Bill Lidicker, Spring 2004. Two lectures + one lab + one field trip per week.

Guest lecture – species and management unit concepts, Smithsonian Conservation Biology Course, Conservation Research Center, Front Royal, Spring 2003.

Museum Biology Training Workshop, organized and taught one-week course at the University of PNG in collaboration with the PNG National Museum and Smithsonian Institution, August 2001.

Wildlife Conservation Biology and Management, a 2-week field course for university students and conservation professionals, Varirata National Park, Papua New Guinea, July and August 2001.

Mentored a Friends of the National Zoo intern for two months, Summer 2001.

Radio telemetry, field course for 3rd and 4th-year university students and wildlife managers, University of Papua New Guinea and Smithsonian Institution, Varirata National Park, PNG, Sept. 2000.

Mentored high school student, Thomas Jefferson High School (Alexandria, VA) Mentorship Program, 1998-99, Mentored a student in 6-month nuclear-gene phylogenetics project.

Teaching assistantships held for the following classes:

THE UNIVERSITY OF CHICAGO

Environmental Ecology, 1996 (Instructor Mathew Leibold).
Field Ecology (lab course), 1993 (Instructor Stephen Pruett-Jones).
Evolution in Human Environments (lab course), 1992 (Instructor Stevan Arnold).
Global Ecology, 1991 (Instructor Monty Lloyd).

CLEMSON UNIVERSITY:

Ornithology (lab course), 1990 (Instructor Sid Gauthreaux Jr).
Ecology (lab course), 1990 (Instructor David Tonkyn).
Animal Behavior (lab course), 1989 (Instructor Sid Gauthreaux Jr).

Introductory Biology lab, 1988, 1989, 1990.Screened, edited, and recommended films for biology video-library, 1989, Clemson University.

Instructor and coordinator, Outdoor Education Program, 1984-1987, Vanderbilt University.

Invited Lectures:

2005 Museum of Vertebrate Zoology, UC Berkeley
2005 Department of Integrative Biology, UC Berkeley
2004 Golden Gate Audubon Society, San Francisco, CA
2004 CAS Science Council; trustees meeting, guest presentation.
2003 San Francisco State University, Biology Department
2003 Smithsonian Bird Identification Course, Front Royal, VA
2003 Smithsonian Conservation Research Center, Explorer's Lecture Series
2003 Telluride Pinhead Institute, Bird Identification lecture, Telluride, CO
2002 California Academy of Sciences, San Francisco, CA

2002 Pinhead Institute, Telluride Colorado
2002 University of California, Berkeley, Museum of Vertebrate Zoology and Integrative Biology
2002 University of Kansas, Ornithology Group and Natural History Museum
2002 University of Texas, Arlington, Biology Department
2001 Smithsonian Vertebrate Biology Group, National Museum of Natural History
2001 University of Connecticut, Storrs CT, Biology Department
2001 Philadelphia Academy of Natural Sciences, Philadelphia, PA
2001 California State University, Los Angeles, Biology Department
2001 Department of Biology, Gettsyburg College, Gettysburg, PA
1999 Sigma Xi Induction Ceremony, Washington, DC chapter
1999 NOAHS (New Initiatives in Animal Health Sciences) Group, Front Royal, VA
1999 National Zoological Park, Public Lecture Series
1998 University of Maryland; Behavior, Ecology, and Evolutionary Biology Sciences
1998 Papua New Guinea National Museum and Art Gallery
1998 University of Papua New Guinea, Biology Department
1998 Conservation Research Center, National Zoo (Front Royal Virginia)
1998 Tracy Aviary, Distinguished lecture series, Salt Lake City
1998 University of Utah, Biology Department
1998 St. Mary's College of Maryland, Division of Science and Mathematics
1998 Villanova University, Department of Biological Sciences
1998 National Zoological Park, Division of Zoological Research
1996 Laboratory of Bio-organic Chemistry, National Institutes of Health
1996 Conservation International, Washington, DC office
1994 Cenderawasih University, Biology Department, Jayapura, Irian Jaya, Indonesia
1992 University of Chicago, Evolutionary Morphology Series; Natural History Seminar Series
1990 Cornell University, Behavioral Ecology Group
1988 Clemson University, Biology Department, South Carolina

Meeting or Symposium Presentations:

2005 Genetics and Taxonomy of Endangered Species, organized for the Department of the Interior, with Sustainable Ecosystems Institute, May 23-24, Washington, DC.

2004 Moving Mountains Symposium, Organizer and MC, Telluride MOUNTAINFILM Festival.

2003 Chemical Signals in Vertebrates, Corvalis, OR – Plenary Speaker.

2002 North American Ornithological Society meetings, New Orleans, LA.

2001 Society for the Study of Evolution, annual meeting, Knoxville, TN.

2000 Southern Hemisphere Ornithological Congress, Brisbane, Australia.

1999 American Ornithologists' Union Meeting, Cornell University, NY.

1998 Society for the Study of Evolution, annual meeting, Vancouver, BC.

1998 North American Ornithologists' Congress (meeting of AOU, WOS, AFO, and COS), St. Louis.

1994 International Ornithological Congress, chemical defense symposium convener, Vienna, Austria.

1993 Cooper Ornithological Society, Centennial Meeting, Sacramento, CA.

Public lectures/Outreach

2005 California Academy of Sciences, Bioforum for High School Teachers.

2005 High Country Passage trip to Greenland, lecturer.

2005 Bear Creek Symposium, Telluride Pinhead Institute, Colorado.

2005 Marin County Audubon Society, California UC Berkeley Darwin Day Lecture.

2004 California Academy of Sciences, Members Lecture, CA.

2003 Smithsonian Conservation Research Center, public evening lecture.

2002 Telluride Pinhead lecture on basic ornithology.

2002 Wildlife Conservation Society, PNG, Lecture.

2002 Department of Environment and Conservation, Papua New Guinea.

Scientific Society Memberships:

American Association for the Advancement of Science (AAAS), American Ornithologists' Union (AOU), Association of Field Ornithologists (AFO), Cooper Ornithological Society (COS), Society for the Study of Evolution (SSE), Society for Systematic Biologists (SSB).

Students Advised

Daniel Levitis, UC Berkeley, PhD candidate (present, Major Advisor).
Becky Williams, UC Berkeley, PhD candidate (present, committee member).

References:

Robert Fleischer, Molecular Genetics Laboratory, National Zoological Park, 3001 Connecticut Ave. N.W., Washington, D.C. 20008, phone (202) 633-4190, fax (202) 673-4648, Fleischer.Robert@NMNH.SI.EDU, (post-doctoral advisor).

Scott Derrickson, Associate Director, Conservation Research Center, National Zoological Park, 1500 Remount Road, Front Royal, VA 22630, phone (540) 635-6510, fax (540) 635-6551, sderrickson@crc.si.edu (Smithsonian Scholarly Studies collaborator).

Stephen Pruett-Jones, Department of Ecology and Evolution, The University of Chicago, 1101 East 57th Street, Chicago, IL 60637, phone (773) 702-3115, fax 773-702-9740, aspj@midway.uchicago.edu (Ph.D. Advisor).

John W. Daly, Laboratory of Bio-organic Chemistry, National Institutes of Health, NIDDK, Building 8, Room 1A-15, Bethesda, MD 20892-0820, phone (301) 496-4024, johnd@bdg8.niddk.nih.gov.

Stevan Arnold, Department of Zoology, Oregon State University, Corvallis, OR 97331, phone (541) 737-3705, fax (541) 737-0501, arnolds@bcc.orst.edu.

Michael Wade, Department of Biology, Indiana University, Jordan Hall, Bloomington, Indiana 47405, phone (812) 856-4680, fax (812) 855-6705, mjwade@bio.indiana.edu.

SCOTT J. STEPPAN

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PROFESSIONAL EXPERIENCE

2004-present	Associate Professor, Florida State University
1998-2004	Assistant Professor, Florida State University
1996-98	Smithsonian Visiting Scientist. (M. J. Braun, R. S. Hoffmann PIs).
1995-96	Smithsonian Fellow
1990-95	Teaching Assistant, University of Chicago.
1986-88	Teaching Assistant, Physical geography labs, San Diego State University.
1986	Research Assistant II. San Diego State University.
1984, 85	Program Assistant II, Coordinator of activities and public education for Earthquake Awareness Day. Lawrence Hall of Science, University of California, Berkeley.
1983	Research Assistant. UCLA/VA Hospital Wadsworth.

EDUCATION

Ph.D.	1995	University of Chicago. Evolutionary Biology. Dissertation title: Phylogenetic relationships of the phyllotine rodents (Sigmodontinae) and the evolution of phenotypic patterns of covariation in *Phyllotis.* (B.D. Patterson advisor).
M.S.	1992	University of Chicago. Evolutionary Biology.
M.A.	1988	San Diego State University. Geography. Thesis title: Geographic variation of flower morphological traits and boundary phenomenon in subspecies of *Lotus scoparius*.
B.A.	1983	University of California, Berkeley. Biology and Geography (with Academic Distinction).

TEACHING EXPERIENCE

FSU

2005	Evolution
	Macroevolution
2004	Evolution (required for Biology seniors)
	Systematics (upper division elective)
	Macroevolution (graduate tutorial)
2003	Evolution (required for Biology seniors)
	Macroevolution (graduate tutorial)
2002	Systematics (upper division elective)
	Macroevolution (graduate tutorial)
2001	Evolution (required for Biology seniors)
	Macroevolution (graduate tutorial)
	Speciation (graduate seminar)

2000	Systematics (upper division elective)
	Systematics (graduate tutorial)
	Evolution (required for Biology seniors)
	Advanced Systematics (graduate seminar)
	Macroevolution (graduate tutorial)
	Vertebrate Evolution (graduate tutorial)
1999	Systematics and Macroevolution (graduate tutorial)
	Evolution (required for Biology seniors)
	Biological Frontiers (guest lecture)

University of Chicago

1995	Diversity of Life Through Time (TA under J. Flynn and G. Mueller)
	Biogeography (Lab TA under B. Patterson)
1993	Mammalian Evolution (Lab TA under J. Flynn)
1992	Biogeography (TA under L. Heaney)
1991	Systematics (Lab TA under B. Chernoff)
	Biogeography (TA under B. Patterson)
1990	Introduction to Research at Field Museum (TA)

San Diego State University

1986-88	Physical Geography Laboratory (8 semester-classes)

FELLOWSHIPS AND AWARDS

2000	Nominated for University Teaching Award (student nomination)
1995	Smithsonian Postdoctoral Fellowship. (M.D. Carleton, R. Thorington advisors).
1995	Ernst Mayr Award for best student paper, Society of Systematic Biologists.
1995	Outstanding Student Presentation, American Society of Mammalogists.
1992-93	Field Museum of Natural History, Rowley Graduate Fellowship.
1989-91	Searle Fellowship, University of Chicago.
1983	American Heart Association Student Internship.
1980-83	Alumni Scholarship, University of California, Berkeley.

GRANTS

2005	"Collaborative Research: Muroid Rodent Phylogenetics Using Multiple Nuclear Genes" NSF, to Scott J. Steppan and Ronald M. Adkins ($400,000)
2005	"Phylogeny of the aeluroid Carnivora: a combined evidence approach" NSF DIG (Jill Holliday) DEB-0508848 ($7,600).
2004	NSF REU Supplement to "Phylogeny, Andean Biogeography, and Multivariate Evolution in Phyllotine Rodents" ($6,650)
2002	"Murid Rodent Phylogenetics Using Multiple Nuclear Genes" NSF DEB-0238837, to Ronald M. Adkins (PI) and Scott J. Steppan (Co-PI), ($100,000)
2001	"Phylogeny, Andean biogeography, and multivariate evolution in *Phyllotis*" NSF DEB-0108422 ($404,453)
	FSU Travel Grant to present paper at ASM Meetings ($600)
2000	FSU First Year Assistant Professor Summer Salary Award ($10,000)
	FSU Travel Grant to present paper at Evolution Meetings ($600)
1997	"Molecular phylogenetics of the squirrels and their relatives." Smithsonian Institution Scholarly Studies Program. Co-PI with Robert S. Hoffmann (PI). ($69,000).
1995	Hinds Fund research grant extension, Committee on Evolutionary Biology, University of Chicago ($700).
1993	Nierman Foundation Award ($1000).

1993 Center for Latin American Studies Travel Grant ($1377).
1993 Sigma Xi Grants-in-Aid of Research ($600).
1993 American Museum of Natural History, Collection Study Grant.
1992 American Society of Mammalogy, Grant-In-Aid of Research ($1000).
1992 Hinds Fund research grant, Committee on Evolutionary Biology, University of Chicago ($1500).
1988 California Native Plant Society Research Grant ($300).
1987 Teaching Micro-Grant for curriculum development, San Diego State University.

GRADUATE STUDENTS SUPERVISED

STUDENT ADVISOR

Jenner Banbury, 2003-2005 (Ph.D. advisor, withdrew 2005)
James Albright, M.S. Dec. 2004 advisor
Brian Storz, M.S. June 2003 co-advisor, (now Ph.D. student at FSU)
Jim Cooper, M.S. Dec. 2000. advisor, (now Ph.D. student at Univ. of Chicago)

1999-present Jill Holliday, (Ph.D. advisor)
2005-present Ken Wray (Ph.D. advisor)

COMMITTEE MEMBER

Vanessa Jackson, M.S. June 2004 (D. Swofford, chair)
Andy Feldman, Ph.D. April 2004 (A. Arnold, Geology, chair, now Asst. Prof., New Mexico Highlands University)
Erin Creech, M.S. April 2003 (G. Erickson, chair)
Sarah Boyce, M.S. Dec. 2001 (L. Abele, chair, now Senior Technician, Woods Hole)
Jamie Kneitel, Ph.D. Aug. 2002. (T. Miller chair, now post-doc, Wash. U.)

2006-present Allison Bauer, Ph.D. (B. Inouye, chair)
2002-present Glen Golden, Ph.D. (T. Houpt, chair)
2002-present Jean Burns, Ph.D. (T. Miller, chair)
2003-present Albert Prieto-Marquez, Ph.D. (G. Erickson, chair)
2003-present Tim Swain, Ph.D. (J. Wulff chair)
1999-2002 Greg Farley, Ph.D. (B. Herrnkind, R. Mariscal chairs)
1997 Warren Young, Smithsonian Minority Intern

PUBLICATIONS

In press **Steppan, S. J.,** Ramirez, O., Banbury, J., Huchon, D., Pacheco, V., Walker, L, and Spotorno, A.O.. A molecular reappraisal of the systematics of the leaf-eared mice *Phyllotis* and their relatives. For Oliver Pearson Festschrift. (Kelt, D., Lessa, E., Patton, J. L., and Salazar-Bravo, J. eds.)

In press **Steppan, S.J.** and Ramirez-Baca, O. Genus *Phyllotis*. In South American Mammals. J. L. Patton ed.

2005 **Steppan, S. J.,** Adkins, R. M., Spinks, P. Q., and Hale, C. Multigene phylogeny of the Old World mice Murinae reveals distinct geographic lineages and the declining utility of mitochondrial genes compared to nuclear genes. *Molecular Phylogenetics and Evolution*. 37:370-388.

2005 **Steppan, S. J.**, Seeing the Forest for the Trees. Book review of "Assembling the Tree of Life." *Science*. 307:677-678.

2004 **Steppan, S. J.,** Adkins, R., and Anderson, J. Phylogeny and divergence date estimates of murid rodents based on multiple nuclear genes. *Systematic Biology*. 53(4):533-553.

2004 Holliday, J. A. and **Steppan, S. J.** Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity. *Paleobiology*. 30(1):108-128.

2004 **Steppan, S. J.** Phylogenetic comparative analysis of multivariate data. In Phenotypic Integration. (eds., Piggliuci, M and Preston, K. A.). Oxford Univ. Press.

2004 **Steppan, S. J.**, Storz, B. L., and Hoffmann, R. S. Nuclear DNA phylogeny of the squirrels (Mammalia: Rodentia) and the evolution of arboreality from c-myc and RAG1. *Molecular Phylogenetics and Evolution*. 30:703-719.

2003 **Steppan, S. J.**, Zawadzki, C., and Heaney, L. R. Molecular phylogeny of the endemic Philippine rodent *Apomys* (Muridae) and the dynamics of diversification in an oceanic archipelago. *Biological Journal of the Linnean Society*. 80:699-715

2002 **Steppan, S.J.**, Houle, D., and Phillips, P.C. Comparative quantitative genetics: evolution of the **G** matrix. *Trends in Ecology and Evolution*. 17:320-327.

2002 Kuch, M., Rohland, N., Betancourt, J., Lattore, C., **Steppan, S.J**., and Poinar, H.N. Molecular Analysis of a 11,700-yr old rodent midden from the Atacama Desert Chile. *Molecular Ecology.* 11:913-924.

2000 **Steppan, S.J.** Flexural stiffness patterns of butterfly wings. *Journal of Research on the Lepidoptera*. 35:61-77.

2000 **Steppan, S.J.** and Sullivan, J. The emerging statistical perspective in systematics and the status of *Andalgalomys* (Rodentia: Sigmodontinae): a comment on Mares and Braun. *Journal of Mammalogy*. 81(1):260-270.

2000 Ortiz, P.E., Pardiñas, U.F.J. and **Steppan, S.J.** A new extinct phyllotine (Rodentia: Muridae) from the Pleistocene of Argentina and a consideration of the phylogenetic relationships of the "*Reithrodon* group." *Journal of Mammalogy*. 81(1):37-51.

1999 **Steppan, S.J.**, Akhverdyan, M. R., Lyapunova, E.A., Fraser, D.G., Vorontsov, N.N., Hoffmann, R.S., and Braun, M.J. Molecular phylogeny of the marmots (Rodentia: Sciuridae): tests of evolutionary and biogeographic hypotheses. *Systematic Biology*.48(4):715-734.

1998 **Steppan, S. J.** and U. Pardiñas. Two new fossil murids from the Pleistocene of Argentina: phylogeny and paleoecology. *Journal of Vertebrate Paleontology*. 18(3):640-649.

1998 **Steppan, S.J.** Phylogenetic relationships and species limits within *Phyllotis* (Rodentia: Sigmodontinae): concordance between mtDNA sequence and morphology. *Journal of Mammalogy*. 79(2):573-593.

1997 **Steppan, S.J.** Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from matrix correlation and Common Principal Component analyses. *Evolution*. 51(2): 571-586.

1997 **Steppan, S.J.** Phylogenetic analysis of phenotypic covariance structure. II. Reconstructing matrix evolution. *Evolution*. 51(2): 587-594.

1996 **Steppan, S.J.** A new species of *Holochilus* (Rodentia: Sigmodontinae) from the middle Pleistocene of Bolivia and its phylogenetic significance. *Journal of Vertebrate Paleontology*. 16(3):522-530.

1995 **Steppan, S.J.** Revision of the tribe Phyllotini (Rodentia: Sigmodontinae) with a phylogenetic hypothesis for the Sigmodontinae. *Fieldiana: Zoology*. n.s. 80:1-112.

1993 **Steppan, S.J.** Phylogenetic relationships among the Phyllotini (Rodentia: Sigmodontinae) using morphological characters. *Journal of Mammalian Evolution.* 1(3):187-213.

1991 **Steppan, S.J.** Geographic distribution of flower morphological traits in subspecies of *Lotus scoparius*. *Journal of Biogeography.* 18:321-331.

ELECTRONIC PUBLICATIONS

In development. **Steppan, S.J.** Order Rodentia, Superfamily Muroidae, Family Sciuridae, Subfamily Sigmodontinae, Tribe Phyllotini, *Phyllotis*, and other pages. *in* Tree of Life: an integrated internet project [online] (D. Maddison and W. Maddison, eds.). Available from World Wide Web: http://tolweb.org/tree?group=Rodentia&contgroup=Eutheria, http://tolweb.org/tree?group=Sigmodontinae&contgroup=Muroidaea, http://tolweb.org/tree?group=Muridae&contgroup=Rodentia http://tolweb.org/tree?group=Sciuridae&contgroup=Rodentia http://tolweb.org/tree?group=Phyllotini&contgroup=Sigmodontinae

PUBLISHED ABSTRACTS

2004 **Steppan, S.J.**, Adkins, R.M., Anderson, J., Hale, C. and Spinks, P.Q. Phylogeny and divergence-dates in muroid rodents based on multiple nuclear genes: comparisons and contrasts to morphological hypotheses. *Journal of Vertebrate Zoology*. 24 (3):117A.

1998 Bond, M., Pardiñas, U. F. J., and **Steppan, S**. Los cricetidos (Rodentia: Cricetidae) más antiguos de la Argentina. *Acta geol. Lill.* 18:155.

1996 **Steppan, S.J.** Phylogenetic relationships of the phyllotine rodents (Sigmodontinae) and the evolution of phenotypic patterns of covariation in *Phyllotis.* (Dissertation Abstract). *Mastozoología Neotropical* 3(1):125.

MANUSCRIPTS IN REVIEW

Adkins, R.M. and **Steppan, S.J**. A molecular timescale of Old World murine evolution. *Molecular Biology and Evolution*.

Albright, J.S. V. Pacheco, U. Pardiñas, O. Ramirez, A. Spotorno, L. Walker and **Steppan, S.J**. Phylogeography of the sigmodontine rodent, *Phyllotis xanthopygus*, and a test of the sensitivity of nested clade analysis to alternative distances. *Molecular Ecology*.

MANUSCRIPTS IN PREPARATION (late draft manuscripts)

Steppan, S. J., Adkins, R. M., Burns, J. H., Zawadzki, C., and Sierra, M. Rapid diversification of the South American sigmodontine mice as revealed by multiple nuclear and mitochondrial genes. For *Evolution*.

Cooper, W. J., and **Steppan, S. J**. Evolution of marsupial forelimbs is constrained by their reproductive strategy. For *Journal of Evolutionary Biology*.

PRESENTED TALKS

INVITED SEMINARS/SYMPOSIA

2005 "Diversification and global biogeography of the most successful mammals, the muroid rodents." University of Florida, Dept. of Zoology.

2004 "Phylogenetic comparative analysis of multivariate data as exemplified by comparative quantitative genetics and the evolution of the **G**-matrix." International Congress of Vertebrate Morphology.

2002 "Evolution of the **G** matrix." Universidad Peruana Cayetano Heredia, Peru.

1998 "'Punxsatawney Phil, this is your life!' plus the evolution of covariance structure in sigmodontines." Carnegie Museum of Natural History.

1997 "Phylogenies for hypothesis testing and the evolution of covariance structure in rodents." Florida State University.

1997 "Systematics, quantitative genetics, and the comparative method in phyllotine mice: the evolution of covariance matrices." Utah State University.

1996 "Phylogenetic analysis of the evolution of phenotypic covariance structure in *Phyllotis*: can quantitative genetics explain macroevolution?" American Museum of Natural History.

1996 "Phylogenetics of the phyllotine mice and an extension of the comparative method: the evolution of covariance matrices." University of Massachusetts, Amherst.

1995 "The evolution of the sigmodontine rodents: how much do we know?" Invited symposium, X[a] Jornadas Argentinas de Mastozoología (SAREM).

1995 "Evolution of the South American mice: nested phylogenies, the evolution of covariance structure, and their role in the Great American Interchange." University of Chicago.

1993 "Evolutionary relationships among the sigmodontine mice and rats of South America." Universidad de Católica, Santiago, Chile.

1992 "Darwin's leaf-eared mice: phylogenetic relationships of the phyllotines." Field Museum of Natural History.

CONTRIBUTED PAPERS

2005 "Biogeographic History of Diversification by Murid Rodents in the Philippine Islands" (Heaney, L.R., Balete, D.S., Jansa, S., Rickhart, E.A., Steppan, S.J.) 9th International Mammalogy Congress, Japan.

2005 "The geography of repeated rapid radiations in both New and Old World clades of mice and rats." (Steppan, S.J., Adkins, R.M., Burns, J.H., Hale, C., Spinks, P.Q., and Zawadzki, C.) Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists

2005 "A molecular timescale of Old World murine biogeography." (Adkins, R.M., and Steppan, S.J.) Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists

2004 "Phylogeny and divergence-dates in muroid rodents based on multiple nuclear genes: comparisons and contrasts to morphological hypotheses" (Steppan, S.J., Adkins, R.M., Anderson, J., Hale, C. and Spinks, P.Q.) Annual Meetings of the Society of Vertebrate Zoology.

2003 "Biogeography and Diversification in Philippine Murids of the Genus *Apomys*" (Heaney, L.R., Steppan, S.J. and Zawadzki, C.) Wildlife Conservation Society, Philippines.

2003 "Biogeography and Diversification in Philippine Murids of the Genus *Apomys*." (Heaney, L.R., Steppan, S.J. and Zawadzki, C.). Annual Meetings of the American Society of Mammalogists.

2002 "Andean phylogeography in the *Phyllotis darwini* species group (leaf-eared mice) and identification of an 11,700 year old packrat midden." Steppan, S.J., Kuch, M., Lattore, C., Spotorno, A., and Poinar, H.) Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists

2002 "Evolution of hypercarnivory: the effect of specialization on character change." (Holliday, J. and Steppan, SJ) Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists

2002 "Robust phylogeny of the muroid rodents using multiple nuclear genes." (Steppan, S.J., Adkins, R, Anderson, J.) Annual Meetings of the American Society of Mammalogists

2001 "Order out of chaos: Multigene phylogeny of muroid rodents." (Steppan, S.J., Adkins, R, Anderson, J.) 8th International Theriological Congress, South Africa.

2001 "Nuclear DNA phylogeny of the squirrels using RAG-1 and c-*myc*." (Steppan, S.J., Storz, B.L., and Hoffmann, R.S.) 8th International Theriological Congress, South Africa

2001 "Resolution of an intractable problem: Multigene phylogeny of muroid rodents." (Adkins, R, Anderson, J., and Steppan, S.J.) Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists.

2001 "Nuclear DNA phylogeny of the squirrels using RAG-1 and c-*myc*." (Steppan, S.J., Storz, B.L., and Hoffmann, R.S.) Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists

2001 "A molecular phylogeny of the endemic Philippine rodent *Apomys* and its biogeographic implications." (Steppan, S.J., Heaney, L.R., and Zawadski, C.) Annual Meetings of the American Society of Mammalogists.

2001 "Hypercarnivory: an evolutionary dead end? The effect of specialization on subsequent character change." (Holliday, J. and Steppan, SJ. Poster) Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists

2001 "Comparative molecular evolution: What do molecules tell us about the evolution and life history of sciurognath rodents " Storz, B.L. and Steppan, S.J. 9th Annual Florida Ecological and Evolutionary Symposium.

1999 "Phylogenetic utility of the nuclear c-*myc* gene applied to the ratite birds." Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists

1998 "Molecular phylogeny of the marmots (Rodentia: Sciuridae): tests of evolutionary and biogeographic hypotheses." (Steppan, S.J., Hakverdyan, M, Lyapunova, E., and Hoffmann, R.S.) Annual Meetings of the American Society of Mammalogists

1997 "Molecular phylogeny of the marmots (Rodentia: Sciuridae) and its significance for Holarctic and amphiberingian biogeography." (Steppan, S.J., Hakhverdyan, M, Lyapunova, E., and Braun, M.J.). Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists.

1996 "Evolutionary constraints and the vertebral column in rodents." Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists.

1996 "The comparative method extended to multivariate data: the evolution of phenotypic covariances in *Phyllotis*." Annual Meetings of the American Society of Mammalogists.

1995 "Phylogenetic analysis of the evolution of phenotypic covariance matrices: from populations to genus." Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists. (Ernst Mayr Award for best student paper).

1995 "Species limits and phylogenetic relationships within *Phyllotis* (Muridae: Sigmodontinae): a comparison of weighting methods for DNA sequence data." Annual Meetings of the American Society of Mammalogists (received outstanding student presentation evaluation).

1995 "Los cricetidos (Rodentia: Cricetidae) mas antiguos de la Argentina." (The oldest cricetids [Rodentia: Cricetidae] from Argentina.) (Bond, M., Pardiñas, U. F. J., y Steppan, S.). XIª Jornadas Argentinas de Paleontologia de Vertebrados.

1994 "Is covariance structure conserved across the evolutionary hierarchy of a species group? Nested research design and preliminary results." Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists.

1993 "A preliminary assessment of phylogenetic relationships among the South American sigmodontine rodents." Annual Meetings of the American Society of Mammalogists.

1992 "Phylogenetic relationships among the Phyllotini (Rodentia: Sigmodontinae) using morphological characters." Annual Meetings of the American Society of Mammalogists.

1988 "*Lotus scoparius* ssp. *scoparius* and *Lotus scoparius* ssp. *brevialatus*: Geographic distribution of flower morphological traits and boundary phenomenon." Annual Meetings of the Association of Pacific Coast Geographers.

1988 "The role of photographic composition in landscape preference studies: a multidimensional approach." EDRA 19, Environmental Design Research Association.

POSTERS

2004 "Of mice and mountains: Nested Clade Analysis assumptions and the Andean leaf-eared mouse. Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists (Albright, J.S. V. Pacheco, U. Pardiñas, O. Ramirez, A. Spotorno, L. Walker and Steppan, S.J)

2003 "Alternative Andean speciation hypotheses and a comparison of nuclear and mitochondrial genes in resolving the phylogeography of *Phyllotis*, a South American rodent. Annual Meetings of the Society for the Study of Evolution/Society of Systematic Biologists (J. Albright, D. Huchon, O. Ramirez, A. Spotorno, S. Steppan, L. Walker)

SOCIETY MEMBERSHIP

American Society of Mammalogists
International Society of Vertebrate Morphologists
Society for the Study of Evolution
Society of Systematic Biologists

SOCIETY SERVICE

2006-present Associate Editor, *Evolution*
2004-present Council Member, Society of Systematic Biologists
2004-present *Systematic Biology* Editorial Board
2003-2004 Society of Systematic Biologists, President's Long Range Planning Committee
2000-present American Society of Mammalogists, Grants-in-Aid Committee

JOURNALS AND GRANTS REVIEWED

Acta Theriologica
Ameghiniana
American Journal of Physical Anthropology
American Museum Novitates
American Naturalist
Belgian Journal of Zoology
Brain, Behavior, and Evolution
Canadian Journal of Zoology
Cladistics
Entomological Society of America
Evolution
Evolution and Development
Fieldiana: Zoology
Genetica

Journal of Biogeography
Journal of Mammalian Evolution
Journal of Mammalogy
Journal of Zoological Systematics and Evolutionary Research
Mammalia
Mastozoología Neotropical
Molecular Biology and Evolution
Molecular Phylogenetics and Evolution
Systematic Biology
Trends in Ecology and Evolution
Zoologica Scripta
Harvard Univ. Press
National Science Foundation, Systematic Biology
National Science Foundation, Population Biology
National Agency for the Promotion of Science & Technology of Argentina
U.S. Civilian Research and Development Foundation
United States-Israel Binational Science Foundation
FONDECYT, Chile