Does Taxonomy Matter in Conservation Biology?

Preble's Meadow Jumping Mouse Says Yes

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Table of Contents

Overview

The U. S. Endangered Species Act (ESA) allows for the listing of any *species*, *subspecies*, or *distinct population segment (DPS)* of any vertebrate fish or wildlife species (USFWS and NMFS 1996). Species and subspecies constitute formal taxonomic categories but, a DPS does not. Furthermore, there is still substantial debate about what constitutes a species (e.g. Mayr 1963; Cracraft 1983; Mayden 1997; Marris 2007) or subspecies (e.g. Haig et al. 2006; Cronin 2007). Given that for vertebrates formal taxonomic recognition is not required for protection under the ESA and the uncertainty regarding what a species or subspecies represents does this mean that taxonomy has little value to conservation biology. I think the case of Preble's meadow jumping mouse *Zapus hudsonius preblei* argues that taxonomy does have conservation value.

Background

Preble's meadow jumping mouse is one of 12 recognized subspecies of meadow jumping mice. As a species, meadow jumping mice occupy about 50% of North America but, Preble's meadow jumping mouse is native only to the eastern foothills of the Front Range in Colorado and Wyoming (Figure 1).

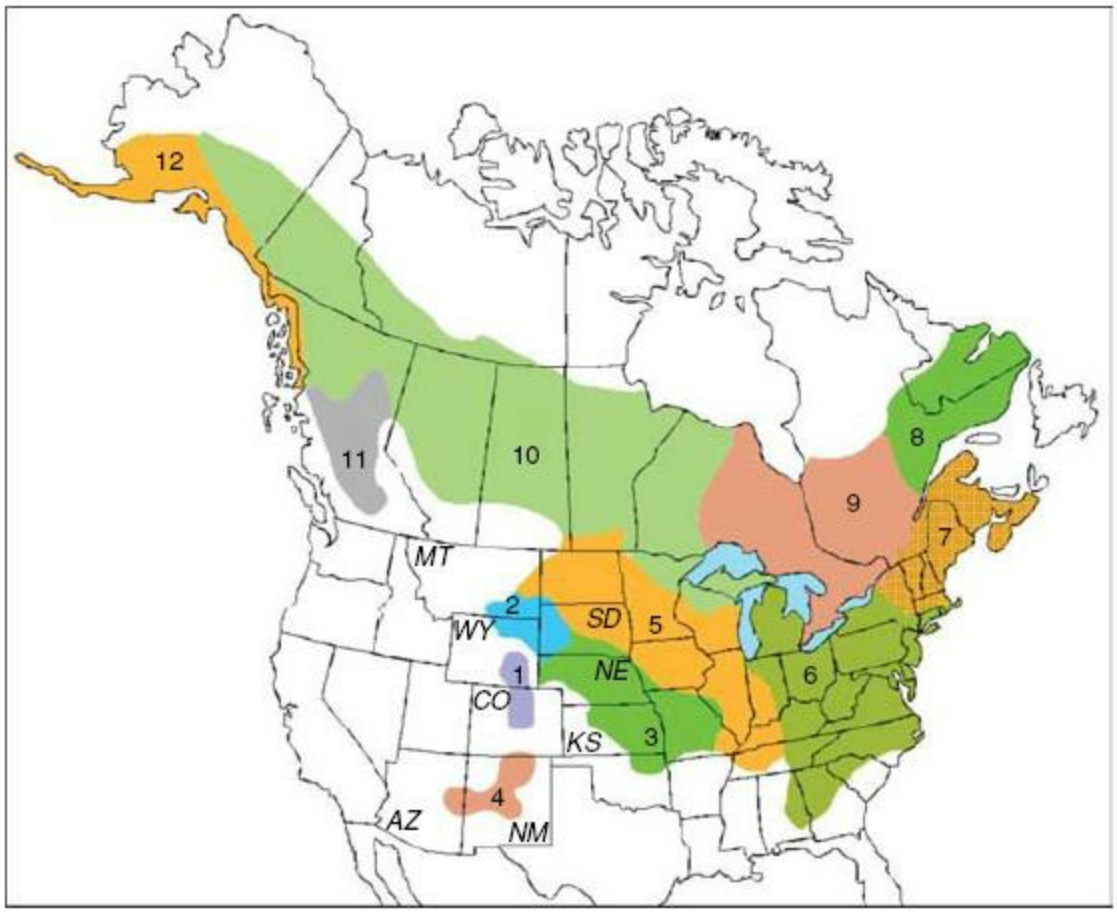
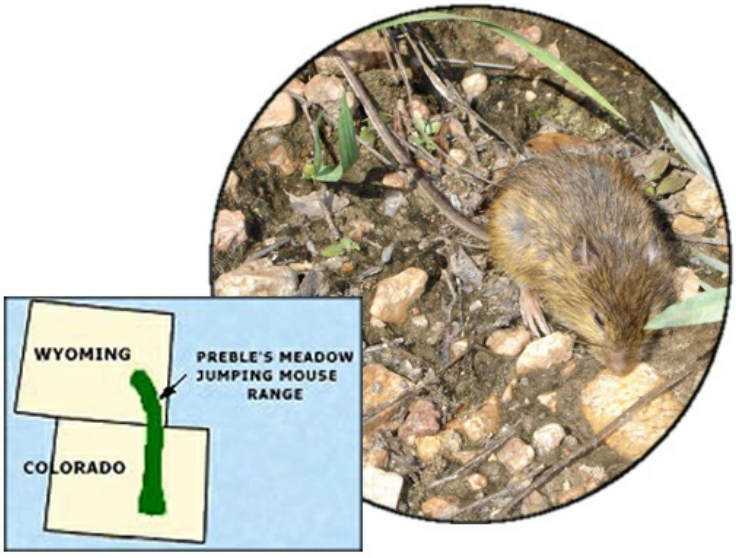


Figure 1. Distribution of 12 subspecies of meadow jumping mice Zapus hudsonius in North America. Subspecies: 1=preblei, 2=campestris, 3=pallidus, 4=luteus, 5=intermedius, 6=americanus, 7=acadicus, 8=ladas, 9=canadensis, 10=hudsonius, 11=tenellus, 12=alascensis. From Ramey II et al. (2005).

It was first recognized as a subspecies by Krutzsch (1954) using a combination of six skull measurements and pelage coloration. Historically they were continuously distributed along the Front Range usually being found associated with riparian and adjacent, drier upland habitat (Ramey II et al. 2005; King et al. 2006). They now exist as isolated northern and southern groups primarily because of the Denver metropolitan area (King et al. 2006).



In 1998, Preble's meadow jumping mouse was listed as a threatened species under the ESA (USFWS 1998). The major factor for listing was considered to be substantial reduction in suitable riparian habitat due to agricultural, residential, and commercial development and associated declines in abundance (USFWS 1998).

The New Data

Ramey II et al. (2005) used nine skull measurements of museum specimens to compare Preble's meadow jumping mouse to the *campestris* and *intermedius* subspecies and sequences of 346 *base pairs* (bp) of *mitochondrial DNA* (mtDNA) and *allele frequencies* from five *microsatellite loci* to compare Preble's meadow jumping mouse to the *campestris, intermedius, pallidus,* and *luteus* subspecies.

Using principle components analysis, they found that Preble's meadow jumping mouse and *campestris* were nearly indistinguishable but, both tended to have significantly larger skulls than *intermedius*. Using the western jumping mouse Z. *princeps* as an *outgroup* to root their *phylogenetic tree*, they found that the mtDNA sequences obtained from Preble's meadow jumping mouse, *campestris, intermedius, pallidus,* and *luteus* were divisible into two well defined *evolutionary lineages* (Figure 2) of which one contained mainly *haplotypes* from Preble's meadow jumping mouse, *intermedius*, and *campestris* and the other mainly haplotypes from *luteus* and *pallidus*. Furthermore, they found that Preble's meadow jumping mouse shared haplotypes in common with *campestris* and that *campestris* and *intermedius* also shared haplotypes (Figure 2).

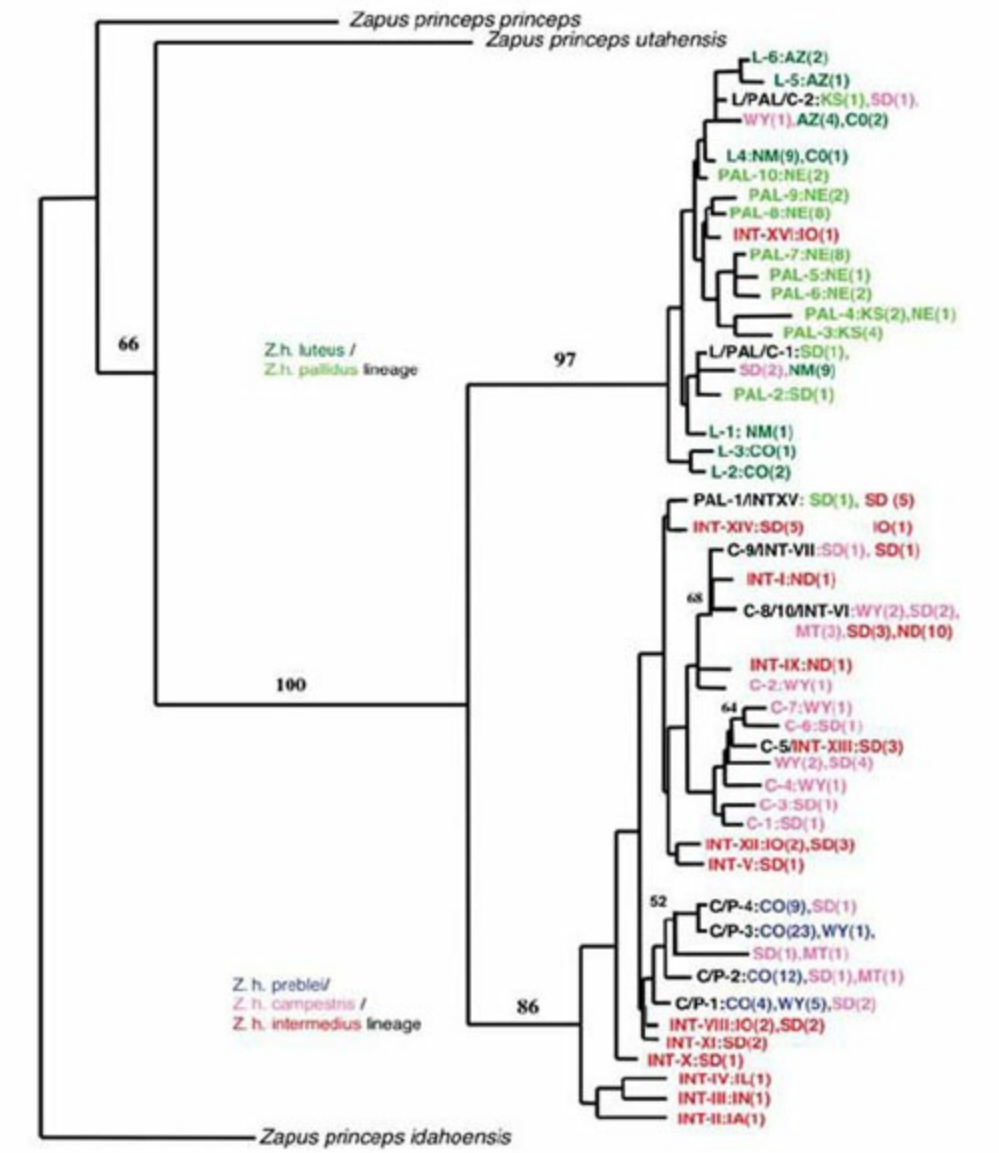


Figure 2. Phylogenetic tree of sequences from 346 bp of mtDNA from Preble's meadow jumping mouse (blue), and the intermedius (red), campestris (pink), luteus (dark green), and pallidus (light green) subspecies. The western jumping mouse Z. princeps was used as an outgroup. For each haplotype, number in parentheses indicates the number of individuals from that subspecies possessing the haplotype. Abbreviations corresponding with haplotypes indicate the state from which the samples were obtained: AZ=Arizona, CO=Colorado, IL=Illinois, IN=Indiana, IO=Iowa, KS=Kansas, MO=Missouri, MT=Montana, ND=North Dakota, NE=Nebraska, NM=New Mexico, SD=South Dakota, and WY=Wyoming. Values on branches represent the confidence that the branch is correct. From Ramey II et al. (2005).

When the total amount of *genetic variation* detected at the microsatellite loci was partitioned into that due to differences among the subspecies and variation within them, differences accounted for 7.5% of the total. When only Preble's meadow jumping mouse and *campestris* were compared, nine percent of the total microsatellite genetic variation was due to differences between them. Finally, although there was no evidence to support this, Ramey II et al. (2005) concluded that there were no adaptive differences between Preble's meadow jumping mouse and adjacent subspecies.

Considering all the data and the purported lack of adaptive differences they concluded that Preble's meadow jumping mouse, *campestris*, and *intermedius* were not distinct subspecies.

Based on the conclusion of Ramey II et al. (2005), the United States Fish and Wildlife Service (USFWS) re-evaluated the status of Preble's meadow jumping mouse under the ESA and proposed it for delisting (USFWS 2005). This prompted a somewhat lively debate in the literature regarding the taxonomic status of the mouse and the appropriateness of implementing conservation measures for it.

The Criticism

Vignieri et al. (2006) strongly criticized the conclusions of Ramey II et al. (2005). They pointed out that of the nine skull characters Ramey II et al. (2005) examined only one was used by Krutzsch (1954) to distinguish the subspecies from *campestris* (1954). Thus, they really did not test the validity of the original morphological description. Furthermore, the only character that Ramey II et al. (2005) analyzed in common with Krutzsch (1954), interorbital breadth, was found by both to be on the average narrower in Preble's meadow jumping mouse than in *campestris*. Overall, therefore, Vignieri et al. (2006) suggested there was no morphological basis to suggest that Preble's meadow jumping mouse and campestris were synonymous.

Ramey II et al. (2005) chose to liberally interpret the lack of data addressing potential ecological differences (i.e. local adaptations) among subspecies to mean such differences did not exist. In contrast, Vignieri et al. (2006) preferred a conservative interpretation. They suggested that since Preble's meadow jumping mouse is separated from all other subspecies by at least 160 km of unsuitable habitat (Figure 1) that they are highly isolated. Preble's meadow jumping mouse and *campestris* also exist in different environments with the former being in a grama-buffalo grass association and the latter in a wheatgrass-needlegrass or a grama-wheatgrass-needlegrass association. Given the lack of *gene flow* and the environmental differences Vignieri et al. (2006) suggested that the existence of local adaptations is likely and, therefore, the lack of direct evidence for this should not be interpreted to mean the two subspecies are synonymous.

The mtDNA *gene tree* (Figure 3) was interpreted by Ramey II et al. (2005) to accurately represent the true evolutionary relationships among the subspecies. Whether or not this is true, however, is questionable (Vignieri et al. 2006). The mtDNA molecule basically represents a single gene and data from only a small 346 bp region were analyzed. The ability of gene trees to accurately reflect the true evolutionary relationships among taxa increases as the number of loci and number of bp used to construct the tree increases. Thus, the tree produced by Ramey II et al.

(2005) was based on minimal data and, therefore, probably should be considered preliminary at best. Furthermore, Ramey II et al. (2005) interpreted the sharing of haplotypes between Preble's meadow jumping mouse and *campestris* to indicate relatively recent gene flow. Another possible interpretation, especially considering the geographic isolation of Preble's meadow jumping mouse, is that this situation simply represents the sharing of an *ancestral polymorphism* between recently diverged taxa. Because of the uncertainty regarding the interpretation of the mtDNA data, Vignieri et al. (2006) suggested they provide no conclusive evidence for synonymy.

Finally, considering the microsatellite data Ramey II et al. (2005) used an ultra conservative criterion for the designation of subspecies; that is, over 50% of the total genetic variation must be attributable to genetic differences between them. This amount of genetic divergence is seldom observed even for comparisons among different species and the value of nine percent for the comparison between Preble's meadow jumping mouse and *campestris* is within the range often observed for comparisons between subspecies of other mammals (Vignieri et al. 2006). Furthermore, considering the amount of genetic diversity detected at the microsatellite loci, even if Preble's meadow jumping mouse and *campestris* were completely divergent (i.e. shared no alleles in common) at most 31% of the total genetic diversity would be due to differences between them. Considering this, therefore, the observed value of nine percent is relatively large. Thus, Vignieri et al. (2006) again argued the data were not sufficient to support the premise of Ramey II et al. (2005) that Preble's meadow jumping mouse and *campestris* were the same subspecies.

The Rebuttal

Ramey II et al. (2006) provided a rebuttal to the criticisms raised by Vignieri et al. (2006). They countered by stating that the assertion of Vignieri et al. (2006) that there was a high probability of local adaptations was speculative and, therefore, had little merit. Personally, I find this argument to be weak as the converse interpretation of Ramey II et al. (2005) that no differences exist is equally as speculative. They criticized Krutzsch's (1954) data set as being weak and theirs as better because they used more characters and multivariate analyses. This, however, does not counter the objection raised by Vignieri et al. (2006) that the data of Ramey II et al. (2005) do not demonstrate that the original description of Preble's meadow jumping mouse was invalid because different sets of characters were used.

Considering the genetic data, Ramey II et al. (2006) simply dismissed the shared ancestral polymorphism scenario proposed by Vignieri et al. (2006) to account for why some haplotypes were found in both Preble's meadow jumping mouse and *campestris*. For the microsatellite data, Ramey II et al. (2006) stated that statistically significant divergence does not necessarily represent biologically significant divergence. Although both of these may be true, it is unknown whether or not they are and with uncertainty it is probably best to err on the conservative side which in this case would not constitute proposing synonymy. Overall, therefore, I found the rebuttal to be quite weak.

Other Challenges

Others also criticized the interpretations of Ramey II et al. (2005). Martin (2006) challenged the conclusion of a lack of local adaptation and suggested that at a minimum the mtDNA and microsatellite data supported the designation of Preble's meadow jumping mouse as a DPS. Thus, indirectly he suggested the data did not warrant delisting of the mouse. Cronin (2007) felt that the data of Ramey II et al. (2005) concerning the subspecific status of Preble's meadow jumping mouse were ambiguous. He suggested that the lack of diagnostic morphological characters and shared haplotypes may support synonymy but, the existence of significant microsatellite divergence and the high degree of isolation enhancing the likelihood of the establishment of local adaptations may not. He concluded that since what constitutes a subspecies is speculative that Preble's meadow jumping mouse may or may not be a subspecies.

More Research

Clearly the arguments in the literature concerning the taxonomic and thus ESA status of Preble's meadow jumping mouse were getting nowhere. Thus, the USFWS in conjunction with others funded an additional genetic comparison of Preble's meadow jumping mouse to other subspecies.

King et al. (2006) sequenced 1,380 base pairs of mtDNA, which included the 346 base pair region sequenced by Ramey II et al. (2005), and obtained allele frequency data from 21 microsatellite loci from collections of Preble's meadow jumping mouse (N=170, 7 locations), *campestris* (N=61, 2 locations), *intermedius* (N=49, 2 locations), *pallidus* (N=48, 2 locations), and *luteus* (N=20, 1 location). They also resequenced mtDNA from 11 *campestris*, 2 *intermedius*, and 2 *pallidus* museum specimens analyzed by Ramey II et al. (2005) that indicated the sharing of haplotypes between subspecies.

Using the microsatellite allele frequencies, they calculated *genetic distances* between all possible pairs of samples and used these to examine the evolutionary relationships among the samples. The resulting tree clearly divided the samples into five distinct clusters corresponding to the five subspecies (Figure 3). Furthermore, when the total amount of genetic variation detected was partitioned into the proportion due to genetic differences among subspecies, genetic differences among collections within subspecies, and genetic variation within collections the former two values were 14.8% and 8.6%, respectively. Overall, these data indicate that at microsatellite loci substantial genetic differences exist among the subspecies and that within subspecies appreciable genetic differences exist among mice collected from different areas. There is more divergence, however, among than within subspecies. Thus, King et al. (2006) suggest these data support the subspecific recognition of these five groups of mice.

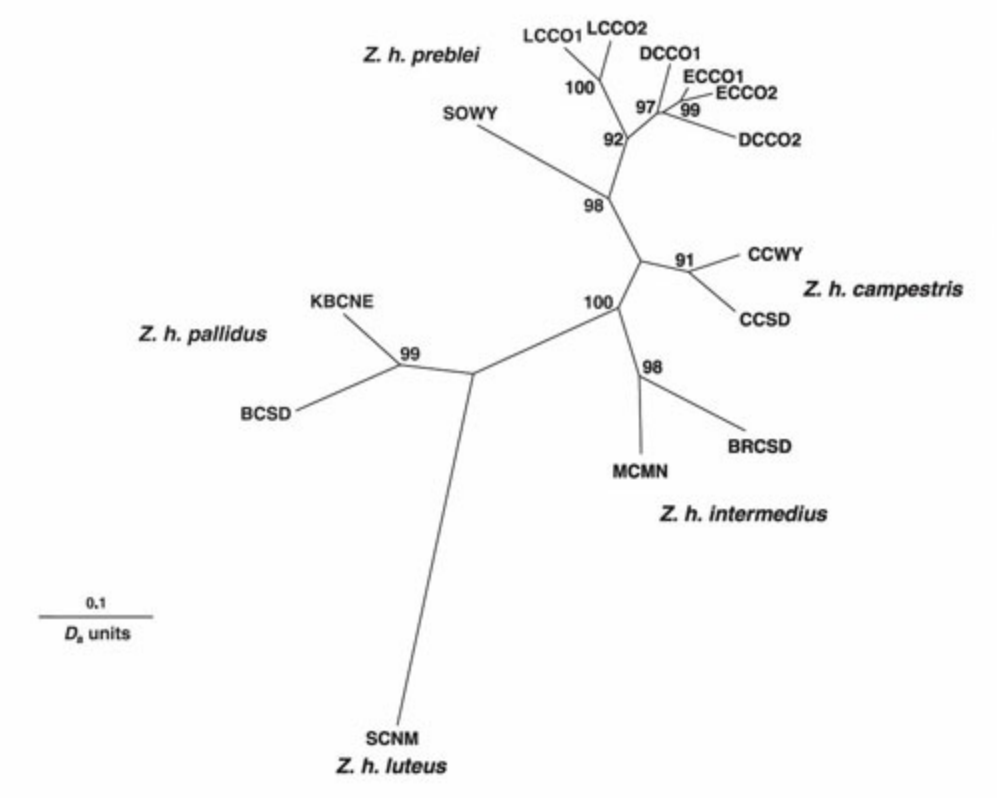


Figure 3. Evolutionary relationships based on allele frequencies at 21 microsatellite loci among five purported subspecies of meadow jumping mice. From King et al. (2006).

Phylogenetic analysis of the mtDNA sequences divided the haplotypes into three groups one of which contained all the *pallidus* haplotypes, another all *luteus* haplotypes, and the other all the haplotypes from the other three subspecies (Figure 4). Furthermore, no haplotypes were shared in common between individuals from different subspecies indicating all of them to be genetically distinct (Figure 4).

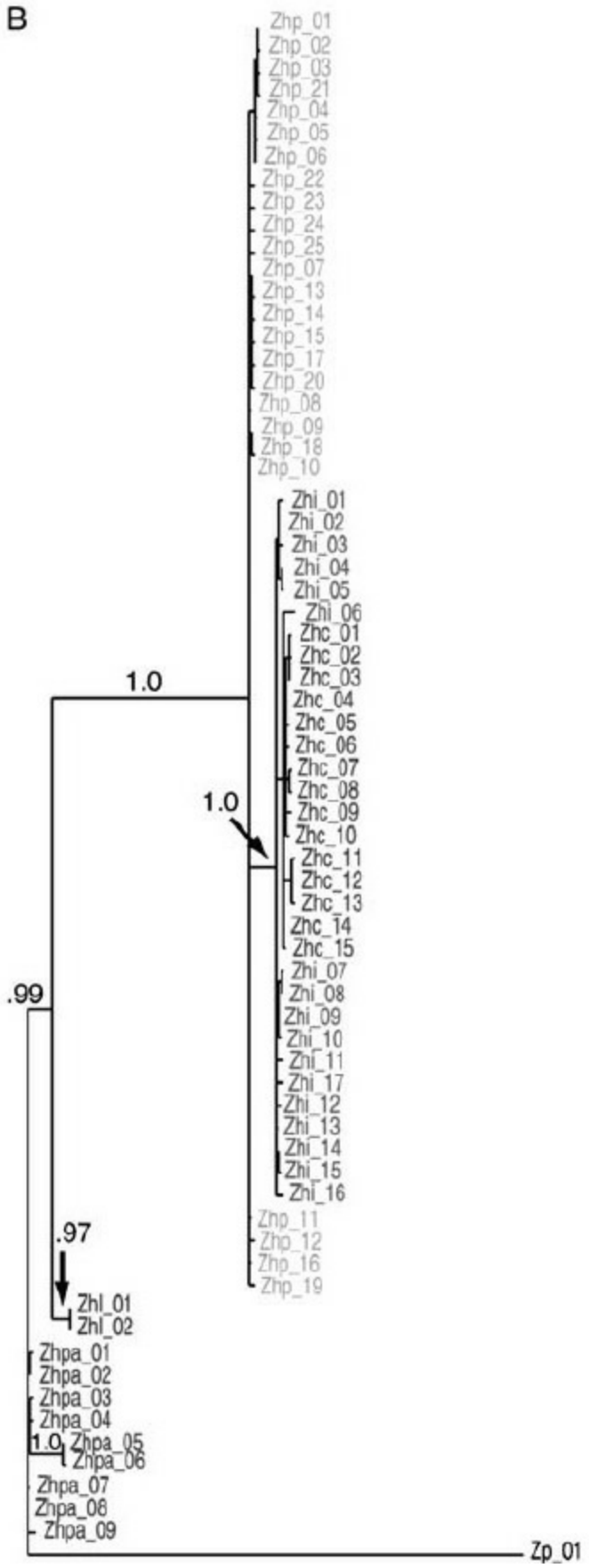

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Figure 4. Evolutionary relationships among 69 unique haplotypes based on sequence data of 1,380 bp of the mtDNA molecule. Zhp=preblei, Zhi=intermedius, Zhc=campestris, Zhl=luteus, Zhpa=pallidus, Zp=Zapus princeps outgroup. Numbers on the branches indicate the confidence that the branch is correct. From King et al. (2006).

When King et al. (2006) compared their mtDNA sequences from the 15 museum specimens analyzed in common with Ramey II et al. (2005), they found discrepancies between 13 of the sequences. Most importantly, King et al. (2006) found that all seven of the *campestris* reported by Ramey II et al. (2005) to have Preble's meadow jumping mouse haplotypes had, based on their data, the common *campestris* haplotype. King et al. (2006) used much more rigorous laboratory procedures than Ramey II et al. (2005) such as sequencing these individuals multiple times and suggested the most likely reasons for the discrepancies to be contamination, mislabeling, or some other procedural problem.

Considering all the data, King et al. (2006) found high concordance to the pattern of genetic divergence observed at both microsatellite loci and mtDNA which corresponded to previously proposed subspecies classifications based on morphology and geographic separation. They also found no haplotypes in common between any of the subspecies. Thus, they concluded that taxonomic revision was not warranted and that the ESA status of Preble's meadow jumping mouse did not require re-evaluation.

The Final Review

Of course Ramey II et al. (2007) challenged, mainly on conceptual and philosophical grounds, the conclusions of King et al. (2006).

Because of the dramatically different conclusions derived from the two studies and failure to reach a resolution in the scientific literature the USFWS had an independent panel of scientists review both the Ramey II et al. (2005) and King et al. (2006) studies (Arbogast et al. 2006). The panel concluded that Ramey II et al. (2005) did not provide sufficient morphological or ecological data to warrant changing the taxonomic status of Preble's meadow jumping mouse.

Their arguments were very similar to those of Vignieri et al. (2006) in that Ramey II et al. (2005) did not analyze the majority of the morphological characters that were used in the original description of the subspecies and the lack of data addressing whether or not local adaptations existed among subspecies in no way constituted evidence none exist. That is, the absence of evidence does not necessarily constitute evidence of absence.

The panel also re-examined the original mtDNA sequences obtained by Ramey II et al. (2005) that showed sharing of haplotypes between subspecies. They concluded that in almost all cases the samples were clearly contaminated as more than one sequence was obtainable from the individuals.

Based on this re-analysis and the data of King et al. (2006) the panel concluded there was no evidence of haplotype sharing among subspecies.

Finally, the panel concluded that in reality there was substantial concordance between the two studies regarding the results obtained from microsatellite allele frequencies. They felt that in regards to the interpretation of the results that the differences between the two sets of authors were mainly philosophical in nature stemming from what constitutes a subspecies and biologically significant divergence. Thus, overall the panel concluded "… 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" (Arbogast 2006; page 4).

Does Taxonomy Matter?

So does taxonomy matter in conservation biology?

Again I feel the case of Preble's meadow jumping mouse argues yes. When it was accorded subspecific status in 1998 it was listed as threatened under the ESA (USFWS 1998). Once Ramey II et al. (2005) proposed it to be synonymous with *campestris* and *intermedius* the mouse's status under the ESA was proposed for re-evaluation and delisting (USFWS 2005). Following the results of King et al. (2006) and the determinations reached by the independent scientific panel (Arbogast et al. 2006), re-evaluation ceased and now the USFWS is in the process of trying to "… specify over what portion of its range the *subspecies* is threatened" (italics mine; USFWS 2007; page 62992).

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