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Genetic evidence for recent spread of springsnails (Hydrobiidae: \emph{Pyrgulopsis}) across the Wasatch divide

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The 370-km-long, north–south-trending Wasatch Mountains separate the eastern Great Basin and upper Colorado River basin in Utah. Smith (1978) identified this mountain range as a strong dispersal barrier for fishes based on the limited species overlap across it. Phylogeographic studies of those fishes that are distributed (naturally) on both sides of the Wasatch Mountains drainage divide (referred to herein as the Wasatch divide) have shown that the (intraspecific) lineages in these 2 areas are not closely related to each other (Catostomus discobolus, Hopken et al. 2013; Oncorhyncus clarkii, Loxtman and Keeley 2012; Rhinichthys osculus, Oakey et al. 2004, Smith and Dowling 2008), providing additional evidence that the Wasatch divide functions as a strong dispersal barrier for this group. However, the biogeographic history of other obligately aquatic organisms in relation to the Wasatch divide has not been investigated aside from a recent study which showed that pebblesnails (Fluminicola coloradensis) share haplotypes and are not significantly
The Toquerville springsnail (*Pyrgulopsis kolobensis*) is a small, gill breathing caenogastropod that is widely distributed in the eastern Great Basin and several adjacent areas (Fig. 54 in Hershler 1998). In the eastern portion of its range, *P. kolobensis* is distributed along the Wasatch Front and its canyons, with one population occurring just across the Wasatch divide in Strawberry Valley (Fig. 1, Kol3). This is the only record of this large genus (139 species; Hershler et al. 2014b) in the upper Colorado River basin. Several alternative scenarios can be envisaged to explain this transmontane distributional pattern. First, the Wasatch Mountains may separate distantly related *P. kolobensis* lineages (i.e., not forming a monophyletic group) as has been documented in several fishes (see above). We note in this context that morphologically cryptic species have been detected in several other springsnails that range across multiple drainage basins (e.g., *P. micrococcus*; Hershler et al. 2013). Second, this distributional pattern could be the product of vicariance associated with the inception of the Wasatch divide, which dates minimally to the early to middle Miocene (10–12 Ma; Bryant et al. 1989). Third, the Strawberry Valley population could have become isolated as a consequence of a subsequent headwater transfer across the Wasatch divide in which case it would be expected to form a distinct lineage that is little differentiated from geographically proximal populations in the eastern Great Basin (consistent with a split during the Quaternary). This hypothesis is supported by geologic evidence that the western portion of Strawberry Valley drained (eastward) into the Provo River basin through Daniels Canyon.
for some time prior to late Quaternary faulting which severed this connection (Nelson and Krinsky 1982, Sullivan et al. 1988). Fourth, the Strawberry Valley population could have been founded by anthropogenic means and thus would be expected to bear the genetic signature of very recent separation (e.g., sharing of haplotypes with populations across the Wasatch Divide). The valley is a popular stop for anglers and there is a long history of introduction of nonnative fishes into Strawberry Reservoir, including several species that are distributed naturally in the eastern Great Basin (Catostomus ardens, Gila atraria; Sigler and Sigler 1996, Lentsch et al. 2001). We note in this context that the New Zealand mudsnail (Potamopyrgus antipodarum), whose spread in the West has been attributed in part to bait bucket release and other fisherman activities, was recently discovered in the Strawberry River (Vinson 2004). There is also a long history of artificial surface water transfers across the Wasatch divide from Strawberry Valley beginning in the late 1800s (La Rue 1916, Nelson 1997) which could have facilitated spread of P. kolobensis into the latter, although this would have required upflow migration in man-made canals. Herein we analyze the genetic structure of P. kolobensis across the Wasatch divide using mtCOI sequence data to discriminate among these competing hypotheses.

METHODS

For this study we collected (in 2012) specimens of P. kolobensis from Strawberry Valley and 4 populations on the other side of the Wasatch divide in the Provo and Weber River drainages (Fig. 1, Koll–5). We also included in our analyses previously published sequences from conspecific populations located in other parts of the eastern Great Basin (Hershler and Liu 2004a, 2004b, 2008) and the lower Colorado River basin (Hurt 2004, Liu and Hershler 2005, Hershler and Liu 2008). Samples were collected with a fine hand sieve and preserved in concentrated (90%) ethanol in the field. Voucher material was deposited in the Smithsonian Institution’s National Museum of Natural History (USNM) collection. Five specimens from each sample were sequenced for mtCOI. Genomic DNA was extracted from entire snails using a CTAB protocol (Bucklin 1992); each specimen was analyzed for mtDNA individually.
LCO1490 (Folmer et al. 1994) and COIH 2390 (Liu et al. 2001) were used to amplify a 900–base pair (bp) fragment of COI; amplification conditions and sequencing of amplified polymerase chain reaction product followed Liu et al. (2001). Sequences were determined for both strands and then edited and aligned using SEQUENCHER™ version 5.0.1. Our molecular phylogenetic analysis also included congener from the eastern Great Basin (P. inopinata, P. plicata) and lower Colorado River basin (P. bacchus, P. morrisoni) that were shown to be closely related to P. kolobensis in prior molecular phylogenetic studies (Hurt 2004, Liu and Hershler 2005). The type species of the eastern North American genus Marsto-

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MRMODELTEST 2.3 (Nylander 2004) was used to obtain an appropriate substitution model (using the Akaike information criterion) and parameter values for the molecular phylogenetic analysis, which was conducted using MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001). Metropolis-coupled Markov chain Monte Carlo simulations were run with 4 chains (using the model selected through MrMODELTEST) for 2,000,000 generations, and Markov chains were sampled at intervals of 10 generations to obtain 200,000 sample points. We used the default settings for the priors on topologies and the HKY + I + G model (Hasegawa et al. 1985) parameters selected by MrMODELTEST as the best-fit model. At the end of the analysis, the average standard deviation of split frequencies was <0.01 (0.0025) and the Potential Scale Reduction Factor (PSRF) was 1, indicating that the runs had reached convergence. The sampled trees with branch lengths were used to generate a 50% majority rule consensus tree with the first 25% of the samples removed to ensure that the chain sampled a stationary portion.

Genetic distances within and between samples of P. kolobensis were calculated using MEGA6 (Tamura et al. 2013), with standard errors estimated by 1000 bootstrap replications with pairwise deletion of missing data. Since MEGA does not contain the HKY model that was selected by MrMODELTEST, we used the uncorrected distance.

**Results**

New sequences were deposited in GenBank (accession numbers KT248032–248042). Ten haplotypes, differing from each other by 1–7 bp, were detected in the 25 newly sequenced specimens of P. kolobensis from Strawberry Valley and the 4 populations on the other side of the Wasatch divide (Table 2). One of these haplotypes (Kol1B) was shared by 2 populations (Kol1, 1 specimen; Kol5, 2 specimens), whereas the other 9 were restricted to single populations. The single haplotype detected in the Strawberry Valley population (Kol3A) differed from haplotype Kol1B by 1 base pair (Table 2). The haplotype (P162A) detected in the Bear River drainage population differed from the newly reported haplotypes by 1–6 bp (Table 2). Collectively the P. kolobensis sequences formed a poorly supported
(52% posterior probability) clade in the Bayesian tree within which the haplotypes detected in samples from along the Wasatch Mountains and Bear River drainage formed a well-supported (96% posterior probability) subunit that we informally referred to herein as the "Wasatch clade" (Fig. 2). The mean sequence divergence among samples in the Wasatch clade ranged from 0.3% to 0.8%, whereas divergence among all \textit{P. kolobensis} samples ranged from 0.3% to 2.9% (Table 3).

**DISCUSSION**

Our finding of shallow phylogeographic structure of \textit{P. kolobensis} across the Wasatch
divide obviously does not support the hypothesis of subdivision (vicariance) coincident with the tectonic development of the Wasatch Mountains, nor does it support a hypothesis that this range separates distantly related lineages. The mean sequence divergence between the Strawberry Valley and other *P. kolobensis* samples ranged from 0.3% to 0.8% (Table 3), which suggests that divergence occurred about 494,000–185,000 years ago (well postdating uplift of the Wasatch Range) based on a geology calibrated COI clock for *Pyrgulopsis* (1.62% of substitutions per million years; Hershler and Liu 2008). This result is consistent with the headwater transfer hypothesis outlined above, although the geologic evidence for this drainage displacement has not been spelled out in detail in the literature, nor is it well constrained chronologically. Although our findings indicate that the Strawberry Valley lineage diverged well prior to historic times, we cannot entirely rule out the possibility of a recent introduction given our incomplete sampling along the western side of the Wasatch divide (Fig. 1). However, we note in this context that there have been no confirmed reports of introduced springsnails anywhere in the West to date (Hershler et al. 2014a). Additional population sampling and use of more rapidly evolving molecular markers will be needed to discriminate between these 2 competing hypothesis for recent divergence across the Wasatch divide.

The phylogeographic pattern detailed herein bears some similarity to that previously reported for another regional caenogastropod, *Fluminicola coloradensis*, although the latter appears to have spread across the Wasatch divide somewhat farther to the north (fig. 1 in Liu et al. 2013). These findings provide an interesting contrast with fishes, which in most cases have failed to cross the Wasatch barrier (Smith 1978) despite their far greater mobility. The ability of these 2 snail species to penetrate into upland headwater habitats (cold-water streams and springs) appears to be the key to their success in crossing the Wasatch (and other) drainage divides.

**Acknowledgments**

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