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Discussion

Comments on the paper "Is the track of the Yellowstone hotspot driven by a deep mantle plume? — Review of volcanism, faulting, and uplift in light of new data" by Kenneth Pierce and Lisa Morgan [J. Volcanol. Geotherm. Res. 188 (2009), 1–25]

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As students of western North American aquatic biogeography we read with great interest the paper by Pierce and Morgan (2009) because it contained a synthesis of recent geological and biological studies relating to the late Cenozoic history of drainage along the track of the Yellowstone hotspot (pages 18–21). We were pleased to be educated about the geological evidence that may conflict with the late Pliocene paleodrainage connecting (what are now) the upper Missouri River (MRB) and Bonneville basins, which we hypothesized based on a molecular phylogenetic study of aquatic gastropods (genus *Pyrgulopsis*) (Hershler et al., 2008), but were troubled by several misleading and/or confusing statements regarding our paper and other biogeographic evidence. Here we briefly discuss and attempt to clarify these statements for the benefit of the reader. Pierce and Morgan suggested that the divergence time between snail lineages across the northern continental divide that we estimated using a molecular clock may not be accurate because the exemplars analyzed from the MRB live in a spring (Blaine Spring, Madison Valley) that is currently used by a fish hatchery and thus may have been recently introduced to this site from elsewhere. However, contrary to what was implied by Pierce and Morgan, our study included not one but two species (*Pyrgulopsis bedfordensis*, *Pyrgulopsis blainica*) from the MRB basin and the estimated time of divergence across the continental divide was based on the split between the clade composed of these two species and the closest relative of this clade, which is distributed in the Bonneville basin (*Pyrgulopsis anguina*). Both of the MRB species are local endemics (*P. bedfordensis* lives in a spring in the Townsend graben) that have not been found elsewhere despite regionally extensive sampling (e.g., see Hershler and Gustafson, 2001, Fig. 7) and both are highly divergent relative to other members of the genus. This information provides a strong basis for treating the Blaine Spring occurrence as native. Note, however, that even if *P. blainica* is removed from our analysis, the (mtCOI) DNA sequence divergence of the other MRB species (*P. bedfordensis*) relative to its close relative (*P. anguina*) in the Bonneville basin (5.167–5.319%) suggests a divergence time (3.28–3.19 Ma) that is closely similar to our original result (3.64–2.52 Ma).

After seemingly dismissing our results because they appear to conflict with their geology-based interpretation of northeastward flowing drainage from central Idaho into the Madison Valley region (Ruby Graben) as late as 4 Ma, Pierce and Morgan state that the "Distribution of the worm (*Rhynchelmis gustafsoni*) studied by Dan Gustafson (personal commun, 2008) provides conclusive evidence that the Madison Valley and upper Henrys Fork area were once connected and drained either to the north or south." This statement is troubling for several reasons. First, it appears to conflict with their previous statements regarding the paleodrainage history of the Ruby Graben area (see above), yet is consistent with our hypothesis of prior southward stream flow from the upper Missouri River Basin (through southeastern Idaho) into the Great Basin based on snail molecular phylogeny. Second, we do not understand how a personal communication can be cited as conclusive evidence in an otherwise rigorously derived scientific paper. Third, the "conclusive evidence" appears to be simply the occurrence of *R. gustafsoni* in both the Madison Valley and upper Henrys Fork (Fend and Brinkhurst, 2000). Biogeographers long ago abandoned the traditional practice using organismal distributions alone to test hypotheses because this information, at best, only suggests that there *may* have been a historical relationship between the areas of concern at some unknown time (Platnick and Nelson, 1978); hence the current emphasis on phylogenetic studies that can delineate relationships and the use of a molecular clock or some other means for dating divergence events (Lomolino et al., 2006). We note that there is some evidence in the literature to suggest that *R. gustafsoni* as currently envisaged may not be an especially suitable "tool" for inferring regional drainage history. A recent molecular phylogenetic study of this genus (Zhou et al., 2010) suggests that the morphologically similar populations assigned to *R. gustafsoni* (which are distributed in other areas in addition to the

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above) do not form a monophyletic ("natural") group and thus this species may require taxonomic revision. Specimens of *R. gustafsoni* from the Henrys Fork area differed from those from other, widely scattered populations identified as this species by 2.64–2.99% mtCOI (sequence data obtained from GenBank; http://www.ncbi.nlm.nih.gov/genbank/); application of a generalized annelid molecular clock (Martin et al., 2010) suggests that divergence of these occurred 2.13–1.88 Ma. Unfortunately, specimens of *R. gustafsoni* from the MRB were not included in this study, thus preventing a test of the postulated historical drainage relationship between the Madison Valley and upper Henrys Fork area.

The point of our letter is not to challenge the conclusions of Pierce and Morgan relating to drainage history in the northern continental divide area, which appear to be sound and derived from solid geological evidence. However, we consider it important that geological and biological evidence should be subjected to the same level of critical review and scrutiny in integrative studies such as this.

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