



Contents lists available at ScienceDirect

## Molecular Phylogenetics and Evolution

journal homepage: [www.elsevier.com/locate/ympev](http://www.elsevier.com/locate/ympev)

## Isolation drives increased diversification rates in freshwater amphipods

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## ARTICLE INFO

## Keywords:

Chihuahuan Desert  
 Dispersal  
*Gammarus*  
 Historical biogeography  
 Vicariance  
 Amphipoda

## ABSTRACT

Vicariance and dispersal events affect current biodiversity patterns in desert springs. Whether major diversification events are due to environmental changes leading to radiation or due to isolation resulting in relict species is largely unknown. We seek to understand whether the *Gammarus pecos* species complex underwent major diversification events due to environmental changes in the area leading either to radiation into novel habitats, or formation of relicts due to isolation. Specifically, we tested the hypothesis that *Gammarus* in the northern Chihuahuan Desert of New Mexico and Texas, USA are descendants of an ancient marine lineage now containing multiple undescribed species. We sequenced a nuclear (28S) and two mitochondrial (16S, COI) genes from gammarid amphipods representing 16 desert springs in the northern Chihuahuan Desert. We estimated phylogenetic relationships, divergence times, and diversification rates of the *Gammarus pecos* complex. Our results revealed that the region contained two evolutionarily independent lineages: a younger Freshwater Lineage that shared a most-recent-common-ancestor with an older Saline Lineage ~66.3 MYA (95.6–42.4 MYA). Each spring system generally formed a monophyletic clade based on the concatenated dataset. Freshwater Lineage diversification rates were 2.0–9.8 times higher than rates of the Saline Lineage. A series of post-Cretaceous colonizations by ancestral *Gammarus* taxa was likely followed by isolation. Paleo-geological, hydrological, and climatic events in the Neogene-to-Quaternary periods (23.03 MYA – present) in western North America promoted allopatric speciation of both lineages. We suggest that Saline Lineage populations include two undescribed *Gammarus* species, while the Freshwater Lineage shows repetition of fine-scale genetic structure in all major clades suggesting incipient speciation. Such ongoing speciation suggests that this region will continue to be a biodiversity hotspot for amphipods and other freshwater taxa.

## 1. Introduction

Biogeographers have long recognized two mechanisms promoting speciation: vicariance and dispersal. Paleogeological events and the ability to disperse long distances both create ecological opportunities for organisms to exploit novel habitats, leading to species diversification that has shaped the current biogeographic patterns of the world's biota (Stace, 1989; Zink et al., 2000; Adamowicz et al., 2010). When a vicariant event, such as sea level change or uplifting of mountain ranges, causes the fragmentation of a widespread taxon, local populations may undergo reproductive isolation, adaptation to local ecological pressures, and/or genetic drift. Maintenance of the isolating barriers, and the resulting lack of dispersal between populations, leads to allopatric speciation (Coyne & Orr, 2004). Alternatively, long-distance

dispersal events allow species to overcome barriers and exploit new regions. Because these events are typically rare and involve only a few individuals, genetic drift places newly founded populations on unique evolutionary trajectories, leading them to diverge from the ancestral population, so-called peripatric speciation (Coyne & Orr, 2004; Murphy et al., 2009; Murphy et al., 2012). Newly founded populations are believed to contribute to high diversification rates initially as new niches are exploited; subsequent saturation of niches may lead to declines in diversification rates over time (Coyne & Orr, 2004; but see Santini et al., 2013). Understanding the roles of vicariance and dispersal is essential for explaining current patterns of global and regional biodiversity, which serve as baselines for understanding issues of conservation associated with current elevated rates of extinction due to human exploitation of the earth.

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The genus *Gammarus* (Crustacea: Amphipoda) provides a particularly interesting example of the interplay of vicariance, dispersal, and diversification. With more than 200 species (Vainölä et al., 2008), this genus occurs in a wide variety of freshwater, brackish, and saline habitats throughout the Holarctic. Following its origin in saline environments of the West Palearctic during the Paleocene (~61 million years ago; MYA), these amphipods underwent rapid diversification upon colonization of freshwater habitats in the Middle Eocene (Hou et al., 2011). Further rapid diversification of freshwater lineages occurred during the Miocene, primarily due to isolation of populations via vicariant events. As a result, the genus currently consists of five lineages distributed throughout the Northern Hemisphere, with the majority of species found in freshwater habitats (Hou & Sket, 2015). All of these freshwater species are endemic to limited areas, save for the cosmopolitan *Gammarus lacustris* (Hou et al., 2011). Based on the relationship of *Gammarus* diversification and geological events, this pattern likely resulted from ecological opportunities that promoted radiation into novel habitats, along with isolation and poor dispersal that led to the maintenance of relict species (Hou et al., 2014).

One of these isolated regions of *Gammarus* diversification is the Chihuahuan Desert in the southwestern United States and northern Mexico. One of the most biologically diverse Neotropical deserts (Ricketts et al., 1999), it is also a World Wildlife Fund Global 200 priority ecoregion for biodiversity conservation due to its species richness, high levels of endemism, and increasing anthropogenic threats (Olson & Dinerstein, 2002). These high levels of biodiversity and endemism are especially evident in the region's aquatic ecosystems (Abell et al., 2000). During most of the Cretaceous (145–66 MYA), the region was inundated by the Western Interior Seaway (Baldrige, 2004); subsequently in the Late Cretaceous, uplifts of the Rocky Mountains and associated basins caused the Seaway to recede and created isolated aquatic habitats (Bousfield, 1958; Holsinger, 1974; Dave Love personal comm. 2011). Furthermore during the Cenozoic (65.5 MYA – present), dynamic geomorphologic events, including formation of the Rio Grande rift; Trans-Pecos volcanic activities; and major fluvial shifts affected the current distribution of aquatic habitats in the region (Snyder et al., 1976; Chapin et al., 2004; Galloway et al., 2011). These geologic events are thought to have had major influences on the current aquatic biodiversity of the region.

*Gammarus* inhabiting springs in the northern Chihuahuan Desert exhibit high levels of species diversity and endemism. This region was originally thought to contain three species based on morphological differences (*G. pecos* Cole & Bousfield, 1970; *G. hyalleloides* Cole, 1976; *G. desperatus* Cole, 1981), each of which was limited to one or two spring systems (i.e., sets of geographically proximate springs sharing groundwater sources). Morphological differences observed in individuals from additional spring systems led to speculation that several undescribed species were also present in the region (Cole, 1985). Recent studies using biochemical and molecular genetics revealed several reciprocally monophyletic clades (Gervasio et al., 2004; Seidel et al., 2009), with each clade being endemic to a single spring system. Subsequently, these studies led to the discovery of a new species, *Gammarus seideli* Cannizzaro, Walters, and Berg, 2017, from Caroline Spring, Terrell County, Texas (Cannizzaro et al., 2017). The same studies showed high genetic divergence among spring systems, suggesting weak passive dispersal of amphipods and extreme geographic isolation of most springs. Such results suggest that each spring system possesses an endemic species. This so-called *Gammarus pecos* species complex (the four known species and the potentially unknown endemic species in the region) was thought to be a marine relict descended from a widespread Cretaceous ancestor that became isolated inland upon the recession of the Western Interior Seaway (Cole, 1985; Seidel et al., 2009; Hou et al., 2011). Furthermore, a study of physiological traits within the species complex found that salinity tolerance was a function of local ambient salinity rather than phylogenetic distance, suggesting that these organisms independently underwent adaptation to local environments

(Seidel et al., 2010).

In this study, we reconstructed the evolutionary history of *Gammarus* amphipods in the northern Chihuahuan Desert using mitochondrial DNA (mtDNA) and nuclear DNA (nDNA) sequences. Specifically, we estimated divergence time, colonization timing, and diversification rates of the *Gammarus pecos* complex. We tested whether the species complex underwent major diversification events due to environmental changes in the area leading either to radiation into novel habitats (vicariance and dispersal), or formation of relicts due to isolation (vicariance and isolation). Specifically, we tested the hypothesis that *Gammarus* in the northern Chihuahuan Desert are descendants of an ancient marine lineage now containing multiple undescribed species. Because spring systems in the region are at great risk due to human exploitation of water resources (USFWS, 2012), our results serve to not only increase understanding of biogeographic processes leading to formation of species, but also to further identify unique taxonomic entities that merit conservation concern.

## 2. Materials and methods

### 2.1. Sampling, DNA extraction, amplification, and sequencing

We sequenced *Gammarus* individuals from desert springs (including seeps, creeks, and desert wetlands) across the northern Chihuahuan Desert in New Mexico and Texas, USA (Table 1 and Fig. 1). We re-sequenced a subset of samples from Seidel et al., (2009) and added another subset of GenBank-deposited sequences from the study to get *Gammarus* samples across 16 springs in the region. We collected animals from the water column, macrophytes, or substrata using hand nets, preserved them in 95% ethanol, and stored them at  $-20^{\circ}\text{C}$  until further processed. Populations we sampled were from eight spring systems which include all known localities for *Gammarus* in this region (Table 1). Four nominal taxa are endemic to the region: *G. desperatus* from Bitter Lake National Wildlife Refuge (BLNWR) in Chaves County, NM; *G. hyalleloides* from the Toyah Basin in Jeff Davis and Reeves counties, TX; *G. pecos* from Diamond Y Preserve in Pecos County, TX; and *G. seideli* from Caroline Spring in Terrell County, TX (Cole, 1981; Cole, 1985; Seidel et al., 2009; Cannizzaro et al., 2017). Because we were unable to place other populations within these species based on morphology, we initially designated them as *Gammarus* sp.

Genomic DNA was extracted from five to eight individuals per spring. We amplified the mtDNA cytochrome *c* oxidase subunit I (COI) and the mtDNA 16S ribosomal RNA (16S) genes. In addition, we amplified the nDNA 28S ribosomal RNA (28S) gene for individuals for which mtDNA sequencing was successful. Because nDNA tends to show low intra-population genetic variation, we sequenced a subset of individuals from each spring (Table 1). For DNA extraction and amplification details see Supplementary Information (detailed methods in Appendix A). PCR products were then isolated by electrophoresis on 2% agarose gels and extracted using Qiagen® QIAquick Spin Columns and buffers (cat. #28106). The PCR products were bidirectionally sequenced using the same primers as PCR, except two additional primers were used to sequence the 28S gene [28SR, 28S-700F, (Hou et al., 2007)] in four segments due to its longer length. Cycle sequencing reactions were carried out using ABI BigDye terminator v3.1 sequencing kits (25 cycles, annealing temperature:  $50^{\circ}\text{C}$ ) and visualized with an ABI 3130 genetic analyzer (Life Technologies). Resulting sequences were aligned using GENEIOUS 4.8.3 (Kearse et al., 2012) and an open-reading frame for the COI gene was verified. Additionally, we re-sequenced individuals from the previous study (Seidel et al., 2009), allowing us to increase the length of the COI sequence from 236 bp to 640 bp for these individuals. We performed multiple sequence alignments using MAFFT v6 (Katoh et al., 2005) with the AUTO setting. We estimated genetic indices for each gene, including mean number of nucleotide differences (K) and mean nucleotide diversity ( $\pi$ ), within each population and over the pooled dataset using DNASP 5 (Librado &

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