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Molecular phylogenetics of American snapping shrimps allied to *Alpheus floridanus* Kingsley, 1878 (Crustacea: Decapoda: Alpheidae)

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Abstract

Widely distributed populations of the snapping shrimp, *Alpheus floridanus* Kingsley, 1878, from the eastern Pacific and western and eastern Atlantic Ocean have long been suspected to represent different species due to extreme morphological variation among conspecifics. A companion study (Bracken-Grissom & Felder 2014) contains redescrptions of two western Atlantic species (*A. floridanus* Kingsley 1878 *sensu stricto* and *A. platycheirus* Boone, 1927), assignments of the original syntypes for *A. floridanus*, descriptions of three new species from the Atlantic and eastern Pacific (*A. hephaestus* Bracken-Grissom & Felder, 2014; *A. roblesi* Bracken-Grissom & Felder, 2014; *A. ulalae* Bracken-Grissom & Felder, 2014), and discussion of the relationship of the eastern Atlantic *A. floridanus africanus* Balss, 1916. The present study underpins all these findings by application of molecular phylogenetic techniques. Analysis of partial sequences of the 16S, 12S, and COI mitochondrial genes separate species throughout the eastern Pacific and the eastern and western Atlantic. Morphological comparisons suggested that the two syntypes of *A. floridanus* belong to different species, and molecular results in this study confirm this separation. Genetic data suggest a strong affinity between the western Atlantic *A. platycheirus* and the eastern Pacific *A. hephaestus*. Close relationships are evident between trans-Atlantic species, *A. floridanus africanus* and *A. floridanus*, a pattern also seen for other cryptic and pseudocryptic species of *Alpheus*. *Alpheus roblesi* and *A. ulalae* represent early-branching lineages within the complex. In some cases, molecular phylogenetic relationships between members of the *A. floridanus* complex can be reconciled with postulated biogeographic history.

Key words: *Alpheus*, Alpheidae, species complex, snapping shrimp, 16S, 12S, COI, mitochondrial genes, phylogenetic analysis

Introduction

Genetic data can provide tools for defining and describing taxa within cryptic and pseudocryptic species complexes. Here we define a “species complex” to be a group of species that are morphologically similar but genetically distinct (“pseudo-sibling species” of Knowlton 1993). Williams *et al.* (2001) demonstrated the usefulness of molecular data in studies of species complexes while conducting the first large-scale phylogenetic study of the genus *Alpheus* based on both mitochondrial and nuclear genes and including several transisthmian pairs. Williams *et al.* (2001) reported evidence of at least seven cryptic species among American species of *Alpheus*, revealing a need for future studies in this genus. With the application of both morphological examinations and DNA analyses, several American complexes of *Alpheus* have been recently revised: *A. formosus* Gibbes, 1850, *A. cristulifrons* Rathbun, 1900, *A. nuttingi* (Schmitt, 1924), *A. websteri* Kingsley, 1880, and *A. armillatus* H. Milne Edwards, 1837 (Anker 2012; Anker *et al.* 2007; 2008a; 2008b; 2008c; Mathews & Anker 2009). *Alpheus floridanus* Kingsley, 1878, which was revised based on morphology and color patterns (Bracken-Grissom & Felder 2014), represents yet another species complex, with five species and one subspecies in the eastern Pacific and tropical eastern and western Atlantic. In the present study, we present the underpinning molecular phylogenetic

depths ranging from 12 to 122 m, where they are collected with trawls, box corers, or dredges. These species also share similarities in morphological traits, such as the length and shape of the antennal scale, structure of the mandible, and elongate major and minor chelae (Bracken-Grissom & Felder 2014; Chace 1972). Applying a molecular clock calculated in previous studies for alpheidids (1.5% divergence per million years in COI sequences; (Anker *et al.* 2007; Knowlton & Weigt 1998; Knowlton *et al.* 1993), suggests that the species pair *A. hephaestus* / *A. platycheirus** diverged many years prior to the closing of the Panamanian Isthmus, approximately 9.1 mya.

While the length and shape of the scaphocerite could suggest an affinity among *A. hephaestus*, *A. platycheirus*, and *A. floridanus africanus*, molecular data instead place *A. floridanus africanus* as the sister species to *A. floridanus*. Although these two species are geographically separated, their genetic affinity is not surprising given a number of closely related decapod species that reside on either side of the Atlantic Ocean (Bracken-Grissom & Felder 2014; Chace & Manning 1972; Wirtz 2004). These often have broad distribution ranges and the potential for interbreeding, perhaps facilitated by the strong westward equatorial currents of the Atlantic Ocean. Many trans-Atlantic sister species pairs are known in mollusks (Lapegue *et al.* 2002), crabs (Weinberg *et al.* 2003), and other groups of snapping shrimps (Anker *et al.* 2008a; 2008c).

The distribution range of *A. floridanus* and *A. platycheirus* in the western Atlantic may be at least in part determined by the Loop Current, which travels northward, entering the Gulf of Mexico through the Yucatan Channel and exiting through the Florida Straits. This current plays a major role in the circulation and transport of water throughout the southeastern Gulf of Mexico and has been suggested to influence the distribution of other species in the region (Bangma & Haedrich 2008; Williams & Williams 1981). One species known so far from only the eastern Gulf of Mexico, *A. ulalae*, represents a distinct lineage in our concatenated molecular analysis (Fig. 1). Undoubtedly, *A. ulalae* is genetically distinct from all other species of *Alpheus* within the *A. floridanus* complex, and morphological differences have been documented (Bracken-Grissom & Felder 2014). The amphiatlantic *A. roblesi* is morphologically the most distinctive species within the *A. floridanus* complex and also the earliest branching lineage within the group (Fig. 1), being characterized by a sinuous shape to the scaphocerite margin, presence of conspicuous spines along the propodus of the fifth pereopod (rarely lacking), and less elongate chelae than in the compared species (Bracken-Grissom & Felder 2014).

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