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Molecular phylogeny of the genus *Lepidophthalmus* (Decapoda, Callianassidae), with re-examination of its species composition

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Abstract

Ghost shrimps (Decapoda: Callianassidae) are common estuarine and marine burrowing organisms of tropical to temperate waters, typically found in intertidal to shallow subtidal habitats. Except for an abbreviated planktonic larval phase, most callianassids live as obligate burrowers and appear to depend on the burrow for shelter, reproduction, and feeding. Recent studies have shown the genus *Lepidophthalmus*, a group largely restricted to estuaries and river mouths, to be surprisingly speciose, but relationships among these taxa and driving forces for their separation remain poorly understood. We include fifteen described species of *Lepidophthalmus* in a molecular phylogenetic analysis based upon sequence analyses of the 16S and 12S mitochondrial genes. Our findings clarify the monophyletic membership of the genus and confirm postulated species separations. We reconfirm validity of *Lepidophthalmus eiseni*, reject two recently proposed new genera for selected members of *Lepidophthalmus*, and define ecologically and morphologically informative clades among congeners. Limited capability for larval dispersal and regional biogeographic history could well account for high diversity and regional endemism observed within the genus. Biogeographic scenarios, including continental drift, closure of the Panamanian Isthmus, and post-glacial dispersals, are invoked to account for proposed reconstructions of historical relationships.

Key words: *Lepidophthalmus*, Callianassidae, ghost shrimp, phylogeny, mitochondrial genes

Introduction

An emerging picture of high species diversity within the genus *Lepidophthalmus* has been previously explained as a likely combination of both reduced larval dispersal and adaptation for life in disjunct, low salinity environments like estuaries and river mouths (Felder & Manning 1997). Larval development of at least *L. sinuensis*, *L. louisianensis*, and *L. siriboia* is known to be abbreviated, and anecdotal evidence suggests this may be generally the case for the genus (Felder *et al.* 1986; Nates *et al.* 1997; Abrunhosa *et al.* 2005; DLF, unpublished data). For the cases in which larval life history is known, there are only two to three zoeal stages that molt to the postlarval stage within 2–4 days, at which time the postlarvae burrow. With rare exceptions, the adults appear to thereafter remain in the burrow as obligate fossorial animals. This abbreviated development may serve to retain offspring within estuaries and thus facilitate dense settlement of the decapodid in the typical adult habitat (Nates *et al.* 1997), and it may also limit gene flow that favors regional adaptation and species endemism.

Dense populations of *Lepidophthalmus* and related callianassid shrimps have long attracted attention in ecological studies of marine soft-bottom benthos, especially given the influence of these animals on sedimentology and geochemistry of the seabed through their bioturbating activities and consequent effect on benthic community structure (Felder & Griffis 1994; Astall *et al.* 1997; Dworschak 2000; Felder 2001). The importance of various Axiidean and Gebiidean species (ghost shrimp or mud shrimp) in sediment turnover and nutrient recycling is well documented (Koike & Mukai 1983; Nickell & Atkinson 1995). These burrowing animals can pump out hypoxic water, ejecta, and excretia directly to the water column through their irrigation activities (Koike & Mukai 1983).