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ON THE CONTRIBUTION OF ALLOMETRY TO MORPHOLOGICAL VARIATION IN A FRESHWATER GASTROPOD *ELIMIA LIVESCENS*

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ABSTRACT. Morphological variation attributable to allometry in the freshwater gastropod *Elimia livescens* Menke, 1830 is described. Geometric morphometric analyses were used to examine shape variation and visual ontogenic deformation patterns for a population of *E. livescens* along the West Fork of the White River, Delaware County, Indiana. A strong allometric slope from more globose and robust shelled smaller individuals to increasingly fusiform shell shapes in larger individuals was identified. The relatively high allometric slope was interpreted as evidence of functional importance and maintenance through selection.

Keywords: gastropods, morphology, allometry

Morphological variation in freshwater gastropods has been attributed to allometry, predation, competition, and environmental variation (Vermeij & Covich 1978; Kemp & Bertness 1984; DeWitt 1998; Dunithan et al. 2011). Shape variation of most taxa can be described with a power function that varies with body size (e.g., allometry; Huxley 1932; Peters 1983). Allometric variation can result from competition among and within age groups (Kemp & Bertness 1984), selection for exaggerated secondary characters (Kodric-Brown et al. 2006), environmental associations (Hollander et al. 2006), and can be present in taxa due to ancestral states. Environmental and biotic variation can also influence morphology through the alteration of allometric trajectories (Kemp & Bertness 1984) or through plasticity at a given point along a growth continuum (Hoverman & Relyea 2007; Bourdeau 2009).

Phenotypic plasticity has been attributed to both habitat and community structure (Minton et al. 2011). For example, DeWitt et al. (2000) and Krist (2002) identified shell morphology variation in freshwater gastropods that supported elongate morphology as a functional response to resist crayfish predation. *Elimia livescens* is a freshwater gastropod that occupies a wide range of habitats and has high morphological variation that covaries with abiotic environmental variables (Dunithan et al. 2011). However mechanisms for the direct cause of this morphological variation are mostly unknown. Although morphological variation that covaries with environmental variation appears to be adaptive, this research area is understudied (Callery et al. 2001). Identifying morphological corollaries can provide further information about ecological and evolutionary patterns (Hollander et al. 2006). The objective of this study was to describe morphological variation in *E. livescens* as a function of allometry.

METHODS

We collected gastropods by hand using visual searches in the West Fork of the White River in Delaware County, Indiana, USA. This reach of the White River is a non-sinuous third order stream with coarse substrate, moderate flow, and mean depth of 1 m. All collected individuals were photographed (Nikon D70 – AF Micro Nikkor Macro Lens) against a scale reference and digitized using tpsDig2 software (Rohlf 2008) with a series of 12 repeated landmarks (Fig. 1), and described using shape regression (tpsRegw; Rohlf 2011) and relative warp analysis (RWA; tpsRelW; Rohlf 2007). Landmark locations were chosen based on previous morphometric analyses of *E. livescens* (see Dunithan et al. 2011). To reduce bias due to landmarks placed along curvatures, landmarks ‘3’ and ‘5’ were considered semi-sliding. Allometry was assessed by regressing relative

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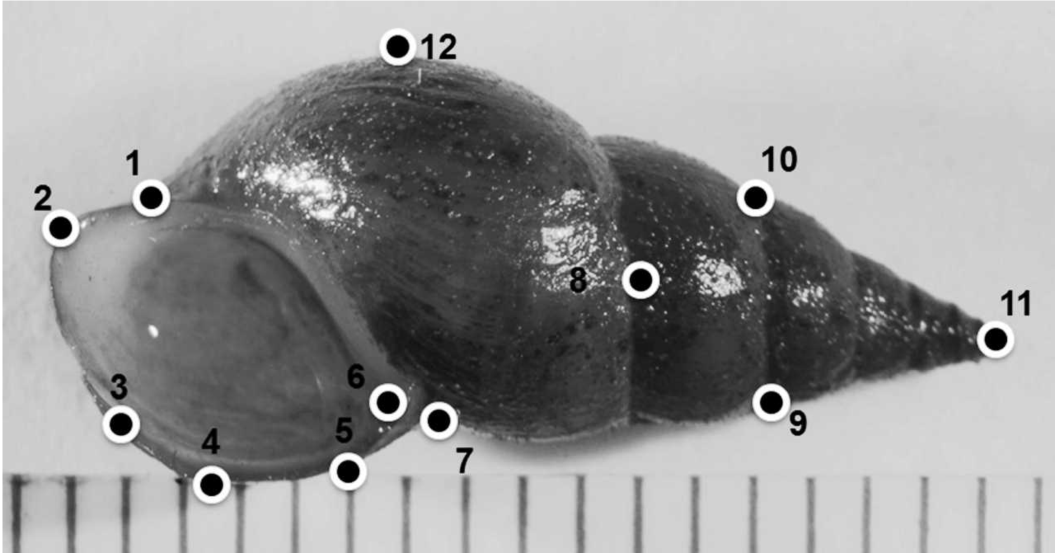

Figure 1.—Landmarks used in morphometric analyses of *Elimia livescens*.

warp scores against body size (e.g. centroid size) for collected individuals that spanned the entire size range present within the White River collecting site. Relative warp axes were used for subsequent description and visualization of the morphological variability present. Visualization of shape change used thin plate splines deformation grids. Following analysis all specimens were vouchered and deposited in the Ball State University invertebrate collection.

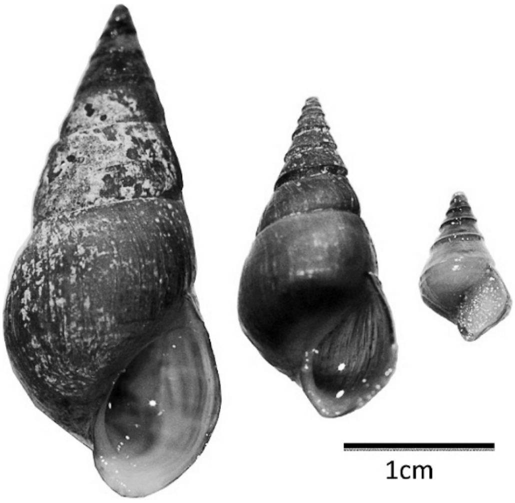

Figure 2.—Three *Elimia livescens* individuals to demonstrate the range of sizes in the White River, Indiana, USA.

RESULTS

Elimia livescens (n=80) with body size ranges 4–17 mm was collected from the White River (Fig. 2). Regression analysis (using tpsRegr; Rohlf 2011) of shape versus size accounted for 22% of the overall allometric variability (Wilks λ 0.14, $F_{20,1560} = 21.6$, $p < 0.001$; Fig. 3). Relative warp analysis resulted in two significant axes that explained 57% of the total shape variation. RWA1 (eigenvalue 180) explained 38% of the total variation among individuals

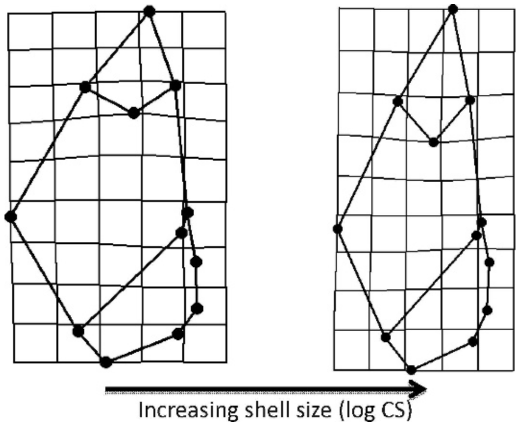

Figure 3.—Thin plate spline deformation grids corresponding to morphology – size (log CS is centroid size) allometry gradient from smaller (left image) to larger (right image) individuals.

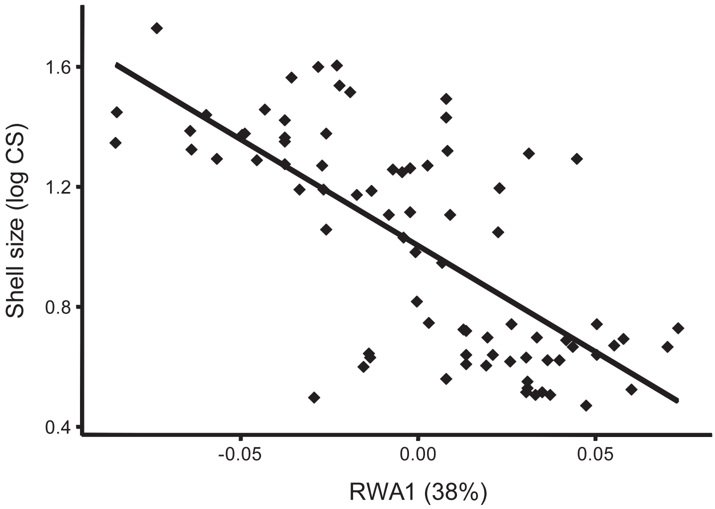

Figure 4.—Scatterplot of *Elimia livescens* shell size (log CS is centroid size) and primary axis morphology.

and had positive loadings for small, robust shape and negative loadings of large, fusiform and elongate shape ($r = -0.72$; $p < 0.001$; Fig. 4). RWA2 (eigenvalue 83) explained 19% of the total variation among individuals and had positive loadings for increased body size and negative loadings for thick spires and large, rectangular apertures ($r = 0.37$; $p < 0.001$).

DISCUSSION

We identified shape change in *E. livescens* concurrent with developmental changes in body size. Although we expected allometry, the high degree of slope with shape implies the potential for maintenance costs (Gould 1968). Allometric slope has been hypothesized to be conserved by phylogeny (Urdy et al. 2010) and influenced by environment (Kemp & Bertness 1984). Thus, it likely varies predictably among populations. We suggest that allometry is a primary source of morphological variation in this taxon and that local habitat (Dunithan et al. 2011), community attributes of predators, competitors, and parasites (Vermeij 1982; Krist 2002, 2009; Covich 2010), and large scale geographic variables (Trussel 1997; Minton et al. 2009) can influence developmental trajectory and adult morphologies through phenotypic plasticity. Functional variation in morphology likely is a response to varying biotic and abiotic conditions to increase survival, dispersal, and population success. Future research should focus on discerning the degree that environment influences morphological allometry and plasticity and to what extent this may influence *E. livescens* ecology.

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