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CHANGES IN SHELL MORPHOLOGY OF *ELIMIA COMALENSIS* (GASTROPODA: PLEUROCERIDAE) FROM THE EDWARDS PLATEAU, TEXAS

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ABSTRACT—Species in the pleurocerid genus *Elimia* are important components of freshwater systems in the eastern United States, but little is known about their natural history. Using dual-simultaneous linear regression and principal components analyses, we show patterns of morphological change in two populations of *E. comalensis* from the Edwards Plateau, Texas. Both populations had similar rates of change for all shell measurements analyzed, and both showed similar decreases in growth as total length of shell increased. However, the size at which growth slowed was different between populations, and small shells tended to have a consistent shape, while larger shells were more variable.

RESUMEN—Aunque las especies del género *Elimia* son componentes importantes de los sistemas de agua dulce del este de los Estados Unidos, se sabe poco de su historia natural. Usando dos análisis, uno de regresión linear dual simultánea y otro de componentes principales, mostramos patrones de cambio morfológico en dos poblaciones de *E. comalensis* del Edwards Plateau, Texas. Las dos tuvieron tazas de cambios similares para todas las medidas de conchas analizadas y las dos tuvieron disminuciones similares en el crecimiento mientras la longitud total de concha aumentaba. Sin embargo, el tamaño al que el crecimiento disminuyó fue diferente entre las poblaciones y las conchas pequeñas tendieron a tener una forma consistente y las conchas más grandes fueron más variables.

Snails in the genus *Elimia* (=*Goniobasis*) often are important components of freshwater systems throughout the eastern United States (Newbold et al., 1983; Richardson et al., 1988). In the southeastern states, where diversity of *Elimia* is greatest (Burch, 1982; Lydeard and Mayden, 1995), *Elimia* may comprise >90% of the total biomass of macroinvertebrates (Newbold et al., 1983; Richardson et al., 1988) and have a species richness rivaling most genera of aquatic insects in the same region (Merritt and Cummins, 1995). As reported for other Pleuroceridae (e.g., Lamberti et al., 1987), *Elimia* has a significant influence on ecological processes at both community and ecosystem levels, e.g., influences on community structure of periphyton (Tuchman and Stevenson, 1991; Morales and Ward, 2000) and macroinvertebrates (Harvey and Hill, 1991). Despite the important ecological impacts of *Elimia*, little has been published with regard to life history. Studies of life history have been almost exclusively limited to examinations of Mobile River basin and Atlantic slope fauna (Dillon and Davis, 1980; Dillon, 1984; Huryn et al., 1994). Accordingly, large gaps of information regarding growth, reproductive age, and variation in shells exist in the literature.

Lack of data on basic biological features of *Elimia* is alarming considering the decline in species richness and distribution throughout the genus. Like many freshwater faunas globally (Lydeard et al., 2004), pleurocerid snails are declining due to a variety of factors including habitat modification, degradation, and destruction. Impacts of this loss have been studied extensively in the Mobile River basin, where pleurocerids historically reached their greatest diversity and where the largest number of extinctions has occurred (Neves et al., 1997). Status of most species in the genus remains unknown, although its range is from Texas to the Atlantic Ocean and from the Florida Panhandle to southern Canada (Burch and Tottenham, 1980). While recent studies have helped sort out evolutionary relationships within and among *Elimia* (e.g., Lydeard et al., 1997, 1998; Dillon and Frankis, 2004), data on basic life history are lacking. Any plan to conserve this fauna must incorporate natural history and evolutionary information to be successful.

One species of *Elimia* that exemplifies a lack of natural-history data and potential conservation issues is *Elimia comalensis* (Pilsbry, 1890). *Elimia comalensis* is known from spring-fed pool and stream systems across the Edwards Plateau and Balcones Escarpment regions of Texas (Neck, 1986; United States Congress, 1993), although its distribution is patchy. Except for original descriptions of it and its subspecies *E. c. fontinalis* (Pilsbry and Ferris, 1906), the species is nearly absent in the literature, except in lists (Turgeon et al., 1998) and in museum, government, and agency reports (e.g., J. C. Britton, in litt.; United States Congress, 1993). The only paper that has addressed the natural history of the species noted that individuals in pool and stream regions of Comal Springs exhibited different distributions of size (Cheatum and Mouzon, 1934). In terms of conservation status, *E. comalensis* is ranked H (possibly extirpated) on the state, national, and global heritage rank scales (NatureServe, www.natureserve.org/explorer), although no extensive surveys for the species have been conducted (R. Howells, pers. comm.). The species appears restricted to the Edwards Plateau, an area of high endemicity containing many threatened taxa (Diamond et al., 1997). Many freshwater organisms in Texas are experiencing declines due to extraction of water (Contreras-Balderas and Lozano-Vilano, 1994), habitat modification, and introduced species (Howells, 2001), including *E. comalensis* (J. C. Britton, in litt.). The species is under additional pressure because it occurs in areas used for municipal water supplies and recreation (McCarl et al., 1993; McKinney and Watkins, 1993; McKinney and Sharp, 1995).

Using regression analysis on museum and recently collected specimens of *E. comalensis*, we attempted to determine rates of growth for two populations living on opposite ends of the Edwards Plateau in Salado and Del Rio, Texas (Fig. 1). We also attempted to quantify changes in shape of individual snails as they grew using factor analysis. Our objective was to generate basic life-history data on *E. comalensis* from across its range for use in future studies of the species and for *Elimia* and pleurocerids in general.

METHODS—Two groups of snails were used in this analysis. Individuals from San Felipe Springs in Del Rio, Texas ($n = 430$), were collected by F. Thompson and L. Appleton in March 2001 and vouchered in the Florida Museum of Natural History (FLMNH). Individuals from Salado Creek, Salado, Texas ($n = 228$) were collected by DMH during summer 2004, and are housed in the Museum of Natural History at the University of Louisiana at Monroe. Both populations contained a continuous series of size classes, with the smallest specimens being consistent in size with recently hatched individuals (Dillon, 2000).

Photographs of individual shells were taken with a tripod-mounted (Kodak EasyShare CX6330) or with a microscope-mounted (Nikon CoolPix 4500) digital camera. Shells were leveled in clay to make the longitudinal axis of the shell parallel to the mounting surface, and a ruler was photographed with all specimens for scale. Four position landmarks were chosen for their homology and repeatability among specimens: apex of shell (landmark 1); anterior end of aperture where it meets body whorl (2); posterior end of the aperture where it meets body whorl (3); and anterior end of aperture at the columella (4), referenced herein as the deflection due to its appearance as a deflection of shell away from the aperture (Fig. 1a). Two additional landmarks spaced 10 mm apart also were included for scaling. Landmarks were digitized using tpsDig 2.04 (F. J. Rohlf, life.bio.sunysb.edu/ee/rohlf/software.html), and care was taken to avoid specimens with heavily eroded apices. Landmark positions were converted to scaled x,y coordinates using CoordGen6f (H. D. Sheets, www2.canisius.edu/~sheets), and all straight-line distances between landmarks were generated in TmorphGen6b (H. D. Sheets, www2.canisius.edu/~sheets).

Distance data were analyzed using a multivariate analysis of covariance (MANCOVA) with population (Salado and Del Rio) as the independent variable and total length of shell as the covariate. Significance was accepted at the $\alpha = 0.05$ level. Regression analyses were performed on data averaged over 0.5 mm size classes to describe the relationship between length of shell and each variable measured using a single line fit. In addition, the software REGRESS (J. A. Muday, www.wfu.edu/~mudayja/prog.html) was used to simultaneously fit two lines to the same data using the method of Yeager and Ultsch (1989). The single-line and two-line regressions were compared (Pearson correlation coefficient) to determine best fit for the variable and group analyzed. To assess differences in shape between populations, principal-components analyses (PCA) were performed on the distances and scatterplots were used to visualize relationships between components.

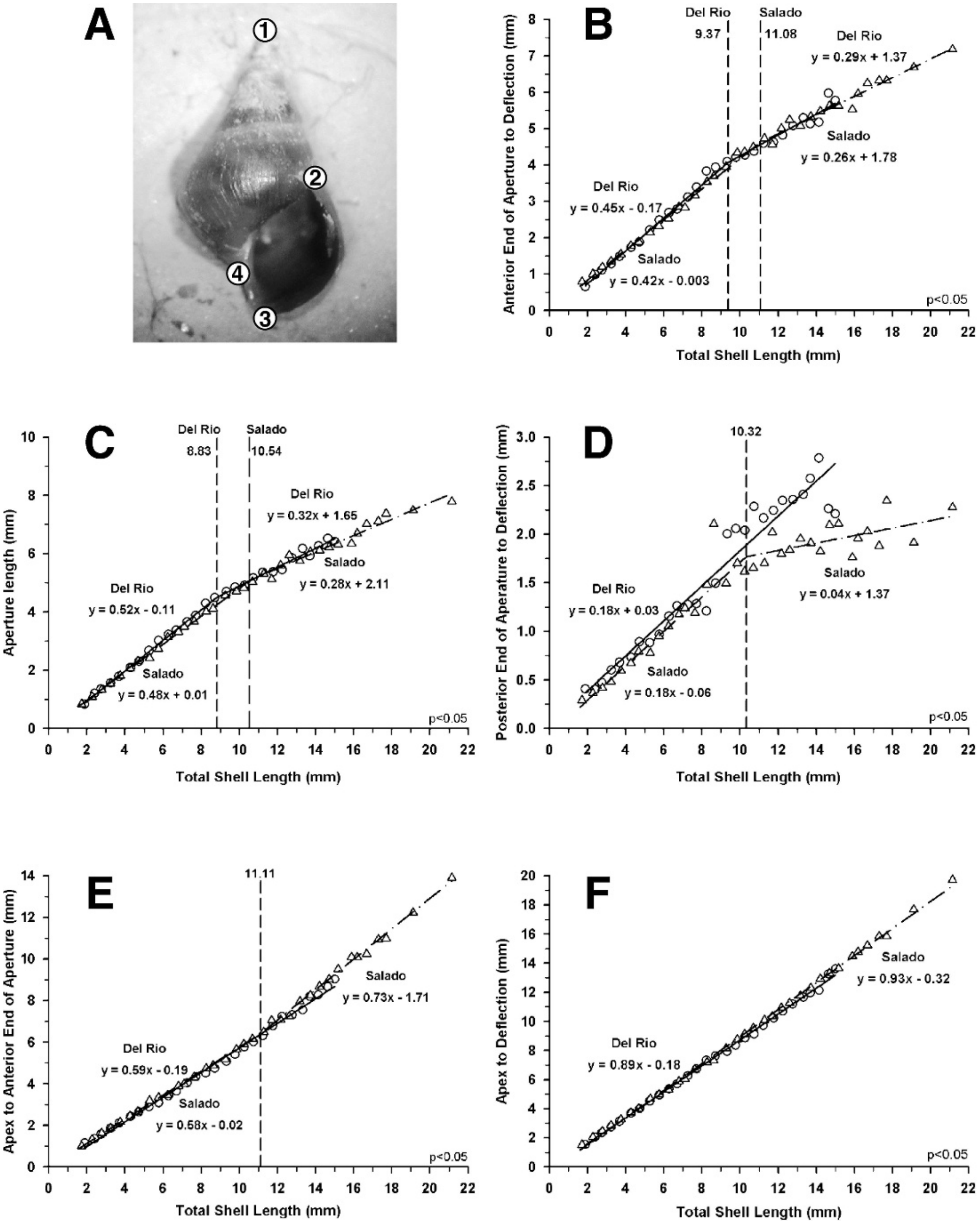

FIG. 1—(a) Landmarks used to obtain measurements of shells of snails, *Elimia comalensis*. Regression analysis of (b) apex to deflection versus total length of shell, (c) length of aperture versus total length of shell (changes in rate of snails from Del Rio occurred at 8.83 and 10.54 mm for snails from Salado), (d) posterior end of aperture to deflection versus total length of shell (changes in rate of snails from Del Rio occurred at 9.37 and 11.08 mm for snails from Salado), (e) apex to posterior end of aperture versus total length of shell (change in rate occurred at 11.11 mm for snails from Salado), (f) anterior end of aperture to deflection versus total length of shell (change in rate occurred at 10.32 mm for snails from Salado). Circles and solid line represent individuals from Del Rio, triangles and dotted lines represent individuals from Salado. Symbols indicate means for each size class.

RESULTS—In general, as the total length of shell (landmarks 1 and 3) increased, each of the other distances increased as well, regardless of population. However, the two populations differed in rates and pattern of growth among measured distances. The distance from apex to deflection (landmarks 1 and 4) increased at almost the same rate as total length (slope = 0.93 for Salado and 0.89 for Del Rio; $r^2 = 0.99$ and $P < 0.05$ for both), although this measure increased slightly faster in snails from Salado than in snails from Del Rio (Fig. 1b). In both groups, length of aperture (landmarks 2 and 3) increased at about one-half the rate of total length of shell initially (slope = 0.48 for Salado and 0.52 for Del Rio; $r^2 = 0.99$ and $P < 0.05$ for both), but was followed by a slowed rate of increase (slope = 0.32 for Del Rio and 0.28 for Salado; $r^2 = 0.99$ and $P < 0.05$ for both) after 8.8 mm in Del Rio and 10.5 mm in Salado (Fig. 1c). This measure consistently increased faster in snails from Del Rio than in snails from Salado. Distance from posterior end of aperture to the deflection (landmarks 2 and 4) increased at about one-half the rate of total length of shell initially (slope = 0.45 for Del Rio and 0.42 for Salado; $r^2 = 0.99$ and $P < 0.05$ for both), but was followed by a slowed rate of increase (slope = 0.29 for Del Rio and 0.26 for Salado; $r^2 = 0.99$ and $P < 0.05$ for both) after 9.4 mm in snails from Del Rio and 11.1 mm in snails from Salado (Fig. 1d). This variable consistently increased faster in snails from Del Rio than in snails from Salado. Distance from apex to posterior end of aperture (landmarks 1 and 2) increased about 60% as fast as total length of shell in both groups of snails (slope = 0.59 for Del Rio and 0.58 for Salado; $r^2 = 0.99$ and $P < 0.05$ for both), but after 11.1 mm length of shell, this variable increased by almost 75% of total length of shell in snails from Salado (slope = 0.73; $r^2 = 0.99$ and $P < 0.05$; Fig. 1e). Distance from anterior end of aperture to the deflection point (landmarks 3 and 4) increased about 20% as fast as total length of shell in both groups of snails (slope = 0.18 for both; $r^2 = 0.94$ for Del Rio, $r^2 = 0.99$ for Salado, $P < 0.05$ for both). However, at a length of shell of 10.3 mm, the increase in this distance slowed to 0.04 ($r^2 = 0.92$ and $P < 0.05$) relative to total length of shell in snails from Salado (Fig. 1f).

Principal-components analysis showed similar patterns as regression analyses. The first component, PC1, accounted for 98.7% of the variation and was a measure of size. The second component, PC2, accounted for 0.9% of the variation and was a measure of size of aperture relative to size of shell. The third component, PC3, accounted for 0.4% of the variation and was a measure of size of aperture to width of shell. Scatterplots of comparisons between PC1, PC2, and PC3 show small individuals from both populations changed shape in a similar fashion (Figs. 2a, b). At points at about 8–11 mm in length, individuals began to deviate from this pattern and variability increased.

DISCUSSION—Like other pleurocerids (e.g., Houp, 1970; Aldridge, 1982; Diamond, 1982), snails in the genus *Elimia* are relatively long-lived (Heller, 1990), with lifespans reported ≤11 years (Dazo, 1965; Stiven and Walton, 1967; Mancini, 1978; Payne, 1979). *Elimia* appear to have perennial life cycles (sensu Calow, 1978), giving populations complex age structures that may obscure growth patterns (Huryn et al., 1994). In those *Elimia* for which life-history information is available, patterns of oviposition, growth, and structure of cohorts are similar (Dazo, 1965; Mancini, 1978; Smith, 1980, Huryn et al., 1994), with growth becoming asymptotic after about 2 years. The existing literature on growth of snails usually fits comparisons of two measures of growth (e.g., width of aperture and mass of body; Huryn et al., 1994) to a single regression line without looking for changes in relationships of data over ontogeny of populations. By using simultaneous linear regressions, we were able to quantitatively document the magnitude and change in rate of growth in *Elimia* as size increases.

Length of aperture, distance from posterior end of aperture to the deflection, and distance from anterior end of aperture to the deflection relative to total length of shell increased faster in snails from Del Rio than in snails from Salado. Distance from apex to aperture increased at about the same rate in all snails compared to total length, but when snails from Salado reached 11.1 mm, the rate of change increased 25%, producing overall faster growth in this dimension. Distance from apex to the deflection compared to total length of shell remained constant throughout growth for all individuals, but this relative distance increased faster for snails from Salado than for snails from Del Rio.

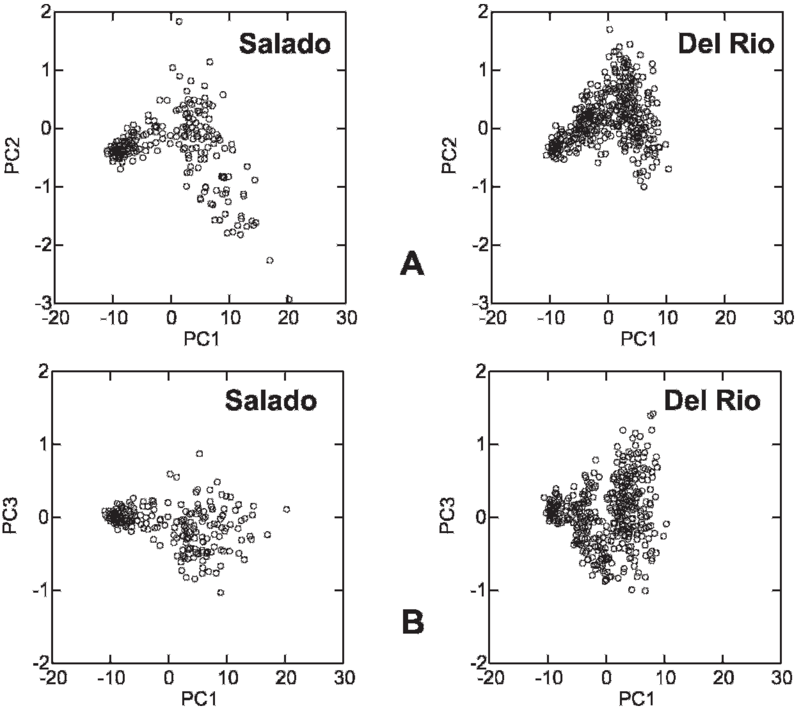

FIG. 2—(a) Scatterplots of PC2 versus PC1 and (b) scatterplots of PC3 versus PC1 resulting from principal-components analyses of size and shape measurements of snails, *Elimia comalensis*.

Increases in distances from apex to aperture, aperture to deflection, and length of aperture started out at about one-half what total length of shell increases were (0.4–0.6), suggesting controlled deposition of shell to affect morphological changes. Deposition of shell is influenced by both genetic and environmental factors (Trussell and Etter, 2001), although our data were not chosen to distinguish between the two. Apparent differences in relative rates of growth may have arisen because we used two-dimensional distances, and shells grow by coiling in three dimensions. However, all changes in growth were significant and clearly showed similar patterns in both populations. The only distance that increased at almost the same rate as total length of shell was from apex to the deflection. Distance from anterior end of aperture to the deflection increased slowly compared to overall increases in length of shell (0.18) initially and snails from Salado slowed almost to a stop (0.04). In snails from Salado, there was a point of inflection at lengths of shell between 10.5 and 11.1 mm where relative rate of change in four of the five variables changed. Only one of these changes in rate was positive (distance from apex to aperture). The other three changes were all decreases in rate, with rate of relative change in length of aperture decreasing 42%, in distance from aperture to deflection decreasing 38%, and in distance from bottom to the deflection decreasing 77%. Snails from Del Rio, however, only had points of inflection for relative rates of increaase in length of aperture and in distance from aperture to the deflection. Interestingly, the percentage change in these rates was the same between the two populations, but occurred earlier in snails from Del Rio.

Because this is the first study to apply simultaneous linear regressions to *Elimia*, direct comparisons of our data to other published sources are not possible. However, like previously cited works (e.g., Huryn et al., 1994), our data suggest growth to an asymptotic point where growth slows. This slowing in growth generally is related to reaching reproductive age in freshwater snails (Dillon, 2000). Our data also suggest that as well as slowing growth at a certain size, shape of shell changes from the growth pattern seen in all shells to an increase in seemingly random variance in shape. Many factors could be affecting this change in shape including population density and predation. One factor we currently are studying is use of habitat in the spring systems. Juvenile *E. comalensis* generally are found among algal filaments, while adults tend to inhabit open water. Preliminary data (RLM and KEP, unpublished) suggest that seasonal and temporal changes in use of habitat may play a role in the observed patterns of growth.

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