Notes and Comments

Experimental Evidence for the Rapid Evolution of Behavioral Canalization in Natural Populations

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ABSTRACT: Canalization—the evolutionary loss of the capacity of organisms to develop different phenotypes in different environments—is an evolutionary phenomenon suspected to occur widely, although examples in natural populations are elusive. Because behavior is typically a highly flexible component of an individual's phenotype, it provides fertile ground for studying the evolution of canalization. Here we report how snail populations exposed for different lengths of time to a predatory crab introduced from Europe to America exhibit different degrees of canalization of an adaptive antipredator behavior: soft tissue withdrawal, measured as angular retraction depth. Where crab-snail contact is shortest (60 years), snails showed the highest behavioral flexibility. Where crabs invaded 110 years ago, snails showed significantly less behavioral flexibility, and where the interaction is ancient (Europe), snails exhibited highly canalized behavior. Selection therefore appears to have acted rapidly to increase canalization in wild snail populations, leading ultimately to the hard-wired behavior seen in European conspecifics.

Keywords: phenotypic plasticity, canalization, biogeography, adaptation, predator-prey, invasive species.

Introduction

Flexible phenotypes should evolve to become less labile—more canalized (Waddington 1942)—under prolonged stabilizing selection and when selection regimes are stable over evolutionary time. Despite general consensus about the conditions favoring the evolutionary loss of phenotypic flexibility (Waddington 1942; Maynard Smith and Sondhi 1960; Scheiner 1993; Rice 1998; Siegel and Bergman 2002; Wilkins 2003; Hollander 2008), examples of canalization in the wild remain elusive. This is true even for behaviors, arguably the most labile component of an animal's phenotype. Here we use the documented invasion history of the European green crab *Carcinus maenas*, introduced to New England from Europe in the nineteenth century (Scattergood 1952), to investigate the evolution of behavioral canalization in a species of prey that has coexisted with this generalist predator for different amounts of time.

In Europe, an intertidal snail, the flat periwinkle *Littorina obtusata*, has coexisted with green crabs since at least the last glacial retreat (approximately 10,000–12,000 years; Roman 2006). In contrast, records place green crabs in the southern Gulf of Maine (United States) at about 110 years ago and in the northern Gulf of Maine at about 60 years ago (Scattergood 1952). The introduction of these crabs to America affected the selection regime and consequently the shell form of native flat periwinkles (Vermeij 1982; Seeley 1986; Trussell 2000; Trussell and Smith 2000; Edgell and Rochette 2008). However, whether or not this altered selection regime also drove changes in the periwinkle's antipredator behavior has received little attention (Edgell et al. 2008).

If canalization can be recognized as trait stability in variable environments, then we can test for canalization in the flat periwinkle by measuring the magnitude of behavioral changes when exposed to different experimental conditions. If canalization exists, behavior should remain stable. Soft tissue withdrawal (i.e., angular retraction; fig. 1) is an adaptive defense in *L. obtusata* faced with shell-entering *C. maenas* green crabs (Edgell et al. 2008). Therefore, if depth of retraction is plastic, periwinkles exposed to effluent from green crabs should retract deeper than controls. If retraction behavior is canalized, however, depths should be similar whether periwinkles are exposed to risk or not. Here we predict periwinkles with a longer interaction history with green crabs will have more canalized behavior, because (1) shell-entry selection has had longer to eliminate individuals that do not maintain a well-

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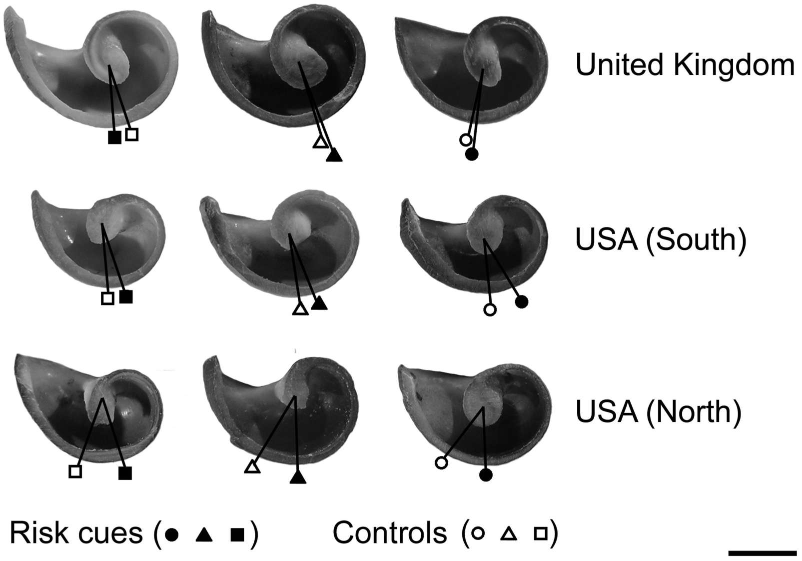

Figure 1: Representative shells illustrating mean angular retraction of snails exposed to chemical risk cues (*solid symbols*) versus controls (*open symbols*) after 35 days in the laboratory. Different symbol shapes indicate different populations within that geographic region, corresponding to symbols in figure 2. Scale bar = 4 mm.

defended posture when crab cues are either missed or temporarily absent or (2) green crab densities have been historically more variable in more recently invaded regions. We predict, therefore, behaviors of United Kingdom (U.K.) periwinkles to be more canalized than U.S. conspecifics, and within the United States, periwinkles from the southern Gulf of Maine to have more canalized behavior than those from the northern Gulf of Maine.

Methods

Littorina obtusata snails (shell breadth 8–11 mm) were collected from rocky shores in the United Kingdom (54°26′29″N, 00°32′09″W; 54°06′25″N, 00°07′52″W; 53°17′00″N, 04°37′02″W) and the northern (44°48′31″N, 66°58′39″W; 44°48′46″N, 66°57′05″W; 44°49′10″N, 66°57′15″W) and southern Gulf of Maine (42°25′13″N, 70°54′14″W; 42°25′48″N, 70°55′32″W; 42°33′48″N, 70°46′13″W). Male *Carcinus maenas* crabs (carapace width 46–73 mm) were from St. Andrews, Canada (45°04′N, 67°02′W). Experiments began within 14 days of first site collection; between collection and the experiment, periwinkles were held in flowing seawater and fed ad lib. with fucoid macroalgae. Experiments were conducted in a quarantined seawater lab at the University of New Brunswick (seawater salinity 32 ppt; temperature 12.5°C).

Angular retraction—the angular withdrawal depth of a snail into its shell after exposure to artificial prodding simulating a shell-entry attack by a crab—was marked on the outer shell wall for each snail at the beginning and end of the experiment (35 days), then measured digitally upon completion of the experiment (following methods described in Edgell and Rochette 2008; Edgell et al. 2008). The pre- and postexperiment measurements were used to calculate percent change in angular retraction between days 0 and 35. Tissue mass was measured nondestructively (Palmer 1982) at the start and end of the experiment to estimate somatic growth rate (mg/d).

Each aquarium (3-L capacity) contained four individually marked snails from one source population. All snails were fed ad lib. with macroalgae. Seawater was aerated and replaced with fresh seawater every 24 h. Crabs were caged in half of each population's 10 aquaria, yielding 5 treatment and 5 control aquaria per population. Snails were enclosed in smaller mesh cages to allow chemical exchange but prevent physical contact with crabs. Crabs were fed 3 g of fish (haddock) twice per week; fish was also added to control cages.

Nested ANCOVA tested for the effects of treatment and region (fixed), population [region] (random), and replicate cage [treatment, region, population] (random). ANCOVA tested for differences in percentage change in angular retraction, using somatic growth as a covariate. ANCOVA for somatic growth included initial body mass as a covariate. When appropriate, nonsignificant interactions involving covariates ($P \geq .25$) were removed (Hendrix et al. 1982). Model residuals conformed to assumptions of normality (Shapiro-Wilk, $P \geq .21$) and equal variances (Levene's, $P \geq .13$). The JMP version 5.1 statistical software was used for analyses.

Testing for Physical Constraints on Retraction

Retraction depth may be physically constrained by (1) body size relative to internal shell volume and (2) shell shape, specifically shell elongation (Vermeij 1987, p. 220). Constraints were tested only among snails exposed to predator cues, because they are expected to retract more deeply than nonthreatened conspecifics.

For *L. obtusata*, body mass is smaller in snails with relatively thick shells, presumably because shells thicken internally, and this can reduce the internal space available to house tissue (Trussell 2000). Therefore, the packing of soft tissues into a shell should become increasingly constrained as body mass increases despite shell size and thickness remaining constant. In other words, if internal shell volume is constraining maximum retraction depth, then the deepest-retracting populations should also have the smallest body mass (per given shell size and thickness). We tested this hypothesis by comparing tissue masses among regions and including size-adjusted shell mass as a covariate in ANCOVA (i.e., size-adjusted shell mass is an indicator of overall shell thickness and thus internal shell volume; residuals were calculated from the shell height by shell mass relationship after ensuring mass increased with height similarly in all regions [ANCOVA slope term: $F_{2,152} = 1.59$, $P = .21$]). Model residuals for ANCOVA met the assumption of normality (Shapiro-Wilk, $P = .65$) and variances were slightly heteroscedastic (Levene's, $P = .03$), but ANCOVAs are robust to such mild departures from equal variance (McGuinness 2002).

Gastropod species with more elongate shells (i.e., shell height divided by breadth) retract more deeply than species with more rotund shells (Edgell and Miyashita 2009), so it was important to test for regional differences in *L. obtusata* shell elongation to ensure shell shape variation did not confound variation in retraction depth. ANCOVA tested for regional differences in angular retractions as a function of shell elongation; model residuals conformed to assumptions of normality (Shapiro-Wilk, $P = .93$) and equal variance (Levene's, $P = .56$).

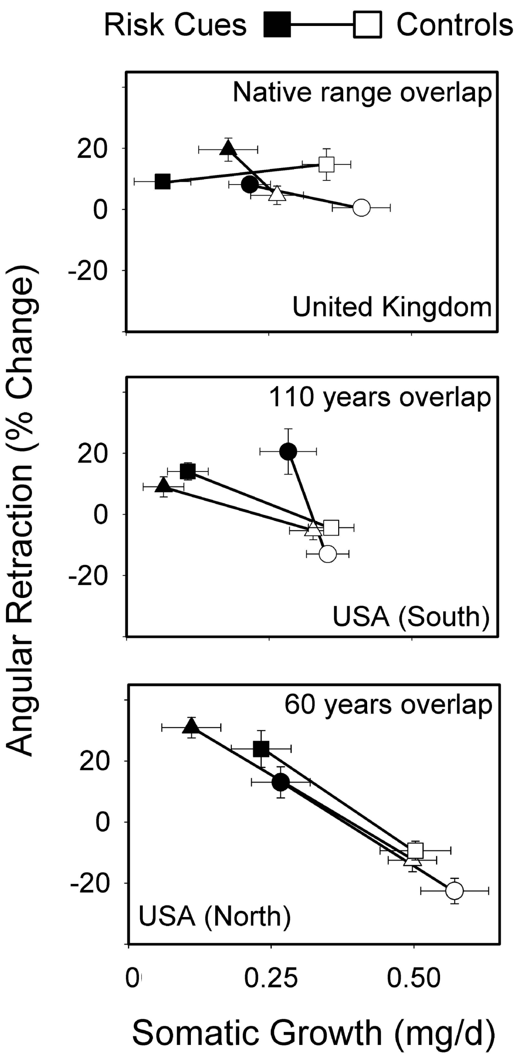

Figure 2: Variation in angular retraction (a measure of withdrawal depth) as a function of variation in somatic growth (wet mass + SEM) in snails exposed for 35 days to predator risk cues (*solid symbols*) versus controls (*open symbols*). Different symbol shapes indicate different populations within that geographic region. Differences in withdrawal depth between snails exposed to crab risk cues versus controls differed among the three geographic regions (ANCOVA, treatment × region effect, $F_{2,72} = 11.06$, $P < .0001$), although withdrawal depth was similar among populations within regions (ANCOVA, treatment × population [region], $F_{6,72} = 1.62$, $P = .15$). Subsequent analysis of withdrawal involving only American regions also showed a significant effect (ANCOVA, treatment × region effect, $F_{1,48} = 6.98$, $P = .0111$). Snails also reduced somatic growth in response to risk (ANCOVA, $F_{1,72} = 66.94$, $P < .0001$), with similar reductions among regions (ANCOVA, treatment × region effect, $F_{2,72} = 1.78$, $P = .18$).

Results and Discussion

Consistent with predictions, regional differences in the flexibility of withdrawal behavior (i.e., size of difference between retraction depth in the presence and absence of crab risk cues) varied as a function of crab-snail coexistence time (fig. 2). The U.S. periwinkles were significantly more flexible than the U.K. periwinkles ($F_{2,72} = 11.06$, $P < .0001$; fig. 3) and periwinkles from the northern United States more so than from the southern United States ($F_{1,48} = 6.98$, $P = .011$; fig. 3). In other words, periwinkles had greatest behavioral flexibility where contact with green crabs is most recent (northern Gulf of Maine), least where

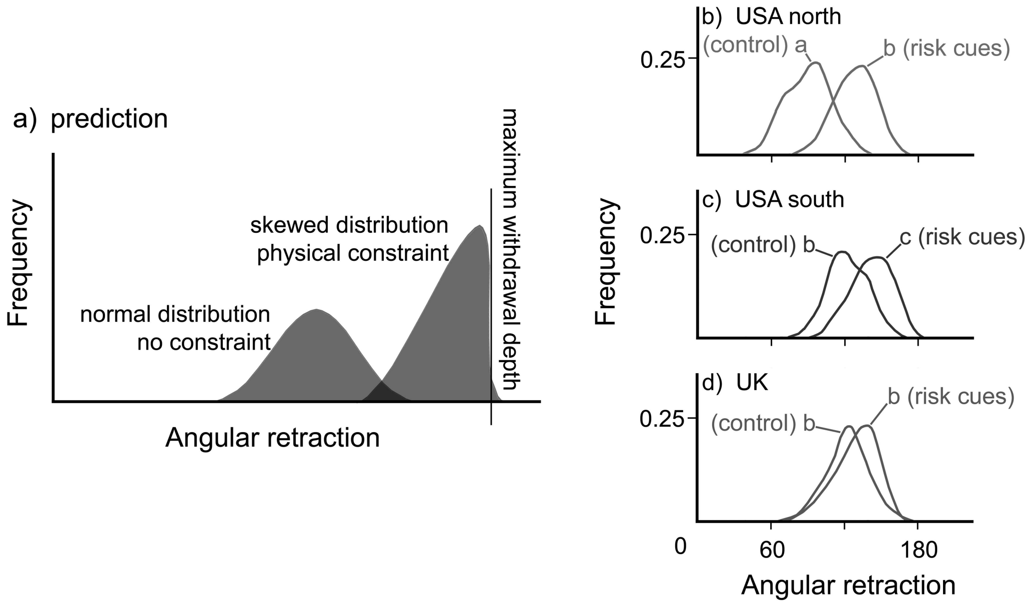

Figure 3: Frequency distributions of angular retraction (a measure of withdrawal depth). *a*, Theoretical test for physical constraints on soft-tissue retraction depth. Observed distributions (*b*–*d*) were fitted with a smooth curve (JMP ver. 5.1 software). All observed data distributions were normal (Shapiro-Wilk test, $P \geq .13$) except for the United Kingdom distribution under risk cues (Shapiro-Wilk test, $n = 53$, $P = .035$). Common letters adjacent to each distribution indicate statistically similar means ($P < .05$, Tukey's multiple comparison test across all regions and treatment groups).

contact is most ancient (United Kingdom), and intermediate where contact is of intermediate duration (southern Gulf of Maine; Tukey's post hoc multiple comparison among all regions and treatment groups, $P < .05$; fig. 3). Furthermore, significantly greater flexibility in northern U.S. populations than in southern U.S. populations (figs. 2, 3) suggests canalization can occur quickly, within 50 years. The prolonged interaction between periwinkles and shell-entering crabs in the United Kingdom appears to have led those snails toward a stereotyped (canalized) behavioral state—perpetually well defended whether in the presence of predation risk cues or not (fig. 3*d*).

Two mechanisms could cause U.K. populations to be more canalized than U.S. conspecifics. (1) Prolonged predation pressure by green crabs has selectively removed ill-defended periwinkles from U.K. populations, unlike in the southern Gulf of Maine and even less so in the northern Gulf of Maine, where green crab predation has had significantly less time to structure the periwinkle phenotype. Hence, centuries of shell-entry predation in the United Kingdom has selectively removed individuals that do not display defensive postures when green crab cues are either missed or temporarily absent—an ongoing process in the Gulf of Maine. (2) Invasive species typically have patchy distributions when they invade a new region, and we suggest that U.S. periwinkles have probably experienced more heterogeneous green crab predation intensity than U.K. conspecifics over the past century. Consistent with results, plasticity theory predicts the phenotypes of periwinkles in the United States should therefore be more plastic than U.K. conspecifics, and conspecifics in the northern Gulf of Maine should be more plastic than those in the southern Gulf. To test hypothesis 2 robustly, however, we would need historical data on green crab density and predation rates, and those data are not available. Incidentally, green crab densities appear to have become more similar in northern and southern parts of the Gulf of Maine, including four of our six collection sites (e.g., data from Edgell and Rochette 2008 support estimates of green crab density at 22 and 56 catches h^{-1} at two northern U.S. sites, compared with 26 and 41 catches h^{-1} in the southern United States).

Regional differences in the diversity or abundance of shell-entry predators other than green crabs may also contribute to variation in predation risk that, in turn, influences behavioral flexibility. For example, during a survey of intertidal communities in the Gulf of Maine in 2003 (data for 26 sites, including four sites used in this study, are available in the appendix in the online edition of the *American Naturalist*), one of us (T. C. Edgell) found that sea stars (*Asterias* spp.), which prey on gastropods via shell entry, were rare at northern sites and common at southern sites. Also, juvenile lobsters (*Homarus americanus*) and Asian shorecrabs (*Hemigrapsus sanguineus*) were common at southern sites despite being absent from northern sites, but this is probably unimportant because these are shell-crushing predators. We know relatively little of the *Asterias*-*Littorina* interaction in this region, although extensive fieldwork throughout the Gulf of Maine leads us to believe that *Asterias* is not an important predator of *Littorina obtusata*, because *L. obtusata* is found primarily in the *Ascophyllum* canopy, whereas *Asterias* spp. are found on hard substrates and typically forage on blue mussels (*Mytilus edulis*). So, although other predator species occur along Gulf of Maine shores, the most common molluscivore found at midshore, in contact and interacting with *L. obtusata*, is the European green crab. A field-based test for regional incidences of shell-entry predation would be enlightening. Such a test in the northern Gulf of Maine says shell entry is important (Edgell and Rochette 2008), though no such tests have been conducted in either the southern Gulf of Maine or United Kingdom regions (with exception of a field experiment in Ireland; Ebling et al. 1964).

Predator-avoidance behaviors such as fleeing from tidal pools, crawling out of water, burrowing into sediments, and hiding under rocks typically yield reduced opportunities to feed (Palmer 1990; Trussell et al. 2004, 2006; Brookes and Rochette 2007). Although our experiments were not designed to monitor avoidance behaviors directly, flat periwinkles from all regions showed lower somatic growth when exposed to crab risk cues (fig. 2), indicating such a trade-off between feeding and hiding probably occurred. The feeding-hiding trade-off may also have fitness consequences because fecundity in gastropods is often a positive function of body size (Spight and Emlen 1976; Hart and Begon 1982). Intuitively, reduced feeding should lower fitness by limiting energy available for reproduction; however, slower growth and smaller body size can also increase fitness of periwinkles that rely on the availability of cracks and crevices to escape predation (Rochette and Dill 2000).

Physical Constraints

Littorina obtusata bodies consist of 72% water ($n = 216$, ± 2.63 SD); therefore, a fixed inner shell volume coupled with a largely incompressible body will hypothetically constrain maximum withdrawal depth. We may detect such a constraint by inspection of the angular retraction frequency distributions: an asymmetrical distribution with an abrupt upper retraction value would indicate a constraint (fig. 3*a*, skewed distribution). Conversely, a normal frequency distribution (fig. 3*a*, normal distribution) suggests no such constraint is operating. Frequency distributions for U.S. periwinkles exposed to risk cues and controls were normal (fig. 3*b*, 3*c*), as was the distribution for U.K. periwinkles in the control treatment (fig. 3*d*). However, U.K. periwinkles exposed to risk cues exhibited a significantly skewed distribution even though they did not retract as deeply as southern U.S. snails (fig. 3*d*), suggesting upper retraction depth was constrained in the United Kingdom but not in the U.S. populations. This hypothesis implies that directional selection for deeper retraction may be acting on both U.S. and U.K. snails; however, different evolution of shell shape imposes constraints on U.K. retraction that is either not realized or has been circumvented by the evolution of U.S. conspecifics. We can investigate this problem further by analyzing two aspects of shell morphology most likely to constrain retraction depth: (1) internal shell volume, a function of size-standardized shell mass or thickness (i.e., littorinid shells thicken internally, and thus, more massive shells per standard shell length have less internal volume than thinner shells; see Trussell 2000; Brookes and Rochette 2007) and (2) shell elongation, whereby species with more elongate shells can retract more deeply into them (Edgell and Miyashita 2009).

Shell thickness may impose a physical constraint on retraction by limiting the amount of flesh that can be withdrawn deeply into the shell. In other words, for a standard shell size, retraction depth should be proportional to internal shell volume (or shell thickness) and inversely proportional to body volume. If the deepest-retracting populations also have the smallest body mass per given shell size and thickness, then results in figure 3 suggest periwinkles from the southern United States (the deepest retractors under risk cues) should have significantly smaller adjusted body masses than conspecifics from either the northern United States or the United Kingdom, and those from the latter two populations should have similar adjusted body masses since they retracted to similar depths when exposed to risk cues (Tukey's, $P > .05$; fig. 3). Although adjusted body mass did indeed vary among regions (ANCOVA, $F_{2,158} = 11.37$, $P < .0001$), differences were not as expected if a physical constraint was limiting retraction depth. For example, the mean adjusted body mass of southern U.S. and U.K. periwinkles was statistically similar (Tukey's, $P > .05$) despite the former being capable of significantly deeper retraction (fig. 3*c*, 3*d*). Conversely, mean adjusted body mass of northern U.S. periwinkles was greater than U.K. periwinkles (Tukey's, $P < .05$) despite retraction angles in both groups being similar (fig. 3).

Shell shape might also constrain retraction depth. Shell elongation has long been suspected to facilitate deeper soft-tissue withdrawal depth in gastropods (Vermeij 1987, p. 220), a hypothesis that was only recently confirmed (Edgell and Miyashita 2009). In general, species with more elongate shells retract more deeply than species with rotund shells. However, this pattern only emerges after contrasting distantly related species or individuals of a species with highly variable shell forms. For example, shell elongation was unrelated to angular retraction within or among four *Littorina* species (i.e., *L. obtusata, L. littorea, L. scutulata, L. sitkana*) despite significant interspecific variation in shell shape. *Littorina obtusata* shell elongation was approximately equal among the three regions studied here (ANCOVA with shell height covariate, population nested in region, $F_{2,6} = 2.4897$, $P = .16$). Therefore, retraction depth can vary substantially without variation in shell elongation (Vermeij 1987; Edgell and Miyashita 2009), and putative differences in shell shape cannot explain the shallow retraction of U.K. periwinkles relative to southern U.S. conspecifics.

Conclusion

Although regional differences in flexibility could be caused by canalization or a physical constraint, our results are more consistent with canalization. Nonetheless, in the eyes of natural selection, the behaviorally inflexible U.K. snails are equally defended against shell-entering *Carcinus* with or without prior detection of waterborne crab cues. This is unlike U.S. conspecifics, whose relationship with *Carcinus* is younger by millennia and which exhibit appropriate fully defensive postures only in the presence of crab scent.

Biological invasions offer an invaluable opportunity to study phenotypic evolution because species' contact histories are uncharacteristically well defined, and interactions occur on a fascinating evolutionary timescale—decades to hundreds of years—longer than the <10-year timescale studied by experimental biologists, yet significantly shorter than the thousand- to million-year timescales studied by paleontologists. Such timescales offer intriguing glimpses of the earliest microevolutionary responses of wild populations. Here we use a known history of range expansion by the U.K. green crab to provide compelling evidence of rapid behavioral canalization in natural populations of flat periwinkle: the longer the interaction with U.K. green crabs, the more hard-wired their antipredator behaviors become.

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European green crab after feast of American littorinid snail (photograph by Timothy C. Edgell).