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Functional Significance of Varices in the Muricid Gastropod *Ceratostoma foliatum*

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Abstract. Functional significance of varices in the muricid gastropod *Ceratostoma foliatum* was investigated from the standpoints of (1) frequency of landing in the two upside-down orientations after short vertical falls of less than five body lengths through seawater and energy costs of righting from these upside-down positions, and (2) scaling relationships of varix areas with other body dimensions. Field manipulations showed that *C. foliatum* occupied habitats that mostly permit short falls of less than five body lengths upon dislodgment, as might occur during predation by fish. After short vertical falls in the laboratory, animals landed 48% of the time on their aperture sides (upright), 15% on their right sides (on right and middle varices), and 37% on their left sides (on left and middle varices). These frequencies differed significantly from the expected frequencies calculated on the basis of the percentage circumference delineated by each varix pair (50%, 31%, and 19%, respectively). Righting from the right-side orientation was slower and four times more energetically costly than from the left-side orientation, underscoring the advantage conferred by animals, if not landing in the upright position after short falls, preferentially landing on their left sides. Removal of individual varices showed that the large, right varix is most influential in producing this "destabilization." Landings are biased to the side from which rightings are easiest due to a combination of the location of center of mass within the left side of the main body whorl and the broad right varix possibly acting as an upward-trailing vane.

Morphometric relationships of shell length, live weight, varix areas, aperture dimensions, and labial spine (tooth) length were investigated over a wide range of body sizes in an attempt to infer varix function. Aperture area scaled allometrically with length. Right-, middle-, and left-varix

areas also grew relatively larger as the animals increased in length. In contrast, combined varix areas around the aperture increased in direct proportion with aperture area, forming a broad shelf surrounding the aperture. We infer from this that, in addition to their effects on landing orientation from both long and short vertical falls, the varices of *C. foliatum* may function to protect the aperture, and thus protect the soft body parts that protrude from it during feeding and locomotion.

Introduction

The function of shell ornamentation in prosobranch gastropods has intrigued scientists for decades. Shell ornamentation is most well-developed in the family Muricidae, where it consists of ridgings, or varices, elaborated from thickenings of the outermost shell edge during growth. In the adult leafy hornmouth snail, *Ceratostoma foliatum*, three such varices predominate (Fig. 1). The newest varix is the right one. New varices are added in growth spurts, which causes the varices to shift position, with the present right one coming to occupy a new middle position, and the present middle one becoming a new left varix.

The precise function of shell sculpturing in *C. foliatum* and other muricid gastropods is not known, although suggestions include (1) stabilizing the shell in shifting substratum; (2) aiding in feeding; (3) supporting or protecting sensory structures; (4) perceiving vibration; (5) protecting the snail from predators; (6) strengthening the shell (as seen for thicker-shelled *Nucella lapillus*, which withstand predatory attacks by crabs better than thinner-shelled varieties); and (7) in *C. foliatum*, destabilizing the falling orientation such that landing is more often in the aperture-down position (Ebling *et al.*, 1964; Kitching *et al.*, 1966; Carter, 1967; Fotheringham, 1971; Spight and Lyons, 1974; Palmer, 1977; Vermeij, 1974, 1979, pers. com.;
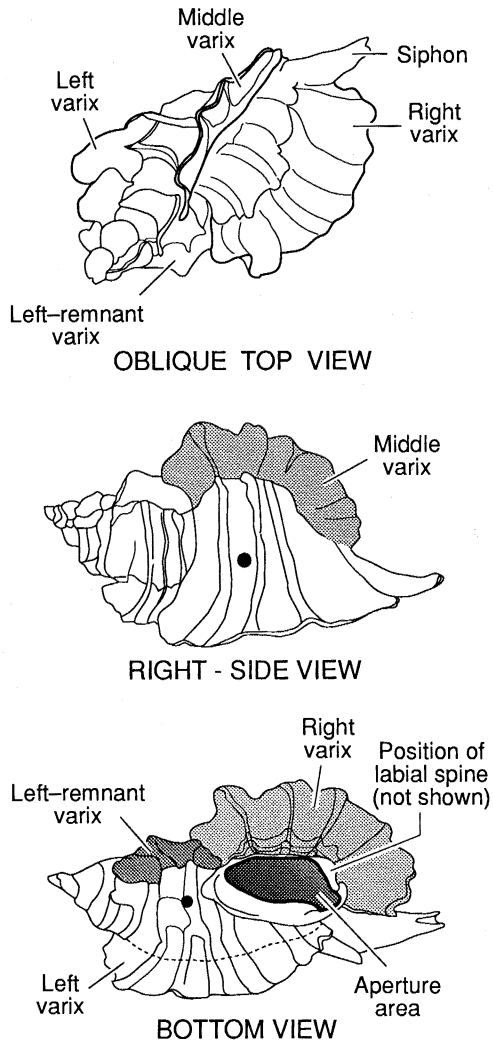
Figure 1. *Top:* Oblique plan view of *Ceratostoma foliatum* to show varix arrangement. *Middle* and *bottom:* Views from the right side and bottom, respectively, to show areas of right-, left-, middle-, and left-remnant varices, and aperture, as measured for allometry. The dots indicate the location of center of mass in a live but withdrawn animal.

servations (shown later) suggest that few individuals of this species occupy positions that permit even five body-lengths of free-fall to the bottom. Most would bump, roll, or slide, even from near-vertical slopes.

Second, Palmer suggests that kelp greenling prey upon *C. foliatum* by dislodging the snails and consuming their feet when they are exposed during righting. However, we have been unable, using the precipitin test of Pickavance (1970), to identify the presence of *C. foliatum* antigens in the stomach contents of 42 kelp greenling fish coexisting with *C. foliatum*. This is despite positive responses from stomach contents of kelp greenling experimentally fed on *C. foliatum*, and a robust response of *C. foliatum* antisera (induced in rabbits) to *C. foliatum* antigen preparations in control tests (unpub. data). *C. foliatum* lives most commonly in the low intertidal and subtidal regions to a depth of 30 m and feeds predominantly on barnacles and bivalves (Spight *et al.,* 1974; Spight and Lyons, 1974; Kent, 1981). Although little is known of its natural biology, its principal predators might be seastars, such as the large, fast-moving sunflower star, *Pycnopodia helianthoides,* rather than fish. If this is the case, dislodgment due to predation is less likely.

Third, although this by no means discounts a destabilizing function for the middle varix of *C. foliatum,* the fact that many other muricids have tri-radiate varices of spines rather than blades suggests that other selective factors are operating.

Finally, if the primary function of varices in *C. foliatum* is to provide a large right varix for protection or stability during locomotion and feeding, then the destabilizing function of the middle varix might be only secondarily important.

Two features of *C. foliatum's* growth are relevant to this introduction of varix function. First, the varices are produced relatively rapidly. Spight and Lyons (1974) recorded varix production about once per year in older animals, each one taking 1–2 months for completion. Our *in situ* scuba observations indicate that varix growth must be as rapid, or more so, in the field. We have only once observed a partially formed varix, indicating that varices are produced in growth spurts of extremely short duration or that they are produced secretively. In either case, it is clear that a fully formed varix is vital to the well-being of the animal. Second, the three-varix morphology of the adult snail is not typical of its entire life. While young (<25 mm), the snail produces multiple axial ribs, up to 7–10 per whorl. This changes to a three-varix pattern in the adult, suggesting that the three-varix morphology, whatever its function, is more important in older stages.

Palmer (1977) constructed his argument for varix function in *C. foliatum* around the premise that, on dislodgment and subsequent free-fall, it would be advantageous for the snail to land upright. He was not concerned

Morris *et al.,* 1980). Other possible paradigms are (8) camouflaging the snail (reminiscent of the shell debris employed by the carrier shell, *Xenophora conchyliophora*); (9) reducing or preventing rolling in currents; and (10) increasing apparent size to deter predators.

The problem for molluscan functional morphologists is that few of these hypotheses are testable. Even the elegant demonstration by Palmer (1977) that the middle varix of *C. foliatum* (see Fig. 1) acts to destabilize the animal's orientation during falling, causing it to land aperture down, is open to question.

First, the requirement for a falling distance of at least 10 body-lengths to ensure 35%–70% landing success (aperture down) would rarely be satisfied in *C. foliatum's* rock- and seaweed-strewn natural habitat. Our field ob-

with landing orientations other than upright, yet the other two landing orientations occurred with 43%–100% frequency, depending on height of fall, in his study (Palmer, 1977). Lacking any other information, similar values could be predicted from falls of the bump-and-roll type. Based on shell shape and angle of the varices (Fig. 2a), and discounting for the present any varix or center of mass influence on falling, an animal that landed randomly might be expected to land 50% of the time on its right and left varices (*i.e.,* upright), 31% on its right and middle varices (right-side posture), and 19% on its middle and left varices (left-side posture).

Two implications derive from these considerations, both of which focus on the advantages of landing in a left-side orientation over a right-side orientation. First, an animal should be able to right itself more readily, that is more quickly and with less energy expenditure, from the smaller-angled left-side orientation (Fig. 2c) than from the larger-angled right-side one (Fig. 2b). This is because the foot has a shorter reach to gain purchase on the substratum. In contrast, from the proposed less-favorable landing position (Fig. 2b), the foot must reach further and the shell be levered through a greater angle to right it. Note that righting from the "easy" orientation exposes the foot to lesser risk of predation than from the "hard" orientation. The second implication is that relative varix height affects the ability of the animal to right itself due to the change in the angles the animal experiences in relation to the substratum (Fig. 2b, c). Thus, a larger middle varix relative to the other varices favors the righting process from both easy and hard orientations by decreasing the distance that the foot must traverse. By the same token, a larger right varix impedes righting from the hard orientation by increasing the distance of foot extension. However, because a large right varix is required to produce eventually a large middle varix, any such argument of effect of relative varix sizes from the hard orientation is self-defeating.

Palmer's (1977) interest was in the destabilizing effect of the middle varix during falls mainly in excess of 10 body lengths in height. We are interested here in dislodgment effects from heights less than this, and especially in the energetic consequences of the animal landing and having to right from the left- and right-side orientations. We are also interested in the relationship of varix areas to other body dimensions, in particular to aperture area, since three varices combine to form a broad shelf surrounding the aperture, which may provide either protection or stabilization (Fig. 1, bottom). Hypotheses to be tested are (1) that landing orientations, other than ones ending with the animal upright, will favor the "easy" side, despite the smaller circumference occupied by this side; and (2) that righting times from the "easy" posture will be shorter than from the "hard" and, correlatively, that
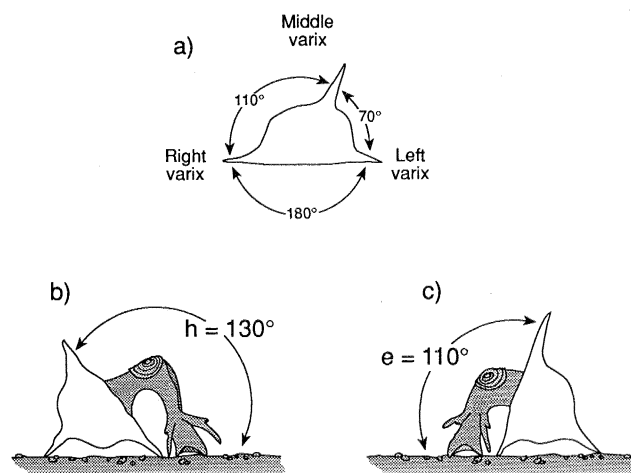

Figure 2. Schematic representation of varices and shell-righting postures in *Ceratostoma foliatum,* from head-on views. (a) Extent of circumference occupied by each varix-pair (110° is equivalent to 31% of the circumference; 70° to 19%). (b) Righting from the "hard" right-side landing orientation (resting on the middle and right varices). The angle "h" denotes the extent of traverse of the foot during righting from the "hard" orientation (130°). (c) Righting from the "easy" left-side landing orientation (resting on the middle and left varices). The angle "e" denotes the extent of traverse of the foot during righting from the "easy" orientation (110°).

energy expenditure will be less. Additionally, morphometric relationships of various shell structures are investigated and interpreted in an attempt to infer varix function.

Materials and Methods

Collection of animals

Animals were collected from subtidal locations in Barkley Sound, on the west coast of Vancouver Island, and in Telegraph Cove, West Vancouver, British Columbia. They were brought to the University of British Columbia and held in tanks supplied with recirculated seawater. Barnacle-encrusted rocks and mussels were provided as sources of food.

Field tests of falling distances

One hundred snails were selected at random during scuba dives at depths of 3–10 m along a 200-m section of Barkley Sound shoreline characterized by large boulders and rock walls. Each snail was manually dislodged and its unimpeded vertical falling distance recorded. The divers moved from habitat to habitat, selecting and testing the first individual of *Ceratostoma foliatum* seen in each. This procedure allowed a variety of habitats to be sampled, such as sloping and vertical rock walls and overhangs. Length of each snail was recorded to determine falling

distance relative to body length (apex to tip of siphonal canal).

VO₂ and righting times

VO_2 (oxygen consumption in microliters of oxygen per hour) of individual animals was measured in a closed respirometry system by means of a polarographic oxygen electrode coupled with a DATACAN data acquisition and analysis program (SABLE Systems Ltd., Salt Lake City). A stir-bar in the chamber ensured continuous and thorough mixing. Temperature was maintained at 12°C, the same as in the holding tanks. Respirometers were made of clear plastic and varied in size (85, 120, and 700 cm³) for use with different-sized animals. The snails were placed in an aperture-down position in the chamber and allowed to rest for 20 min while the system equilibrated. Oxygen consumption was then measured for 20 min to establish a resting VO_2. A narrow-gauge wire hook inserted into the chamber through a small hole in the top was used to flip each snail randomly to either its right ("hard") side or its left ("easy") side. It took less than 5–10 s to flip a snail onto its side. The snails were observed as they righted themselves and times of the following specific events were recorded: (1) appearance of the snail's foot from under the operculum, (2) attachment of the snail's foot to the bottom of the chamber, and (3) completion of righting, as defined by the settling of the shell onto the back of the snail. Righting time was measured as the time from first appearance of the snail's foot to when the shell settled over the back of the snail. Oxygen consumption was recorded during the righting episode. After the 20-min rest period, the snail was flipped onto its other side and the procedure repeated. Three VO_2 values were generated for each animal from this procedure: (1) normal upright resting VO_2 (snails that crawled in the chamber were not tested), (2) VO_2 when righting from the easy orientation, and (3) VO_2 when righting from the hard orientation.

VO_2's were multiplied by righting times from each upside-down orientation to give absolute cost in microliters of oxygen for each righting episode. Costs in microliters of oxygen were converted to joules by multiplying by an oxycalorific coefficient (Q_{ox}) of 21.10 mJ · µl O_2^{-1}, representing an accepted value for catabolism of carbohydrate (Elliot and Davison, 1975). This value was chosen because most gastropods rely on glycogen stores for energy during activity (Carefoot, 1987).

Landing frequencies

To determine the frequency of landing in each of the three orientations, upright, left side (easy), and right side (hard), 137 snails of varying size were dropped in aquaria with seawater depths about 5 times the length of the snail. We chose this depth because (1) we did not wish to invoke

the destabilizing effect of the middle varix, shown by Palmer (1977) to occur at depths greater than 10 bodylengths, and (2) we believed from our field observations that short falls, or bump-and-roll falls, would be most commonly experienced by snails in the field. Each snail was held just below the water surface and released. Release positions were random. Each snail was tested 10 times and the average landing frequency calculated. After this, the length of each snail was measured.

In another series of experiments to test the effect of varix removal on landing frequency, snails were dropped 20 times from random release positions and their landing orientations noted, then dropped 20 more times after removal of a single varix. Varices were removed by grinding them down flush with the shell surface with a rotary grinder. Fifty snails were used for each of the three treatments, or 150 snails total. A given landing orientation was calculated as the mean percentage of 50 animals each dropped 20 times. Before-and-after comparisons were done on arcsine-transformed percentage values using either paired Student's t tests or Wilcoxon signed-rank tests, depending on whether the data were normally distributed.

Varix angles and righting angles

A protractor was used to measure the angles between varices shown in Figure 2a. To standardize the measurements, the middle of the protractor was aligned with the siphon and upward-facing middle varix. Angles through which a snail's foot had to traverse during righting from the two upside-down landing positions shown in Figure 2b and 2c were also measured with a protractor. In this case, the middle of the protractor was aligned with the upward-facing varix in each position. The angles were determined for 88 shells ranging in length from 25–82 mm.

Center of mass

Center of mass with the snail in the withdrawn position was ascertained by suspending five live snails of varying sizes (16–37 g) from threads attached at about midpoint in their right and middle varix edges, and from a point near the siphon. Each snail was suspended in seawater successively from each of the three positions. Centers of mass were estimated from the point of intersection of the three lines generated by following the visual extensions of the threads from which the animals were hung down into the body of the snail. Penciled reference marks on the shells were used to help assess the point of intersection of the three lines. Changes in center of mass on removal of varices were estimated in the same way, except that hanging positions were adjusted depending on which varix was being removed.

Morphometry

The following morphometric measurements on perfect, uneroded *C. foliatum* shells were made: areas of the three main varices and left-remnant varix (described below), aperture area, aperture length, total shell length including siphon, labial spine (tooth) length, and live body weight (measured in air with the animal retracted into its shell). The left-remnant varix constitutes a remnant of the previous left varix that abuts on the current right varix to form a combined right-shelf area of larger dimension (see Fig. 1, bottom). This abutment is often not perfect, yet visual analysis of many shells suggests that the animal may use this remnant as a guide to where to terminate growth of each new varix. The end result of the juxtaposition of these two varices, and the surface area of the left varix, is a broad shelf surrounding the aperture.

The labial spine projects downward from the anterior-right aperture margin. It is an extension of a shallow collar that borders the aperture on the right-hand side. It is this collar that ultimately extends during growth to form the new right varix, and the spine remnant can be seen embedded in the upper surface of each preceding varix. Its function may be to anchor the snail during feeding, as surmised for other gastropods (Paine, 1966). Spine length was defined as the magnitude of its extension above the rim of the collar.

Varix and aperture areas were determined by drawing their outlines at 8-power magnification using a Leitz drawing tube, then analyzing with a SIGMA-SCAN area-measurement software system (Jandel Scientific, California).

Allometric or isometric relationships between the morphological features were investigated with standard least-squares linear regressions calculated on log-transformed values for several combinations of variables. The slope (*b*) of a regression is often underestimated due to error in measurements of the independent variable (LaBarbera, 1989). To compensate for this underestimation, reliability ratios (*k*) were calculated (as described below) and the log-log transformed slope (*b*) was multiplied by k^{-1} to produce a corrected log-log slope (β) (Fuller, 1987; Harvey and Pagel, 1991; Johnson and Koehl, 1994). To calculate *k* for length measurements, the lengths of 10 shells were measured three times. The first set of values was regressed on the second set of values, the first on the third, and the second on the third. The mean *r* for these regressions was used as the value of *k*. To calculate *k* for area measurements, the areas of 10 circles were calculated in two ways: (1) from measured radii, and (2) using the SIGMA-SCAN software system described above. The values of the two sets of data were regressed and the resulting *r* was used as the value of *k*. β was then tested against the predicted slope for isometry for each scaling relationship using a *t* test.

Results

Field tests of falling distances of 100 snails encountered in random sampling of rocky subtidal habitats showed that 18 resided on horizontal surfaces from which falling did not occur, 28 resided on inclines from which a bump-and-roll response without free-fall occurred, 28 resided on inclines from which bump-and-roll responses followed by free-fall occurred, and 26 resided on vertical slopes from which only free-fall occurred. Of the 54 animals that experienced free-fall, 40 (74%) fell less than 5 body lengths, while the remaining 14 (26%) fell more than 5 body lengths. However, no animal fell further than 8.4 body lengths. Thus, most of the specimens sampled occupied rocky habitats from which only a short unimpeded vertical fall was possible, while the rest did not experience free-fall.

Righting times from the right-side (hard) orientation were significantly greater than from the left-side (easy) orientation ($W = 681$, $p < 0.001$, Wilcoxon signed-rank test; Fig. 3). A 10-g animal took 6.3 min to right from the hard orientation and 2.9 min from the easy orientation.

Significant differences were shown between all VO_2 rates ($p < 0.001$, Friedman repeated measures ANOVA) and the data segregated into three statistically homogeneous subgroups representing each activity (Newman-Keuls test, $p < 0.05$; Fig. 4).

Righting costs (mJ) from the hard orientation were 4-fold greater than from the easy orientation (expressed in
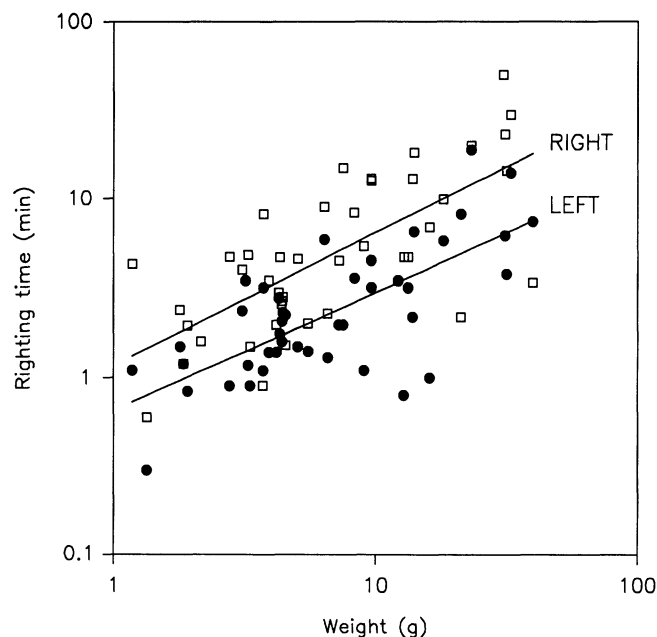

Figure 3. Righting times from right ("hard") and left ("easy") landing orientations in *Ceratostoma foliatum* as a function of body weight (including shell). Regression statistics are, for RIGHT: log $Y = 0.0626 + 0.7382 \log X$, $r^2 = 0.494$, $n = 43$ and, for LEFT: log $Y = -0.1830 + 0.6495 \log X$, $r^2 = 0.494$, $n = 43$.
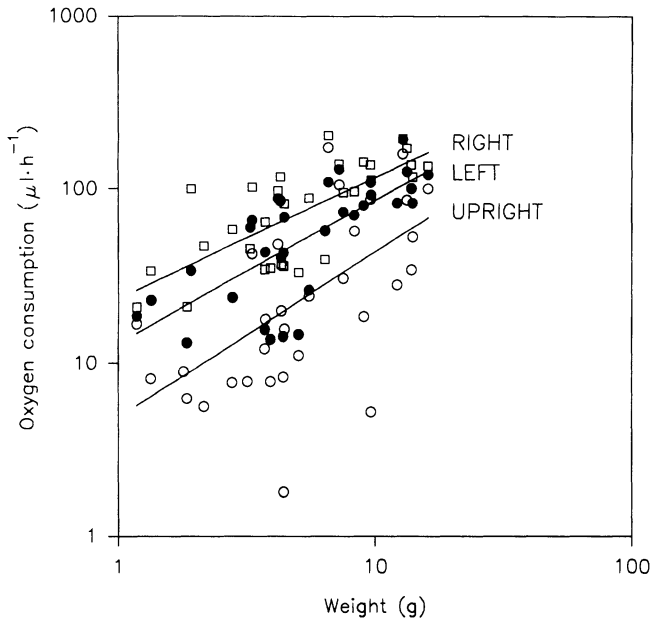
Figure 4. Rates of oxygen consumption during righting from the right ("hard") and left ("easy") orientation compared with that in the upright (resting) orientation as a function of body weight (including shell) in *Ceratostoma foliatum*. Regression statistics are for RIGHT: log Y = 1.381 + 0.665 log X, r^2 = 0.522, n = 32; for LEFT: log Y = 1.092 + 0.814 log X, r^2 = 0.529, n = 32; and for UPRIGHT: log Y = 0.688 + 0.919 log X, r^2 = 0.349, n = 33.

Table I for an equivalent 10-g animal). The higher costs from the right side are explained by the greater angle (130°) through which the foot must traverse to gain a purchase on the substratum, as compared with that of the left side (110°). These angles are constant through a wide weight range (1–41 g, n = 88) and variances are small: right-side angle = 130° ± 4 SD, left-side angle = 110° ± 5 SD. It should be noted that these righting angles do not correspond directly with the varix angles depicted in Figure 2a because, as the shell lies on its side, the angle is determined by the relative heights of the varix-pair and the different balance points of the shell on these varices.

A summary of landing frequencies when dropped through seawater of depths of five body lengths (Table II)

indicates that the animals landed in a pattern that differed significantly from that expected based on the proportion of circumference delineated by each varix-pair (X^2 = 20.9, p < 0.001). Thus, although the right-side varix-pair occupied 31% of the circumference (see Fig. 2a), the animals landed on it only 15% of the time. The left-side varix-pair, from which righting was easiest, occupied only 19% of the circumference, but was landed on 37% of the time. The aperture-down landing position occurred 48% of the time, conforming closely to the 50% circumference that it represented.

The reason for the disproportionate landings on the left-side varix-pair becomes clear when the snail's center of mass is known. When representative-sized snails were suspended from threads attached to their individual varices, points of intersection were located within the largest, most recent whorl, slightly to the left of the longitudinal axis of the snail, and about midway between the aperture and the top of the main body whorl (see Fig. 1). Thus, the tendency during falling was for the shell to rotate to its most stable orientation, with the center of mass downwards. This falling orientation was probably aided and further stabilized by the broad right varix, which presumably acted as a rudder as it trailed. Thus, most animals not landing aperture down actually landed on the left-side varix pair from which subsequent righting was easiest.

Removal of the varices affected this landing pattern as follows (Table III). Right-varix removal caused the animals to land significantly more on their right sides and significantly less on their left sides and upright. Middle-varix removal led to a similar pattern of landing, but with even greater frequency of landings on the right side. In contrast, left-varix removal greatly increased the probability of landing upright at the expense of both left-side and right-side landings. Varix removal was accompanied by shifts in center of mass: right-varix removal produced a slight shift dorsally, middle-varix removal produced a slight shift ventrally, and left-varix removal produced a slight shift to the right.

There was no relationship between landing orientation and length in *C. foliatum* (t values all < 1.52, p values all > 0.135, t test of significance of regression; Zar, 1984).

Table I

Righting costs of Ceratostoma foliatum *(n = 34) from the right-side ("hard") and left-side ("easy") orientations*

Orientation	Angle (°)	Regression equation	r^2	Righting cost (mJ) for 10-g animal
Right-side ("hard")	130	log Y = 0.969 + 1.447 log$X$	0.703	261
Left-side ("easy")	110	log Y = 0.557 + 1.265 log$X$	0.606	66

The angle is the degree through which the snail's foot must traverse during righting from each orientation. Righting cost is the product of rate of energy expenditure and total righting time. The regression equations were generated by regressing the log transformation of energy needed to right (mJ) against the log transformation of body weight including shell (g). Righting costs were calculated for a 10-g animal from the regression equations.

Table II

Landing frequencies of Ceratostoma foliatum *(n = 137) onto the right side, the left side, and the normal aperture-down position*

Orientation	Mean landing frequency % ± 1 SD	% circumference occupied by each varix-pair
Aperture-down (right and left varix pair)	48 ± 19	50
Right-side (right and middle varix pair)	15 ± 16	31
Left-side (left and middle varix pair)	37 ± 17	19

Each snail was dropped 10 times in an aquarium tank with a seawater depth of 5 body lengths. These data were combined into a grand aggregate for all animals, from which the landing percentage values were calculated. Percentage circumference data were taken from Figure 2.

Regression analyses on log-log transformed data showed that there were significant relationships between most shell-parts as well as body weight and shell-parts (Table IV). Right-, middle-, and left-varix areas scaled allometrically to shell length (corrected log-log slopes equal to 2.15, 2.38, and 2.38 respectively; all significantly greater than 2.0, t = 2.72, 5.78, and 5.22, respectively, p all < 0.01), as did aperture area (β = 2.24, significantly different than 2.0, t = 6.24, p < 0.001). Of interest was the fact that right-varix area scaled to shell length with a constant log-log slope of 2.15 (Fig. 5a). Thus, animals of the largest size recorded here (82 mm shell length) were producing new varices in a constant allometric proportion to length. Combined varix area (right, left, and left-remnant varices) increased linearly with aperture area. The log-log slope of the regression of right-varix area compared to aperture area (β = 0.93, r^2 = 0.918) differed significantly from 1.0 (t = 2.24, p < 0.05), but when the left-varix and left varix-remnant areas were successively added to the right-varix

area (the three components combine to produce a flat shelf surrounding the aperture), progressive improvements in fit were seen: right + left *vs.* aperture: β = 0.96, r^2 = 0.931 and right + left + left-remnant *vs.* aperture: β = 0.98, r^2 = 0.941. The addition of the left varix and the left-remnant varix also changed the log-log slopes of the lines in a progressive manner such that they no longer differed significantly from 1.0 (right + left *vs.* aperture: t = 1.58, p > 0.10 and right + left + left-remnant *vs.* aperture: t = 0.81, p > 0.20). This shows that as the aperture grows in size in *C. foliatum,* so the shelf surrounding it grows in proportional scale, with the best fit being realized when all three shelf components are included.

To ensure that our two populations from Barkley Sound and Telegraph Cove did not differ in any respect of morphometry, we compared log-log slopes and, if necessary, intercepts of regression lines for each morphometric comparison generated independently for each population. In no instance was a significant difference shown (all comparisons: t < 1.96, p > 0.05, tests of slope and intercept differences; Zar, 1984).

Labial-spine length scaled allometrically to body length (β = 1.87, significantly different than 1.0, t = 12.67, p < 0.001; Table IV). There was no indication in our data of any break in this relationship, at least over the size range represented by our collection (25–82 mm length).

Discussion

Several notable findings have arisen from this study. First, aerobic righting costs from the right-side, or hard, orientation are significantly greater than aerobic costs from the left-side, or easy, orientation. This was expected in view of the greater angle that the foot must traverse, requiring a greater period of time and a greater absolute need for oxygen. Also in accordance with our prediction was that landings after short vertical falls were preferen-

Table III

Landing frequencies of Ceratostoma foliatum *after removal of single varices*

Following removal of	Landing orientation (%)			Upright *vs.* upright	Right *vs.* right	Left *vs.* left
	Upright	Right	Left			
Right varix	33	44	23	t = 3.16	t = 11.21	t = 5.65
Control	44	16	40	p = 0.003	p < 0.001	p < 0.001
Middle varix	16	73	11	t = 12.03	t = 20.93	t = 8.96
Control	48	13	39	p < 0.001	p < 0.001	p < 0.001
Left varix	85	6	9	t = 12.05	W = 431	t = 13.59
Control	50	13	37	p < 0.001	p < 0.001	p < 0.001

Drops were in seawater of 5 body-length depth. N = 50 snails for each treatment, with 20 drops for each snail before (control) and after removal of varix. Values presented are mean percentage landings in each orientation for 20 drops for each of 50 animals, tested intact (control) and then following removal of a single varix. t: paired t test; W: Wilcoxon signed-rank test.

Table IV

Scaling relationships of shell and body parts of Ceratostoma foliatum *(n = 88)*

Relationship (Y vs. X)	loga	b	r^2	k	β	Predicted slope for isometry
weight *vs.* shell length	−3.829	2.83	0.984	0.999	2.83*	3
aperture area *vs.* shell length	−3.599	2.24	0.975	0.999	2.24*	2
labial spine length *vs.* shell length	−2.808	1.87	0.882	0.999	1.87*	1
right-varix area *vs.* shell length	−3.099	2.15	0.946	0.999	2.15*	2
middle-varix area *vs.* shell length	−3.707	2.38	0.938	0.999	2.38*	2
left-varix area *vs.* shell length	−3.860	2.38	0.925	0.999	2.38*	2
right-varix area *vs.* aperture area	0.358	0.93	0.918	0.999	0.93*	1
right + left varix area *vs.* aperture area	0.511	0.96	0.931	0.999	0.96	1
right + left + left remnant varix area *vs.* aperture area	0.550	0.98	0.941	0.999	0.98	1

Regression statistics are for the equation $\log Y = \log a + b \log X$. β is the corrected slope calculated by multiplying b by the reliability ratio, k (see text for explanation).

* Indicates that corrected log-log slope (β) differs significantly from the predicted slope for isometry, p all < 0.05.

tially on the left-side varix-pair, which offered the smaller angle for the foot to traverse.

Our data suggest that it is the presence of the right varix that most contributes to this result. Its effects are both through its potential vanelike influence and through its large size (weight). In the absence of the right varix the animal lands more on its right, or more vulnerable, side, probably because the trailing-edge stabilizing function of the broad right varix is missing (see Table III). Now the animal falls with the middle and left varices trailing upwards in winglike fashion, but rotated slightly clockwise by an accompanying dorsalward shift in center of mass. This produces a bias towards a right-side landing. In the absence of the middle varix the animal falls with center of gravity down (aperture up), with right and left varices extending outwards, and lands on the main body whorl. On impact, the imbalanced weight of the right varix tends to roll the animal onto its right side, even from landing orientations that, in the presence of the middle varix, would have resulted in a left-side posture. Thus, 73% of landings with the middle varix absent are on the right side. The slight ventral shift in center of mass on removal of the middle varix was not enough to affect this falling orientation. A similar falling orientation is produced in the absence of the left varix. Now the animal falls with center of mass downwards, stabilized by the right and middle varices, which project out in winglike fashion. However, because of the disproportionate weight of the right-varix, this falling orientation is not perfectly symmetrical; rather, it is skewed somewhat to a right-side-down orientation, perhaps aided by a slight shift to the right in center of mass on removal of the varix. Thus, mostly aperture-down landings result. Where this skewing is less, landing is still mostly on the main body whorl previously occupied by the left varix, and the heavy weight of the right varix rolls the animal onto its aperture. Thus,

85% of landings in the absence of the left varix lead to an upright position. In all cases where a varix was absent, subsequent landing orientation was greatly influenced by the two trailing varices, especially the right one in its presence. Whereas Palmer (1977) attributed a slight, but significant, destabilizing effect of the middle varix, leading to more upright landings from falls of 10 body lengths or greater, we show that the right varix is mainly responsible for the type of "destabilizing" event recorded here. Obviously these functions are inter-related, as the right varix ultimately becomes the middle one.

Based on these considerations, then, the optimal shell design (ignoring other possible varix functions) would be to have only right and middle varices, and not a left varix. But, because of the way the snails grow, varices can only be partially removed after they are laid down. Thus, the method of growth constrains C. foliatum to a less-than-optimal shell shape with respect to the feature of landing orientation after falling.

Our morphometric analyses failed to indicate the diminution of growth that was noted for San Juan Island, Washington, populations of C. foliatum by Spight and Lyons (1974) and Spight et al. (1974). These authors suggested that growth stops in mature snails, with the animals subsequently appearing to shrink in size as the varices, siphon, and spire erode. Our data indicate that animals are still adding undiminished right varices up to 82 mm length; but, as this is also equivalent to the largest size recorded by Spight and colleagues, it may represent a maximum for the species in this geographical area. Furthermore, the allometry of labial spine size to body length was consistent over the complete size range (25–82 mm length) found in our populations. There was no break discernible in the relationship corresponding to the spine reaching its "mature" form at 60 mm body length; a break
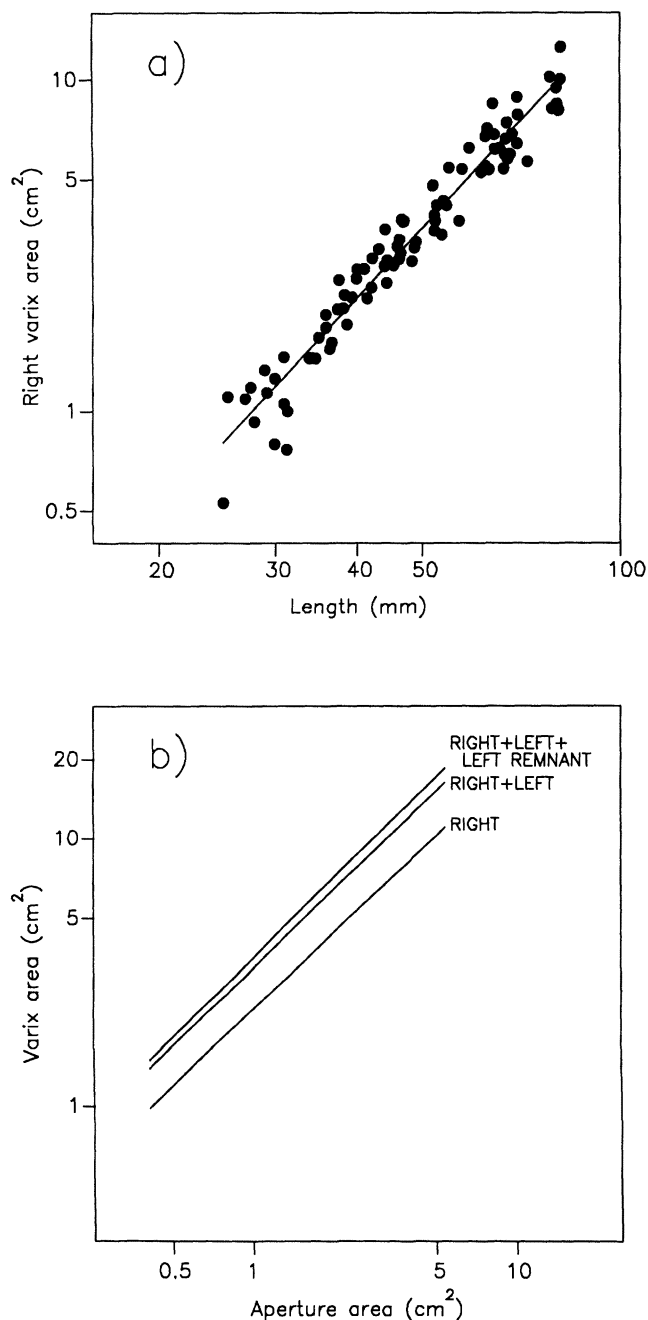
erential upright landings during long falls—the truth is probably that the varices serve multiple functions. Our inclination on viewing *C. foliatum,* and from our morphometry data, is to believe that the extended platform surrounding the aperture formed from the combined right and left varices could serve for protection of the soft parts during feeding and locomotion or, as suggested by Palmer (1977), for providing a stable platform during drilling of its prey. These ideas are supported by the juxtaposition of the previous left-varix remnant with the present right varix, which increases this area. In fact, we showed that the combined right-, left-, and left remnant-varix areas scaled isometrically with aperture area ($\beta = 0.98$), suggesting a related function.

Such hypotheses of protection and stability are testable, and could provide provocative areas for future work, especially if incorporated into a larger comparative study. Several other muricid species (in the genera *Ceratostoma* and *Pteropurpura*) on Pacific Ocean coasts have tri-varix morphology similar to that of *C. foliatum.* Most are large (4–8 cm) and all are carnivorous, but data on their habitat preferences and other aspects of their biology are scanty. A comparison of varix morphometries of a few of these species relative to aperture areas, combined with tests of their susceptibility to nipping or enveloping predators and their stability in currents, could lead to further insights on optimal shell design in gastropod molluscs.

Acknowledgments

Figure 5. (a) Right-varix area as a function of shell length in *Ceratostoma foliatum.* (b) Areas of various varix combinations around the aperture plotted against aperture area in *C. foliatum.* The combined right + left + left-remnant varix area represents the flat shelf that surrounds the aperture. Regression statistics for the relationships are given in Table IV. $N = 88$ for each regression.

was noted for San Juan populations of *C. foliatum* by Spight and Lyons (1974).

Despite the attractiveness of a dual destabilizing-effect theory for the function of the varices during falls—that is, that the right one leads to preferential landing on the easy side during short falls and the middle one to pref-

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