Function of Shell Sculpture in Marine Gastropods: Hydrodynamic Destabilization in *Ceratostoma foliatum*

Abstract. *The gastropod* Ceratostoma foliatum *(Gmelin) possesses three bladelike varices on the body whorl of the shell. The precise positioning and relative width of these varices destabilize the animal as it falls through the water, substantially increasing the chances that it will land upright (aperture down). For a gastropod pulled off rocks and dropped by predatory fish, such a mechanism could considerably reduce its probability of being eaten.*

Ceratostoma foliatum (Gmelin), a muricid gastropod of the subfamily Ocenebrinae, is characterized by "three large, thin, foliaceous varices per whorl" (*1*, p. 185) (Fig. 1). It is the oldest extant member of the genus, dating back to the mid-Pliocene, and is also the most broadly distributed (*2*). The species occurs from Alaska to California and is abundant in both the Puget Sound region and on the open coast (*1, 3, 4*), typically inhabiting lower intertidal or subtidal, steeply sloping to vertical rock walls.

Little is known about the functional significance or adaptive value of external sculpturing in marine gastropods. Intraspecific variation in the spine length of *Murex brandaris* has been correlated with habitat type (*5*); this correlation suggests that some spines may function as stabilizers on soft substrates. A more generally accepted hypothesis is that most strong external sculpturing acts in some way to reduce susceptibility to predation (*6*). However, to my knowledge, essentially no experimental work has been done documenting the means by which a particular sculpture acts to assist or defend a particular species.

In this report I present evidence that the three evenly spaced bladelike varices of *C. foliatum* act to destabilize the animal as it falls through the water. This instability in falling orientation can be shown to increase significantly the probability that an individual will land aperture down, with its foot protected, if it has become dislodged from the substratum. In a habitat prowled by predatory fishes that bite off gastropod feet, landing aperture down could substantially reduce the chance of the gastropod's being eaten.

A series of experiments was conducted to characterize landing success as a function of individual size, length of fall, and starting orientation. Individuals of various lengths were dropped over depths of 10 to 200 cm from two starting orientations, aperture up or aperture down (Table 1) (*7*). Two other species were used as controls: (i) *Fusitriton oregonensis* (Cymatidae), which lives in the same habitat as *C. foliatum* but is covered with a hairy periostracum and has no varices, and (ii) a morph of *Thais (Nucella) lamellosa* (Muricidae), which lives intertidally and subtidally and has 8 to 15 bladelike varices per whorl.

Rather than cause the aperture to orient stably downward as the animal falls, the varix arrangement in *C. foliatum* results in a cyclic "flopping" behavior, with the aperture rotating about the axis of coiling alternately facing up and then down (Fig. 2). Over distances less than ten body lengths, landing success is strongly a function of initial orientation (*8*). As falling distance increases, the probability of successful landing stabilizes between 35 and 70 percent independent of the starting orientation. The mean probability of successful landing for all individuals for falling distances greater than 20 body lengths is 56.7 percent (*9*).

These results contrast sharply with those of the controls. Both control species, once having fallen more than five body lengths, consistently land aperture up, regardless of starting orientation. An examination of a variety of species has indicated that nearly all other gastropod shell forms with elongate columellar axes have a stable falling orientation with the aperture facing up (*10*), simply because there is more shell material dorsal to the plane described by the axis of coiling and the outer lip of the aperture than ventral to it. *Ceratostoma foliatum*, by virtue of its particular external sculpturing, is a striking exception.

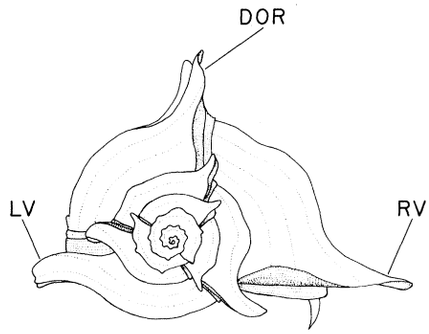

Fig. 1. Apical view of *Ceratostoma foliatum* illustrating the regular varix arrangement: *DOR*, dorsal varix; *LV*, left ventral varix; *RV*, right ventral varix.

To determine the degree to which individual varices contribute to this hydrodynamic instability, I measured landing success for similar-sized individuals from three groups after they fell a fixed distance. A particular varix was then filed flush with the body whorl for all the individuals of each group, after which they were allowed to fall again (Table 2).

The results show that, of the three varices, the dorsal varix is the most important in determining falling behavior. Its removal leads to a nearly stable falling orientation with the aperture facing up regardless of starting orientation and hence significantly reduces landing success. Removal of the left ventral or right ventral varix appears to have little effect.

The adaptive value of *C. foliatum*'s falling behavior becomes apparent when one examines the gut contents from freshly caught kelp greenling (*Hexagrammos decagrammus*), a common predatory rockfish in the Pacific Northwest whose geographic distribution parallels that of *C. foliatum* (*11*). Two of 23 individuals from various sites in the San Juan Islands, Washington, were found to have positively identifiable remains of *Fusitriton oregonensis* feet in their guts (*12*). Since *Hexagrammos* does not have the capacity to crush the shells of this large gastropod and there were no shell fragments in the guts, it appears that the feet were bitten off leaving the remainder of the animal behind. Removal of gastropod feet has been noted in other predatory fishes (*13*) and is consistent with *Hexagrammos* behavior in the laboratory. Individual fish have been observed to sit patiently next to an inverted gastropod, and, as the animal extended its foot to right itself, the fish attempted to bite it off (*14*). Opercula and feet of *Calliostoma ligatum* (Trochidae), a much smaller gastropod, have also been found in *Hexagrammos* guts (shell fragments were absent) (*12, 15*), an indication that this technique may be applied to smaller gastropod prey as well.

The sculptural pattern of three regularly spaced varices occurs in several other gastropods, including six of the remaining seven extant *Ceratostoma* species (*16*). Whether it functions in a similar manner remains to be tested. On the basis of the falling behavior of *C. foliatum* individuals with weakly developed sculpturing, it appears that the varices must be bladelike and must extend relatively far from the body whorl in order to substantially disrupt the otherwise even flow about the shell.

Actual proof of the functional significance of a particular morphology is nearly impossible, as one must rely on infer-

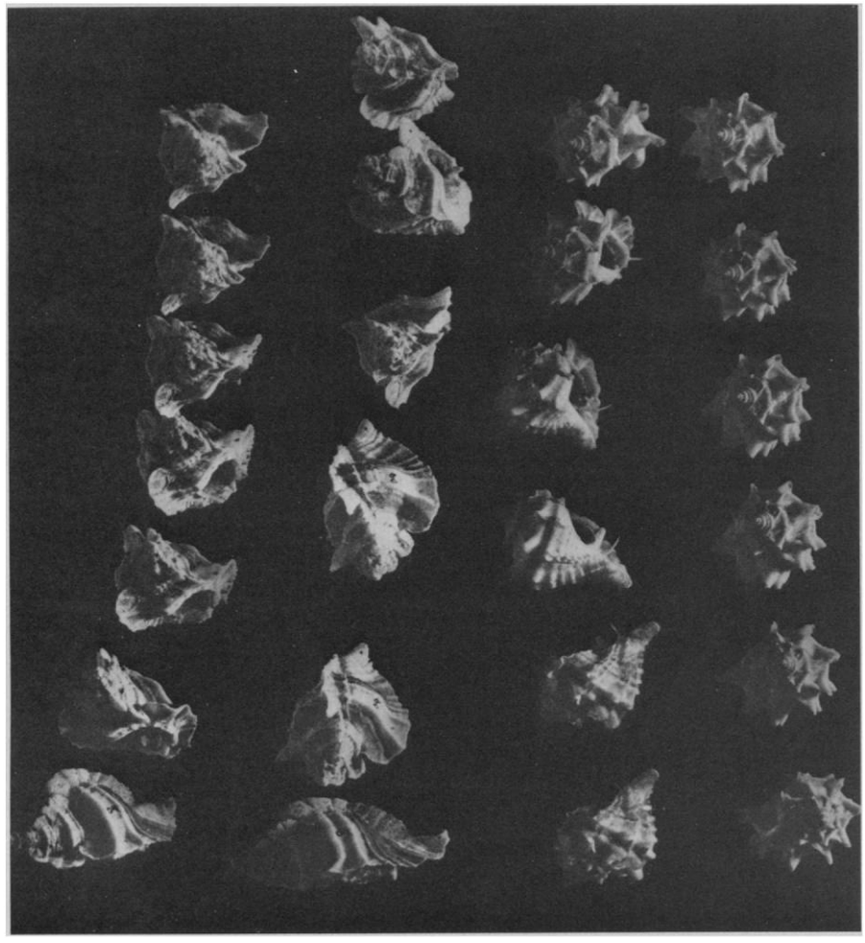

Fig. 2. Sequential patterns of falling behavior. The sculptural arrangement of *Ceratostoma foliatum* substantially increases the chance that it will land upright after falling through the water (first and second columns). The typical, aperture-up falling behavior of nearly all other gastropod shell forms is illustrated for *Thais (Nucella) lamellosa* (third and fourth columns). Approximately one-half actual size; flashes at eight cycles per second.

ential evidence (*17*). Moreover, the possibility that the morphology has evolved in response to a stress to which the species is no longer subject can never be excluded. However, ruling out plausible alternative hypotheses can provide some additional strength for a particular argument. The right ventral varix certainly acts to reinforce the lip of the aperture for *C. foliatum*. Such reinforced lips have been clearly demonstrated to reduce susceptibility to predation by crabs in at least one gastropod species (*18*). However, this hypothesis offers no explanation for the regular spacing of the varices. In addition, the virtual absence of repaired crab damage marks and the rarity of crabs capable of such damage in the habitats where *C. foliatum* is common also weaken this hypothesis. The ventral varices of *C. foliatum* may provide additional stability in conjunction with its labial spine while the animal

Table 1. Landing success as a function of length of fall for eight individuals of *Ceratostoma foliatum* of various lengths and for the two control species, dropped from two different starting orientations, aperture facing up or aperture facing down. The values listed correspond to the percentage of times an individual landed aperture down out of 20 falls. The repeated values for 0 to 5 body lengths fallen represent landing success for falling distances of 100, 200, and 300 mm, respectively. Abbreviations: U, up; D, down.

Number of body lengths fallen	Length for																			
	Ceratostoma foliatum individuals of																*Fusitriton oregonensis*		*Thais lamellosa*	
	85.4 mm		85.2 mm		58.9 mm		56.0 mm		50.7 mm		44.8 mm		28.2 mm		27.9 mm		72.8 mm		34.7 mm	
	U	D	U	D	U	D	U	D	U	D	U	D	U	D	U	D	U	D	U	D
0 to 5	0	100	0	100	0	40	0	100	0	0	0	75	100	0	100	100	0	100	0	0
0 to 5	100	25	5	75	80	0	90	100	100	0	85	70					0	0		
0 to 5	100	0	10	80	85	10	30	85									0	0		
6 to 10			50	30					50	100	80	65	60	100	100	100	0	0	0	0
11 to 15	20	0	20	0	45	50	60	25	40	50			0	50	100	100	0	0	0	0
16 to 20	45	40	35	20	60	25	20	40	75	40	50	55					0	0	0	0
21 to 25	60	95	40	45	40	60					60	40	35	70	70	80	0	0	0	0
26 to 30							45	50	40	45							0	0	0	0
30 to 35					40	75					50	40	75	80	60	65				

Table 2. Change in the landing success of *Ceratostoma foliatum* with the removal of individual varices. The values listed correspond to the mean (Y) and standard deviation (s) of landing success for 20 falls of 70 cm for three groups of four individuals each, both before and after varix removal. Lengths range from 38.6 to 59.0 mm (mean = 48.9mm). Probabilities are computed from a Mann-Whitney U test; N.S., not significant.

Varix manipulated	Starting orientation up				Probability	Starting orientation down				Probability
	Varix present		Varix removed			Varix present		Varix removed		
	Y	s	Y	s		Y	s	Y	s	
Right ventral	47.5	25.00	30.0	8.16	N.S.	46.3	18.87	47.5	36.63	N.S.
Dorsal	45.0	14.72	0.0	0.00	$P < .025$	46.3	12.50	6.3	12.50	$P < .025$
Left ventral	58.8	14.36	56.3	30.38	N.S.	57.5	22.17	70.0	18.26	N.S.

drills barnacles or mussels (*19*). The dorsal varix, however, would not contribute to this stability and would tend to make the animal more sensitive to water movement. It is also quite possible that the varix arrangement of *C. foliatum* represents a combined response to several factors, of which fish predation is only one.

A linking of form with function is the closest approximation of adaptive significance that one can achieve for species whose evolutionary history is not precisely known. The correlated occurrence of *C. foliatum*'s unique falling behavior with a known source and specific type of mortality strongly suggests an adaptive response.

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References and Notes

1. R. T. Abbott, *American Seashells* (Van Nostrand Reinhold, New York, 1974). Produced at the outer lip of the shell as the animal grows and often representing temporary cessations of growth, varices in muricids may take the form of conical nodes (*Ocenebra*, *Purpura*, *Thais*), blunt ribs (*Aspiella*, *Oceanebra*), delicate spines (*Homolocanthus*, *Murex*, *Poirieria*), or broad, thin blades (*Boreotrophon*, *Ceratostoma*, *Pteropurpura*, *Pterynotus*).
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7. The individuals selected for these experiments were chosen because of their unworn, well-developed varices. Although no particular starting orientation is more likely than another in nature, preliminary trials indicated that, after the animal had fallen from three to six body lengths, the axis of coiling of all individuals including controls would orient perpendicular to the direction of the fall, regardless of starting orientation. Aperture up and aperture down with the axis of coiling parallel to the bottom were arbitrarily chosen because they represented the extreme positions of *C. foliatum*'s natural "flop" cycle and permitted more reliable replication. All the experiments were carried out in aquariums with running seawater or off the dock of Friday Harbor Laboratories. The substratum upon which the animals were dropped was flat and perpendicular to the direction of fall. "Landing success" refers to the precentage of all times dropped that an individual landed aperture down.
8. There is a significant negative correlation ($r = -.47$, $P < .05$, Spearman coefficient of rank correlation) between landing success when dropped aperture up and landing success when dropped aperture down for all individuals falling distances less than ten body lengths. This does not include the 27.9-mm individual which, over short distances, fell stably aperture down regardless of initial orientation.
9. What is increasing with the distance of fall is landing success independent of starting orientation rather than landing success per se. Hence, absolute length of fall is not important, only the position of the animal in the "flop" cycle when it reaches the bottom. Smaller individuals cover less distance over a complete cycle than larger ones.
10. Genera examined included *Acanthina*, *Bursa*, *Cantharus*, *Conus*, *Crassilabrum*, *Cymatium*, *Fasciolaria*, *Hexaplex*, *Latirus*, *Leucozonia*, *Littorina*, *Morula*, *Muricanthus*, *Pisania*, *Planaxis*, *Purpura*, *Searlesia*, *Strombus*, *Thais*, and *Vitularia*.
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12. L. Moulton, personal communication.
13. T. Scott, *Annu. Rep. Fish. Bd. Scotland* **20** (No. 3), 486 (1901), *Gadus morhua* (Gadidae); L. R. Brightwell, *Proc. Zool. Soc. London* **123**, 61 (1953), *Squalus caniculus* (Squalidae); J. E. Randall, *Stud. Trop. Oceanogr.* **5**, 665 (1967), *Epinephelus striatus* (Serranidae), *Lutjanus analis* (Lutjanidae); E. S. Hobsen, *Natl. Oceanic Atmos. Adm. (U.S.) Fish. Bull.* **72**, 915 (1974), *Chaetodon lunula* (Chaetodontidae).
14. A. R. Palmer, personal observation.
15. That these fish are quite capable of removing firmly attached mollusks is dramatically supported by the finding of 31 chitons in the gut of a single *Hexagrammos* (L. Moulton, personal communication).
16. This sculptural pattern is perhaps most common in the Muricidae but also occurs among species of the Cymatiidae and Cerithiidae.
17. M. J. S. Rudwick, *Br. J. Philos. Sci.* **15**, 27 (1964). Circumstances where induced morphological changes occur in response to the presence or absence of a specific stress are exceptions to this generalization, for example, production of more and longer spines by a rotifer in the presence of a rotiferan predator [J. J. Gilbert, *Science* **151**, 1234 (1966)] and the presumed induction of thicker-shelled thaidid gastropod populations in the presence of crab predators [J. A Kitching, A. Muntz, F. J. Ebling, *J. Anim. Ecol.* **35**, 113 (1966); A. R. Palmer, unpublished data].
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20. Portions of this study were supported by NSF grant OCE 74-02307 A01 to R. T. Paine. I thank A. O. D. Willows, director of the Friday Harbor Laboratories, for allowing me use of the laboratory facilities. L. Moulton generously shared unpublished thesis data on stomach contents from kelp greenling. I thank R. T. Paine and A. J. Kohn for critically reading the manuscript. I also thank an anonymous reviewer for suggestions which have improved the manuscript.

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Auditory Evoked Potentials as Probes of Hemispheric Differences in Cognitive Processing

Abstract. *The amplitude of auditory evoked potentials recorded from the cerebral hemispheres to pairs of task-irrelevant tones was related to differential hemispheric engagement in ongoing cognitive activity (for example, verbal versus musical). The hemisphere hypothesized to be most engaged in the ongoing cognitive task, as compared to the unengaged hemisphere, produced a greater potential difference between the temporal and reference electrode to the second of the tone pairs. These findings are related to "fast habituation" and "recovery cycle."*

Evidence from clinical and behavioral studies has indicated that, for the majority of right-handed people, the left hemisphere plays the more active role in the processing of analytical (for example, linguistic) information, and the right hemisphere plays the more active role in holistic (for example, spatial and musical) information processing (*1*). Recently, attempts have been made to study this lateralization of brain function in intact subjects by using neurophysiological techniques such as the electroencephalogram (EEG) and evoked potential (*2–5*). Although these investigations have tended to support the clinical-behavioral observations, the results have not been overwhelmingly convincing and many have been criticized for their methodological shortcomings (*6*). For example, Galambos *et al.* (*7*, p. 282) concluded, "The interhemispheric electrophysiological differences reported to date, however, are so tiny as to be barely believable. Hence, either the evoked response method is virtually blind to the crucial events we believe must be there, or the hemispheric differences are barely present in the conditions under which the measurements are currently being made."

In previous auditory evoked potential (AEP) studies of cerebral lateralization, AEP's were elicited directly by relevant speech or nonspeech stimuli (*2, 3, 6, 7*). Further, most previous studies had little control over the subject's level of arousal or his involvement in the task. For example, subjects may have been told to simply listen to the incoming stimuli (*2, 4*).

We now report a study in which we have successfully assessed lateralization of brain function by using the AEP as a "probe" of ongoing cognitive processing of information. We were able to obtain reliable AEP changes that were related to the subject's mode of ongoing cognitive processing by using pairs of task-irrelevant auditory tone pips superimposed on linguistic and musical auditory information presented to the subject. We were also able to confirm independently each subject's involvement in the task to assure us of his or her continuous cognitive processing of the information presented during the recording period.

The use of tone pairs allowed us to investigate hemispheric AEP differences in what has been described by Callaway (*8*) as "fast habituation." Essentially, fast habituation is defined as a reduction in AEP amplitude that occurs when less than 10 seconds elapses between pairs of stimuli; it is generalized to AEP components from 100 to 300 msec, shows response decrements from 30 to 80 percent or more of maximum depending on the interstimulus interval, shows less decrement to stimuli that are relevant to a task the subject is performing or to stimuli the subject cannot anticipate, is a form of