

## LOCOMOTION RATES AND SHELL FORM IN THE GASTROPODA: A RE-EVALUATION

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### ABSTRACT

A reconsideration of data from Linsley (1978a) indicates that the association between crawling speed and shell form is not likely to be a causal one. The correlation between speed and form is due largely to multiple adaptations to different habitats (particulate versus rocky substrates). In addition, a conservative estimate of the energy saved by reducing drag experienced at crawling speeds is shown to be more than three orders of magnitude less than the energy expended during normal activity. One may be able to distinguish surface dwelling from burrowing gastropods in the fossil record based on shell form, but not "fast" from "slow" moving species.

### INTRODUCTION

Linsley (1978a,b) has recently advanced the proposition that shell form in marine gastropods may be related to rates of locomotion, finding that more rapidly moving animals have subjectively lower drag shells than slower moving ones in general. The purpose of this paper is to examine some alternative hypotheses accompanied by additional data which suggest this correlated association is not a causal one, but is very likely a consequence of other covarying biological and environmental factors.

The additional information I have compiled (Table 1) falls into three categories: 1) type of locomotion (muscular waves of various types versus cilia); 2) habitat type (predominantly sand versus rock); and 3) some estimates of the actual drag forces experienced by snails at crawling speeds in relation to their tenacity. I present this information only for the species that Linsley (1978a) has considered, and while much more extensive data exist on the rates of locomotion for many prosobranch species (Miller, 1972, 1974a) the general conclusions adequately obtain from his smaller sample.

### PROCEDURES AND RESULTS

In Table 1, I have arrayed species in the five 'form rank' categories of Linsley (1978a) where increasing rank relates to presumed

increases in drag experienced by the shells. This is a compound subjective ranking based on some measure of bilateral symmetry (presumably symmetry with respect to the direction of motion rather than with respect to the axis of coiling, though this is not clear in his description of methods) and on the amount of shell ornamentation, where both greater asymmetry and more extensive sculpture are believed to increase drag. Species followed by an 'M' carry their shell at least partially covered either by the mantle or foot during locomotion.

Locomotor types have all been identified from the appendix of Miller (1974b). For species not listed in this appendix, I have assigned the mode of locomotion determined either for other members of the same genus or the same family. Such inferences are indicated by the subscripts G and F respectively in column 2 of Table 1. The details of the different locomotor types are illustrated and discussed in Miller (1974b).

The habitat information is unfortunately crude but I think sufficient for the distinctions I would like to make. It has been collected from several sources identified by the footnotes at the top of each column (columns 3-7, Table 1). The column headed 'summary' (column 8) indicates what is considered to be the "average" or "typical" habitat of the species based on these varied sources and it is this habitat assignment to which I refer in subsequent discussion. As with locomotory modes, a G or F superscript indicates an inference from

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TABLE 1. Habitat, estimated drag at crawling speed and tenacity of the species from Linsley (1978a) and from various other sources. Species followed by an 'M' in column 1 carry their shell at least partially covered by the mantle or foot during locomotion. Locomotor type abbreviations: Arhyth.—A rhythmic muscular waves (discontinuous, indistinct and terminating); Lat. mon.—Lateral monotaxic muscular waves; Dir. dit.—Direct ditaxic muscular waves; Ret. dit.—retrograde ditaxic muscular waves (including diagonal retrograde ditaxic waves); Ret. mon.—Retrograde monotaxic muscular waves. Habitat abbreviations: AC—associated with coral or coral reefs; AS—associated with sand or mud (i.e. sometimes found on rocks or in rubble); Go—on gorgonians; Gr—in or on seagrasses; Ma—on mangrove roots, pilings or driftwood; RI—rocky intertidal; Ro—rocky habitat (not restricted to the intertidal); Ru—in rubble, either coral or rock; S—sand or mud; UR—under rocks; X—species not listed in that reference;—species listed but no habitat information provided. Under 'drag calculations' L refers to approximate adult shell length; D to approximate adult shell diameter; Re to Reynolds number; and  $C_d$  to the drag coefficient. G or F superscripts to locomotor type, habitat or tenacity indicate the information has been inferred from other members of the same genus or family respectively. See text for a more detailed discussion.

Species	Locomotor type <sup>2</sup>							Habitat			Drag calculations							
	References							References			Speed <sup>1</sup> (mm/s)	L (mm)	D (mm)	Re	$C_d$	Drag (dyn)	Tenacity (dyn × 10 <sup>8</sup> ) <sup>3</sup>	
	3	4	5	6	7	Sum- mary	3	4	5	6								7
Form Rank 21	Arhyth. F	S	X	S	S	--	X	X	X	X	X	4.0	255	114	1020	0.5	408.3	--
<i>Busycyon contrarium</i>	Ciliary	Go	Go	Go	Go	Go	Go	Go	Go	Go	Go	1.3	30	12	39	1.6	1.5	--
<i>Cyphoma gibbosum</i> (M)	Lat. mon. G	Gr	--	--	--	--	X	X	X	X	Gr	2.8	130	71	364	0.6	99.3	--
<i>Cypraea cervus</i> (M)	Lat. mon. G	X	UR	AC	UR, AC	UR, AC	UR, AC	UR, AC	UR, AC	UR, AC	Ru	4.3	30	19	129	0.9	23.1	--
<i>C. cinerea</i> (M)	Lat. mon. G	X	UR	Ru	Ru	Ru	Ru	Ru	Ru	Ru	Ru	3.4	25	14	85	1.1	9.6	--
<i>C. spurca acicularis</i> (M)	Ciliary F	Ru	--	AC	UR	UR	S, Ru	S, Ru	S, Ru	S, Ru	AS	5.6	50	36	280	0.7	114.9	4.0F
<i>Cypraeacassis testiculus</i>	Ret. dit. G	X	X	X	--	--	X	X	X	X	SG	4.6	70	31	322	0.7	54.3	--
<i>Fasciolaria liliium hunteria</i>	Ret. dit.	X	Gr	S, Gr	--	--	S, Gr	S, Gr	S, Gr	S, Gr	S	6.5	140	58	910	0.5	284.6	--
<i>F. tulipa</i>	Ciliary F	X	UR	--	--	--	UR, AC	UR, AC	UR, AC	UR, AC	Ru	3.5	12	4	42	1.5	1.2	--
<i>Hyalina avena</i>	Ciliary F	X	X	SF	UR	UR	SF	SF	SF	SF	AS	3.0	15	8	45	1.5	3.5	--
<i>Marginea guttata</i> (M)	Ciliary F	X	X	SF	UR	UR	SF	SF	SF	SF	AS	1.8	6	3	11	3.0	0.4	--
<i>M. lactea</i> (M)	Ciliary F	X	--	SF	--	--	SF	SF	SF	SF	S	3.4	10	6	34	1.7	2.4	--
<i>M. pruniosum</i> (M)	Ciliary F	X	X	X	S, Gr	S, Gr	S, Gr	S, Gr	S, Gr	S, Gr	S	3.4	10	6	34	1.7	2.4	--
<i>Mitrella ocellata</i>	Ret. dit. G	X	X	X	UR	UR, S	UR, S	UR, S	UR, S	UR, S	AS	1.9	12	5	23	2.1	0.8	5.2F
<i>Nitidella nitida</i>	Ret. dit. F	X	Ru	AC	Ru	UR	UR	UR	UR	UR	Ru	2.0	12	5	24	2.0	0.7	5.2F
<i>Oliva sayana</i> (M)	Ciliary G	X	X	S	S	S	S	S	S	S	S	8.4	55	21	462	0.6	70.9	0.5G
<i>Polinices duplicatus</i> (M)	Ciliary	S	X	S	S	S	X	X	X	X	S	5.6	45	40	252	0.8	151.7	--
<i>P. lacteus</i> (M)	Ciliary G	X	X	S	S	S	S	S	S	S	S	3.4	30	22	102	1.0	21.7	--
<i>Tonna maculosa</i>	Ciliary	S	--	AC	--	--	S, AC	S, AC	S, AC	S, AC	S	3.6	90	58	324	0.7	1.2	--

Form Rank 3	Ret. dit.	X	--	S,Gr	UR	UR,AC	AS	0.9	15	8	13	2.8	0.6	5.2F
<i>Columbella mercatoria</i>	Arhyth.G	S	X	S	--	X	S	3.6	75	41	270	0.8	64.2	--
<i>Melongena corona</i>	Arhyth.	X	X	X	--	X	SG	2.4	115	69	276	0.7	78.6	--
<i>M. melongena</i>	Ciliary <sup>G</sup>	X	S	S	S	S	S	5.0	12	6	60	1.3	4.6	1.2G
<i>Nassarius vibex</i>	Ciliary ? <sup>G</sup>	X	--	Ro	Ro	X	Ro	0.8	10	6	8	3.5	0.3	--
<i>Trivia maltbiana (M)</i>	?	X	X	X	--	X	?	0.5	265	115	132	0.9	11.3	--
<i>Turbinella angulata</i>														
Form Rank 4	Ciliary	Ru	--	Ro	RI	RU	RU	1.8	100	74	180	0.8	54.3	4.0G
<i>Cassis flammea</i>	Ret. dit.	RI	Ro	RI	RI	X	RI	0.9	60 <sup>9</sup>	60	54	1.4	15.6	--
<i>Cittarium pica</i>	Arhyth.F	X	X	X	UR	X	Ru	0.4	20	8	8	5.0	0.2	--
<i>Crassispira cubana</i>	Ret. dit.	Ma	Ma	Ma	Ma	Ma	Ma	2.4	25	13	60	1.3	4.9	1.9G
<i>Littorina angulifera</i>	Ret. dit. <sup>G</sup>	RI	RI	RI	RI	RI	RI	0.6	15	8	9	4.5	0.4	1.9G
<i>L. ziczac</i>	Ret. dit.	X	--	--	Ru	Ro	Ru	1.6	85	39	136	0.9	13.1	1.7F
<i>Murex pomum</i>	Ret. mon. <sup>G</sup>	RI	--	--	--	RI	RI	2.4	20	18	48	1.4	10.5	16.5G
<i>N. versicolor</i>	Ret. mon. <sup>G</sup>	RI	RI	RI	RI	X	RI	2.6	20	18	52	1.4	12.0	16.5G
<i>Pisania auritula</i>	Ret. mon. <sup>G</sup>	Ru	--	X	--	Ru,Ac	Ru	2.3	30	18	69	1.2	8.1	--
<i>Planaxis nucleus</i>	Ret. dit.	X	RI	RI	--	X	RI	1.7	12	8	20	2.2	1.6	--
<i>Tegula fasciata</i>	Ret. dit. <sup>G</sup>	X	UR	UR	UR	X	Ru	1.8	20 <sup>9</sup>	20	36	1.7	8.5	5.2G
<i>T. lividomaculata</i>	Ret. dit. <sup>G</sup>	X	UR	UR	UR	X	Ru	0.9	20 <sup>9</sup>	20	18	2.4	3.0	5.2G
<i>T. lividomaculata</i>	Dir. dit.	RI	RI	--	--	RI	RI	2.4	40	23	96	1.0	12.2	4.6G
<i>Thais rustica</i>	Ret. dit. <sup>G</sup>	X	--	--	--	Ru	Ru	1.5	75 <sup>9</sup>	75	113	0.9	46.7	6.8G
<i>Turbo canaliculatus</i>	Arhyth.	Ru	--	--	--	X	Ru	0.3	83	51	26	2.0	1.8	--
<i>Vasum muricatum</i>														
Form Rank 5	Ret. dit. <sup>G</sup>	X	--	UR	UR	Ro,AC	Ru	0.5 <td>20</td> <td>11</td> <td>10</td> <td>4.0</td> <td>0.5</td> <td>--</td>	20	11	10	4.0	0.5	--
<i>Leucozonia ocellata</i>	Ret. dit.F	RI	RI	RI	RI	RI	RI	0.6	15	12	9	3.3	0.7	1.9F
<i>Nodilittorina tuberculata</i>	Ret. dit. <sup>G</sup>	X	--	X	--	X	Ro <sup>G</sup>	0.3	6	3	2	16.0	0.04	0.7G
<i>Ocenebra minirosea</i>	Dir. dit.	Ro	RI	RI	RI	RI	RI	0.6	40	27	24	2.0	2.1	4.6G
<i>Thais deltoidea</i>	Ciliary <sup>G</sup>	X	X	X	--	Ro,SG	AS	0.5	20	8	10	3.2	0.2	--
<i>Vexillum dermestinum</i>														
Form Rank 6	Ret. dit.	X	--	Gr	Gr	Ro,Gr	Gr	0.4 <td>60<sup>9</sup></td> <td>60</td> <td>24</td> <td>2.0</td> <td>4.6</td> <td>31.8G</td>	60 <sup>9</sup>	60	24	2.0	4.6	31.8G
<i>Astraea phoebia</i>	Ret. dit.	X	--	UR,Gr	UR,Gr	X	Gr	0.3	259	25	7	5.0	1.1	31.8G
<i>A. tecta americana</i>	Ret. dit.	X	--	--	--	X	Gr <sup>G</sup>	0.4	259	25	10	4.0	1.6	31.8G

<sup>1</sup>Linsley (1978a), <sup>2</sup>Miller (1974b); <sup>3</sup>-personal observation; <sup>4</sup>Warmke & Abbott (1961); <sup>5</sup>Abbott (1968); <sup>6</sup>Abbott (1974); <sup>7</sup>Rios (1970); <sup>8</sup>Miller (1974a); <sup>9</sup>for turbinata shells diameter is used instead of length.

species in the same genus or family respectively.

Drag has been estimated using the following equation (Alexander, 1968, eq. 28):

$$\text{Drag} = \frac{1}{2} \rho v^2 A C_d$$

where  $\rho$  refers to the fluid density (essentially 1 gm/cm<sup>3</sup> for seawater);  $v$  is the velocity of the object relative to the fluid (for these computations, crawling speeds from Linsley, 1978a);  $A$  is the measure of the area of the object [I have used frontal area, the projected area in the direction of motion, which for this analysis may be approximated as a circle whose diameter corresponds to the diameter of the body whorl (column D under shell size)]; and  $C_d$  is a drag coefficient whose numerical value has been determined from the empirical relation between  $C_d$  and Reynolds number (Tietjens, 1934, fig. 54) assuming the object to be a sphere of diameter  $L$  (the approximate length of the adult shell). This obviously unrealistic assumption of spherical snails introduces some error, but comparison of the  $C_d$ /Reynolds number relationship for spheres and cephalopod shells (Chamberlain & Westermann, 1976, fig. 4) indicates that this error is probably slight. The crawling speeds are those measured by Linsley (1978a). Approximate adult shell sizes, both lengths ( $L$ ) and diameters ( $D$ ) were compiled from Abbott (1974) using the mean of the range of sizes given in the species' description.  $R_e$  values are Reynolds numbers, assuming a kinematic viscosity of 0.010 cm<sup>2</sup>/s for seawater, which were computed for shells using adult length and crawling speed. The drag values thus provide a rough approximation of the force required to push a shell of a given size through the water at crawling speeds and do not include any frictional resistance between the sole of the foot and the substrate.

Finally, tenacities (force required to dislodge an attached animal) as measured normal to the substrate have been compiled from Miller (1972) for comparison with the drag forces. Her tenacity values in gm/cm<sup>2</sup> of foot area have been converted to dyns through multiplication by the foot area and gravitational constant and are expressed as dyn  $\times 10^5$ .

Table 2 summarizes the information in Table 1 for locomotor types and habitat. In addition to the correlation between shell form and speed noted by Linsley (1978a) there are also strong associations between shell form and 1) the manner in which the mantle and/or foot covers the shell; 2) whether the species use ciliary locomotion or muscular waves and 3) whether species live in a sand environment or in the rocky intertidal. Nearly two-thirds of the species of form rank 2 (presumed low drag shells) envelop their shell with either the mantle or the foot while moving so that the shell itself is not responsible for drag, yet no species in the higher drag categories (4-6) exhibit this behavior. Approximately half of the species of form ranks 2 and 3 utilize ciliary locomotion, whereas nearly all the species of ranks 4 through 6 (presumed high drag shells) use muscular waves. Finally, two-thirds to three-quarters of the species with presumed low drag shells (ranks 2 and 3) are sand dwellers and none live in the rocky intertidal. Rocky intertidal dwellers are restricted to categories 4 and 5. Category 6 contains species from only one genus associated with rocky substrates and seagrasses.

Table 1 also tabulates the estimated drag forces experienced by the various species while moving through the water and it is clear by comparing these with what information is available on tenacities (Miller, 1974b) that the estimated drag forces at the speeds gastropods move is three to six orders of magnitude less than the force required to dislodge an

TABLE 2. Proportions of species of different locomotor types and from different habitats as a function of form ranking.

Form Rank	N	Enveloping mantle	Locomotion type		Habitat		
			Ciliary	Muscular waves	Sand	Rocky intertidal	Other
2	18	0.61	0.56	0.44	0.67	0.0	0.33
3 <sup>1</sup>	5	0.20	0.40	0.60	0.80	0.0	0.20
4	15	0.0	0.07	0.93	0.0	0.47 <sup>2</sup>	0.54
5	5	0.0	0.25	0.75	0.20	0.40	0.40
6	3	0.0	0.0	1.0	0.0	0.0	1.0

<sup>1</sup>Not including *Turbinella angulata* for which information is not available.

<sup>2</sup>Includes *Littorina angulifera*, living intertidally on mangrove roots.

animal while moving. Note that this is assuming no movement of water relative to the shell except that due to locomotion, i.e. no wave action or tidal current.

#### DISCUSSION AND RE-EVALUATION

Linsley's proposition (1978a) that drag reducing morphologies in marine gastropods may have evolved in response to higher locomotion rates derives from a correlation between average crawling speeds and a ranking of shell form based on presumed drag resistance. Considering the above results, it would appear that this correlation is due largely to a more complicated association of several other biologically or ecologically important factors. First, ciliary locomotion is on the order of two to three times faster than either retrograde monotaxic or retrograde ditaxic and nearly three times faster than arhythmic muscular waves on the average (Miller, 1974a, table 1). This is particularly true for smaller gastropods (less than 15 mm). If one only compares crawling speeds of *Conus* species, the mean speed of species using ciliary locomotion (1.56 mm/s, N = 5) is more than three times that of species using some form of muscular waves (0.43 mm/s, N = 13; Miller, 1972) and this difference is highly significant ( $P < 0.001$ , Mann-Whitney U test). Hence, the faster average speeds observed among species in form categories 2 and 3 are due at least in part to differences in locomotion modes. This does not affect the interpretation of the correlation between speed and form, it only provides a partial explanation for the differences in mean speed observed among the different form categories.

Second, species using ciliary locomotion are mostly sand dwellers (10 of 14, Table 1; 30 of 34 species identified in Miller, 1974a in her table 2). In fact, Miller (1974a: 146) states that "Ciliary and discontinuous locomotion in prosobranchs appear to be primarily adaptations to soft substrata." In addition, gastropod crawling speeds for ciliary locomotion are 1.5 to 2 times faster on Plexiglas than on sand (Miller 1974a: table 3). Thus crawling speeds of ciliary movers measured on Plexiglas will most likely be faster than those the animals experience in their natural environment, and this artifact may also contribute to the mean speed differences among form categories.

Third, species living in sandy environments spend at least some time burrowing in the sediment. This is true for *Busycon* (Paine,

1963), *Cassis* (Hughes & Hughes, 1971), *Fasciolaria* (Snyder & Snyder, 1971), *Melongena* (Hathaway & Woodburn, 1961), *Polinices* (Edwards & Huebner, 1977), and *Oliva* (Marcus & Marcus, 1959). The energy expended while burrowing has been measured at nearly 10 times that while crawling on the surface in a sand dwelling nassariid, *Bullia* (Trueman & Brown, 1976) presumably largely as a result of the increased resistance experienced while moving through sand. Consequently one would expect species that burrow to possess less sculpture and present a smaller cross-sectional area in the direction of movement than those species that do not burrow. This should be particularly true for shell sculpture since the markedly higher viscosity and lower crawling speeds in a sand/water "solution" will result in a lower Reynolds number and thus a relatively greater contribution of surface friction to overall drag. Given that two-thirds to three-quarters of the species in rank categories 2 and 3 are sand dwellers (Table 2) it is not surprising that they exhibit such lower drag shells. Much of the variation in drag reducing morphology between the form rank categories can thus be attributed to habitat constraints rather than crawling speed. Hence, because drag reducing morphologies and ciliary locomotion are both associated with a sandy environment where burrowing efficiency may be an important selective force, the association between surface crawling speed and shell form appears due in large part to the co-evolution of multiple adaptations for inhabiting particulate substrates and not because of a direct response of shell form to open surface crawling speed per se.

Another habitat dependent factor is shell sculpture. Open surface (e.g. rocky intertidal) dwelling gastropods may be more exposed to shell crushing predation particularly by fishes than sand dwelling species. This is supported to some extent by Vermeij's observation (1978: 131) that while "the most profound interoceanic variations in architecture occur on open rocky surfaces," changes in sand dwelling species are considerably less pronounced. Consequently, sculptural defenses against crushing (Vermeij, 1978; Palmer, 1979) may be of greater importance to open-surface dwelling gastropods. Such a relative advantage of shell sculpture in open surface dwelling species compared to sand dwellers would be further augmented by its tendency to increase the drag experienced while burrowing among sand dwellers. The restriction

of rocky intertidal species to rank categories 4 and 5 (Table 2) is due largely to a greater development of shell sculpture.

Further complicating the interpretation of hydrodynamic drag with respect to shell sculpture are conflicting observations of intra-specific variation related to wave action. The degree of sculptural development has been found both to increase (James, 1968; Sakai, 1972) and decrease (Struhsaker, 1968) intra-specifically in different species of *Littorina* in response to increasing wave action. At certain water velocities, sculpture may actually decrease drag (Chamberlain & Westermann, 1976). Thus, sculpture per se cannot always be assumed to increase the hydrodynamic drag experienced by surface dwelling gastropods.

Finally, and perhaps most importantly for a streamlining argument, is the consideration of water velocities experienced by gastropods independent of their movement. Koehl (1977) has measured water velocities of up to 160 mm/s in tidal currents and 1300 mm/s in wave surge. These are 2 to 3 orders of magnitude greater than gastropod crawling speeds. Given that environmental water velocities are so much greater than crawling speeds, the marginal increase in water velocity relative to the shell due to locomotion would seem to be insignificant. Further, if water velocity is such an important factor influencing shell form, one would predict that open surface dwelling species should exhibit low drag shells, and the data in Table 2 do not support this prediction. Rocky intertidal species are restricted to form categories 4 and 5 (presumed high drag shells) while species living in rubble or under rocks generally occur in all categories.

To place the drag experienced by snails at crawling speeds in perspective, it is informative to estimate the energy expended to overcome this drag and compare it to values for locomotory metabolism. A single example illustrates the point. From Table 1, the estimated drag on *Thais rustica* at crawling speed is 12.2 dyn (measured values for drag on an unsculptured morph of *Thais* (= *Nucella*) *lamellosa* of comparable size at a water velocity of 2 mm/s are less than one tenth of this; Palmer, unpublished). The power, or energy per unit time to overcome this force, equals the force times the crawling velocity, yielding a value of 2.4 ergs/s (12.2 dyn  $\times$  0.2 cm/s). Oxygen consumption in a comparable sized *Thais* (= *Nucella*) *lapillus* during

"intermittent low activity" has been measured at approximately 70  $\mu$ l/hr (Bayne & Scullard, 1978) which converts to  $3.9 \times 10^3$  ergs/s [ $(1.9 \times 10^{-2} \mu$ lO<sub>2</sub>/s)  $\times$  ( $4.8 \times 10^{-3}$  cal/ $\mu$ lO<sub>2</sub>)  $\times$  ( $4.2 \times 10^7$  ergs/cal)]. The total energy expended to overcome drag is thus more than three orders of magnitude less than that expended during low levels of activity. Since one is really interested in energy saved due to relative differences in drag attributable to shell orientation or sculpture rather than total drag, the energy saved will be even a smaller fraction of the energy expended moving. Hence, even though one might argue that reducing drag at crawling speeds still represents an energy savings, this savings will be vanishingly small.

The preceding discussion has analyzed the relation between crawling speed and drag reducing morphologies without examining how various shell features contribute to drag. As already mentioned, certain kinds of shell sculpture can reduce drag in rapidly moving water though they may tend to increase drag due to surface friction at lower water velocities (Chamberlain & Westermann, 1976). However, shell shape will also affect drag, particularly pressure drag (that drag due to the momentum transferred by the moving body to the fluid in the form of eddies and turbulence in the wake). Species with low apical half-angles [i.e. more elongate spires like *Fasciolaria tulipa* (Linné)] should experience less pressure drag than those with high apical half-angles [shorter spires like *Busycon contrarium* (Conrad)] because more gradually tapering trailing edges will tend to reduce wake size (Alexander, 1968: 218). Note that both of these species are considered presumed low drag shells (rank category 2). Caution should be exercised when trying to assign complex forms such as marine gastropod shells to categories based on presumed differences in an equally complex physical stress such as hydrodynamic drag. In the absence of any empirical evidence, such assignments must be considered highly tentative.

## CONCLUSIONS

Interpreting the adaptive value of gastropod shell form based on single factor correlations is risky for a variety of reasons, not the least of which is that alternative causal factors may account for the observed association. In such correlative studies, the safest procedure is to

identify as many plausible causal hypotheses as possible and examine the degree to which different hypotheses present different predictions. Linsley (1978a,b) has examined the hypothesis that locomotory rates may have exerted an important influence on shell form. His prediction that faster moving snails should have lower drag shells is supported by a correlation between shell characteristics believed to reduce drag, and increased crawling speed. However, this association can just as readily be explained as a compound adaptive response to differences in habitat as I have discussed above. If one compares non-sand dwelling species whose shell is exposed to the water during movement (i.e. whose shells are not enveloped by the mantle or foot since in these situations it is the mantle or foot that is responsible for the drag, not the shell itself), there are no significant differences in crawling speeds between species with presumed low drag shells (rank categories 2 and 3 pooled) and high drag shells (rank categories 4 through 6 pooled,  $P > 0.10$ , Mann-Whitney U test). The inference that drag reducing morphologies are an adaptive response to increased surface crawling speed and the subsequent interpretation of life modes in Paleozoic gastropods based on this inference (Linsley, 1978a,b) do not appear justified in light of the preceding analysis.

The strong association between shell form and habitat (Vermeij, 1978 and above) suggests that a safer interpretation of life modes from shell form may be based on the differences between surface dwelling and burrowing species. Species exhibiting strong external sculpture will most likely have been restricted to an open surface existence while those whose shells are very smooth and streamlined are likely to have been associated with some degree of burrowing.

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