

# Orientational and Anatomical Trends Related to Detorsion among Prosobranch Gastropods<sup>1</sup>

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*Abstract.* Extant prosobranchs were placed into three groups based upon (1) the angle between the coiling axis of the shell and the antero-posterior axis of the foot during locomotion and retraction of the animal into its shell, (2) the angle between pallial water currents and the antero-posterior axis of the foot, (3) the relative proportions of the shell aperture, and (4) the manner in which the foot was folded during retraction. In Condition I (archaeogastropods and lower mesogastropods) the shell axis is at a 30 to 60° angle to the foot during locomotion and retraction, the pallial water currents are at a 60 to 85° angle to the foot, the shell aperture is nearly round, and the foot most often folds transversely during retraction. In Condition II (higher mesogastropods and neogastropods) the shell axis is at a 0 to 10° angle to the foot during locomotion but a 30 to 80° angle during retraction, the pallial water currents are at a 10 to 30° angle to the foot, the shell aperture is nearly round, but with a siphonal notch, and the foot most often folds transversely during retraction. In Condition III (higher mesogastropods and neogastropods) the shell axis is at a 0 to 10° angle to the foot during locomotion and retraction, the pallial water currents are at a 0 to 20° angle to the foot, the shell aperture is elongate, and the foot folds longitudinally during retraction.

## INTRODUCTION

ALTHOUGH MUCH ATTENTION has been given to the geometry of gastropod shells, there has been relatively little work on the more subtle functional and orientational relationships of these secretions to the soft parts that produce them and to the environments within which they exist. NAEF (1913) was one of the first to investigate the ways in which shells of different shapes are carried by the animals secreting them, noting that shells of extant prosobranchs are asymmetrically deposited in drawn-out, helical patterns—the “typical” snail shapes. These he termed anisostrophic shells, which are in contrast to primitive isotrophic shells, such as those borne by the extinct bellerophonites. In that group the whorls lay in a single plane. Naef concluded that anisostrophic shells, in spite of their

asymmetry, are carried in balanced positions by two simultaneous adaptations. The first of these he termed regulatory detorsion, whereby the spire of the shell has become shifted toward the posterior end of the animal; the second is inclination, whereby the coiling axis has become tilted upwardly from its original horizontal position.

Naef outlined some theoretical evolutionary steps leading to regulatory detorsion, and more recent authors, most notable RISBEC (1955) and LINSLEY (1978a), observed that in those gastropods with shell spires directed posteriorly, regulatory detorsion approaches 90°. These are the more highly evolved snails in which the coiling axis lies virtually parallel with the longitudinal axis of the extended foot (MORTON & YONGE, 1964).

The development of anisostrophy, and the related appearance of regulatory detorsion and inclination, was accompanied by profound alterations in the disposition and anatomy of the pallial organs and reno-pericardial complex (NAEF, 1913; YONGE, 1947), primarily the reduction

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and final loss of the post-torsional right members of previously paired structures.

Beginning with Raup's development of a mathematical model for coiled shells (RAUP, 1961, 1966), there has been a renaissance in the study of the functional morphology of gastropod shells. VERMEIJ (1971) described the interrelationships between angle of inclination of the coiling axis and adaptive diversity of shell form. He found that the small angles of inclination characteristic of siphonate gastropods are related to a diversity of shell shape greater than that possible among more primitive forms with large angles of inclination. GRAUS (1974) reported a latitudinal gradient in the morphological diversity of shells and postulated that the greater diversity in tropical latitudes is a function of increased availability of calcium carbonate for shell deposition. LINSLEY (1977, 1978a, b) noted that gastropods with large angles of inclination are detorted less, better adapted to hard substrata, and have lower rates of locomotion than do gastropods with low angles of inclination. PALMER (1980) proposed that locomotion rates and shell form are but two of several co-evolving adaptations to different habitats. MCNAIR *et al.* (1981) found that gastropods with elongate apertures have elongate feet and are found primarily on soft substrata.

There has remained to be undertaken a systematic study of the magnitudes of regulatory detorsion and of its phylogenetic trends within the orders of the Prosobranchia. Moreover, relationships between regulatory detorsion, the proportions of the shell aperture, and mode of folding of the foot during retraction have not been considered by prior investigators. The present report describes some of the major evolutionary changes within the prosobranch framework in relation to these parameters.

Preliminary results of this study were presented to the American Society of Zoologists (GAINNEY, 1979).

## MATERIALS AND METHODS

Living specimens of prosobranchs were collected at the following localities: Jupiter Inlet and Lantana Beach, Palm Beach Co.; Missouri Key and Long Key, Monroe Co.; Turkey Point and Alligator Point, Franklin Co. (all in Florida); Cape Elizabeth, Cumberland Co., Maine; and Bodega Bay, Sonoma Co., California. Additionally, living Indo-Pacific specimens of 30 species were observed by the junior author while on an expedition to Fiji in 1973 (Table 4). Precise angular measurements were not taken from the Fijian species. However, the position of the coiling axis of the shell with respect to the antero-posterior axis of the foot during locomotion and during retraction of the animal into the shell, as well as the manner in which the foot was folded during retraction, were noted. These initial observations provided the framework for our subsequent, more precise, measurements.

The following parameters were observed in living, adult specimens:

(1) The *locomotion angle* is the angle formed between

the antero-posterior axis of the foot and the coiling axis of the shell, projected onto the horizontal plane (Figure 1A). The locomotion angle was measured from above a snail as it crawled on a horizontal surface.

(2) The *retraction angle* is that formed between the longitudinal axis of the foot and the coiling axis of the shell after retraction of the animal into its shell (Figure 1B). Where the locomotion angle and retraction angle differ in a species, the retraction angle represents the degree of twisting of the shell relative to the median plane of the body after withdrawal. As a matter of practicality, the retraction angle was often measured as the head and foot emerged from the shell cavity. Either mode of observation yielded the same angular measurement.

(3) The *water-current angle* is the angle between the inhalant pallial water current and the longitudinal axis of the foot (Figure 1A). In species with siphonal notches in the shell, the angle was calculated from a line connecting inhalant and exhalant regions of the aperture; for forms with apertures that lack notches, the water-current angle was observed and measured with the aid of fine particles of graphite or carmine placed in the water surrounding the living specimens.

(4) The *proportions of the shell aperture* ( $b/a$ ) were measured as follows: the "length" of the aperture ( $b$ ) is the greatest linear dimension in an abapical-adapical direction, excluding the siphonal notch (Figure 1C); the "width" ( $a$ ) is the greatest linear dimension perpendicular to the "length" of the aperture. As a result of procedural differences, the aperture ratios reported here are slightly larger than those described by VERMEIJ (1971). He defined "b" as the greatest linear dimension of the aperture coplanar with the coiling axis, and "a" as the greatest linear dimension perpendicular to "b." Our measurements relate to the full functional extent of the area passed through by the soft parts as they expand from and contract into the shell cavity. The dimensions of apertures of small species were measured with the aid of camera lucida drawings of the apertures.

(5) The manner in which the foot is folded during retraction into the shell was also noted (Figure 1B). Longitudinal folding refers to creasing of the foot along its longitudinal axis. Transverse folding refers to creasing of the foot along a line at right angles to its longitudinal axis and perpendicular to the plane of the sole.

## OBSERVATIONS

We discerned three distinct arrangements in the orientations of shell and body among the prosobranchs we observed:

First, there was a group in which the coiling axis of the shell forms a wide angle with respect to the median plane of the head and foot. This angle is typically about 60°, and does not alter upon retraction of the body into the shell cavity.

Second, there was a group in which the coiling axis is

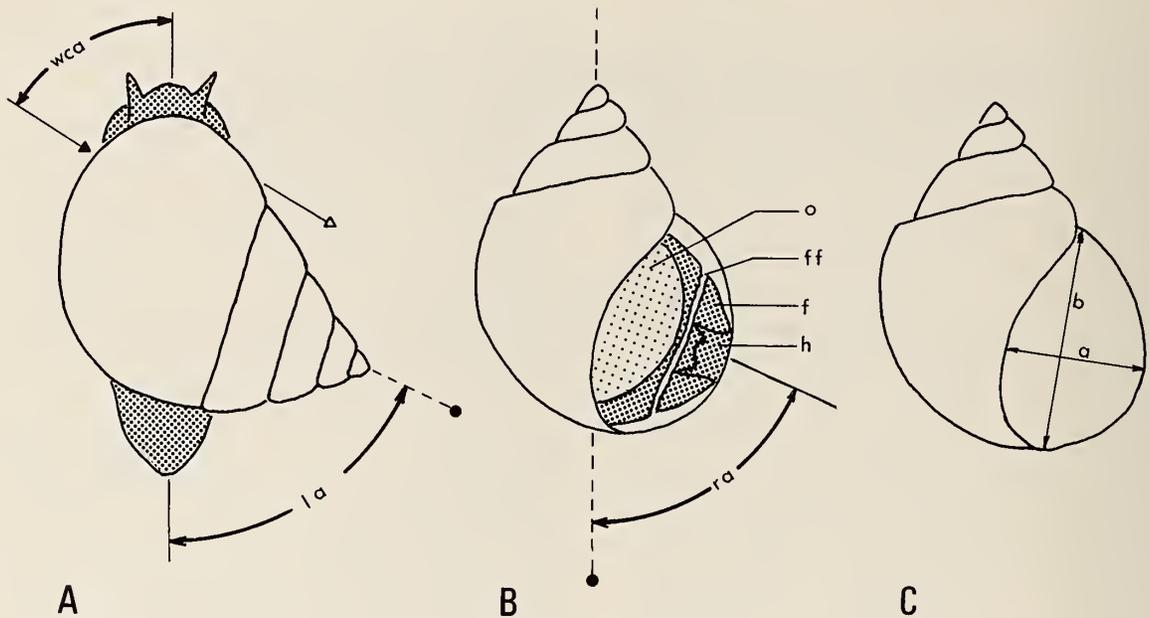


Figure 1

Orientalional and anatomical parameters measured on living gastropods.

A:  $la$ , locomotion angle;  $wca$ , water current angle.

B:  $ra$ , retraction angle;  $ff$ , foot folding (transverse in this example);  $h$ , head;  $f$ , foot;  $o$ , operculum.

C: aperture ratio,  $b/a$ .

Solid arrow shows inhalant current; open arrow shows exhalant current. Solid lines mark antero-posterior axes of foot; dashed lines with terminal dots mark coiling axes.

parallel to, or forms an acute angle with, the median plane of the head and foot. This orientation is altered dramatically upon retraction.

Third, there was a group in which the coiling axis is virtually parallel to the median plane of the foot, an arrangement that does not alter upon retraction.

These situations form the basis for recognition of three conditions that involve not only shell-body orientations, but also the pallial water currents, proportions of the aperture, and modes of folding of the foot.

#### Condition I

All species exhibiting Condition I are archaeogastropods and non-siphonate mesogastropods (Tables 1, 4). Locomotion and retraction angles are the same and fell between 30 and 60°. That is, during locomotion the shell is carried obliquely at a fairly constant orientation with respect to the foot axis, and upon retraction the body and shell do not twist relative to one another.

There are two major arrangements with respect to ctenidial water currents. Most trochaceans possess incurrent and excurrent siphons formed by epipodial lobes, the former to the left, the latter to the right of the head. The angle between inhalant and exhalant streams is approxi-

mately 120°. In the remaining groups, the inhalant and exhalant water currents lie in a virtual straight line, which formed an angle ranging from 70 to 85° with respect to the longitudinal axis of the foot. Except for *Viviparus*, epipodial siphons are lacking in these forms.

Aperture ratios ranged from 0.9 to 1.8; thus, the aperture is broadly open. Among the archaeogastropods the aperture ratios averaged 1.2, whereas among the mesogastropods the average was 1.4.

The foot typically folds transversely as it is withdrawn into the shell aperture. There are exceptions (Figure 2a-d). In *Astraea longispina* and *Turbo castanea* the foot is withdrawn without folding. In *Calliostoma jujubinum*, *Tectus maximus*, *T. pyramis*, and *Trochus maculatus* the foot folds longitudinally. Among the latter three species, the folded ventral surface of the foot faces the outer shell lip at various angles, which affects the use or lack of use of the operculum in blocking the aperture.

#### Condition II

Many siphonate mesogastropods and some neogastropods are characterized by Condition II (Tables 2, 4). Among the mesogastropods, locomotion angles ranged from 0 to 40° (average 12°) and retraction angles from 30 to

Table 1  
Species of gastropods typifying Condition I.

Animals	Locomotion angle	Retraction angle	Water-current angle	Aperture ratio	Foot folding
ARCHAEOGASTROPODA					
Trochidae					
<i>Tegula funebris</i> (A. Adams, 1855)	60°	60°	60°	1.1	transverse
<i>Calliostoma jubinum</i> (Gmelin, 1791)	60°	60°	60°	1.3	longitudinal
Turbinidae					
<i>Turbo castanea</i> Gmelin, 1791	50°	50°	60°	1.2	none
<i>Astraea americana</i> (Gmelin, 1791)	50°	50°	63°	1.2	longitudinal
<i>Astraea phoebia</i> Roding, 1798	60°	60°	60°	0.9	none
<i>Astraea tuber</i> (Linné, 1767)	55°	55°	60°	1	none
Neritidae					
<i>Neritina reclinata</i> (Say, 1822)	60°	60°	75°	1.5	transverse
<i>Neritina virginea</i> (Linné, 1758)	60°	60°		1.4	transverse
<i>Nerita tessellata</i> Gmelin, 1791	60°	60°	80°	1.1	transverse
<i>Nerita versicolor</i> Gmelin, 1791	60°	60°	70°	1.2	transverse
MESOGASTROPODA					
Vivipariidae					
<i>Viviparus malleatus</i>	55°	55°	85°	1.4	transverse
Littorinidae					
<i>Littorina littorea</i> (Linné, 1758)	60°	60°	80°	1.3	transverse
<i>Littorina lineolata</i> Orbigny, 1840	60°	60°		1.3	transverse
<i>Littorina ziczac</i> (Gmelin, 1791)	60°	60°		1.6	transverse
<i>Littorina angulifera</i> (Lamarck, 1822)	30°	30°		1.4	
<i>Nodilittorina tuberculata</i> (Menke, 1828)	60°	60°		1.3	transverse
<i>Tectarius muricatus</i> (Linné, 1758)	60°	60°		1.3	transverse
Modulidae					
<i>Modulus carchedonius</i> (Lamarck, 1822)	60°	60°		1.3	transverse

60° (average 52°). Among the neogastropods, the locomotion angles ranged from 0 to 10° (average 2°) and the retraction angles from 30 to 80° (average 60°). In every species, the locomotion and retraction angles are unequal—there is a twist of the shell as the body retracts into its cavity. This twist is counterclockwise when the animal is viewed from above.

Those species that carry the shell with its axis subparallel to the locomotion angle (e.g., *Planaxis lineatus*) bear a short siphonal notch. The inhalant siphon, which extends from the notch, is carried in front of the head, or else is actively swept in an arc from side-to-side in front of the head during locomotion. Most of the species characterized by Condition II are capable of moving their shells in wide arcs during locomotion. This movement allows water to be drawn into the mantle cavity from a variety of directions and to “zero in” on sources of olfactory stimuli. In every case, water leaves the mantle cavity on the posterior right side of the organism.

The water-current angles listed in Table 2 were measured from specimens while their shells were being carried at the locomotion angles. The range of the water-current angles among the mesogastropods was 15 to 31° (average 24°), whereas among the neogastropods the range was 10

to 30° (average 15°). Although all species of Condition II are siphonate, the Potamididae lack a siphonal notch in the shell aperture.

The aperture ratios in these organisms ranged from 1.2 in *Urosalpinx perrugata* to 2.2 in *Terebra dislocata*, the average among the mesogastropods being 1.6, that among neogastropods 1.5.

During retraction into the shell cavity the foot typically folds once in the transverse plane (Figure 2f, l). Among the exceptions (Figure 2g, j-o) are *Cantharus cancellarius*, in which the foot is folded longitudinally, and species of *Terebra*. There is no folding in *Terebra dislocata* or in *T. duplicaria*, whereas in *Terebra maculata* and *T. dimidiata* there is an oblique folding of the foot.

### Condition III

Some mesogastropods and some neogastropods represent Condition III (Tables 3, 4), characterized by a permanent disposition in which the coiling axis of the shell is subparallel to the longitudinal axis of the foot, whether during locomotion or after retraction.

On the average, the inhalant current enters the mantle cavity at 5° to the midline of the foot in the mesogastro-

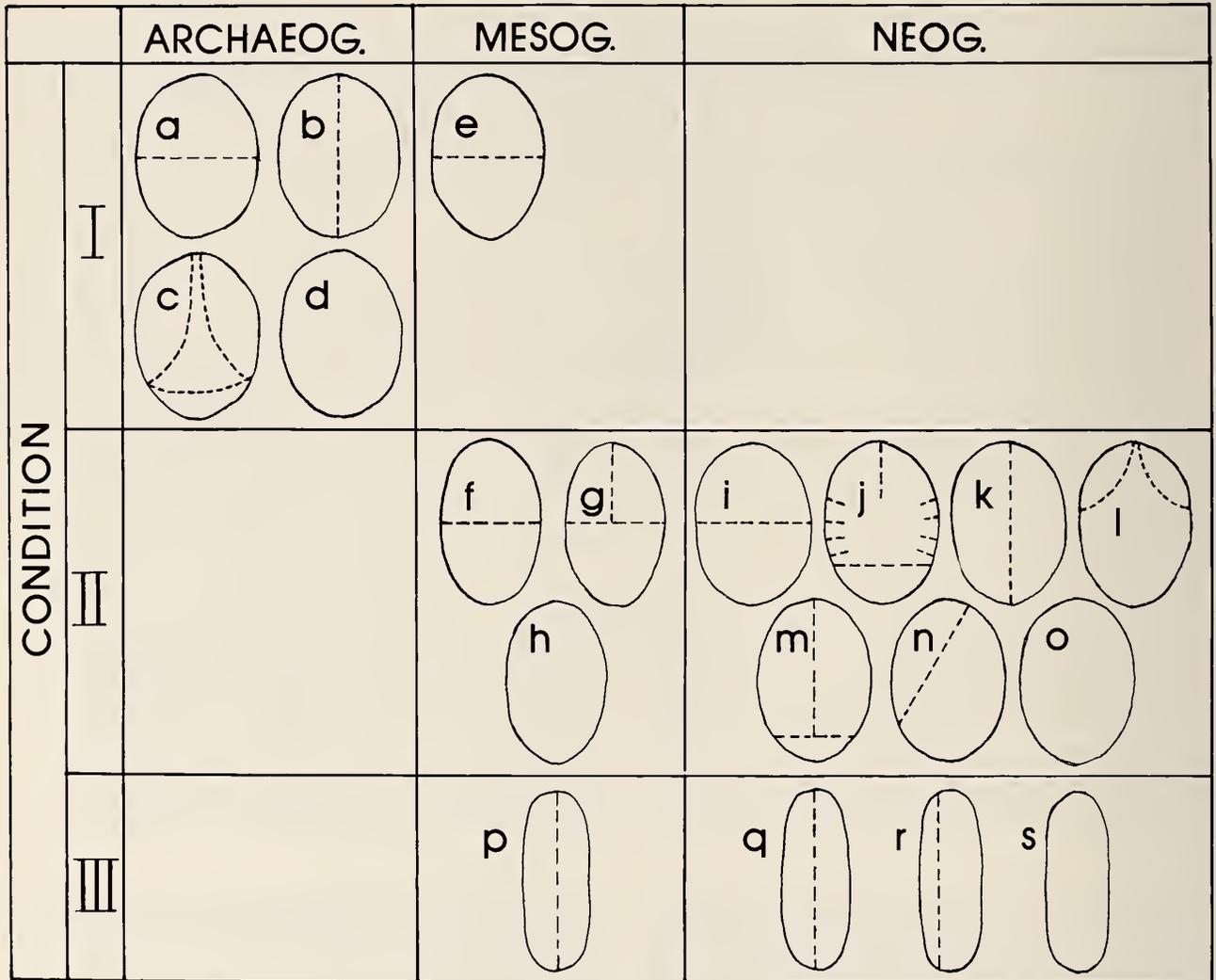


Figure 2

Some foot-folding patterns observed among prosobranchs; ventral views of sole. Anterior ends are upward in the diagrams. In instances of multiple creases, the anterior portions fold first upon retraction. Within each category, the presumed primitive state is shown first. a—(transverse) *Tegula*, *Nerita*; b—(longitudinal) *Tectus*, *Calliostoma*; c—(three flaps) *Nerita*; d—(no folding) some Turbinidae; e—Vivipariidae, Littorinidae, Naticidae, etc.; f—*Cerithidea*, *Cerithium*, *Cymatium*; g—Bursidae (unident. sp.); h—*Contumax nodulosus*; i—*Murex*, *Thais*, *Nassarius*, *Fasciolaria*; j—*Nassarius arcularius* (with lateral crumpling); k—*Cantharus*; l—*Latirus* (two lappets); m—*Terebra* (unident. sp.); n—*Terebra maculata*, *T. dimidiata*; o—*Duplicaria duplicaria*, *Terebra dislocata*; p—Cypraeidae, Cassidae; q—Columbellidae, Olividae, etc.; r—*Conus litteratus*, Mitridae; s—Conidae.

Pods,  $14^\circ$  in the neogastropods, and forms a virtual straight line with respect to the exhalant current, which is located far posteriorly on the right side of the body.

The shell aperture is always much longer than wide, the ratio averaging 6.7 for mesogastropods and 4.6 for neogastropods. The foot never folds transversely (Figure 2p-s), but either creases longitudinally or, as in species of *Conus*, simply slips unfolded along the columella into the shell cavity with the sole facing the outer lip of the shell.

We have not incorporated into our research a study of the operculum. However, it should be noted that the size of this structure, where present, and its position upon the foot are closely related to folding of the foot and to proportions of the aperture. In species with transverse folding, the operculum is attached to the section posterior to the fold, which retreats last into the aperture. This arrangement ensures closure of the opening by the operculum. Among forms with narrow apertures and longitu-

Table 2  
Species of gastropods typifying Condition II.

Animals	Locomotion angle	Retraction angle	Water-current angle	Aperture ratio	Foot folding
<b>MESOGASTROPODA</b>					
Potamididae					
<i>Batillaria minima</i> (Gmelin, 1791)	0°	60°	30°	1.5	transverse
<i>Cerithidea costata</i> (daCosta, 1778)	0°	30°	31°	1.2	transverse
Cerithiidae					
<i>Cerithium eburneum</i> Bruguière, 1792	0–40°	50°	30°	1.3	transverse
<i>Cerithium muscarum</i> Say, 1832	0°	60°	30°	1.3	transverse
Planaxidae					
<i>Planaxis lineatus</i> (daCosta, 1778)	30°	60°	15°	1.8	transverse
Cymatiidae					
<i>Cymatium parthenopeum</i> (von Salis, 1793)	0°	60°	15°	1.5	transverse
<b>NEOGASTROPODA</b>					
Muricidae					
<i>Murex florifer</i> A. Adams, 1855	0°	60°	10°	1.4	transverse
<i>Urosalpinx perrugata</i> (Conrad, 1846)	0°	60°	10°	1.2	transverse
<i>Thais rustica</i> (Lamarck, 1822)	0°	60°	20°	2	transverse
<i>Nucella emarginata</i> (Deshayes, 1839)	0°	60°	10°	1.5	transverse
<i>Nucella lapillus</i> (Linné, 1758)	5°	70°	10°	1.7	transverse
Buccinidae					
<i>Cantharus cancellarius</i> (Conrad, 1846)	0°	30°	10°	1.7	longitudinal
Melongenidae					
<i>Melongenella corona</i> (Gmelin, 1791)	0°	80°	10°	1.4	transverse
<i>Busycon contrarium</i> (Conrad, 1840)	0°	70°	10°	1.7	transverse
Nassariidae					
<i>Ilyanassa obsoletus</i> (Say, 1822)	10°	60°	20°	1.4	transverse
<i>Nassarius vibex</i> (Say, 1822)	10°	40°	20°	1.4	transverse
Fascioliidae					
<i>Fasciolaria lilium hunteria</i> (G. Perry, 1811)	0°	60°	15°	2	transverse
Terebridae					
<i>Terebra dislocata</i> (Say, 1822)	0°	60°	20°	2.2	none

dinal foot-folds, the operculum is generally reduced or lacking. Independent trends toward reduction and loss of the operculum have taken place both in the mesogastropods (Cassididae, Cypraeidae) and in the neogastropods (Conidae, Mitridae) of Condition III.

### CONCLUSIONS AND DISCUSSION

Observed prosobranchs fall into any one of three anatomical groups, here termed Conditions I, II, and III. Each condition is composed of features that may be analyzed separately, but are here interpreted as having evolved in closely interrelated fashions. Of the qualities concerned, orientation of the shell axis with respect to the extended foot, presence or absence of a twist of the shell over the foot during its retraction into the shell cavity, and the angle formed between pallial water currents and the axis of the foot were considered of primary importance in placing species in one of the three conditions. The relative proportions of the aperture and the manner in which the foot folds were considered of secondary importance, be-

cause there are overlaps and exceptions among these qualities within the three conditions. Typical arrangements are illustrated in Figure 3.

To set an evolutionary context for our observations, we agree with the view that modern gastropods found their origins in an extinct superfamily of archaeogastropods, the Bellerophontacea (Figure 3; see STASEK, 1972:26). These primitive forms were isostrophic and have been deduced to have possessed two bipectinate ctenidia, and hence paired reno-pericardial organs (NAEF, 1913; YONGE, 1947). The locomotion and retraction angles were probably 90°; that is, detorsion would have been 0° (Figure 3). There would have been no twist of the shell over the body during retraction. Moreover, the aperture ratio would have been low, a conclusion reached from illustrations in KNIGHT *et al.* (1960). If the foot folded at all during retraction, it was probably transverse to the longitudinal axis. Thus, based upon the parameters that define existing prosobranchs of Conditions I, II, and III, the bellerophonts would form another group—Condition "0" (Figure 3).

Steps away from bellerophont shell morphology in-

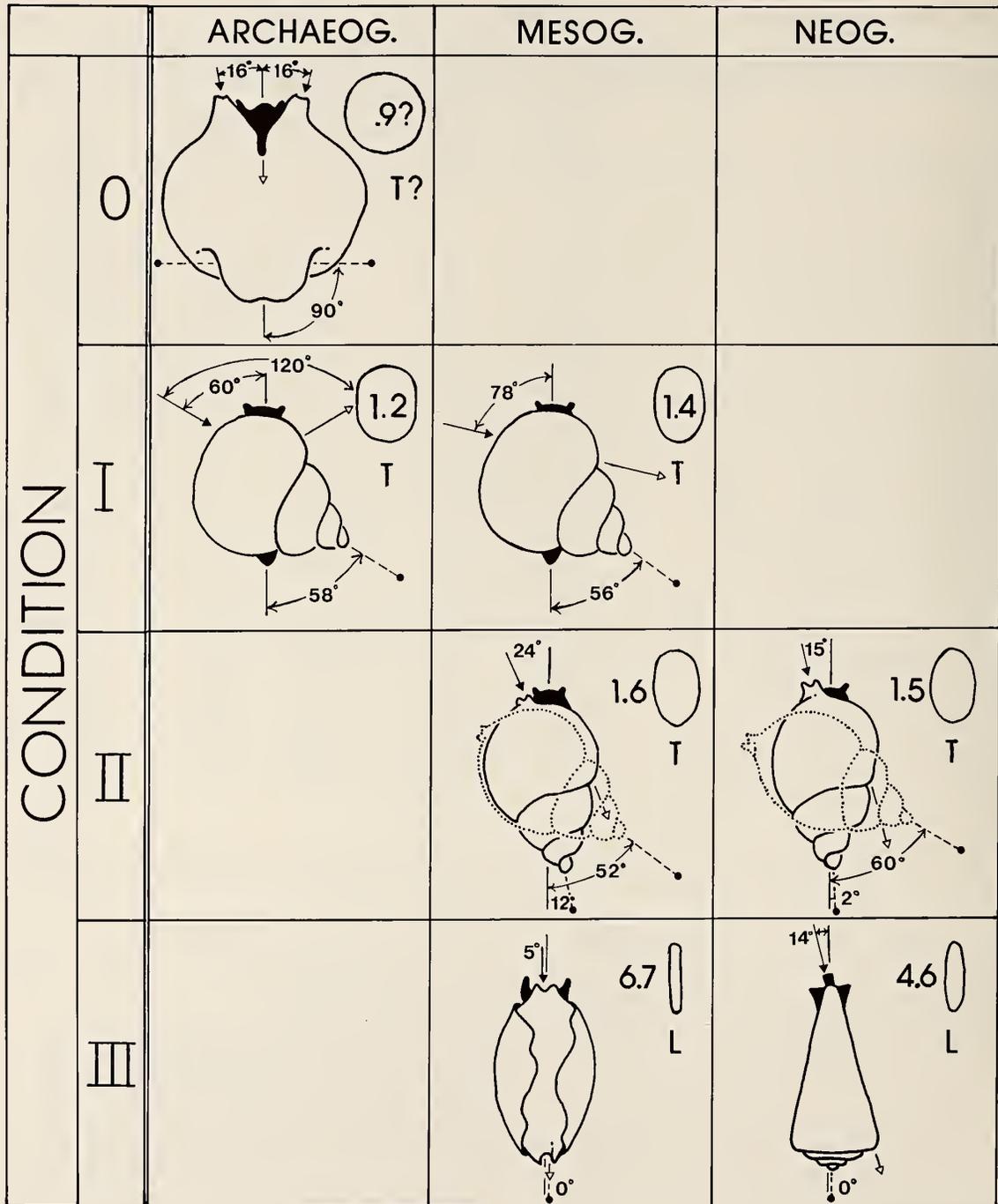


Figure 3

Summary of conditions relating locomotion, retraction, and water-current angles, aperture ratios, and foot folding among the prosobranch orders. Measurements are rounded-off averages from Tables 1, 2, and 3, except for the locomotion angle and retraction angle among the neogastropods of Condition III, for which measurements from *Mitrella lunata* have been excluded. Aperture ratios are indicated by ovals, not by outlines of actual apertures. Dotted outlines in Condition II represent the extent of twisting of the shell over the body upon retraction of the foot. The bellerophonts are represented in Condition "0" by *Knightites multicornutus* (modified from COX, 1960: 195). Solid arrows show inhalant currents; open arrows show exhalant currents. Solid lines mark antero-posterior axes; dashed lines with terminal dots mark coiling axes; L, longitudinal folding; T, transverse folding of the foot.

Table 3  
Species of gastropods typifying Condition III.

Animals	Locomotion angle	Retraction angle	Water-current angle	Aperture ratio	Foot folding
<b>MESOGASTROPODA</b>					
Eratoidea					
<i>Trivia pediculus</i> (Linné, 1758)	0°	0°	0°	9	longitudinal
Ovulidae					
<i>Simnia uniplicata</i> (Sowerby, 1848)	0°	0°	0°	4	longitudinal
Cassididae					
<i>Cassis tuberosa</i> (Linné, 1758)	0–10°	0–10°	15°	7.2	longitudinal
<b>NEOGASTROPODA</b>					
Columbellidae					
<i>Columbella rusticooides</i> Heilprin, 1887	0°	0°	11°	5	longitudinal
<i>Mitrella lunata</i> (Say, 1826)	10°	10°	16°	2	longitudinal
Olividae					
<i>Oliva sayana</i> Ravenel, 1834	0°	0°	6°	5.3	longitudinal
<i>Olivella pusilla</i> (Marrat, 1871)	0–5°	0°	20°	3.1	longitudinal
Marginellidae					
<i>Marginella apicina</i> Menke, 1828	0°	0°	10°	6.7	longitudinal
Conidae					
<i>Conus floridanus</i> Gabb, 1868	0°	0°	15°	7.8	longitudinal
Turridae					
<i>Cryoturris cerinella</i> (Dall, 1889)	0°	0°	20°	2	longitudinal

volved the formation of a spired shell, inclination of the coiling axis, and regulatory detorsion (NAEF, 1913; YONGE, 1947; LINSLEY, 1977). These qualities are borne by *Pleurotomaria*, regarded on anatomical grounds as among the most primitive living archaeogastropods. We have not observed *Pleurotomaria*, but we predict that it will have a locomotion angle of 60°, a shell and body that do not twist relative to one another during retraction, and a foot that folds transversely upon withdrawal into the shell cavity. These qualities would make *Pleurotomaria* a basic representative of Condition I.

The elements that comprise Condition I are found among recent non-patelliform archaeogastropods and non-siphonate mesogastropods. These animals are similar in their general appearance: detorsion ranges from 30 to 60°, and all of them have a rather high angle of inclination of the coiling axis (VERMEIJ, 1971). Moreover, most of them are grazers that are, with few exceptions, restricted to hard substrata. Based upon accepted views of gastropod phylogeny, we conclude that the qualities that define Condition I are primitive. To date, we have observed no neogastropods with the conformation of Condition I.

The mesogastropods and neogastropods characterized by Condition II bear shells the coiling axes of which are carried virtually parallel to the longitudinal axis of the extended foot. The inhalant and exhalant streams lie in a straight line, with the inhalant position much closer to the midline of the head than in forms typified by Condition I. These orientations alter upon retraction of the foot into the shell cavity in that the coiling axis swings counter-

clockwise when viewed from above. The twist of an average mesogastropod is about 40°; the shell moves even more, on the average, among the neogastropods. The species of Condition II are permanently detorted to about the same degree as those of Condition I, and temporarily detorted during locomotion by an additional 40 to 58° in mesogastropods and neogastropods, respectively. The orientation of the two axes in the retracted state is practically identical to the permanent arrangement of the more primitive forms characterized by Condition I.

As in Condition I, transverse folding of the foot during retraction is regarded as primitive, and the proportions of the length to width of the aperture of the shell are about the same as, or only slightly longer with respect to width, than those typical of Condition I. Species of *Terebra* are more variable in the matter of foot-folding than those of any other genus observed (Figure 3m, n, o).

Mechanisms relating to unequal locomotion and retraction angles vary within Condition II. In species with fusiform shells, the siphon is brought to an anterior position by muscular action, whereas species with high-spired shells that taper to slender points employ a purely passive mechanism (such as dragging on or in the substratum) to bring the siphon around in front (GAINNEY, 1976). Considering PONDER'S (1973) views on gastropod phylogeny, there has been convergent evolution of both fusiform and high-spired shells among mesogastropods and neogastropods.

The functional significance of high-spired shells is unclear. GRAUS (1974) noted that shells of this kind are

Table 4  
Fijian species observed in relation to Conditions I, II, and III.

	Archaeogastropoda	Mesogastropoda	Neogastropoda
Condition I	Trochidae <i>Trochus maculatus</i> <i>Tectus maximus</i> <i>T. pyramis</i> Neritidae <i>Nerita</i> spp.	Littorinidae <i>Littorina</i> sp. Nauticidae <i>Polinices pyriformis</i>	
Condition II		Cerithiidae <i>Contumax nodulosus</i> <i>Cerithium</i> sp. Bursidae "Bursa" sp.	Thaididae <i>Mancinella mancinella</i> <i>Morula granulata</i> Nassariidae <i>Nassarius arcularius</i> Fascioliariidae <i>Latirus gibbulus</i> Terebridae <i>Terebra maculata</i> <i>T. dimidiata</i> <i>Duplicaria duplicaria</i>
Condition III		Ovulidae <i>Volva</i> sp. Cypraeidae <i>Cypraea tigris</i>	Olividae <i>Oliva mustellina</i> Mitridae <i>Mitra mitra</i> <i>Vexillum sanguisugum</i> <i>V. vulpecula</i> <i>V. gruneri</i> <i>Neocancilla papilio</i> <i>Pterygia dactylus</i> Conidae <i>Conus livatus</i> <i>C. arenata</i> <i>C. litteratus</i> <i>C. ebraeus</i>

usually confined to burrowing species, and he speculated that drag would be reduced as a result of elongation in the direction of locomotion. VERMEIJ (1977, 1978) observed that an increase in spire height reduces predation by calappid crabs, and that the appearance of antipredatory features of gastropod shells in the Mesozoic was paralleled by an increase in their predators. High-spined shells, for example those of the extinct Murchisoniacea and Loxonematacea, thought to be ancestral to the Cerithiacea (Cox, 1960:143), are known from the Paleozoic, which would seem to preclude a solely antipredatory function of the shells of those groups.

The mesogastropods and neogastropods of Condition III exhibit a greater departure from the ancestral form than do those of Condition II. The temporary virtual alignment of shell and foot characteristic of Condition II is here permanent, with no twisting upon retraction. The angle at which the water current enters the mantle cavity with respect to the median plane is much more acute in the mesogastropods of Condition III, less so in the neogastropods. In keeping with the elongate apertures, which may be as much as nine times longer than wide, the foot

folds longitudinally as it is withdrawn, or slips unfolded into the shell cavity with the sole of the foot facing the outer shell lip. Again, there have been parallel evolutionary trends of these factors among mesogastropods and neogastropods. An additional factor in such parallelism has involved the probable independent appearance in the two higher prosobranch orders of inhalant siphons and of siphonal notches in their shells (PONDER, 1973).

FRETTER (1965) concisely summarized the anatomical arrangements found among the Prosobranchia, noting two major grades of organization—the Diotocardia, which we here term the Archaeogastropoda, and the Monotocardia, which is composed of the Mesogastropoda and Neogastropoda. Each of the latter two groups was considered by Fretter to represent an additional grade of organization. The conditions recognized in the present paper may also be considered grades of organization, but referring primarily to orientational relationships, rather than to anatomical conditions, as are those described by Fretter. Thus, Figure 3 represents a cross-indexing of anatomical grades in the vertical columns and orientational grades along the horizontal axis.

We have, then, the *anatomical* grade of the Archaeogastropoda, within which anatomical and orientational bilateral symmetry of the bellerophonts was lost through suppression of the post-torsional members of several previously paired organ systems and through the appearance of anisotrophy.

It was with the shell and body disposed in the *orientational* grade of Condition I that the Prosobranchia evolved the higher *anatomical* grades of organization: the monoplicate ctenidium, as well as the complete loss of right members of the pallio-renopercardial complex and the straightening out of the water currents. The primary taxobasis used by many to delineate the Mesogastropoda, the taenioglossate radula, made its appearance among forms characterized by Condition I.

Subsequent alterations in *orientational* relationships (that is, the temporary situation of Condition II and the permanent reorganization toward permanent external bilaterality of Condition III) took place independently within each of the higher two grades of *anatomical* organization. One, the Mesogastropoda, is extremely diverse, but with many herbivorous groups; the Neogastropoda consists mainly of carnivorous forms. Mode of feeding is, therefore, independent of orientational relationships, not only in Conditions II and III, but also in Condition I. It was with that primitive organization that the carnivorous Naticidae made their appearance.

There was, in the earlier stages of both the mesogastropods and neogastropods, some slight narrowing of the apertures (Condition II); but, independently in both those orders, the apertures became greatly elongated adapically-abapically. There are several functional advantages that have been proposed for this elongation. For example, in the Conidae, Olividae, Volutidae, and Mitridae, various aspects of shell form, including an elongate aperture and foot, have been seen as adaptations to living on or in soft substrata (GRAUS, 1974; MCNAIR *et al.*, 1981). VERMEIJ (1978, 1979) has presented extensive and convincing evidence that elongate shell apertures are particularly effective as a means of reducing predation, especially by crabs. It seems probable to us, as is the case in high-spined shells, that there are several adaptive advantages operating within the same species that would select for the traits characteristic of Condition III.

Finally, the primitive situation whereby the foot folds transversely during retraction into a broadly rounded aperture is replaced in both the mesogastropods and neogastropods by an elongate foot that either folds longitudinally or slips unfolded into a long, narrow aperture.

Orientation of the shell in relation to the body, positions of inhalant and exhalant water currents, retractor mechanisms of the foot, and proportions of the aperture of the shell have been shown to be interrelated attributes of gastropod functional anatomy. That the observed arrangements within any one order comprise a system of co-evolving elements is indicated by the parallelism that exists within the independent lineages of the Mesogastropoda

and Neogastropoda. At the same time that this clarifies some of the major evolutionary trends within the subclass Prosobranchia, we do not wish to imply "straight-line" phylogenies: that there has been convergent evolution and perhaps polyphyly finds much support. Yet, observed correlation of multiple traits reveals that we are dealing with matrices of co-evolving qualities, both anatomical and orientational.

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