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Adaptive Morphology of the Shell in Bivalves and Gastropods

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I. Introduction and Perspectives

In general, we know more about the meaning of shell shape in bivalves than in gastropods. The reason for this disparity appears to be the more intimate association of the bivalve shell with the substratum. The bivalve shell rests on or lies within a hard or soft medium, and its position and mode of stabilization or locomotion in association with this medium have led to a wide variety of evolutionary changes, the adaptive nature of which are often readily amenable to mechanical analysis. The gastropod shell, especially of an epifaunal species, confronts the investigator with more subtle challenges. When a gastropod shell is separated from the substratum by a creeping foot, its shape is of relatively minor importance to locomotion and must reflect the influence of other factors. It is important to appreciate that within the Bivalvia many widespread relationships between form and habit break down at small body (and shell) size because scaling factors greatly reduce many problems that beset larger animals (Stanley, 1972). The elongate saclike foot of a bivalve species of average size cannot support the animal epifaunally, but many minute bivalve species move about on a creeping foot.

A discussion of the functional morphology of the molluscan shell might be divided into sections that address particular skeletal features. The topics of this chapter, however, are arranged in an alternative way, with particular function or sets of adaptations forming primary sections. In effect, this organizes the discussion along ecological and physiological

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lines. Intraspecific variations in shape, which are often ecophenotypic rather than genetic in nature, are not considered in this review.

II. Locomotion

While the adaptive zone of gastropods is in general broader than that of bivalves with regard to locomotion, bivalves perhaps display a larger set of shell adaptations than that of shelled gastropods. Most mobile bivalves move through resistant sediment or at high speeds through water, and for this reason their shell morphology commonly reflects response to problems of locomotion. A typical mobile gastropod, in contrast, crawls slowly with its shell held largely or entirely above the substratum. For such an animal, slow velocity and the low viscosity of the medium that resists shell movement render shell form relatively unimportant to locomotion.

A. Bivalves

It has long been recognized that living bivalves that are not burrowers have evolved directly or indirectly from burrowers (Yonge, 1962; Stanley, 1972). This does not necessarily imply that infaunal or semiinfaunal habits have characterized the earliest Bivalvia (Tevesz and McCall, 1976), but that the laterally compressed shape that characterizes the class, and the typical foot, which lacks a sole, suggest that such habits are primitive. Support for this inference also comes from the existence of Paleozoic bivalvelike monoplacophorans with narrow shells having restricted apertures that would have prevented clamping to a firm substratum (Linsley and Peel, 1983). As would be expected from the fact that inflated bivalve shells require more force for penetration of sediment than slender shells (Trueman et al., 1966), there is a general correlation between the shape of the bivalve shell and rate of burrowing, as measured by the burrowing rate index ($\sqrt[3]{\text{mass (g)}}$/burrowing time (sec) × 100), in which shape is factored out by employing the cube root of mass as a measure of size (Stanley, 1970). Here burrowing time is the interval between the instant when the shell is supported by the foot and the instant it is fully buried. As might be expected, very few species with equant shapes (shapes of a high sphericity) are rapid burrowers (have a burrowing rate index ≥ 2), whereas most species whose shells are disklike, bladelike, or cylindrical are rapid burrowers (Stanley, 1970).

It might initially seem that the shape of the typical bivalve—a shape in which the anterior is blunter than the posterior—would oppose rather

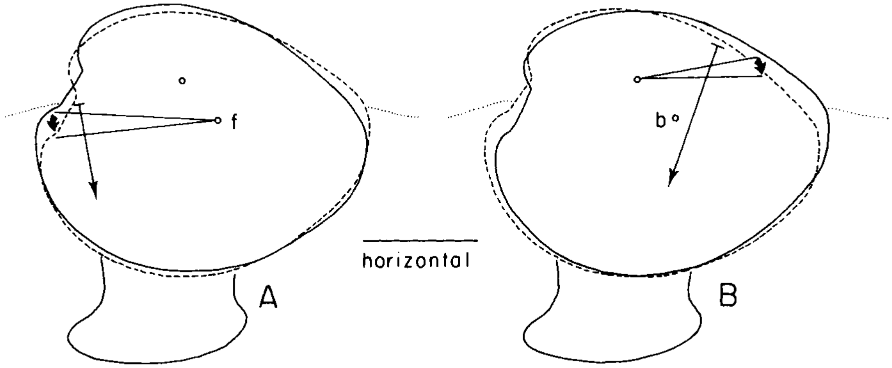
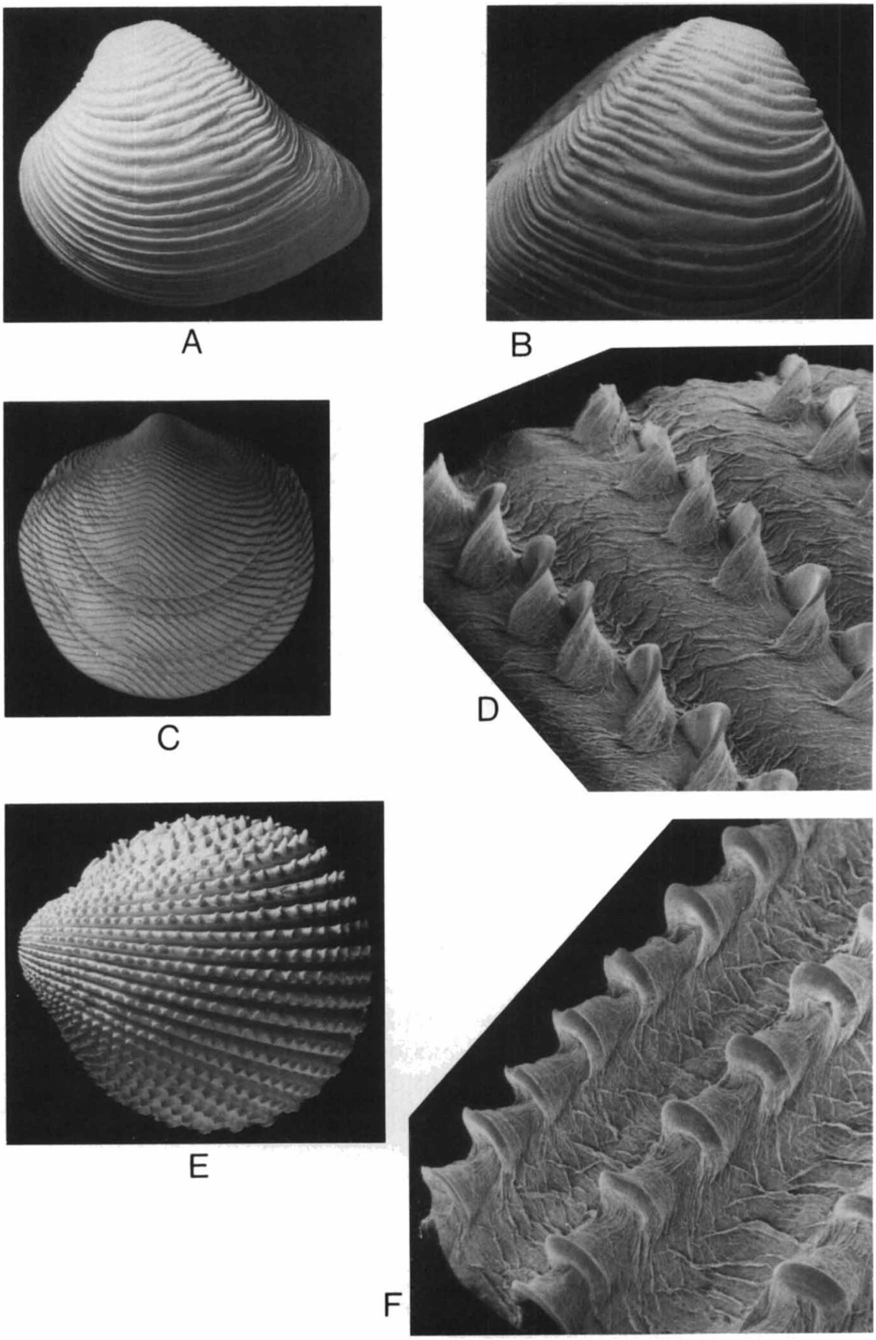


Fig. 1. Burrowing mechanism of *Mercenaria mercenaria,* illustrated by a single forward-and-backward rocking motion as documented by cinematography. The dotted line in each figure depicts the sediment surface. (A) A partly buried animal rocking forward about axis f, from the position in which the foot gains anchorage (solid outline) to the position of maximum forward rotation (dashed outline). (B) Backward rotation about axis b, from the position of maximum forward rotation (solid outline) to the position at which the foot will probe deeper and reanchor itself (dashed outline). In each diagram, the slender arrow represents orientation of the pedal retractor muscle causing rotation and heavy arrow indicates angle of rotation. The shift of the axis of rotation, caused by the jamming of the blunt anterior of the shell against the sediment during backward rotation, causes the animal to "walk" downward into the sediment. [After Stanley (1975b).]

than facilitate penetration of the substratum. This shape results from the prosogyrous condition (forward-directed umbones) and, often, from a nearly flat lunule. The advantage of this shape results from the rocking motion of the shell (Stanley, 1975b), in which the anterior pedal muscles rotate the anterior end of the shell downward and the posterior pedal muscles rotate the posterior end of the shell backward (Trueman et al., 1966). If the axes of forward and backward rotation were coincident, the animal would fail to achieve net movement. In the actual rotational motion, analyzed by means of cinematography, the axis of backward rotation lies anterior to the axis of forward rotation so that the animal "walks" its way into the sediment (Stanley, 1975b). In this motion, the anterior component of the force administered by the posterior pedal muscle jams the blunt anterior end of the shell against the sediment (Fig. 1). Because of this effect, the axis of backward rotation is shifted forward. Ideally the anterior end of the shell (the lunule and umbones) would lock into the sediment, serving as a fulcrum for rotation. In fact, the anterior slips upward a bit, so that the axis of backward rotation is not positioned so far forward, yet nonetheless lies to the anterior of the axis of backward rotation.


A
B
C
D
E
F

The influence of the blunt anterior of the shell on the position of the axis of backward rotation has been demonstrated by means of robots caused to burrow artificially by application of forces at the positions of attachment of the pedal muscles (Stanley, 1975b). The axis of rotation for a robot molded from a real shell was positioned closer to the anterior than the corresponding axis for a robot that was identical except for the addition of a smooth, disklike anterior. In addition, the robot of normal shape consistently "burrowed" more deeply into the sediment than the altered robot when the two were subjected to 25 forward-and-back rocking movements. The small, triangular genera *Donax* (Tellinacea) and *Mesodesma* (Mactracea) do not rotate appreciably in this way but burrow very rapidly simply be wedging into the sediment. Their shape facilitates this movement, and the large anteroventral sector of the shell also houses an exceptionally large foot, which provides for rapid burrowing (Stanley, 1970).

Apparently because of inertial problems that obtain during rocking movements, the capacity for rapid burrowing is rare among species in which the volume of shell material is at least 50% as large as the volume of the body cavity (the space between the valves). Most rapid burrowers are thin shelled (Stanley, 1970). Also, as might be expected, very few species with shell sculpture that stands in high relief are rapid burrowers (Stanley, 1970). On the other hand, asymmetric, ratchetlike sculpture aids bivalves in burrowing (Stanley, 1969, 1970, 1981; Seilacher, 1972, 1973). Because of their asymmetric cross-sectional shape, elements of this sculpture slide through sediment with little resistance and then grip the sediment during backward rotation. This effect has been demonstrated experimentally by removal of the asymmetric spines of *Trachycardium* (Cardiidae) (Figs. 2 and 3) and by application of neutrally buoyant wax to valleys between asymmetric ridges of *Anomalocardia* (Veneridae) (Figs. 2 and 4).

Savazzi (1982) similarly showed that burrowing is facilitated by the ribs of *Scapharca* (Arcidae) and *Acanthocardia* (Cardiidae), although these groups are symmetrical in cross section. Savazzi suggested that the ribs prevent backward slippage of the shell while the umbones are pushed downward during forward rotation and also while the foot probes before a sequence of rotation [the latter idea was also suggested by Thomas (1975)]. The second function is likely, but it would seem more probable

Fig. 2. Functional patterns of sculpture on bivalve shells. (A) *Anomalocardia brasiliana* has asymmetric ridges that grip the sediment (B) during backward rotation. (C) Divaricate asymmetric ridges on *Divaricella quadrisulcata;* the posterior ridges grip the sediment during forward rotation and the anterior ridges during backward rotation. (D) Cuplike posterior spines of *Trachycardium egmontianum* (E), which reduce scour and flared anterior spines (F), which grip the sediment during backward rotation. [After Stanley (1975a, 1981).]

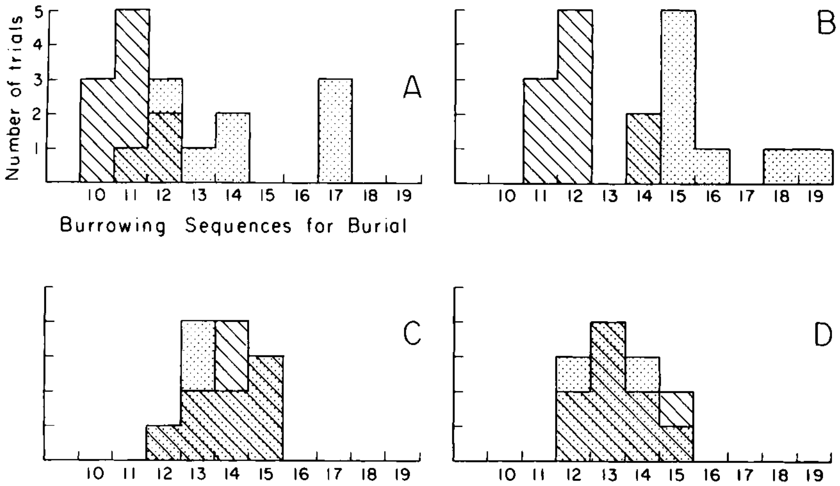


Fig. 3. Results of experiments revealing the effects on burrowing of the cuplike anterior spines of *Trachycardium egmontianum* (Fig. 2F). Two individuals (A and B) were each allowed to burrow 10 times in their normal state (crosshatched bars) and 10 times with the anterior spines removed (dotted bars). For each animal, the number of burrowing sequences (forward-and-backward rocking movements) required for burial was significantly increased by the alteration. For two control animals (C and D), removal of the posterior spines (Fig. 2D), which function in reducing scour (Fig. 11), had no effect on burrowing ability. [After Stanley (1981).]

that the ribs function like the blunt anterior of a typical bivalve during backward rotation than during forward rotation, when the shell rotates within the cavity it has already occupied so that the ribs are not pressed firmly against the substratum.

Shingle- and barb-shaped periostracal structures, like asymmetric sculptural features of the calcareous shell, serve to aid burrowing in both glycymerids (Thomas, 1975) and arcids (Savazzi, 1982).

The precise mechanical function of asymmetric shell surface features that aid burrowing during shell rotation has never been analyzed. The question in any particular case is whether the external structures grip the sand (like the blunt anterior of many species) or whether they excavate sand and transport it upward, making room for the shell to descend. While the former mechanism may characterize many species, excavation may be the mechanism in *Divaricella*, the genus in which the general function of asymmetric sculpture was first recognized (Stanley, 1969). In *Divaricella*, the shell is nearly circular (Fig. 2) and the axes of forward and backward rotation are quite close together, so that many rocking movements (an average of ~27) are required for burial (Stanley, 1970).

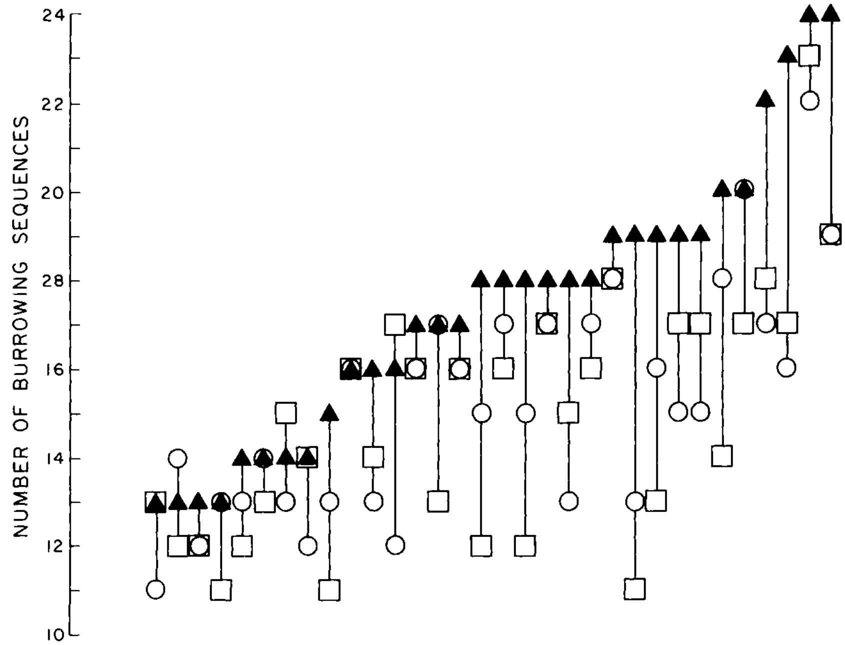


Fig. 4. Number of burrowing sequences (forward-and-backward rocking movements) required by 32 individuals of the species *Anomalocardia brasiliana* for complete burial of the shell. Filling the valleys between the ridges of the shell (Fig. 2A) with neutrally buoyant wax produced a highly significant increase in the number of burrowing sequences required. ▲, Anterior valleys waxed; □, unaltered; ○, posterior valleys waxed. [After Stanley (1981).]

The ligament, which opens the bivalve shell, serves an important function in burrowing, stabilizing the shell by spreading the valves against the surrounding sediment while the foot probes (Trueman, 1964). The ligament is no more powerful in burrowing bivalve species than in many epifaunal species (Trueman, 1964), but Thomas (1976, 1978) has cogently argued that the duplivincular ligament of the arcoids is so weak that it has inhibited the infaunal adaptive radiation of this group by eliminating the potential for rapid burrowing. In the duplivincular ligament, the lamellar layer and fibrous segments are separated on either side of the hinge axis in such a way that both spring the valves open, the lamellar layer through tension and the fibrous layer through compression. Furthermore, in the arcoids the lamellar ligament, which bears the brunt of the responsibility for valve opening, is positioned so that it must grow allometrically relative to other shell features during ontogeny (Thomas, 1976).

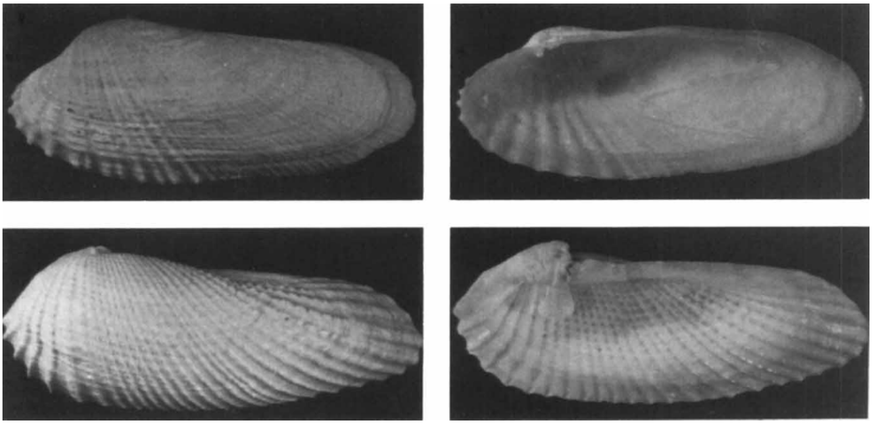


Fig. 5. Similar shell forms of two unrelated bivalve genera that bore into hard substrata: *Petricola pholadiformis* (Veneracea) above (left and right) and *Pholas* sp. (Pholadacea) below (left and right).

The role of the bivalve shell in species that bore into solid substrata has long been a mystery. If the larvae of *Hiatella* settle on a substratum that is solid but soft and weak, the adult will bore into the substratum. *Hiatella* remains byssally attached to hard, solid substrata, however, and its shell exhibits no special morphological features for boring (Russell Hunter, 1949). *Hiatella,* like most other mechanically boring bivalves, apparently excavates its dwelling by rocking the valves about a dorsoventral axis by means of alternate contraction of the anterior and posterior adductor muscles. This is also the boring mechanism of pholad ocean bivalves, in which the ligament is appropriately constricted and the hinge teeth have been lost (Nair and Ansell, 1968). It is apparently not the mechanism in the Gastrochaenacea, however, because in this group the hinge is elongated and not amenable to rotation about a dorsoventral axis. Possibly in this group, rotation about an anteroposterior axis contributes to boring activity (Carter, 1978).

It remains poorly understood how the fragile shells of pholadaceans, petricolids, hiatellaeans, and gastrochaenaceans abrade hard substrata. The marked evolutionary convergence between pholadaceans and petricolid veneraceans (Fig. 5) in association with the boring habit represents powerful evidence that the common shell form of these groups is associated with this habit (Stanley, 1970). The thin nature of the shell indicates that a thick shell is not necessary to withstand abrasion. The cuplike spines clearly serve to excavate the substratum, but possibly function

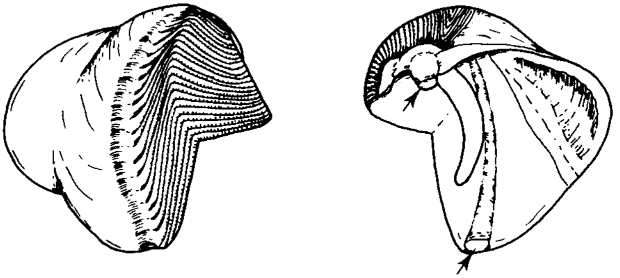


Fig. 6. External and internal views of the teredinid shell. Serrated ridges on the anterior sector of the shell function in boring, during which ball joints on the hinge and ventral margin (arrows) permit the valves to rotate about a dorsoventral axis.

partly through the application of grains that become lodged within them to serve as tools. In some gastrochaenaceans the most recently formed, comarginal shell ridge is abraded, suggesting that it excavates the substratum, but in other species aragonite spikes embedded in the periostracum seem to serve this function. *Tridacna,* which includes the largest living bivalves, bores into coral reefs by rocking in the plane of the commissure with the byssus acting as a fulcrum; in this movement, the scalloped ridges on the shell surface abrade the substratum (Yonge, 1936).

The Teredinidae are perhaps the bivalves most spectacularly adapted for physical, as opposed to chemical, boring. The teredinid shell is reduced in size but effectively shaped for excavating wood (Fig. 6). The hinge forms a ball joint, and another such joint is located opposite it on the ventral margin of the shell. Together these joints form a dorsoventral axis about which the valves rock in relation to one another during boring, in which the sculptured shell constitutes the tool. Between discrete abrasive movements of the shell, the suckerlike foot rotates the shell slightly. Many successive steps rotate the shell through 180° and then back in the opposite direction. Two parts of the shell function in boring, each leaving marks of its ornamentation on the burrow wall. The anterior lobe, with serrated ridges, serves as an "advance boring tool," and the adjacent anterior sector of the shell, which is coarsely denticulated, enlarges the tube (Miller, 1924).

In the mytilacean *Lithophaga,* which bores into calcium carbonate substrata by chemical means, a thick periostracum protects the shell. Bivalve species that burrow in soft substrata under acidic conditions employ conchiolin layers within the shell to terminate leaching of shell material when the periostracum has been abraded. Included here are the marine Corbulidae (Lewy and Samtleben, 1979) and the nonmarine Unionidae and Margaritiferidae (Kat, 1983).

Because of the primitive specialization of the bivalve foot for burrowing (evolutionary sacrifice of the creeping sole for flexibility and development of a large hemocoel), few bivalves are efficient epifaunal crawlers. The only exceptions are very small species such as philobryids (Tevesz, 1977) and leptonaceans. These are animals so small that scaling factors (especially weight–strength ratios) permit many morphological configurations to function in a variety of ways that would not be possible at larger body size (Stanley, 1972).

The habit of swimming by jet propulsion has evolved in only a small number of bivalves. This is accomplished in tubular taxa like *Solemya* (Drew, 1900; Morse, 1913; Stanley, 1970) and *Ensis* (Stanley, 1970) by rapid adduction of the valves. In *Ensis* retraction of the pluglike foot aids in the expulsion of water. Brief underwater "flights" are also undertaken by the "eggshell cockle," *Laevicardium laevigatum,* by valve adduction and pedal kicking (Stanley, 1970). All of these species possess thin shells, which reduce negative buoyancy, as do the swimming scallops (Pectinidae) and those limids that are weak swimmers (Studnitz, 1931; Stanley, 1970). The plicate structure of most scallop shells appears to be an adaptation to strengthen the shell by permitting it to remain light for swimming. Scallops, which are apparently unique among bivalves in swimming with the commissure horizontal, typically have lower valves that are more convex than their upper valves. Thus, they can gain lift only by positioning the commissure at an angle to the direction of movement (Stanley, 1970). An exception is *Placopecten magellanicus,* which because of the lesser convexity of the lower valve forms a good hydrofoil even when swimming parallel to the plane of the commissure, as is its habit (Stanley, 1970; Gould, 1971). Having wide umbonal angles, species of scallops that are free living (unattached) and thus swim frequently expel water for jet propulsion nearly parallel to their direction of movement for efficient swimming (Fig. 7). As a result of their wide umbonal angles, the shells of these species are also broader perpendicular to the direction of movement than are the shells of scallops that are normally byssally attached and swim rarely. This breadth increases the aspect ratio of free-living scallops, providing for greater lift (Stanley, 1970). Scallop species that are free living as adults are byssally attached as juveniles, however, and these species accordingly display an ontogenetic increase in umbonal angle. Gould (1971) has shown that this is one of several ontogenetic changes that enable large scallops to swim in the face of scaling problems. Permanent gapes are also present between the valves of free-swimming scallop species in the region where water is expelled (Stanley, 1970).

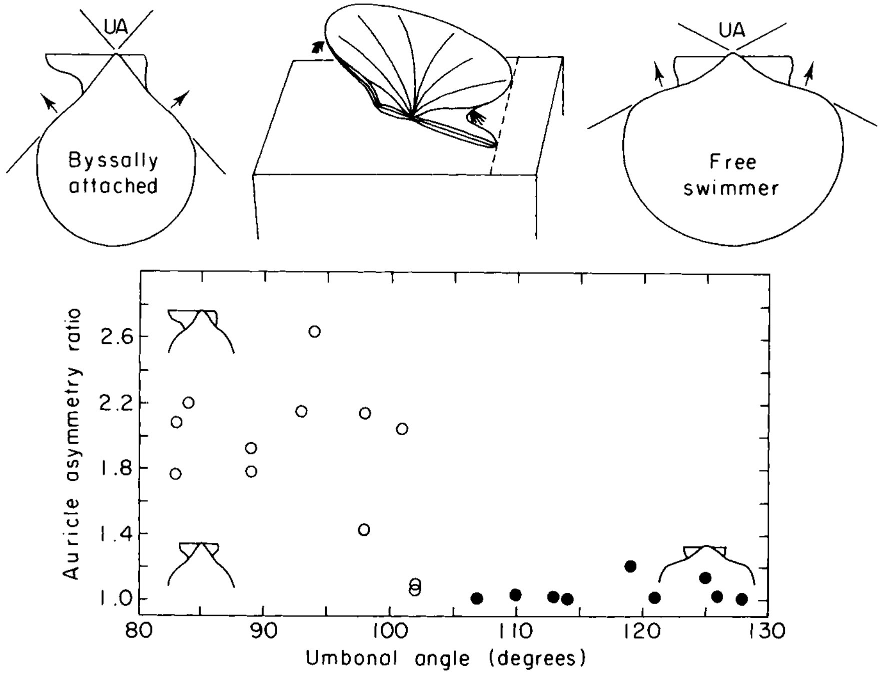


Fig. 7. Adaptations of the pectinacean shell. Byssally attached species employ a narrow umbonal angle (UA) and an elongate anterior auricle for stability. The central block diagram shows how these features provide the byssus with considerable leverage against an overturning force (curved arrow) by forming a fulcrum (dashed line) far from the point of byssal attachment. Free-swimming species (●) employ a wide UA to increase the aspect ratio and direct the propulsive jets (arrows) nearly parallel to the direction of locomotion. [After Stanley (1970).]

B. Gastropods

Because they must displace sediment rather than travel over it, burrowing gastropods might be expected to exhibit more conspicuous adaptations of shell form to locomotion than do epifaunal gastropods. This prediction has been borne out by observations.

The functional morphology of turritelliform snails that burrow has been especially well studied (Signor, 1982a,b, 1983). These have high-spired, many-whorled shells lacking a siphonal canal. Signor found that certain other morphological traits characterize turritelliform species with burrowing habits. Moving parallel to the coiling axis and needing to extend the foot in the direction of movement, these forms seldom have displaced tangential apertures (apertures that are coplanar with the ventral side of the shell). Internally, the large majority have columellar folds (spiral

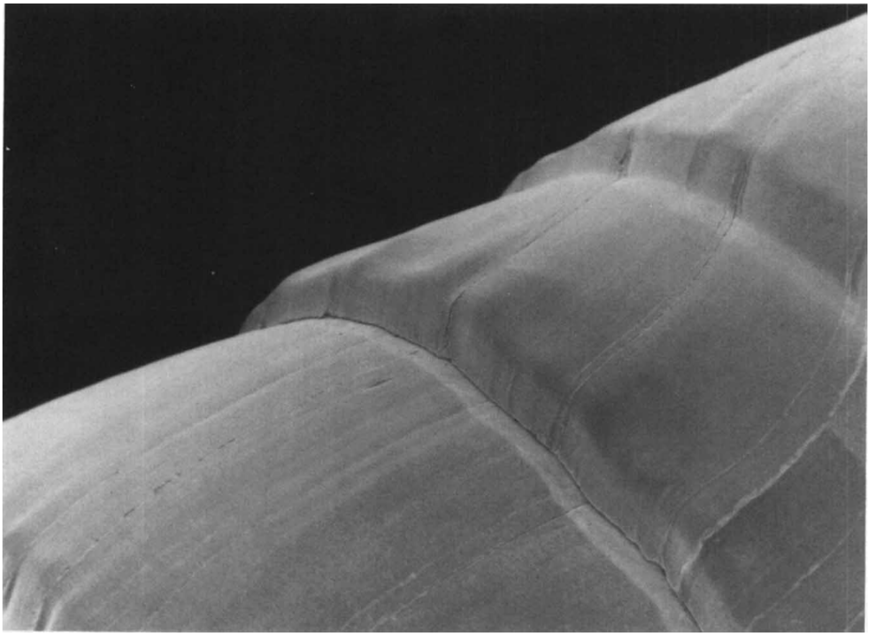


Fig. 8. Scanning electron micrograph of ratchetlike sculpture in *Terebra dimidiata* (see also Fig. 9). The "steps" are ~1 mm in height. The apex is toward the left, so that the steep slopes of the sculpture brace the shell while the foot probes. (Courtesy of P. W. Signor.)

ridges on the columella), which Signor and Kat (1982) interpreted as functioning to prevent the columellar muscles from shifting along the columella during forceful contraction. In addition, these snails have smooth flanks (flat whorls lacking strong ornamentation), which reduce drag. Ratchetlike ornamentation seems also to be restricted to those turritelliform species that are burrowers (Fig. 8). Experiments with this ornamentation intact and removed reveal that it serves as an aid to burrowing. It tends to lock the shell in the sediment so as to reduce backward movement during protrusion of the foot (Signor, 1983). Turritelliform species whose shells have a wide spiral angle burrow more rapidly than species with a narrow spiral angle. This might seem anomalous because a wide shell might be expected to offer greater resistance to sediment penetration, but this kind of shell also harbors a larger foot with a longer reach. Species with wide spiral angles also have columellar muscles that are less tightly coiled than those of narrower snails. Signor (1982a) noted that both of these features are compatible with the observation that the number of burrowing cycles required for shell burial is smaller for species with wide

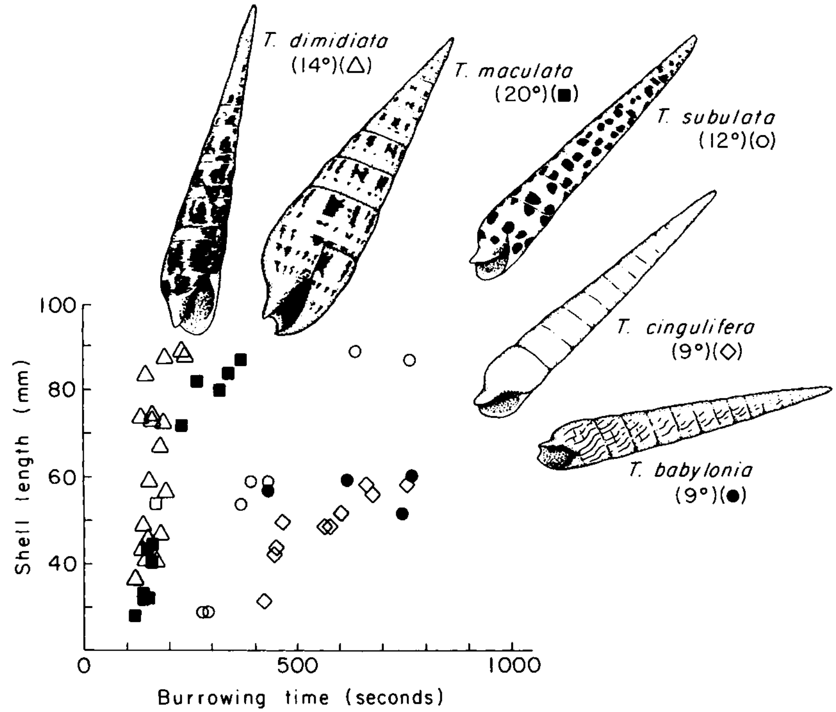


Fig. 9. Association in species of *Terebra* of rapid burrowing with a wide apical angle (in parentheses after species name). Burrowing time here is defined as the period of time between initial shell penetration of the sediment and submergence of the apex. [After Signor (1982a).]

shells (Fig. 9). Clearly, at some unknown apical angle the increased resistance of a wide shell must outweigh these muscular and pedal advantages so that, at least with regard to these factors, shape is optimized.

Although experimental verification is lacking, there can be little question that the smooth bullet-shaped shells of genera like *Bullia* and *Oliva* have also evolved as adaptations for rapid burrowing. There is, however, no absolute rule that within the Gastropoda an elongate shape is necessary for effective burrowing. As analyzed by Trueman (1968), *Polinices* employs both blood and water to expand the foot to the degree that the globose shell is engulfed in soft tissue.

Epifaunal gastropods display a modest number of shell features that have been considered to relate to locomotion. Linsley (1978a) proposed that the shape and orientation of the snail shell are adaptations for reducing shell drag. In fact, Reynolds numbers in snail movement are so low that the term "streamlined" is inappropriate as a description for shell form, and Palmer (1980) has shown that energy saved by reducing crawling speeds is three orders of magnitude lower than energy expended during normal locomotion. More probable is a relationship between shell thickness and rate of locomotion, but this seems not to have been tested. The thin shells of terrestrial pulmonates presumably represent adaptation to a mobile life in a medium of low density, although scarcity of calcium may also play a role.

McNair et al. (1981) found a close correspondence in prosobranchs between the shape of foot and shape of shell aperture. Inasmuch as foot shape is related to substratum preference (Miller, 1974), it can be concluded that apertural form is in part a passive trait, the evolution of which is governed by adaptive changes in the foot, which the aperture houses. McNair et al. (1981) also noted that species that are fundamentally epifaunal but have a foot that penetrates the sediment (e.g., *Busycon* and *Fasciolaria*) often have a flared aperture that penetrates the sediment when the animal clamps down or plows sediment aside when the animal crawls.

Perhaps the most bizarre adaptive relationship between shell form and locomotory mechanism in the Gastropoda is found in *Xenophora,* which is classified as a leaper (Linsley, 1978b). The shell of this animal has built-in stilts, which consist of empty, elongate shells of other species that have been cemented to the shell margin (Fig. 10). The animal normally hangs upside down within the protective cage formed by the stilts, but it moves by thrusting its foot down against the substratum and hopping forward to a new resting position.

III. Fixation and Stability

For immobile animals, shell adaptations for stability are often antithetical to ones that enhance locomotory capacities of mobile forms. One variable illustrating this principle is shell thickness. A thick shell promotes stability but inhibits rapid movement. Another is shell sculpture. In ways that will be discussed below, certain types of pronounced sculpture favor stability but impede locomotion. These conditions suggest the frequent occurrence of evolutionary compromise, in that stability and mobility ultimately may serve the same purpose. Among bivalves, for example, one solution to maintaining an infaunal position is having the ability to reburrow quickly if exhumed. Another is being able to avoid exposure in the first place. Certain kinds of shell ornamentation enhance one of these capacities and certain kinds enhance the other.

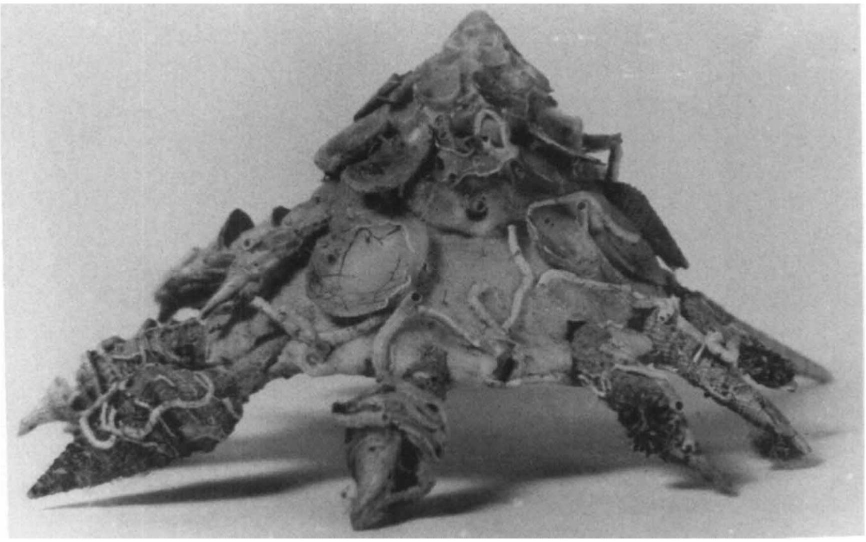


Fig. 10. Shell of *Xenophora pallidula,* to which elongate shells of other species are cemented as props. (Courtesy of R. M. Linsley.)

A. Bivalves

Infaunal bivalves gain stability simply by virtue of their situation within the substratum. On the other hand, most remain mobile and can be disinterred by water currents. It is not movement of the shell that is the fundamental problem, however. As water currents accelerate, sediment begins to move before a partly exposed bivalve shell is mobilized. Sediment is scoured preferentially from around a partly exposed shell, because here water currents are accelerated. The phenomenon can be understood first by recognizing that, because of drag, water currents flow more slowly near the sediment–water interface than higher in the water column. The water can then be viewed as passing over the bottom with a rotational component of movement (vorticity). As a vortex approaches an obstacle such as the posterior end of a bivalve shell protruding from sediment, it is stretched around the obstruction so that its diameter is reduced. As a result, vorticity increases because the product of vorticity and cross-sectional area must remain constant. Stretched vortex tubes that accumulate around an obstruction cause scour if a critical velocity is reached (Stanley, 1977). Experiments have shown that both ridges and spines on the surface of shells can reduce scour (Stanley, 1975a, 1981). In

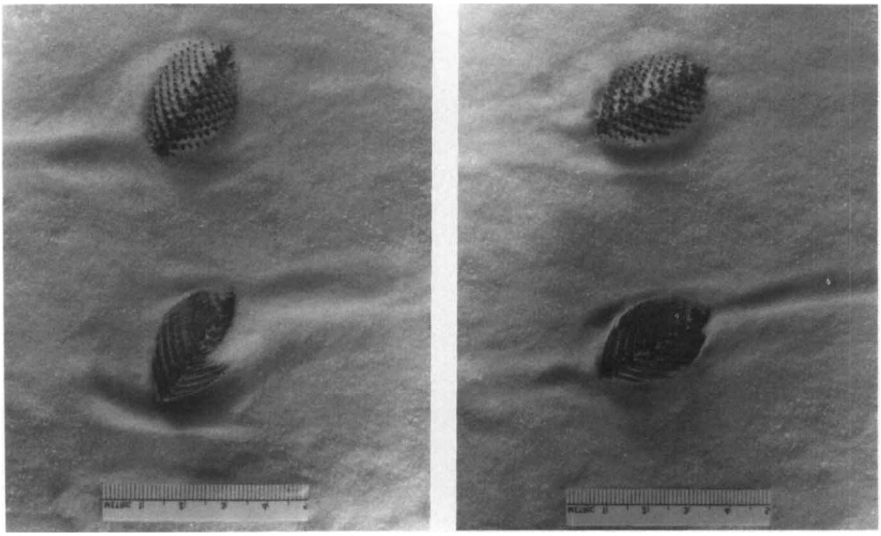


Fig. 11. Results of an experiment in which two black replicas of the shell of *Trachycardium egmontianum,* one unaltered and one with posterior spines (Fig. 2D) removed, were mostly buried in sand and subjected to oscillating water movements parallel to the scale. The altered specimen (below in these top views) suffered a larger amount of scour for both of the shell orientations shown here. [For details see Stanley (1981).]

the genus *Trachycardium,* flared spines on the anterior yield strong frictional asymmetry during shell rotation and thus aid in burrowing (Fig. 3), whereas cuplike spines on the posterior serve to reduce scour (Fig. 11). The mechanism by which scour is reduced here is uncertain. One effect of the ornamentation may be to trap sediment; another may be to disrupt currents adjacent to the shell, dispersing them as turbulence.

In certain species, periostracal spines perform the same kind of stabilizing function (Bottjer and Carter, 1980). The spikes of calcium carbonate that stud the periostracum of *Laternula* have been interpreted as adaptations that promote stability by gripping the sediment, but an alternative hypothesis would be that they simply protect the periostracum against abrasion, which would leave the shell vulnerable to dissolution by acidic interstitial waters.

Scour is also reduced by the low pyramidal shape of many shallow-burrowing bivalves such as arcids and cardiids (Stanley, 1970). This shape results from the configuration of the posterior dorsal flanks of the shell and from truncation of the posterior margin. The alleged importance of an unusually thick shell in stabilizing burrowing bivalves (Stanley, 1970) has not been investigated experimentally. A potentially competing hypothe-

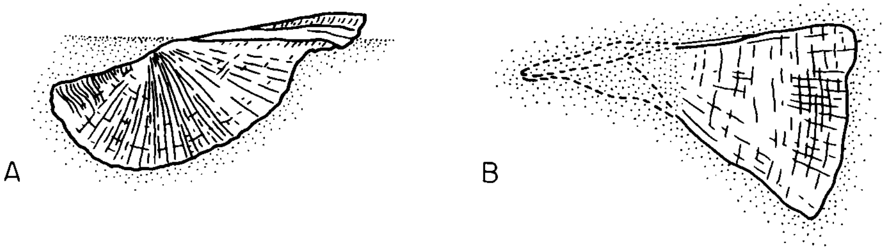


Fig. 12. Life position of *Trisidos*. (A) Cutaway lateral view. (B) Top view. [After Tevesz and Carter (1979).]

sis—although the two are not mutually exclusive—is that a thick shell serves to thwart predators, and this will be considered in Section IV.

Endobyssate bivalves (those that are byssally attached in positions of partial or complete burial) are more stable than free burrowers simply by virtue of their attachment. On the other hand, endobyssate taxa when detached are less mobile than nearly all free burrowers, so that dislodgement is quite hazardous. Thus, it is no surprise that the arcid *Trisidos* has evolved a twisted shape, so that while its anterior region sits buried in the sediment with the commissure vertical, the posterior portion of the shell rests flat on the sediment with its commissure horizontal (Fig. 12). This condition permits the posterior to become greatly expanded so as to separate the inhalant and exhalant currents. Posterior expansion, if the commissure were vertical, would create strong eddies and lead to scour of sediment from around the shell (McGhee, 1978; Thomas, 1978; Tevesz and Carter, 1979).

Among epifaunal bivalves the ultimate adaptation for stabilization is cementation to the substratum. The fossil record reveals that this mode of attachment did not evolve until the Permian Period. Epibyssate (byssally attached epifaunal) bivalves are typically elongate, which provides stability against rotation parallel to the plane of commissure. In the Arcacea, for example, epibyssate species differ from infaunal species in having a length–height ratio >1.35 (Stanley, 1970; Thomas, 1978). In the Arcacea, a pluglike byssus passing through a ventral gape between the valves provides especially strong anchorage. The Anomiidae are equipped with a similar byssus, which passes through what amounts to an aperture in the lower valve, an opening formed by the evolutionary migration of a marginal embayment to an interior position (Yonge, 1977). This permits the lower valve of anomiids to become xenomorphic—to conform to the configuration of the substratum for tight fixation. The Mytilidae, which possess a weaker byssus consisting of an array of discrete threads, are

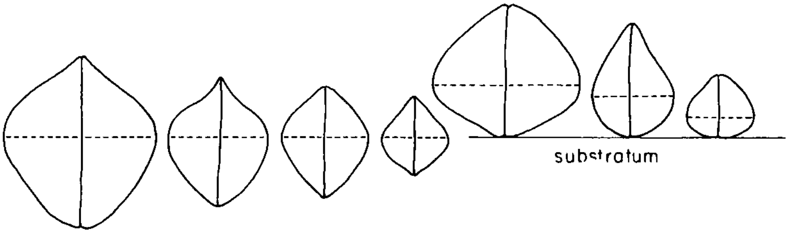


Fig. 13. Cross sections of bivalve species of the Mytilidae. Left: Four endobyssate species (*Modiolus modiolus, M. americanus, Geukensia demissa, Brachidontes citrinus*). Right: Three epibyssate species (*Mytilus edulis, Brachidontes recurvus, B. exustus*). [After Stanley (1972).]

less firmly attached. Epibyssate mytilids gain stability, however, from lateral expansion of the ventral region (Fig. 13). In effect, this increases the lever arm of the shell when tilted from the side by a potentially disruptive force (Stanley, 1970, 1972). At the same time, reduction of the

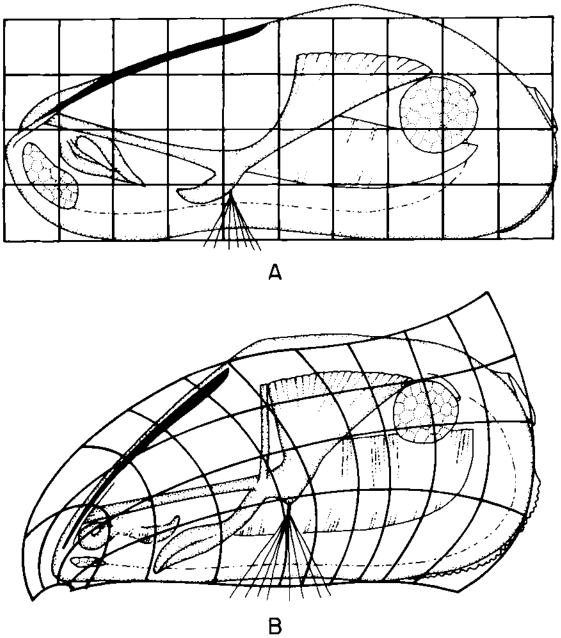


Fig. 14. Comparison of the shape of *Geukensia demissa* (A) to that of *Mytilus edulis* (B) by means of deformation coordinates. Points of intersection in the grid on A are replotted at homologous points on B. (The enlarged foot of *Mytilus* is ignored in this example.) Anterior reduction and posterior expansion result in enlarged and almost vertically oriented byssal retractor muscles in *Mytilus*. [After Stanley (1972).]

anterior portion of the body and shell and expansion of the posterior region (Fig. 14) result in enlargement of the byssal attachment muscles and a resultant vector of muscle contraction that is oriented nearly at right angles to the substratum (Stanley, 1970, 1972).

Byssate pectinaceans (scallops) are even more weakly attached, a condition rendered less problematical by their ability to swim when detached. Two features of the pectinacean shell outline represent adaptations for tighter fixation (Stanley, 1970) (Fig. 7). One is the narrower (<95°) umbonal angle than that of free-living pectinaceans; the other is an elongate auricle adjacent to the byssus (auricle asymmetry ratio is usually >1.4). Both of these features increase the lever arm of the byssus against potential overturning forces. In addition, the comblike ctenolium on the edge of the byssal notch spreads the byssal threads into a ribbonlike configuration so that it better resists rotation of the shell in the plane of commissure (Waller, 1984).

B. Gastropods

As might be expected, the least mobile gastropods display adaptations of shell form clearly related to stability. *Vermicularia,* an evolutionary descendant of the regularly coiled Turritellidae, secretes a coiled juvenile shell but then partly uncoils in subsequent growth to take on an irregular shape (Fig. 15). One function of this uncoiling is that it allows *Vermicularia,* a suspension feeder that cements to the substratum, to grow upward along and around irregular substrata for tight attachment. The uncoiling is looser on vertical than on horizontal substrata and near the bottoms of vertical substrata than near the tops (Gould, 1969).

Snails with limited mobility also exhibit shell adaptations for stability. Prime examples are species characterized by the limpet shape, which are found in a great variety of taxa including the Aplysiacea, Fissurellacea, Patellacea, Cocculinacea, Trochacea, Neritacea, Hipponicacea, Calyptreacea, Lamellariacea, Siphonariacea, Lymnaeacea, Acroloxacea, and Ancylacea. The limpet shape appears to increase stability in two ways: (1) it affords the foot with a broad surface area for clamping to the substratum, and (2) it is streamlined, so as to reduce the impact of strong water movements. Obviously it is no accident that many species of limpets inhabit wave-swept rocky shores.

In pulmonates, it seems that maintenance of a large foot surface–body volume ratio is of great importance for stability, and this condition is reflected in allometric changes during ontogeny (Gould, 1968).

The stability of gastropods of various shapes against strong water movements has never been studied. It seems evident, however, that tur-

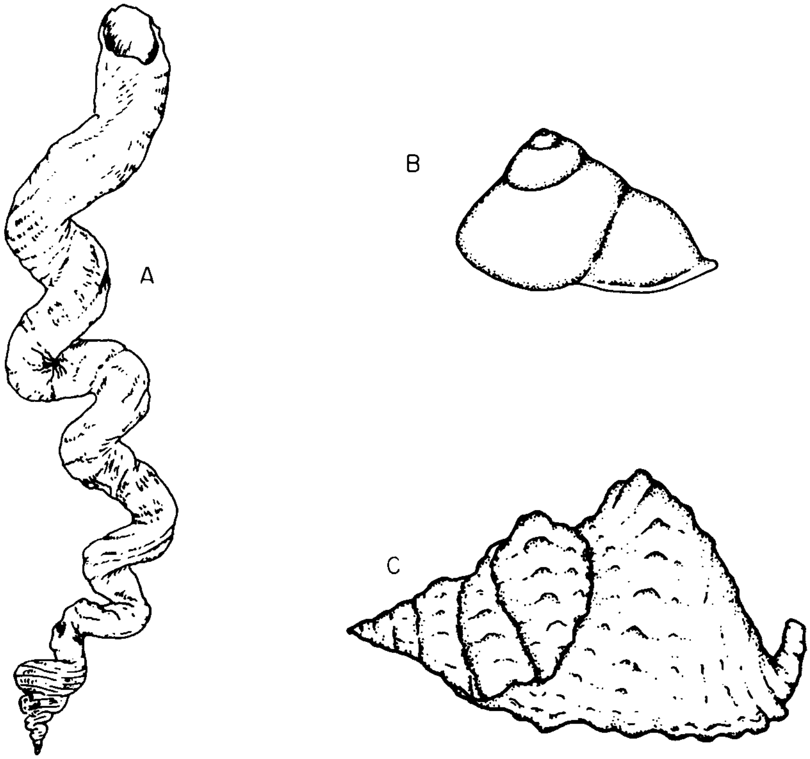


Fig. 15. Stabilizing features of the shells of three gastropod taxa. (A) *Vermicularia,* in which irregular uncoiling provides for attachment to hard substrata. [After Gould (1969.] (B) A terrestrial pulmonate, in which the final whorl is deflected downward for cementation during estivation. [After McNair et al. (1981).] (C) *Distorsio,* in which helical coiling is periodically distorted in such a way that the aperture lies parallel to the axis of coiling. [After Linsley (1977).]

biniform and trochiform species, standing well above the substratum, must be more vulnerable to disruptive water movements than a species that carries its shell with the coiling axis at a low angle. As Vermeij (1971) noted, species of the latter type often exhibit elongate shell apertures, and as Linsley (1977) noted, the evolution of this condition necessarily followed the evolution of the pectinibranch gill, which channels water asymmetrically through the mantle cavity.

Linsley's "second law" of gastropod shell form states that a shell of more than one volution with an aperture that is tangential to the body whorl is positioned in life with the plane of the aperture parallel to the substratum. The validity of this law is based on the need for the gastropod to clamp to the substratum, and this need is manifested in a variety of other shell adaptations. In gastropods that cling to rocks and thus require strong pedal adhesion, the shell aperture, reflecting the shape of the foot, has a nearly circular outline (McNair et al., 1981); examples are *Nerita, Littorina, Turbo,* and *Trochus.* In many terrestrial pulmonates, during ontogeny the body whorl becomes deflected downward so that the plane of the aperture, which in juveniles lies at an angle of ~30° to the coiling axis, comes to lie at an angle of ~60° (Fig. 15); this allows for effective clamping to the substratum during estivation (McNair *et al.,* 1981). It has been alleged that in the pulmonate *Cerion,* populations with large apertural lips tend to live on rocky substrata in windy settings (Woodruff, 1978). Particularly anomalous is the marine gastropod *Distorsio* (Fig. 15). This genus grows in an abnormal way that permits it, by growing in spurts, to maintain the plane of commissure parallel to the axis of coiling for close contact with the substratum (Linsley, 1977).

A set of apertural spines or a flared lip serves to orient some marine gastropods on the substratum. Often these are features only of the adult shell or are secreted periodically after rapid, episodic growth. To what extent such features serve to reduce the chance of overturning and exposure of the animal remains untested, but the thickness of the apertural lip of genera like *Strombus* suggests that the lip serves this kind of stabilizing function. Also apparently untested is the hypothesis that knobs projecting from the "shoulders" of shells such as *Busycon* or the juvenile *Strombus* serve as anchors that prevent rolling under the influence of external water movements.

Among the most unusual adaptation for maintenance of life position may be the bladelike varices of the muricid *Ceratostoma foliatum* (Palmer, 1977). This marine species commonly inhabits steeply sloping rock walls. When dislodged, its chance of landing with the aperture undermost is greatly increased by the presence of the varices. Thus, its chance of reattaching to the substratum before succumbing to predation is increased.

IV. Thwarting Predation

Certain adaptations of bivalve and gastropod shells obstruct predators directly, but others achieve the same result indirectly. Included in the second group are the large majority of adaptations discussed in the preceding two sections: adaptations that improve capacities for locomotion, fixation, or stability and thus render potential victims less vulnerable to predation. This section, then, focuses on skeletal traits that represent direct physical or (rarely) chemical barriers to predation.

A. Bivalves

Obviously the primitive function of the bivalve shell was in part one of protection, yet relatively few specific features of the modern bivalve shell can be assigned antipredator functions (Stanley, 1970; Vermeij, 1980; Boulding, 1984). If a shell provides protection against predators, a thick shell provides more protection than a thin shell. It is difficult to assess the trade-off between the benefit of secreting a thick shell and the accompanying sacrifice in burrowing speed (Stanley, 1970), although Boulding (1984) has shown that thick shells are more resistant to crab predation than thin shells. Energy expenditure in shell secretion is also difficult to evaluate.

The dangers of both physical instability and predation are reduced for deep burrowing bivalves, and these animals typically have thin shells (Stanley, 1970). The fact that many deep burrowers also have valves that are separated by permanent gapes, which facilitate crab predation (Boulding, 1984), suggests that deep within the sediment there is indeed a greatly reduced risk of predation: If certain species are successful in deep burrowing modes of life despite having permanent gapes, there is no reason for these species to expend energy secreting thick shells. Deep burrowing by a rapidly burrowing bivalve fleeing a predator is potentially hazardous, however, in that upward escape from deep burial may be difficult. This may explain the curved, razorlike shape of *Ensis* (Fig. 16). This shape causes an animal to burrow along a curved path, which eventually brings the animal, which began burrowing downward, up to the surface again (Stanley, 1970).

Gastropods that bore through bivalve shells by chemical solution are thwarted by conchiolin layers in the shells of small, otherwise vulnerable species of the Corbulidae (Lewy and Samtleben, 1979), although, as in the Unionidae and Margaritiferidae, these layers may also function as obstructions to shell solution by acidic interstitial waters (Kat, 1983).

Escape from predation simply by growing to large size is well documented for certain species of the Mytilidae (Paine, 1976; Boulding, 1984). Escape by size is suggested for some species of the Pectinitae in which adults are very large and become colonized by heavy barnacles and other epibionts that prevent or otherwise inhibit swimming, which in smaller species is necessary for predator avoidance.

Spines and other forms of shell sculpture almost certainly reduce levels of predation in some species of bivalves, but the details remain to be elucidated experimentally. Fewer infaunal species than epifaunal species exhibit spines that might function in this way. This might be interpreted as reflecting the reduced susceptibility of infaunal species to predation, but it

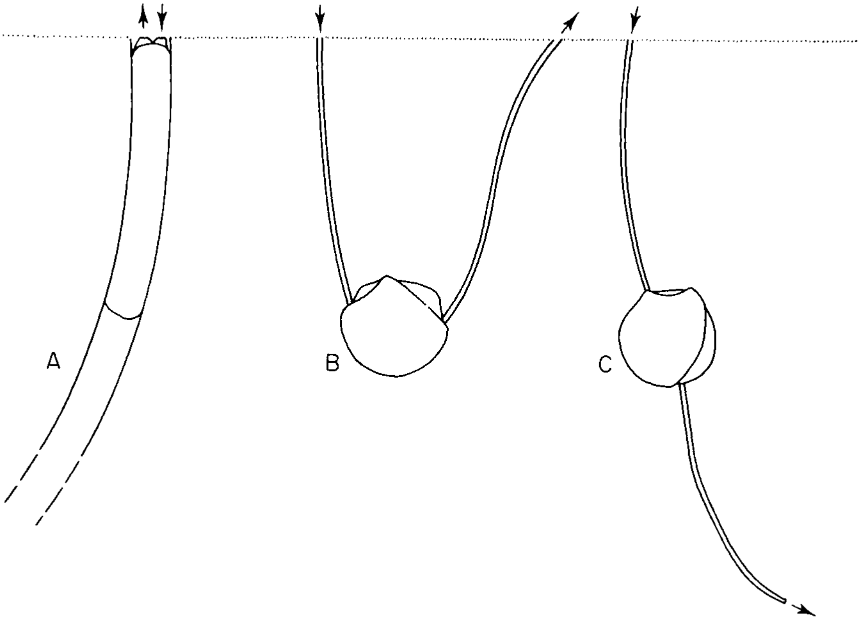


Fig. 16. Features of bivalve shell outlines that relate to modes of life. (A) Curvature of *Ensis*, which appears to function to prevent the animal from burrowing to great depth when pursued by a predator. (B) A typical lucinid, which contrasts with *Lucina pensylvanica* (C), in which the anterior (inhalant) mucous tube is directed upward from a projection along the shell margin.

could also reflect the fact that large spines would inhibit burrowing. The burrowing genus *Hysteroconcha*, an otherwise typical venerid, grows long, sharp spines in the posterior region of its shell (Fig. 17). These have been interpreted as obstructions to predaceous starfish and gastropods (Carter, 1967) but, because of their restricted position, seem more likely to protect the bivalve's siphons from fish predation (Stanley, 1970). The amputation of siphons by fishes is a common problem for the Bivalvia (Trevallion et al., 1970). The two families of epifaunal bivalves in which long spines are most widely deployed are the Chamidae and Spondylidae. Both include many species that are denizens of tropical coral reefs, where predation is intense, and many species that are encrusted with epibionts that may also serve a protective function.

Marginal scalloping or denticulation has been postulated to represent an antipredator adaptation (Carter, 1968b), but this idea is open to question. In the first place, there is no evidence that this configuration thwarts the entry of a starfish's stomach, as alleged. Second, scalloping of the shell margin is often simply the marginal expression of radial ribbing,

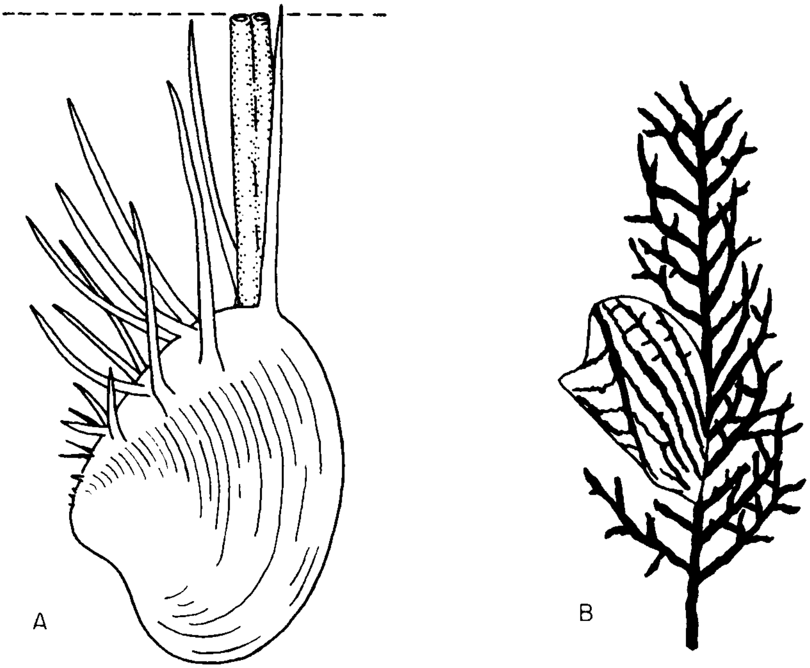


Fig. 17. Antipredator adaptations of bivalve shells. (A) *Hysteroconcha,* in which sharp spines apparently serve to protect the siphons. [After Stanley (1975a).] (B) *Electroma* (*Pterelectroma*) *zebra,* which exhibits protective coloration for life on alcyonarians.

which has other functions. Third, denticulation along the inner surface of an otherwise planar commissure seems simply to represent a mechanism for precise alignment of the valves on closure (only approximate alignment being achieved by the hinge teeth). Denticulation snaps valves into alignment if the initial offset of the valves at closure is less than one-half of the wavelength of the denticulation.

Proper valve alignment can be viewed as functioning primarily to obstruct predators, inasmuch as the fundamental protective function of the shell is diminished if the two valves are misaligned so as to expose the body. In species such as those of the Cardiidae and Trigoniidae in which the foot is exceptionally thick and muscular, the wide angles of gape required for pedal extrusion would result in frequent valve misalignment were it not for the presence of special guides (Stanley, 1977). The problem is that centrally positioned hinge teeth that maintain alignment well at small angles of gape are wedge shaped so that substantial shearing of the valves relative to one another is possible at wide angles of gape. In the Cardiidae the special guides that reduce this shearing are large lateral

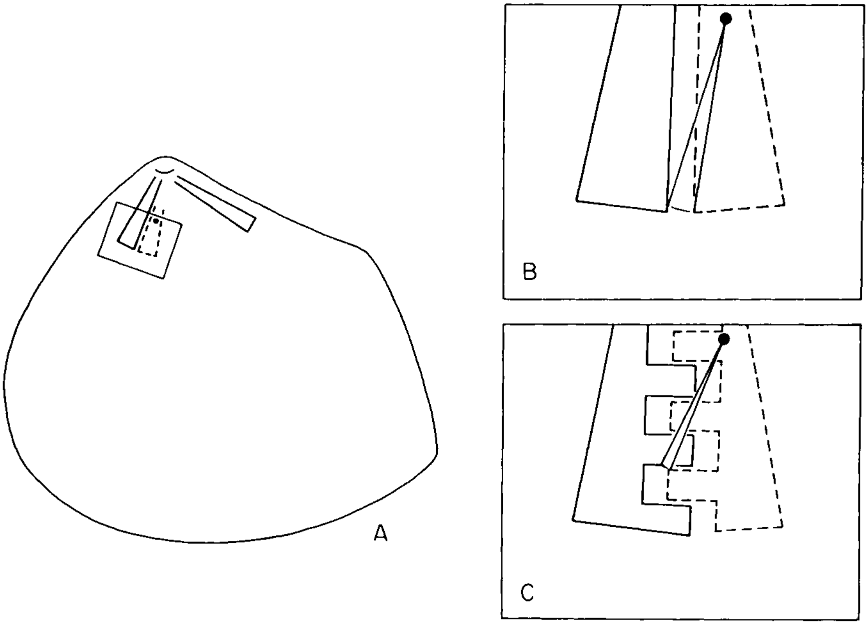


Fig. 18. Diagrammatic illustration of the function of secondary dentition in *Neotrigonia*. (A) The dot shows a potential axis of rotation of one valve relative to the other. (B) Enlargement of dentition, showing the large angle of shearing that would be permitted in the absence of secondary dentition. (C) Similar enlargement with secondary dentition present shows how only a small angle of shearing is permitted. [After Stanley (1977).]

hinge teeth that project far out from the hinge plate. In the Trigoniidae, the same function is performed by transverse secondary hinge teeth on the articulating surfaces of the primary teeth (Fig. 18).

Many thin-shelled epifaunal and semiinfaunal bivalve species avoid predation by secreting a shell much larger than is necessary to house the viscera and ctenidia. Examples are species of *Isognomon* (Kauffman, 1969) and the Pinnidae in which the viscera lie far from the valve margins and are relatively inaccessible to predators. This strategy is less evident among fully infaunal species in which fewer predator attacks are directed at the shell margin. The portion of the valves of the Pinnidae that extends beyond the viscera is formed largely by the outer shell layer, which is flexible. This flexibility is also a special adaptation that allows the valves to close in the face of predation by adductors even though the ligament no longer opens the valve (Seilacher, 1982).

Color patterns on bivalve shells thwart visual predators. Perhaps the most remarkable example is the zigzag pattern on *Electroma (Pterelec-*

troma) zebra, which mimics the alcyonarian to which it is normally attached (Fig. 17). The tellinacean *Donax,* though infaunal, lives along sandy shores where it is frequently dislodged by waves. The widely varied color patterns of individual species of *Donax* may function to prevent visual predators from forming precise search images (Moment, 1962; Smith, 1971, 1975).

B. Gastropods

Probably the original function of the gastropod shell was as a barrier to predation, so it is to be expected that particular features of modern gastropod shells serve as antipredator devices. The basic protective function of the univalve shell of creeping Mollusca seems to have been realized only after the evolution of torsion, which, in causing the head to be retracted

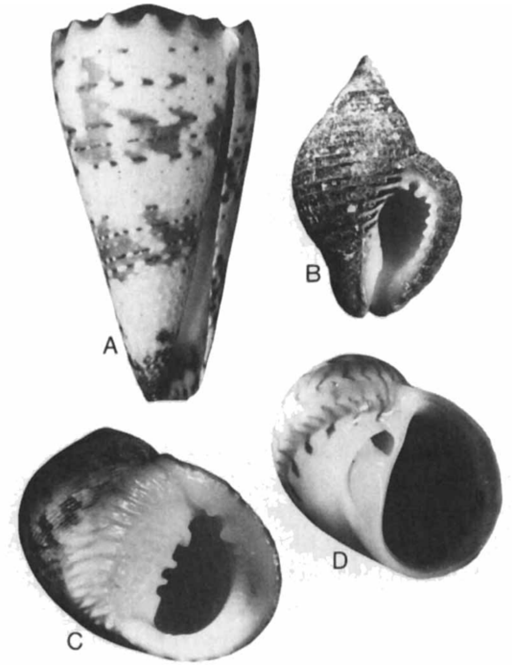


Fig. 19. Features of snail shells that offer resistance to predators. (A) *Conus imperialus,* illustrating a narrow aperture. (B) *Pollia undosa,* displaying a thickened, toothed aperture. (C) *Nerita undata,* in which the aperture is partly occluded by a toothed, shelflike structure. (D) *Natica canrina,* which secretes an umbilical plug.

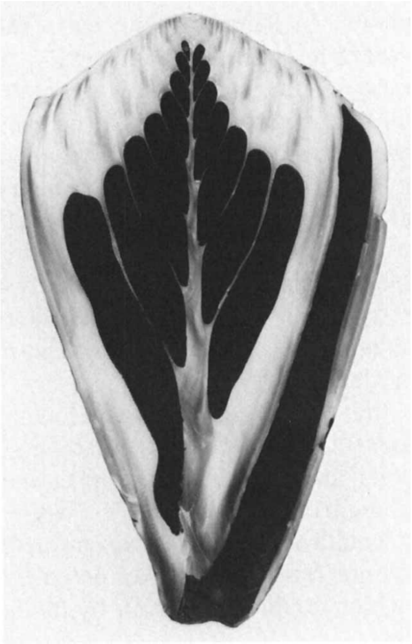


Fig. 20. Section through *Conus lividus,* showing removal of calcium carbonate from inner whorls and thickening of outer wall. [After Kohn et al. (1979).]

into the shell first, permitted an operculum to be employed to seal the shell aperture (Stanley, 1982).

Vermeij (1977, 1979, 1982) concluded that a number of other traits of marine gastropod shells are specifically antipredator adaptations (Fig. 19). These include thickening of the shell, external sculpture, a narrow, elongate aperture, apertural dentition and varices, tight coiling, a low spire, and an umbilical plug. The efficacy of several of these features at thwarting predatory crabs has been confirmed by experimentation or by examination of "dead" shells to detect predation patterns (Bertness and Cunningham, 1981; Vermeij, 1982). Apertural barriers serve primarily to resist spiral peeling of the shell by crabs such as *Calappa*. A thick shell, tight coiling, a low spire, and an umbilical plug all provide strength against crushing.

Remodeling of the shell interior strengthens some taxa, such as *Conus,* in which shell material of inner whorls is dissolved away while the outer whorl is thickened (Fig. 20) (Kohn et al., 1979). Open coiling, in which adjacent whorls are out of contact, is rare among modern gastropods, occurring in just 15 known species (Rex and Boss, 1976); the incidence of open coiling was greater in Paleozoic and early Mesozoic time, when crushing predators were less common and less sophisticated (Vermeij, 1977). Palmer (1979) argued that stout spines and nodes in the exterior of a gastropod shell would be ineffectual against the crusher claw of a crab, which would fit between them for crushing or would peel the shell along a path between them. With the support of experiments, Palmer concluded that stout spines and nodes function instead to thwart predation by fishes, which apply pressure over a broad segment of the shell surface. The precise nature of the physical resistance is unknown but may entail (1) increase in the effective shell diameter, (2) distribution of stress over a broad area, (3) localization of stress at the thickest part of the shell, and (4) damage to the predator.

It has been shown that there is an increase in lower latitudes in the shell defenses of gastropods and in the strength and diversity of crushing crabs (Vermeij, 1976; Vermeij and Currey, 1980; Zipser and Vermeij, 1978) and the diversity of crushing fishes (Palmer, 1979). While it is reasonable that tropical gastropods would have evolved strong defenses in the face of heavy predation, it is not clear why weaker defenses are present in temperate gastropods, which could also benefit by having strong ones (Vermeij and Currey, 1980).

The extraordinary range of color polymorphism exhibited by the land snail *Cepaea* has been related to visual selection by predators. Birds preferentially select snails that are least well camouflaged against their background (Cain and Sheppard, 1954). Polymorphism is maintained by another process, which is the tendency of predators to take a disproportionate percentage of common varieties, apparently as a result of the formation of search images (Clarke, 1962).

V. Feeding and Respiration

Water currents that supply a gastropod or bivalve with oxygen commonly provide food or permit the animal to orient toward food. For this reason, nearly all adaptations of the shell that are associated with respiration are also associated with feeding.

A. Bivalves

Fundamental to infaunal bivalves is the problem of obtaining water for respiration and, in some species, food. Many species employ siphons for effective or long-distance channeling of water currents, and a few infaunal groups such as the Poromyacea and the venerid *Anomalocardia* have shells with rostrate posteriors, which take the place of long siphons. The most bizarre structures of this type are the very elongate tubelike structures of the Gastrochaenacea, Pholadacea, and Clavagellacea (Savazzi, 1982). These are secondary calcareous envelopes rather than true shell structures, and are thus excluded from this review. Those species that employ large siphons formed by fusion of the mantle margins would be unable to retract them without an inflection of the pallial line. This is the line of muscular attachment of the mantle to the shell, on which the line is visible when the mantle is removed. This inflection, or pallial sinus, has long been employed by paleontologists as an indication of the presence of siphons and as an estimation of their length.

Other species exhibit morphological specializations of the siphonal region of the shell that relate to the disposition of the siphons. Most members of the Tellinidae are deposit feeders that lie buried in the sediment, not with the commissure vertical, but with the left valve undermost. This posture permits many tellinid species to maintain a fixed depth within the sediment as they move from place to place while deposit feeding (Stanley, 1970). In the majority of these species, the posterior region is twisted to the right, which creates a gentle curvature of the inhalant siphon where it exits from the shell, so that the inhalant current encounters reduced resistance. *Lucina pensylvanica* is unusual among Lucinidae in living with its shell rotated backward so that the anterior mucous tube (the inhalant structure secreted by the elongate foot) exits more nearly straight upward than in other lucinids (Fig. 16). The anterior region of the shell is constricted, elevating the sector from which the mucous tube emerges (Stanley, 1970).

It is clear that the shell form of certain epifaunal species also enhances current flow. The elongate posterior auricle ("wing") of *Pteria,* a genus that attaches to alcyonarians (Fig. 17), serves to protect the exhalant current from external water currents that would sweep it back into the inhalant area of the commissure (Stanley, 1970, 1972). The animal attaches to the alcyonarian stalk in an orientation that directs the auricle and exhalant current diagonally upward. In certain oysters, a curved shell appears to funnel used water effectively away by concentrating exhalant currents in the concavity of the shell so that they form a single current and that resistance to their flow is reduced (Carter, 1968a). It has been proposed that the zigzag commissure of certain oyster species results in the exposure of a broad gill surface to the inhalant water flow for more effective filtration (Carter, 1968a).

Semiinfaunal bivalve species that employ symbiotic algae for nutrition display unusual adaptations to increase the productivity of the algae. The body and shell of *Tridacna* are greatly hypertrophied in the siphonal region, which harbors the algae; severe reduction of the anterior region then allows the ventral byssus to pass downward to attach to the substratum while the siphonal (posterior) region with the symbiotic algae is directed upward (Yonge, 1936; Stasek, 1961). The margin of the shell is scalloped, but the margins of the two valves do not meet; the projections of each valve do not fill the corresponding embayments of the other. This condition apparently serves to expand the area of algae-bearing siphonal tissue exposed when the valves gape and allows some photosynthetic activity even when the valves are apposed (Stanley, 1970).

Within the Bivalvia, the most unusual shell adaptation for feeding may be the rasping sculpture of the Teredinidae (Fig. 6), species of which consume and digest wood shavings produced by their boring activities.

B. Gastropods

The siphonal canal of the neogastropod serves to protect the partly retracted siphon, which draws in water for respiration and for detecting prey. The evolution of an elongate shell aperture was possible only after the loss of one gill (Linsley, 1977). Thus, it would seem to be no accident that carnivory is not well developed in more primitive gastropods, which cannot draw in water through a single narrow channel.

In a sense, exhalant slits like those of *Pleurotomaria* and holes like those of limpet-shaped gastropods serve to aid feeding and respiration because they funnel used water efficiently from the shell. This reduces the reuse of water, and it also increases the rate of inhalant flow, which cannot exceed the exhalant rate.

The irregularly coiled genus *Vermicularia,* a descendant of *Turritella* or a close relative, exhibits a somewhat irregular pattern of uncoiling. Gould (1969) noted that this growth habit of *Vermicularia,* which is associated with a mode of life of attachment to corals or other hard substrata, enables the animal to extend its feeding region quickly to an open area where food is plentiful. Few other suspension-feeding gastropods seem to possess special adaptation for positioning their inhalant regions propitiously for drawing in food.

Similarly, it is difficult to relate shell features other than a siphonal canal to carnivory. Taxa like *Fasciolaria* and *Busycon* open bivalves with the lip of their shell, but each genus displays no more special adaptation for this than a relatively thin shell, which is apparently suitable for prying apart the valves of prey but nonetheless strong enough to withstand the resulting stresses. The species *Ceratostoma foliatum* does employ a spe-

Fig. 21. Oblique apertural view of the gastropod *Ceratostoma foliatum*, showing the marginal tooth employed to pry barnacles from the substratum.

cial tooth on the outer lip of its shell to dislodge barnacles from rocky surfaces (Fig. 21).

A large shell interior can be viewed as advantageous for carnivorous gastropods in enabling them to consume large prey. Thus, Kohn et al. (1979) interpreted shell resorption in *Conus* (Fig. 20), a process that enlarges living space, as an adaptation permitting the consumption of large prey.

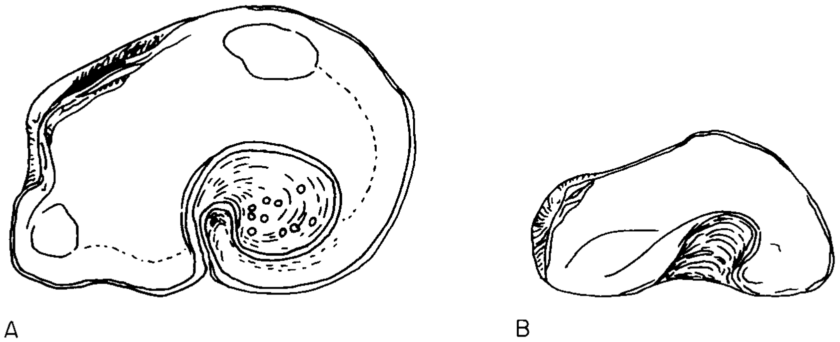


Fig. 22. Brood pouches in the shells of carditids. (A) *Thecalia concamera;* shell, 14 mm long. (B) *Milneria kelseyi;* shell, 5 mm long. [After Yonge (1969).]

VI. Reproduction

Molluscan shells, by way of preserved prodissoconchs, commonly reveal a planktonic or nonplanktonic larval history (see review in Jablonski and Lutz, 1983). Much less conspicuous are adaptations of the adult shell associated with mode of reproduction or with reproductive output.

A. Bivalves

Certain species of bivalves display sexual dimorphism, but in many cases the functional significance remains unknown. In some astartid and carditid species that brood their larvae, the shells of females are more convex than those of males, the most notable examples being members of the freshwater Unionidae (Heaslip, 1969; Kauffman and Buddenhagen, 1969). In the carditid subfamily Thecaliinae, shell adaptations are far more conspicuous (Dall, 1903). Here the ventral region of the female shell grows aberrantly to form a reentrant that serves as a marsupium (Fig. 22).

B. Gastropods

There are also gastropods that use the large umbilicus of their shell as a nest for their eggs. In one of these, the trochid *Margarites vortificerus,* the sexual dimorphism associated with this habit is so pronounced that the male and female were described as separate species (Lindberg and Dobberteen, 1981).

A novel but promising suggestion has been advanced by Davis (1979) for the function of shell sculpture patterns in the Pomatopsidae, and it

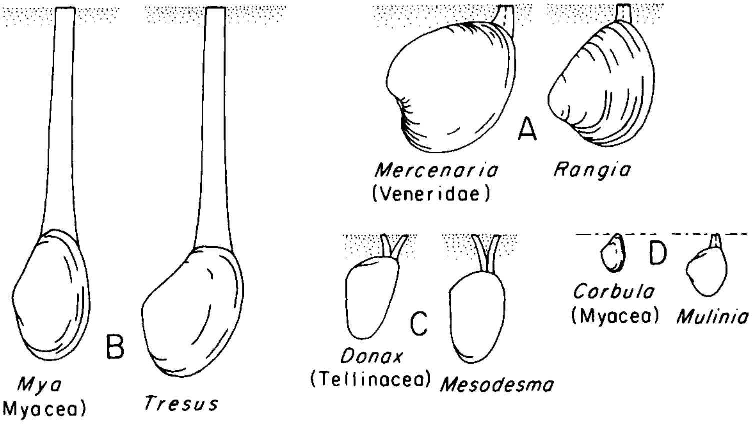


Fig. 23. Evolutionary divergence within the Mactracea (right-hand member of each pair) and convergence with members of other taxa. (A) Shell large and thick, for stability and anterior blunt for effective burrowing. (B) Shell elongate and tubular with gapes for both foot and long siphons; hinge teeth lost so that valves can rock about a dorsoventral axis during pedal and siphonal movements. All of these features, and secretion of a thin shell, are permitted by deep life position, which excludes most predators. (C) Shell with elongate anterior, to accommodate a large foot for rapid burrowing along sandy beaches; shell wedge shaped and moderately smooth, for reduced resistance of sediment; posterior truncate so that foot, which emerges at right angles to hinge axis, is directed toward narrow end of shell; valves thick, for physical stability. (D) Shell small, for flotation in soupy mud. [After Stanley (1970).]

may apply to other taxa as well. This is the idea that species-specific sculpture patterns serve as a basis for mate recognition under conditions of high species diversity in freshwater habitats.

VII. Evolutionary Convergence

One of the strongest lines of evidence favoring any alleged relationship between form and function is the presence in two or more distantly related taxa of both the morphological feature and the function in question. The implication is that the form has arisen more than once in association with the function, by evolutionary convergence.

Examples of such convergence have been noted above: the independent evolution in numerous taxa of the limpet shape for firm attachment to hard substrata, for example, and the evolution in both the Pholadacea and Veneracea of a thin, elongate shell with cup-shaped spines for boring into hard substrata (Fig. 5). Another example of evolutionary convergence is illustrated in Fig. 23, which compares the shell form of burrowing genera within the superfamily Mactracea to genera having similar shapes and habits but belonging to other higher taxa.

References

Bertness, M. D., and Cunningham, C. (1981). Crab shell-crushing predation and gastropod architectural defense. *J. Exp. Mar. Biol. Ecol.* **50,** 213–230.

Bottjer, D. J., and Carter, J. G. (1980). Functional and phylogenetic significance of projecting periostracal structures in the Bivalvia (Mollusca). *J. Paleontol.* **54,** 200–216.

Boulding, E. G. (1984). Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *J. Exp. Mar. Biol. Ecol.* **76,** 201–223.

Cain, A. J., and Sheppard, P. M. (1954). Natural selection in *Cepaea. Genetics* **39,** 89–116.

Carter, J. G. (1978). Ecology and evolution of the Gastrochaenacea (Mollusca, Bivalvia) with notes on the evolution of the endolithic habitat. *Yale Univ. Peabody Mus. Nat. Hist. Bull.* **41,** 1–92.

Carter, R. M. (1967). The shell ornament of *Hysteroconcha* and *Hecuba* (Bivalvia): a test case for inferential functional morphology. *Veliger* **10,** 59–71.

Carter, R. M. (1968a). Functional studies on the Cretaceous oyster *Arcostrea. Palaeontology* **11,** 458–485.

Carter, R. M. (1968b). On the biology and paleontology of some predators of bivalved Mollusca. *Palaeogeogr., Paleoclimatol., Palaeoecol.* **4,** 29–65.

Clarke, B. (1962). Balanced polymorphism and the diversity of sympatric species. *Syst. Assoc. Publ.* **4,** 47–70.

Dall, W. H. (1903). Synopsis of the Carditacea and of the American species. *Proc. Acad. Nat. Sci., Philadelphia* **54,** 696–716.

Davis, G. M. (1979). The origin and evolution of the gastropod family Pomatiopsitae, with emphasis on the Mekong River Triculinae. *Acad. Nat. Sci. Philadelphia Monogr.* **20,** 1–120.

Drew, G. A. (1900). Locomotion in *Solenomya* and its relatives. *Anat. Anz.* **17,** 257–266.

Gould, S. J. (1968). Ontogeny and the explanation of form: an allometric analysis. *J. Paleontol.* **42,** 81–98.

Gould, S. J. (1969). Ecology and functional significance of uncoiling in *Vermicularia spirata:* an essay on gastropod form. *Bull. Mar. Sci.* **19,** 432–445.

Gould, S. J. (1971). Muscular mechanics and the ontogeny of swimming in scallops. *Palaeontology* **14,** 61–94.

Heaslip, W. G. (1969). Sexual dimorphism in bivalves. *In* "Sexual Dimorphism in Fossil Metazoa and Taxonomic Implications" (G. E. G. Westermann, ed.), pp. 60–75. Schweizerbart, Stuttgart.

Jablonski, D., and Lutz, R. A. (1983). Larval ecology of marine benthic invertebrates: paleobiological implications. *Biol. Rev. Cambridge Philos. Soc.* **58,** 21–89.

Kat, P. W. (1983). Conchiolin layers among the Unionidae and Margaritiferidae (Bivalvia): microstructural characteristics and taxonomic implications. *Malacologia* **24,** 298–311.

Kauffman, E. G. (1969). Form, function, and evolution. *In* "Treatise on Invertebrate Paleontology, Part N, Mollusca 6, Bivalvia," pp. 129–205. Geol. Soc. Am. and Univ. of Kansas Press, Lawrence.

Kauffman, E. G., and Buddenhagen, C. H. (1969). Protandric sexual dimorphism in Paleocene Astarte (Bivalvia) of Maryland. *In* "Sexual Dimorphism in Fossil Metazoa and

Taxonomic Implications" (G. E. G. Westermann, ed.), pp. 76–93. Schweizerbart, Stuttgart.

Kohn, A. J., Myers, E. R., and Meenakshi, V. R. (1979). Interior remodeling of the shell by a gastropod mollusk. *Proc. Natl. Acad. Sci.* **76,** 3406–3410.

Lewy, Z., and Samtleben, C. (1979). Functional morphology and palaeontological significance of the conchiolin layers in corbulid pelecypods. *Lethaia* **12,** 341–351.

Lindberg, D. R., and Dobberteen, R. A. (1981). Umbilical brood protection and sexual dimorphism in the Boreal Pacific gastropod, *Margarites vorticiferus* Dall. *Int. J. Invertebr. Reprod.* **3,** 347–355.

Linsley, R. M. (1977). Some "laws" of gastropod shell form. *Paleobiology* **3,** 196–206.

Linsley, R. M. (1978a). Locomotion rates and shell form in the Gastropoda. *Malacologia* **17,** 193–206.

Linsley, R. M. (1978b). Shell form and evolution of gastropods. *Am. Sci.* **66,** 432–441.

Linsley, R. M., and Peel, J. S. (1983). Gonad pouches in a new clam-like monoplacophoran from the Silurian of Sweden. *Lethaia* **16,** 273–280.

McGhee, G. R. (1978). Analysis of the shell torsion phenomenon in the Bivalvia. *Lethaia* **11,** 315–319.

McNair, C. G., Kier, W. M., LaCroix, P. D., and Linsley, R. M. (1981). The functional significance of aperture form in gastropods. *Lethaia* **14,** 63–70.

Miller, R. C. (1924). The boring mechanism of *Teredo. Univ. Calif., Berkeley, Publ. Zool.* **26,** 41–73.

Miller, S. L. (1974). Adaptive design of locomotion and foot form in prosobranch gastropods. *J. Exp. Mar. Biol. Ecol.* **14,** 99–156.

Moment, G. B. (1962). Reflexive selection: a possible answer to an old puzzle. *Science* **136,** 262–263.

Morse, E. S. (1913). Observations on living Solenomya. *Biol. Bull.* (*Woods Hole, Mass.*) **25,** 261–281.

Nair, N. B., and Ansell, A. D. (1968). The mechanism of boring in *Zirphaea crispata* (L.) (Bivalvia: Pholadidae). *Proc. R. Soc. London, Ser. B* **170,** 155–173.

Paine, R. T. (1976). Size-limited predation: an observational and experimental approach with the *Mytilus–Pisaster* interaction. *Ecology* **57,** 858–873.

Palmer, A. R. (1977). Function of shell sculpture in marine gastropods: hydrodynamic destabilization in *Ceratostoma foliatum. Science* **197,** 1293–1295.

Palmer, A. R. (1979). Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution* **33,** 687–713.

Palmer, A. R. (1980). Locomotion rates and shell form in the Gastropoda: a reevaluation. *Malacologia* **19,** 289–296.

Rex, M. A., and Boss, K. J. (1976). Open coiling in recent gastropods. *Malacologia* **15,** 289–297.

Russell Hunter, W. (1949). The structure and behavior of *Hiatella gallicana* (Lamarck) and *H. arctica,* with special reference to the boring habit. *Proc. R. Soc. Edinburgh, Sect. B* **63,** 271–289.

Savazzi, E. (1982). Shell sculpture and burrowing in the bivalves *Scapharca inaequivalvis* and *Acanthocardia tuberculata. Stuttg. Beitr. Naturkd. A* **353,** 1–12.

Seilacher, A. (1972). Divaricate patterns in pelecypod shells. *Lethaia* **5,** 325–343.

Seilacher, A. (1973). Fabricational noise in adaptive morphology. *Syst. Zool.* **22,** 451–465.

Seilacher, A. (1982). The kinetic valves of *Pinna. Neues Jahrb. Geol. Palaeontol., Abhandl.* **164,** 236–238.

Signor, P. W. (1982a). Influence of shell shape on burrowing rates in infaunal turritelliform snails. *North Am. Paleontol. Conv. Proc., 3rd* **2,** 483–487.

Signor, P. W. (1982b). Resolution of life habits using multiple morphologic criteria: shell form and life-mode in turritelliform gastropods. *Paleobiology* **8,** 378–388.

Signor, P. W. (1983). Burrowing and the functional significance of ratchet sculpture in turritelliform gastropods. *Malacologia* **23,** 313–320.

Signor, P. W., and Kat, P. W. (1982). Functional significance of columellar folds in turritelliform gastropods. *J. Paleontol.* **58,** 210–216.

Smith, D. A. S. (1971). Polymorphism and population density in *Donax rugosus* (Lamellibranchiata: Donacidae). *J. Zool.* **164,** 429–441.

Smith, D. A. S. (1975). Polymorphism and selective predation in *Donax faba* Gmelin (Bivalvia: Tellinacea). *J. Exp. Mar. Biol. Ecol.* **17,** 205–219.

Stanley, S. M. (1969). Bivalve mollusk burrowing aided by discordant shell ornamentation. *Science* **166,** 634–635.

Stanley, S. M. (1970). Relation of shell form to life habits in the Bivalvia. *Geol. Soc. Am. Mem.* **125,** 1–296.

Stanley, S. M. (1972). Functional morphology and evolution of byssally attached bivalve mollusks. *J. Paleontol.* **46,** 165–212.

Stanley, S. M. (1975a). Adaptive themes in the evolution of the Bivalvia (Mollusca). *Annu. Rev. Earth Planet. Sci.* **3,** 361–385.

Stanley, S. M. (1975b). Why clams have the shape they have: an experimental analysis of burrowing. *Paleobiology* **1,** 48–58.

Stanley, S. M. (1977). Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves. *Palaeontology* **20,** 869–899.

Stanley, S. M. (1981). Infaunal survival: alternative functions of shell ornamentation in the Bivalvia (Mollusca). *Paleobiology* **7,** 384–393.

Stanley, S. M. (1982). Gastropod torsion: predation and the opercular imperative. *Neues Jahrb. Geol. Palaeontol., Abh.* **164,** 95–107.

Stasek, C. R. (1961). The form, growth, and evolution of the Tridacnidae (giant clams). *Arch. Zool. Exp. Gen.* **101,** 1–40.

Studnitz, G. von (1931). Die Morphologie und Anatomie von *Lima inflata* der Feilenmuschel, nebst biologischen Untersuchungen an *Lima hians* Gmel. *Zool. Jahrb. Abt. Anat. Ontog. Tiere* **53,** 199–316.

Tevesz, M. J. S. (1977). Taxonomy and ecology of the Philobryidae and Limopsidae (Mollusca: Pelecypoda). *Yale Univ. Peabody Mus. Postilla* **171,** 1–64.

Tevesz, M. J. S., and Carter, J. G. (1979). Form and function in *Trisidos* (Bivalvia) and a comparison with other burrowing arcoids. *Malacologia* **19,** 77–85.

Tevesz, M. J. S., and McCall, P. L. (1976). Primitive life habits and adaptive significance of the pelecypod form. *Paleobiology* **2,** 183–190.

Thomas, R. D. K. (1975). Functional morphology, ecology, and evolutionary conservatism in the Glycymerididae. *Palaeontology* **18,** 217–254.

Thomas, R. D. K. (1976). Constraints of ligament growth, form and function on evolution in the Arcoida (Mollusca: Bivalvia). *Paleobiology* **2,** 64–83.

Thomas, R. D. K. (1978). Shell form and the ecological range of living and extinct Arcoida. *Paleobiology* **4,** 181–194.

Trevallion, R. R., Edwards, C., and Steele, J. H. (1970). Dynamics of a benthic bivalve. *In* "Marine Food Chains" (J. H. Steele, ed.), pp. 285–295. Oliver & Boyd, Edinburgh.

Trueman, E. R. (1964). Adaptive morphology in paleoecological interpretation. *In* "Approaches to Paleoecology" (J. Imbrie and N. D. Newell, eds.), pp. 45–74. Wiley, New York.

Trueman, E. R. (1968). The mechanism of burrowing of some naticid gastropods in comparison with that of other molluscs. *J. Exp. Biol.* **48,** 663–678.

Trueman, E. R., Brand, A. R., and Davis, P. (1966). The effect of substrata and shell shape on the burrowing of some common bivalves. *Malacol. Soc. London Proc.* **37,** 97–109.

Vermeij, G. J. (1971). Gastropod evolution and morphological diversity in relation to shell geometry. *J. Zool.* **104,** 153–160.

Vermeij, G. J. (1976). Interoceanic differences in vulnerability of shelled prey to crab predation. *Nature* (*London*) **260,** 135–136.

Vermeij, G. J. (1977). The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* **3,** 245–258.

Vermeij, G. J. (1979). Shell architecture and causes of death of Micronesian reef snails. *Evolution* **33,** 686–696.

Vermeij, G. J. (1980). Drilling predation of bivalves in Guam: some paleoecological implications. *Malacologia* **19,** 329–334.

Vermeij, G. J. (1982). Gastropod shell form, breakage, and repair in relation to predation by the crab *Calappa*. *Malacologia* **23,** 1–12.

Vermeij, G. J., and Currey, J. D. (1980). Geographical variation in the strength of Thaid snail shells. *Biol. Bull.* (*Woods Hole, Mass.*) **158,** 383–389.

Waller, T. R. (1984). The ctenolium of scallop shells: functional morphology and evolution of a key family-level character in the Pectinacea (Mollusca: Bivalvia). *Malacologia* **25,** 203–219.

Woodruff, D. S. (1978). Evolution and adaptive radiation of *Cerion:* a remarkably diverse group of West Indian snails. *Malacologia* **17,** 223–239.

Yonge, C. M. (1936). Mode of life, feeding, digestion, and symbiosis with zooxanthellae in the Tridacnidae. *Great Barrier Reef Exped., 1928–1929, Br. Mus. Sci. Rep.* **1,** 283–321.

Yonge, C. M. (1962). On the primitive significance of the byssus in the Bivalvia and its effects in evolution. *J. Mar. Biol. Assoc. U.K.* **42,** 113–125.

Yonge, C. M. (1969). Functional morphology and evolution within the Carditacea (Bivalvia). *Proc. Malocological Soc. London* **38,** 493–527.

Yonge, C. M. (1977). Form and evolution in the Anomiacea (Mollusca: Bivalvia)—*Pododesmus, Anomia, Patro, Enigmonia* (Anomiidae): *Placunanomia, Placuna* (Placunidae Fam. Nov.) *Philos. Trans. R. Soc. London, Ser. B* **276,** 453–527.

Zipser, E., and Vermeij, G. J. (1978). Crushing behavior of tropical and temperate crabs. *J. Exp. Mar. Biol. Ecol.* **31,** 155–172.