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Functional Shell Morphology of
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INTRODUCTION

An understanding of the adaptive significance of shell form in the Bivalvia permits us to make advances in two other important areas of research. First, we can interpret the life habits of extinct taxa and thus bring to light the ways in which these creatures functioned in their habitats and the roles that they played within ancient ecological communities. Second, we can explain how evolutionary trends uncovered in the fossil record reflect changes in level of adaptation or, more fundamentally, in basic mode of life.

Because the Bivalvia are highly diverse in the modern world and also have a rich and ancient fossil record, it has been possible to investigate their functional skeletal morphology in considerable detail through the study of living species and to apply the results to numerous fossil forms. Of course, the functions of some curious skeletal features of extinct species have been analyzed in ways that do not rely fully on what we know of extant taxa. Through studies of functional morphology, a composite picture has emerged of changes in the spectrum of bivalve life habits through time, one that entails adaptive innovations, evolutionary radiations, and extinctions (see *Treatise Online*, Part N, Revised, Volume 1, Chapter 19, p. 1–2).

APPROACHES TO FUNCTIONAL MORPHOLOGY

In 1964, Martin RUDWICK introduced the paradigm approach to the study of extinct organisms (RUDWICK, 1964). The recommended procedure entails hypothesizing potential functions for a problematical morphologic feature, then envisioning the ideal morphology (paradigm) for the performance of each function, and finally comparing the actual feature to the various paradigms. The closest match is then taken to identify the most likely function.

Although the paradigm method is beneficial in orienting researchers toward hypothesizing functions for morphologic features of extinct taxa, four factors pose problems for this method, as described below.

1. Morphological structures often perform or otherwise relate to more than one function. The result is a compromise: evolution will then pull in more than one direction, so that the structure in question will not closely resemble the imputed ideal morphology for any single function being considered. For example, a shallow-burrowing bivalve that is occasionally swept over by strong currents would, for purposes of stability, benefit from possession of long spines angled downward so as to anchor the shell firmly in place. It appears that no infaunal bivalve has ever evolved such spines. Why is this? It is

undoubtedly because the spines would be useful only against scouring. Scouring would nonetheless occasionally be strong enough to dislodge the animal. This would necessitate reburrowing, which would be greatly hindered by the anchoring spines. The sluggish bivalve would then be highly vulnerable to predation or transport to a hostile environment.

2. There is a less direct factor that results in evolutionary compromises: many morphological features are influenced by multiple genes, and also many genes influence more than one morphological feature (pleiotropy); natural selection cannot single out one function under such circumstances.
3. In postulating an ideal morphology, one must take into account the biology of the higher taxon under consideration. Although it is seldom possible to deny absolutely that a particular species could evolve a particular structure, unrecognized epigenetic interactions between developing tissues and organs may impose morphogenetic constraints, making evolution of a potentially useful structure so improbable that it can be discounted as a possibility. As just one kind of constraint, one can consider the following scenario. The adaptation of a taxon to a certain environmental condition may have been improved by evolution in a particular morphological direction because genetic raw material for this evolution happened to appear, so that it could be selected for. Nonetheless, it might happen that evolutionary change in a different direction would have led to even better adaptation, and yet once evolution had shifted morphology some distance in the direction it did, evolutionary restructuring in the optimal direction became virtually impossible.
4. Natural selection operates on variation within a population, and variation is a result of mutation and recombination, both of which entail chance, and a partic-

ularly useful variant may require millions of years to appear. Thus, evolution takes time and often moves forward haltingly. At a particular time in its history, a taxon being analyzed may have moved only part way along the path of adaptive improvement that it might ultimately follow with regard to a particular function. In fact, the last surviving species of the taxon may have been suboptimally adapted with regard to the function in question.

A different approach to functional morphology entails bypassing construction of a paradigm and simply testing hypothetical functions. For living organisms, it may be possible actually to observe the structure performing the function in question. If uncertainty remains, it may be possible to alter the structure to determine experimentally whether the function is impaired or enhanced according to prediction; this approach can also be employed for extinct species, sometimes by way of physical replicas of fossils.

There is also a third approach. For a variety of taxa that are not closely related, a strong statistical correlation between form and some observed function can point to a likely causal relationship that for unrelated reasons seems quite plausible.

It must be borne in mind that not all genetically based morphological features are adaptive, although in principle it is impossible to demonstrate with certainty that any feature is nonadaptive (it is always possible that the actual function has not been considered). The existence of nonadaptive features has been emphasized by SEILACHER (1970), who, in the area of science he termed constructional morphology, recognized the influence of morphogenetic constraints, in addition to phylogenetic and adaptive factors, in determining morphology.

BODY SIZE AND SCALING

Intrinsic relationships between body size and body shape yield perhaps the most fundamental principle underpinning func-

tional morphology: the principle of similitude. Three-dimensional features, such as total volume of tissue or body weight of an animal (which depend on nutrition and oxygen supply), scale with the cube of linear dimensions. In contrast, two-dimensional features, such as surface area of ctenidia (which are devoted to feeding and respiration) and cross-sectional area (and, hence, strength) of muscles, scale only with the square of linear dimensions. Here we see a fundamental limitation for body size in bivalve evolution. There have certainly been very few thick-shelled bivalve species lacking the nutritional benefit of symbionts that have had a commissure area as large as 300 cm³. The fact that many species with symbionts have grown larger than this indicates that food acquisition rather than oxygen supply has generally determined the upper limit for body size in bivalves. A relatively high rate of food supply by the environment may elevate maximum body size to a degree, but the scaling limitation still applies.

When we consider the other end of the body-size spectrum, it is evident that scaling problems are relatively unimportant for very small bivalves: they can live in a variety of ways, regardless of their shell form. This can make interpretation of their functional morphology problematical.

Scaling factors also come into play for bivalves that live on or in fine-grained, soupy sediment. Most bivalve species occupying such substrata are small because surface area-to-weight ratio is inversely related to body size.

Although, because of scaling factors, growth slows down during the ontogeny of a bivalve, growth to large size offers a special benefit. Small animals are more vulnerable than large animals to predators that bore into or break shells. Thus, growth to a relatively large size can provide what is known as a refuge in size from predation, although it sometimes does not guarantee escape but simply reduces the probability of being eaten.

ECOLOGICAL FACTORS AND FUNCTIONAL SHELL MORPHOLOGY

Predation and physical disturbance are the most significant ecological factors limiting the distribution and abundance of bivalve species. These factors generally restrict the sizes of bivalve populations to levels below those that would be determined by living space or food supply. In fact, bivalves can survive for substantial intervals of time on little or no food, reducing their metabolic rates and losing weight. Various species have been raised in the laboratory without food for two or three months without suffering higher mortality than control groups that were provided with food (e.g., YANG & others, 2001; PECK, PORTNER, & HARDEWIG, 2002).

Feeding does, however, influence functional morphology because good nutrition influences both aspects of natural selection. It provides energy for both reproductive output and survival via rapid growth (which can provide an escape in size from predators). As a result, deposit feeders that do not occupy organic-rich, muddy substrata must generally be adept burrowers in order to relocate efficiently after having depleted the food resources at a feeding station. Also, a variety of epifaunal suspension feeders have morphologies that separate inhalant from exhalant water currents, so that they obtain fresh supplies of food and oxygen. Of course, siphons or similar structures formed by the posterior mantle margin perform a similar function for infaunal bivalves.

Only a few bivalve taxa can effectively execute escape movements from predators. All swimming bivalves, other than solenids, solemyids, and the most adept pectinid swimmers, swim awkwardly. These forms can nonetheless frequently escape from slow-moving predators, as can forms such as cardiids, trigoniids, and solenids that have the ability to leap with a muscular foot. In general, however, bivalves avoid predators by way of skeletal defenses or refugial life

habits. Those that do not have a cryptic mode of life (burrowing, boring, or nesting) often possess a thick or spiny shell. A few taxa secrete organic layers within the shell that thwart chemical borers.

Some fishes habitually nip off the ends of siphons of infaunal bivalves. This is seldom fatal for a bivalve but requires expenditure of energy for regrowth, which reduces the rate of overall growth (for review, see TOMIYAMA & OMORI, 2007). As will be illustrated below, some bivalves employ spines in the siphonal region to thwart siphon predators. Some deep-burrowing and boring bivalves, being relatively invulnerable to predation, can afford to leave their long siphons protruding slightly when retracted, a condition facilitated by the presence of a gaping shell anterior.

Infaunal bivalves possess behaviors and skeletal features, to be reviewed subsequently, that reduce their probability of being dislodged by strong water movements and needing to reburrow. If dislodged, however, they can avoid predators by burrowing to resume their infaunal life position. Thus, physical disturbance and predation are related. Nonetheless, physical disturbance alone can lead to mortality when animals are swept to hostile environments.

Functional morphology is related to rate of burrowing, which in turn tends to be related to the strength of water movements in preferred habitats. Animals that occupy shifting sands are generally rapid burrowers with shell morphologies that enhance their burrowing abilities; deep burrowers that occupy relatively stable substrata are mostly slow burrowers, and their shell morphologies reflect this condition (STANLEY, 1970).

The second ecological trait associated with rapid burrowing is deposit feeding. Nuculoids living in muddy substrata thrive as only moderately rapid burrowers because their organic-rich substratum normally provides abundant food and requires only infrequent lateral movements. On the

other hand, deposit-feeding tellinids and semelids, which vacuum organic matter from the sediment surface, rapidly deplete the food at a feeding station and need to move efficiently to another. The only tellinid and semelid deposit feeders that I have found to be only moderately rapid, rather than rapid, burrowers are *Merisca martinicensis* (D'ORBIGNY, 1853), *Macoma tenta* (SAY, 1834 in SAY & CONRAD, 1830–1834), *Macoma balthica* (LINNAEUS, 1758), and *Cumingia tellinoides* (CONRAD, 1831). All of these species habitually occupy muddy, organic-rich substrata (STANLEY, 1970).

IS EVOLUTION REVERSIBLE?

Dollo's Law states that evolution is irreversible. In the strict sense, after evolution has progressed considerably in a particular direction, the law is valid because the odds of retracing every genetic change are virtually nil. On the other hand, evolution is broadly reversible, in the sense that some members of a taxon can return to an ancestral morphology and resume life habits that were abandoned in their previous evolution. There have been many episodes of such evolutionary reversals in the Bivalvia, although the details have seldom been brought to light. Such reversals have been easily accomplished when the ancestral morphology has been retained in the early ontogeny of descendant forms. For example, in their juvenile state, extant epibyssate mytilids retain the morphology of their endobyssate ancestors (notably, an elongate shape with an anterior lobe). Similarly, in their juvenile state, endobyssate carditids retain the equant shell outline of their free-burrowing ancestors (see *Treatise Online*, Part N, Revised, Volume 1, Chapter 19, Fig. 9). These conditions indicate that each life habit group can give rise to the other via heterochrony, and the fossil record suggests that this kind of evolutionary oscillation has been quite common (STANLEY, 1972).

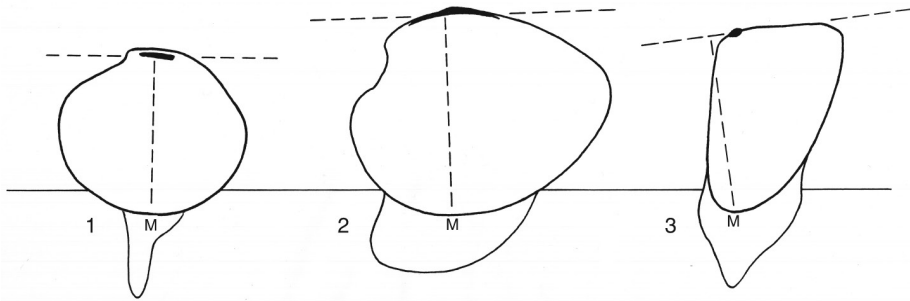


FIG. 1. Typical location of emergence of the central axis of the bivalve foot close to the maximum shell gape (*M*), which is the point on the shell margin farthest from the hinge axis (*dashed line*); this results in the hinge line being approximately horizontal during burrowing; 1, a lucinid; 2, a venerid; 3, a donacid (STANLEY, 1970).

GENERAL FEATURES OF BIVALVE FUNCTIONAL SHELL MORPHOLOGY

The fundamental body plan of the Bivalvia entails folding of the shell about a decalcified central axis, combined with lateral compression of the body. Whether or not this lateral compression originated in association with a burrowing mode of life, it lent itself to burrowing. An important relationship that results from the hinged morphology is that the maximum gape between the valves is located at the point along the commissure positioned farthest from the hinge axis. In the absence of a shell gape to accommodate the foot, it is normally at this position of widest gape that the foot will be centered when extruded from the shell for burrowing (STANLEY, 1970) (Fig. 1).

THE PROBLEM OF SHEARING

Given its flexibility, the ligament and the two valves attached to it are vulnerable to shearing along the plane of the commissure. Among other things, shearing can provide a space for a predator to gain access to a bivalve's viscera or it can expose a lip of each valve for a predatory claw to grasp. Hinge teeth provide at least a partial solution to the problem of shearing. If hinge teeth are wedge-shaped, however (and most are), they permit an increased amount of play as

the gape widens. If the valves are sheared substantially out of alignment as the valves open, they will tend to remain so as the valves are closed. A fluted, zigzag, or denticulated shell margin, however, will bring the valves into alignment during closure, as long as the misalignment is less than one half the wavelength of the skeletal feature performing the alignment (STANLEY, 1977a). Such aligning features are present in both epifaunal and infaunal bivalves. Certainly, as will be discussed below, plications and zigzag shell margins can have other functions as well. The problem of shearing is sometimes reduced by a flexible shell closure mechanism, which produces a wide band of contact between the valves along the commissure plane. The degree of development of this feature correlates generally with reduction of hinge dentition (CARTER & TEVESZ, 1978, p. 372). Flexible shell closure probably originated first to help exclude predators that chip at the shell margins, with subsequent reductions in hinge dentition.

THE LIGAMENT

The most fundamental aspect of the bivalve ligament is that it (or part of it) can be either internal or external relative to the axis of shell rotation during gapping. Any portion of the ligament that is internal is compressed when the valves are closed; any portion that is external is stretched.

Ligaments vary in their mechanical properties. The inherent weakness of the duplivincular ligament of arcoids has imposed an adaptive limitation in that it requires assistance from the foot to spread the valves apart (THOMAS, 1976). The calcified inner layer of the pectinoidean ligament, characterized by a small opening moment and high efficiency, contributes to the rapid clapping of the valves for swimming (TRUEMAN, 1953).

THE PERIOSTRACUM AND ORGANIC SHELL LAYERS

Periostracal structures serve a variety of protective functions in the Bivalvia. When covering the shell surface, periostracum obviously obstructs chemical borers. Similarly, it protects boring lithophagins from the corrosive fluid that they themselves employ to bore into calcareous substrata. A periostracum protects other taxa from acidic conditions of the physical environment. As an illustration of the latter function, the periostracum is commonly abraded from the anterior end of the endobysate mytilid *Geukensia* VAN DE POEL, 1959, which occupies the acidic sandy peat of intertidal marshes, and the resulting dissolution often penetrates to the mantle cavity, necessitating shell repair. Many endolithic mytilids secrete protective organic sheets within the inner shell layer beneath portions of their shell damaged by their own chemical or mechanical boring process (OWADA, 2009). Secretion of one or more conchiolin layers within each valve of the Corbulidae prevents chemical borers from fully penetrating the shell (LEWY & SAMTLEBEN, 1979).

BOTTJER and CARTER (1980) assessed the functional significance of projecting periostracal structures of bivalves, as well as hairy adventitious structures (actually pedal byssal secretions) sometimes secreted on top of them. They concluded that these features serve a variety of functions: stabilizing animals in the substratum, reducing sediment scour, warding off encrusters and borers, serving as camouflage, and providing extended tactile perception. SAVAZZI (1982) found

that, after removal of its periostracum, the arcid *Scapharca inaequivalvis* (BRUGUIÈRE, 1789 in BRUGUIÈRE, DESHAYES, & HWASS, 1789–1832) required an increased number of burrowing sequences to bury itself.

Thick periostraca can also serve to provide a water-tight seal between the shell valves upon closure, as in *Mytilus* LINNAEUS, 1758. This can be advantageous for intertidal, epifaunal taxa that are often subaerially exposed (CARTER, 1990). Such periostraca also provide a small correction factor for valve misalignment, so the species with such a feature can often tolerate minimal hinge dentition.

MUSCLES AND MUSCLE SCARS

Adductor muscles, whether two in number (the plesiomorphic condition) or one in number (a derived condition), vary among species in their size and lever arm length. Fortunately, scars on the shell interior permit the size and position of the adductors to be inferred for many fossil forms. Adductor muscles have two components, the quick muscle, which shuts the valves, and the slow muscle, which holds them shut. These two types of muscle can be distinguished in some fossils. YONGE (1936, 1967) asserted that the importance of the quick muscle for expelling bivalves' pseudofeces has led to relatively larger quick muscles in mud-dwelling taxa than in sand-dwelling taxa. Also, as will be discussed below, the two muscle types differ in relative size for swimming and sedentary scallops. The anteriors of middle Paleozoic megalodontids were extremely thick and housed extremely narrow mantle cavities. An anterior adductor with a shallow depression for attachment would have provided an inadequate amount of extension and contraction (the maximum amount being determined by muscle length). Evolution solved this problem by producing a deeply recessed cavity to house much of the length of the adductor within each thick valve (see *Treatise Online*, Part N, Revised, Volume 1, Chapter 19, Fig. 13).

Similarly, pedal and byssal retractor muscle scars are commonly preserved in

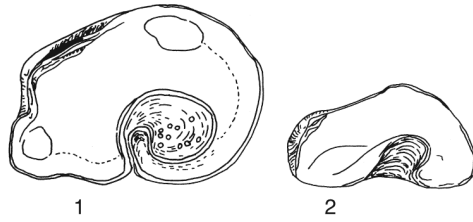


FIG. 2. Marsupia in the shells of carditids; 1, *Thecalia concamerata* (BRUGUIÈRE, 1792 in BRUGUIÈRE, DESHAYES, & HWASS, 1789–1832), $\times 2.5$; 2, *Milneria kelseyi* DALL, 1916, $\times 5$ (YONGE, 1969).

fossils; as a result, their functions can be assessed. For example, they are generally larger in epifaunal mytilids than in endobysate mytilids, which gain support from the surrounding substratum, and they also pull in a ventral direction (toward the surface of attachment) for epifaunal mytilids.

The muscle attachment of the mantle to the shell (the pallial line) is also important, especially in revealing the presence or absence of a pallial sinus, which accommodates withdrawn siphons—and also the size of a pallial sinus, which generally relates to siphon length and depth of burrowing. Scars of small muscles supporting the ctenidia may also be present, although they have little bearing on life habits.

FEATURES RELATED TO REPRODUCTION

The prodissoconch is the initial shell of a bivalve, located at the tip of the umbo and often discernable as a discrete portion of the shell. Well-preserved fossil bivalves can display prodissoconchs, the sizes of which, with a relatively high degree of certainty, reveal a mode of life that was nonplanktonic (entailed direct development), lecithotrophic (entailed a planktonic nonfeeding larva), or planktotrophic (entailed a feeding planktonic larva). Lecithotrophic prodissoconchs (~ 135 – 230 μm in diameter) are usually larger than planktotrophic ones (~ 70 – 150 μm in diameter) because they inherit a relatively large yolk from the egg, and nonplanktonic prodissoconchs are even larger (~ 230 – 500 μm in diameter), reflecting a very large yolk (OCKELMANN, 1965).

In addition, some bivalve species that employ direct development and brood their offspring display sexual dimorphism, with the females having more inflated shells than the males (HEASLIP, 1969; KAUFFMAN & BUDDENHAGEN, 1969). In the carditid subfamily Thecaliinae, a large reentrant on the ventral region of the shell forms a marsupium (Fig. 2) (YONGE, 1969).

Planktonic larval development represents a highly opportunistic life history strategy, in that large numbers of larvae are produced, each with a very small chance of becoming a breeding adult. Species of small adult body size cannot produce large numbers of small larvae and are best served by direct development entailing a small number of large, yolk-rich eggs; these have a much higher probability of survival than eggs that become planktonic larvae. Thus, the percentage of bivalve taxa with nonplanktonic development is inversely related to adult body size; this mode of development characterizes most species for which the geometric mean of adult shell length and height is less than one centimeter. In addition, the percentage of bivalve species with direct development increases toward polar regions; lecithotrophic larvae display the same pattern to a lesser degree, and the percentage of bivalve species with lecithotrophic larvae also increases dramatically with water depth (OCKELMANN, 1965). These spatial patterns obviously reflect the availability of food for planktotrophy.

Larval modes of life are relevant for paleobiogeographic and evolutionary studies (review by JABLONSKI & LUTZ, 1983). In

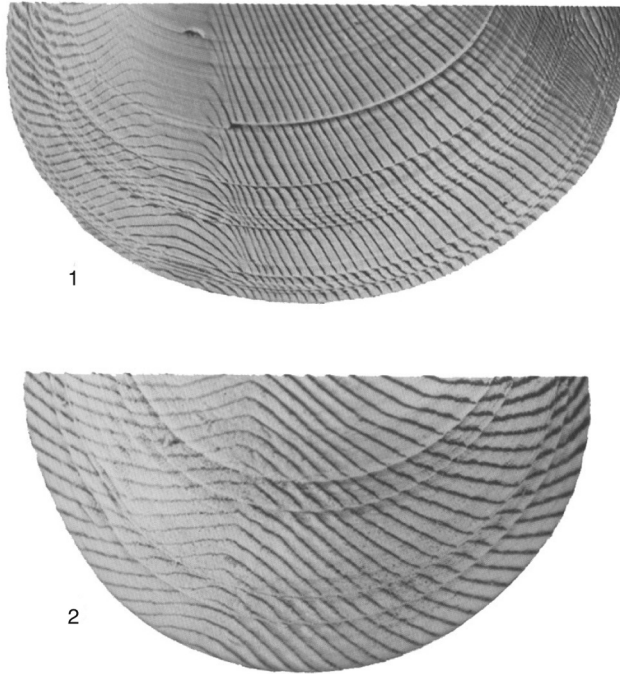


FIG. 3. Discordant rib growth in the tellinid *Strigilla* TURTON, 1822 (1), $\times 4.5$ and lucinid *Divalinga* CHAVAN, 1951 (2), $\times 3.25$; the angle of discordant ornamentation is the resultant vector of lateral migration of the site of ridge secretion at a more or less constant rate and the variable rate of shell growth; when shell growth slows down, the angle of the discordant ornamentation relative to the tangent at the adjacent shell margin decreases. During intervals when no shell growth occurs and a check shape forms on the shell surface, the lateral migration of the site of ridge secretion continues, and the ridge becomes offset (Stanley, 1969, 1970).

general, species characterized by direct development have smaller geographic ranges, and therefore shorter geologic durations, than species with planktonic larvae. On the other hand, species with direct development tend to experience high rates of speciation because their poor dispersal ability tends to produce spatially isolated subpopulations.

SHELL ORNAMENTATION

Strong ornamentation on a bivalve shell presumably offers resistance to crushing and drilling predators (VERMEIJ, 1978, p. 83). As will be described subsequently, certain kinds of shell ornamentation serve as aids to burrowing or boring. Some of these are radially arrayed protuberances, generally spines or knobs. These, and spines that thwart predators, require episodic alteration of the secretion pattern of the mantle

margin. Discordant ridges aid many species in burrowing, and these must be produced by lateral migration of the site of ridge secretion along the mantle margin. The angle of a discordant ridge is the resultant vector of the rate of this lateral migration and the rate of radial shell growth; intervals of relatively slow radial growth result in a decrease of the angle between a discordant rib and the tangent to the adjacent shell margin. In addition, where interruptions of shell growth have occurred, ribs are offset. These patterns imply that the site of rib formation migrates laterally at a more or less constant rate that is independent of the rate of marginal shell accretion (Fig. 3) (STANLEY, 1969).

ZIGZAG COMMISSURES

A variety of bivalve taxa, many belonging to the Ostreidae, have evolved a zigzag

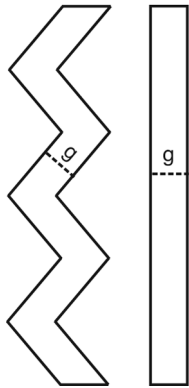


FIG. 4. Increase in the total area of gape of a bivalve with a zigzag commissure relative to one with a planar commissure having the same width of gape between the valves (g); this diagram illustrates the increase for a zigzag commissure with angles of 90° , which is approximately 40% ($2^{1/2}$) (new).

commissure. It is appropriate that this feature be considered here because it is present in some noncemented species (e.g., the free-living ostreids *Agerostrea* VIALOV, 1936, and *Arctostrea* PERVINQUIÈRE, 1910, and the byssate inoceramid *Actinoceramus* MEEK, 1864, all of Cretaceous age). RUDWICK (1964) proposed that a zigzag commissure served to reduce the size of unwanted particles that might enter the mantle cavity, but this is unlikely for lunate oysters, many of which live on muddy regions of the sea floor (CARTER, 1968). RUDWICK'S second hypothesis, that a zigzag commissure increases the amount of sensitive warning tissue at the shell margin, is unlikely to account for the strong selection pressure required to produce a zigzag commissure. CARTER (1968) suggested instead that the zigzag commissure serves to spread inhalant currents across the entire width of the W-shaped gill. Overlooked has been a very fundamental advantage of a zigzag commissure. It increases the total rate of flow of water into the mantle cavity for a given width of valve gape by increasing the length of the gape. For a zigzag commissure with 90° angles, this increase is approximately 40% (Fig. 4).

ADAPTATIONS OF BURROWERS

TRUEMAN (1966) employed electrodes to reveal what amounts to a stereotypical pattern for bivalve burrowing. First, the adductors relax enough to permit the valves to gape sufficiently for muscular extrusion of the foot. The foot then probes downward. Next, the mantle cavity is sealed by joining of the mantle lobes and closure of the siphons, if present. Then the adductors contract, pulling the valves toward one another; the water in the mantle cavity, being incompressible, squeezes blood from the viscera into the distal portion of the foot, where it forms a bulbous structure; also, some water escapes ventrally from the mantle cavity, loosening the sediment below the animal. With the foot anchored, the anterior pedal retractor contracts, rocking the shell forward, then the posterior pedal retractor contracts, rocking the shell backward. Thus, the animal, in effect, takes a step downward.

The typical morphology of a burrowing bivalve is that of most venerids, in which the front of the shell is blunt, consisting of the lunule and the adjacent portions of the coiled shell, including the umbos. On the face of it, this configuration might seem maladaptive, because the animal moves forward as well as downward when burrowing. However, the blunt anterior actually serves as an aid to burrowing, locking into the sediment during backward rotation so that a substantial downward step is taken (STANLEY, 1975). If the forward and backward rotations took place about the same axis, the animal would go nowhere. Downward movement is only achieved by separation of the two axes, with the one for backward rotation positioned to the anterior of the one for forward rotation (Fig. 5). To envision how this works, one can imagine the most extreme (though unrealistic) condition, in which the axes of rotation would be at the anterior and posterior tips of the shell. Then, with alternating forward and backward rotations, the shell would take

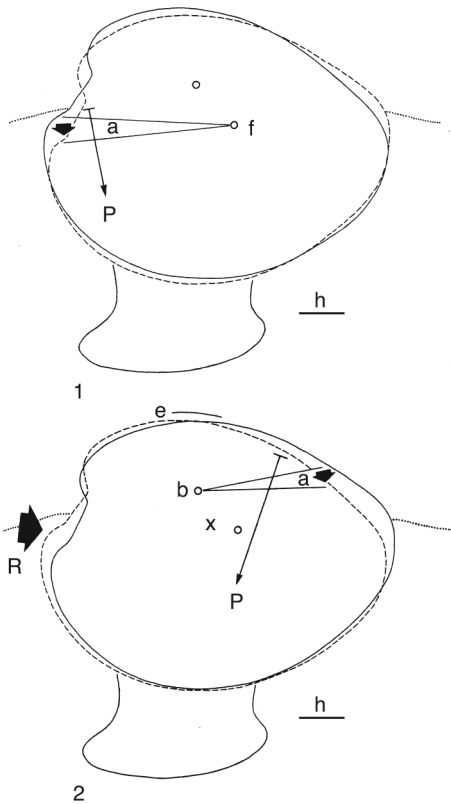


FIG. 5. Mechanics of burrowing of a typical bivalve; the location of the of axis of backward rotation (b) anterior to the axis of forward rotation (f) for the burrowing bivalve *Mercenaria mercenaria* (LINNAEUS, 1758) results in a downward step via a forward and backward rocking movement; 1, forward rotation; 2, backward rotation; films were used to locate the axes of rotation: points on a grid (applied to the image of the shell) that underwent no movement during rotation; the direction of contraction of the pedal retractor muscles (P) results in the rotation through a small angle (a); the blunt anterior produces a large force (R) that causes the sediment in front of the animal to resist upward slippage of the shell anterior; the forward-and-back rotation result in downward movement of the dorsal margin from the initial erect probing position (e); the line h is horizontal (Stanley, 1975).

huge downward steps. Experiments showed that a replica of *Mercenaria* SCHUMACHER, 1817, made more downward progress when induced to rotate backward and forward, as in life, than a model of the same shell fitted with a discoid false front that provided less resistance to upward slippage of the shell

during backward rotation; also, it turned out that, as expected, the two axes of rotation were farther apart for the model with normal morphology (STANLEY, 1975). The prowlike false front slipped upward enough during every backward rotation to reduce the size of each downward step.

SHELL PROFILE IN LATERAL VIEW

A bivalve species that has a flattened posterior region and very short siphons, or none at all, normally lives at the sediment-water interface, oriented with this flattened region horizontal. Among the species with this morphology are many cardiids, including *Fragum* RÖDING, 1798, and *Americardia* STEWART, 1930, and many arcoids, including *Noetia* GRAY, 1857 (Fig. 6).

An elongate, somewhat pointed posterior typically serves like siphons, to position an animal's viscera relatively deep within the sediment. Thus, for many species with the shape of a typical venerid, the long axis of the shell in life is oriented closer to vertical than horizontal. Figure 6 illustrates this life position for *Astarte undata* GOULD, 1841, and *Anomalocardia* SCHUMACHER, 1817. The rostrate posterior of the latter genus is an indication of a vertical life orientation for the long axis of the shell. The more rounded posterior of *Astarte castanea* (SAY, 1822) is consistent with the species' typical upside-down position in coarse sediment (STANLEY, 1970).

When a shell is circular and also laterally compressed, as in *Dosinia* SCOPOLI, 1777, the weak resistance of sediment more than compensates for the absence of a broad, blunt anterior: the animal slices readily downward and is a rapid burrower (STANLEY, 1970). *Dosinia* is also a deeper burrower than nearly all other venerids. Most lucinid species are also deep burrowers that are roughly circular in outline (see *Phacoides* AGASSIZ, 1845, and *Lucina pensylvanica* [LINNAEUS, 1758] of Fig. 6). Thus, the suggestion that deep burrowers are generally elongate (KAUFFMAN, 1969) is invalid. Elongation would serve no purpose for lucinids, for which the life orientation

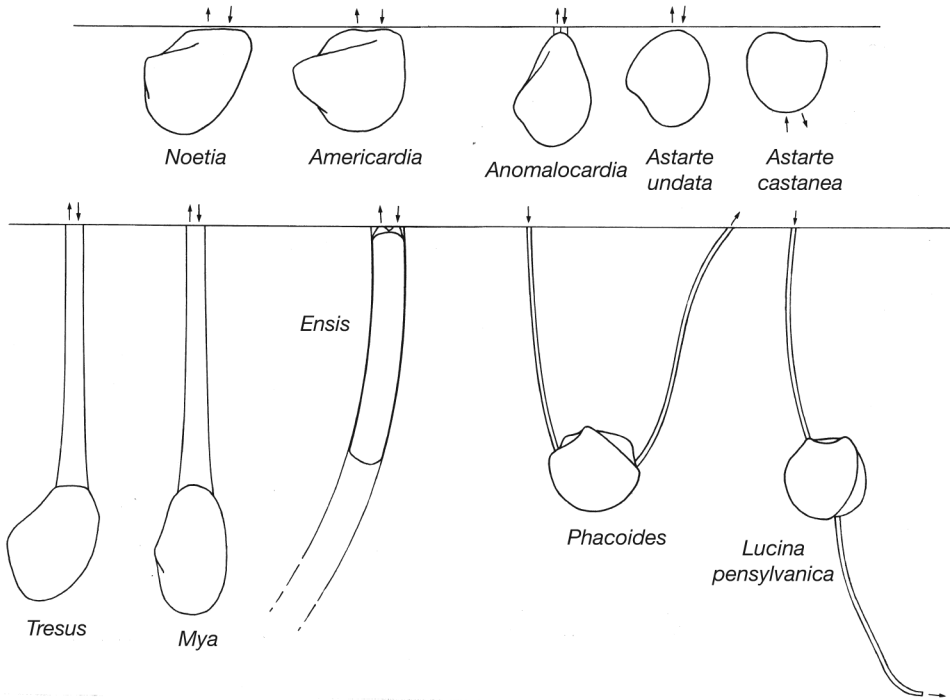


FIG. 6. Relation of lateral shell outline to life position for burrowing bivalves; for explanations, see text (Stanley, 1970).

(in which the anteroposterior axis is horizontal) represents a compromise, positioning the anterior mucous-lined inhalant tube and posterior exhalant siphon so that they emerge from the shell at nearly the same depth below the sediment-water interface. *Lucina pensylvanica* is exceptional among lucinids in directing its posterior siphon downward. Its reduced anterior (compact lunule), and a blunt projection where the mucus tube meets the shell, slightly reduce the required length of the mucous-lined tube.

Because for most burrowing bivalves the central axis of the foot emerges close to the point on the shell commissure farthest from the axis of the ligament, where the gape is widest, the hinge axis is more or less horizontal when the foot probes downward (Fig. 1). Elongate taxa, such as *Tresus* GRAY, 1853, *Mya* LINNAEUS, 1758 (Fig. 6), and *Tagelus* GRAY, 1847 (Fig. 7), circumvent this

constraint with a built-in gape that permits the foot to emerge parallel to the ligament axis. These forms usually also employ a posterior siphonal gape. Many of them are deep burrowers with long siphons that, even when retracted as far as possible, are slightly emergent. These forms can afford to expose soft tissue because they live at depths in the sediment that are reached by few predators.

Many solenids are also highly elongate. Although possessing short siphons and feeding with the shell close to the sediment-water interface, they typically live in cohesive fine sand and maintain an open burrow which extends down many centimeters. Often living intertidally, they descend into this burrow at low tide, and they also retreat into it when threatened by a predator. *Ensis* SCHUMACHER, 1817, known as the razor clam because of its gentle curvature (Fig. 6), benefits from this shape when pursued by a persistent predator. Rather than moving

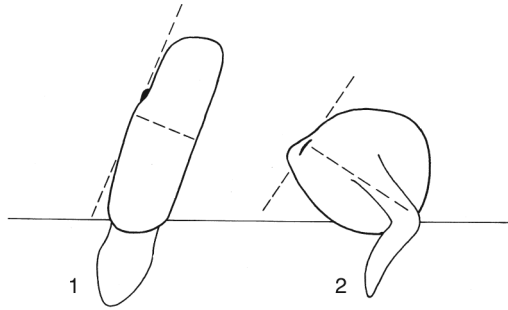


FIG. 7. Morphologies that permit the foot to probe downward with the hinge axis at a high angle; 1, an anterior gape, exemplified by *Tagelus* GRAY, 1847; 2, the muscular L-shaped foot of cardiid (the T-shaped foot of trioniids functions in a similar way) (Stanley, 1970).

inexorably downward, it automatically takes a U-shaped path, eventually emerging at the surface. There it can put its leaping ability to good use. (Once, when pursuing a very small animal, I observed this phenomenon.)

Donax LINNAEUS, 1758, and *Mesodesma* DESHAYES, 1832 in BRUGUIÈRE, DESHAYES, and HWASS, 1789–1832, have a highly elongate, somewhat pointed anteroventral region, which houses a large foot. They exemplify a different solution to the geometric constraint on pedal extrusion (STANLEY, 1970). Truncation of the posterodorsal region of the shell of these forms positions the hinge axis so that the maximum shell gape is at the anteroventral tip of the shell, where the large foot emerges (Fig. 1.3). Rather than rocking back and forth, these genera wedge straight downward in a rapid series of burrowing sequences. They are exceptionally rapid burrowers and thus are adapted to life along sandy beaches, where they can frequently be seen being washed out by waves while feeding and, after the retreating waters of a wave carry them seaward again, reburrowing quickly to avoid menacing crabs and shorebirds.

Middle Paleozoic megalodontids, early ancestors of the rudists, lived semi-infaunally with their long axes at a high angle and attained large sizes, which indicate farming of endosymbiotic algae. They were strongly prosograte, which positioned the maximum

shell gape in the incurrent region of the shell margin, an adaptive necessity (see *Treatise Online*, Part N, Revised, Volume 1, Chapter 19, Fig. 13).

SHELL PROFILE IN FRONTAL VIEW

For rapid burrowers, the maximum shell width lies closer to the dorsal margin than the ventral margin of the shell; this reduces the resistance of the sediment to penetration (Fig. 8).

In most of the very shallow-burrowing forms, for which the flat posterior shell margin, where the inhalant and exhalant currents are located, is oriented parallel to the substratum in life position (Fig. 6), the shell posterior is roughly triangular in cross section (tent-shaped in three dimensions). Included here are a large number of arcoid, trionioid, and cardioid species. Because of scour or incomplete burrowing, these forms often end up with their posterior shell regions at least partly exposed above the substratum. When a horizontal force impinges on this structure at an angle close to the plane of commissure, it will be diverted around it. Simple vector analysis (Fig. 9) shows that, when such a current impinges on such a structure at a high angle to the plane of commissure, the result is a strong downward force, pushing the animal against the substratum, but only a weak horizontal force, which, if stronger, might dislodge the animal.

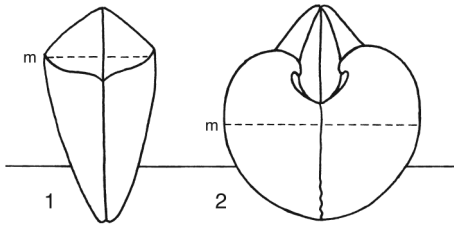


FIG. 8. Position of the maximum shell width near the anterior end of typical burrowing bivalves closer to the dorsal margin than the ventral margin of the shell; 1, *Donax* LINNAEUS, 1758, a rapid burrower; 2, *Anadara notabilis* (RÖDING, 1798), a sluggish, partial burrower (Stanley, 1970).

Overlap of one valve by another, though relatively rare, may increase resistance to compressive force applied by a crushing predator (VERMEIJ, 1987, p. 295, citing R. D. K. THOMAS). On the other hand, the overlapping valve is vulnerable to the application of a crab claw.

THE PALLIAL SINUS

A pallial sinus has traditionally been taken to indicate an extinct taxon's possession of siphons. In addition, the length of the pallial sinus has been taken to provide a measure of siphon length. It should be understood, however, that short siphons do not require a pallial sinus, as evidenced by extant cardiids. Even some relatively long, tissue-grade siphons, when not accompanied by a tissue-grade incurrent siphon, are not associated with a pallial sinus, as in the mytilid *Botula* MÖRCH, 1853, and the Lucinidae. Furthermore, the area of a pallial sinus provides a better estimate of siphon length than the length of the sinus because the siphons are elastic and squeeze into whatever space is available. In fact, it is the volume of the available space that matters, and this relates also to the degree of inflation of the shell. Another issue is that some deep-burrowing taxa, such as tellinids and lucinids, have very thin siphons, which are accommodated in a pallial sinus that, for their length, is relatively small. Other taxa, such as *Mya* LINNAEUS, 1758, and *Panopea* MÉNARD DE LA GROYE, 1807, have very thick siphons

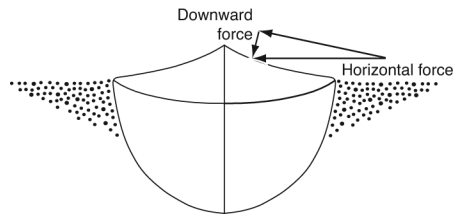


FIG. 9. Adaptive significance of the tent-shaped posterior region of shallow-burrowing bivalves, which reduced the horizontal component of force of water movements that might exhume the bivalve, and increases the downward component of force, which tends to hold an animal in the substratum (new).

that, for their length, require a much larger storage area; in fact, as previously noted, they are not fully retractable. Furthermore, some bivalves invert their siphons at the base and stuff the inverted portion into the ventral mantle cavity when fully retracted: for example, the gastrochaenid *Lamychaena hians* (GMELIN, 1791) (see CARTER, 1978).

MEASUREMENT OF BURROWING RATES

The size of a bivalve must be taken into account in assessing how rapidly it burrows relative to other bivalves—how long it takes for the uppermost margin of the shell to descend below the surface of the substratum after the shell has been elevated to an erect position for the start of burrowing. The interval of time required for a particular kind of muscle to contract by a given percentage is proportional to the length of the muscle. For this reason, the time for a bivalve of a given species to burrow is roughly proportional to its linear dimensions, including shell length (STANLEY, 1970). Length divided by burrowing time would therefore provide a measure for comparison of species, except that species vary in shape. Substitution of $(\text{mass})^{1/3}$ for length removes this shape bias. Indeed, plots of $(\text{mass})^{1/3} \times 100$ versus burrowing time for individual species turn out to be generally linear (Fig. 10). This yields the following burrowing rate index for bivalve species (STANLEY, 1970): $[(\text{mass})^{1/3} / \text{burrowing time}] \times 100$. The overall shape and shell thickness

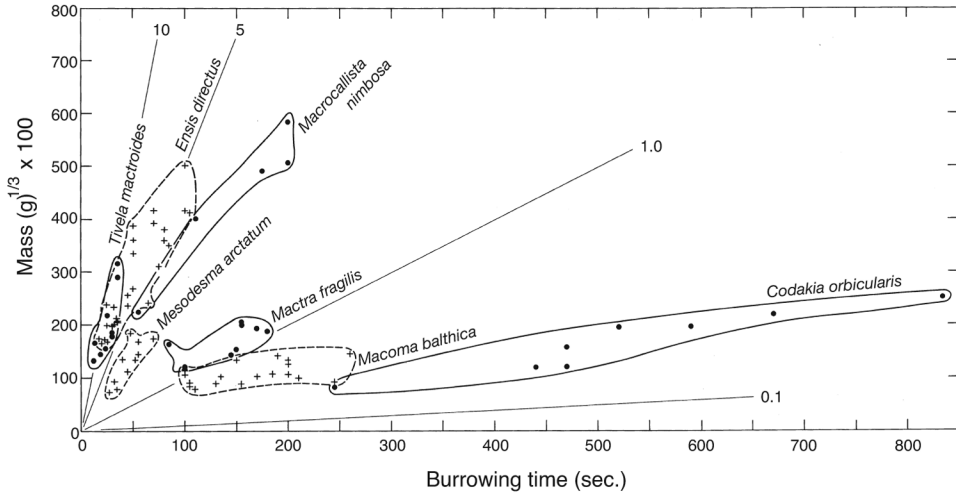


FIG. 10. Graph of the cube root of mass versus burrowing time for seven bivalve species, $\times 100$ (Stanley, 1970).

of various burrowing bivalves show general relationships to the rate of burrowing, as do the configuration and height of ornamentation on the shell exterior.

OVERALL SHAPE AND BURROWING RATE

TRUEMAN, BRAND, and DAVIS (1966) showed that bivalve species with laterally compressed shells move into the substratum more readily than species with inflated shells. Bivalves which are roughly bladelike or cylindrical (and, as described above, burrow in a direction parallel to their long axis) also face less resistance from sediment when burrowing than do globose forms of similar volume, and they therefore tend to be more rapid burrowers (Fig. 11). The most striking exceptions are the cardiids, which, though typically globose, burrow rapidly by virtue of their muscular foot; and elongate deep burrowers, which are often slow burrowers because, unless they are deposit feeders or occupy shifting sands, are seldom required to burrow, except to move slightly downward as they grow.

BILATERAL ASYMMETRY

In general, burrowing bivalves are bilateral symmetrical. Those that are not are

generally positioned in life with the commissure horizontal or at a low angle. The largest taxon of this latter type is the Tellinidae, for which a horizontal life position helps these animals, as deposit feeders, maintain a constant depth below the sediment-water interface while periodically migrating laterally to new feeding stations (Fig. 12.1); an upward twist of the posterior tip of the shell provides for upward bending of the siphons without constriction at the shell margin (Fig. 112.3) (STANLEY, 1970). For extinct tellinids, this twist is an indication of a deposit feeding habit.

SHELL THICKNESS

Growth of a thick shell requires energy that could instead be used for soft tissue growth or reproduction. Furthermore, a thick shell adds inertia that slows rotation in burrowing, so that thick-shelled bivalve species tend to be slower burrowers than thin-shelled species (Fig. 13). One conspicuous exception is *Tivela stultorum* (MAWE, 1823), the pismo clam, which, although very thick shelled, is a rapid-burrowing inhabitant of sandy beaches in the Eastern Pacific; it is a member of the Mactridae, which, as a group, are rapid burrowers.

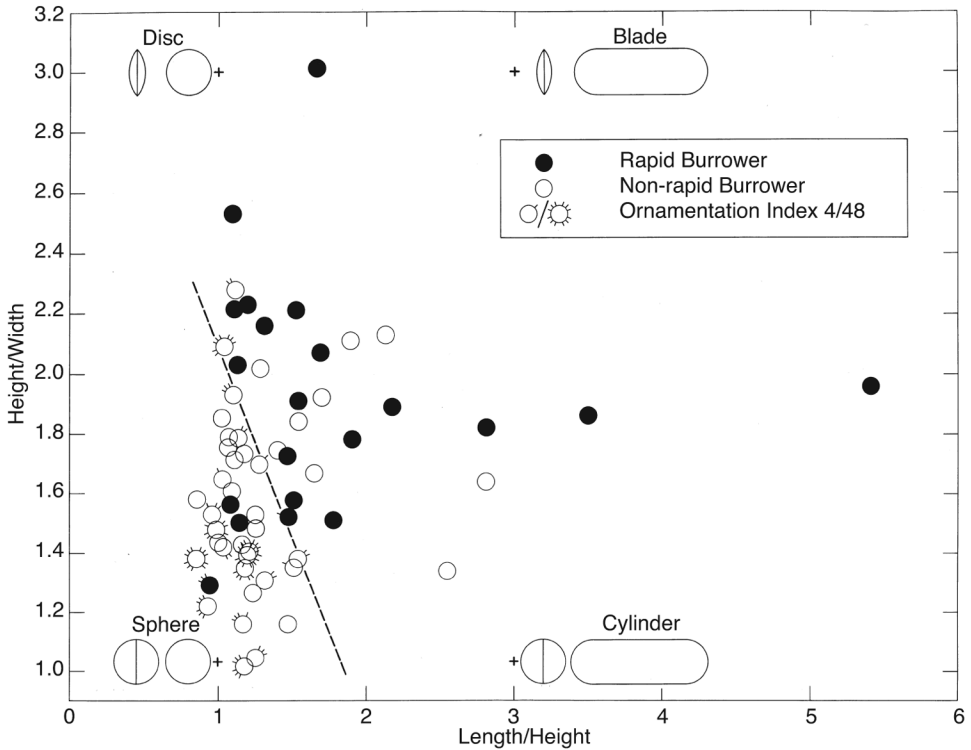


FIG. 11. Relation of burrowing rate to ornamentation and overall three-dimensional shell shape; the dashed line separates the morphologic region that contains mostly rapid burrowers from the one that contains mostly slow burrowers; the ornamentation index is the ratio between the surface relief formed by the ornamentation in the midventral region of the shell and the geometric mean of shell height and shell length (Stanley, 1970).

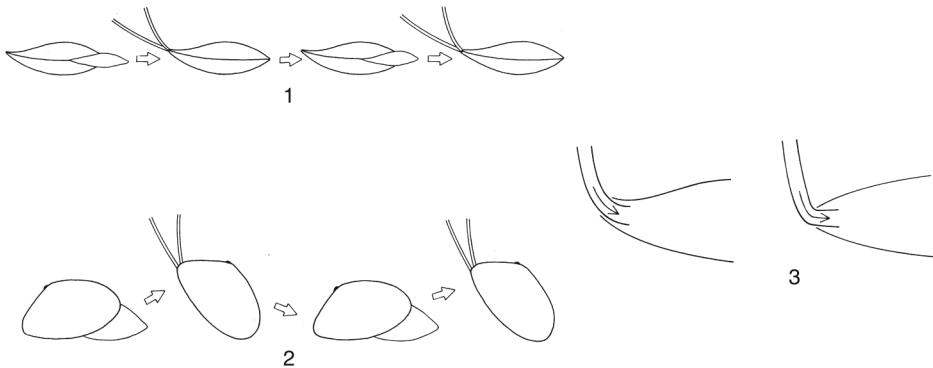


FIG. 12. The life position of tellinids; 1, deposit-feeding animal's maintenance of a constant depth while migrating laterally after exhausting the food supply at any location; 2, a hypothetical life position with the commissure plane vertical, which would permit accidental upward and downward shifts; 3, streamlining of the flow of water through the siphons by the twist at the posterior end of the shell (Stanley, 1970).

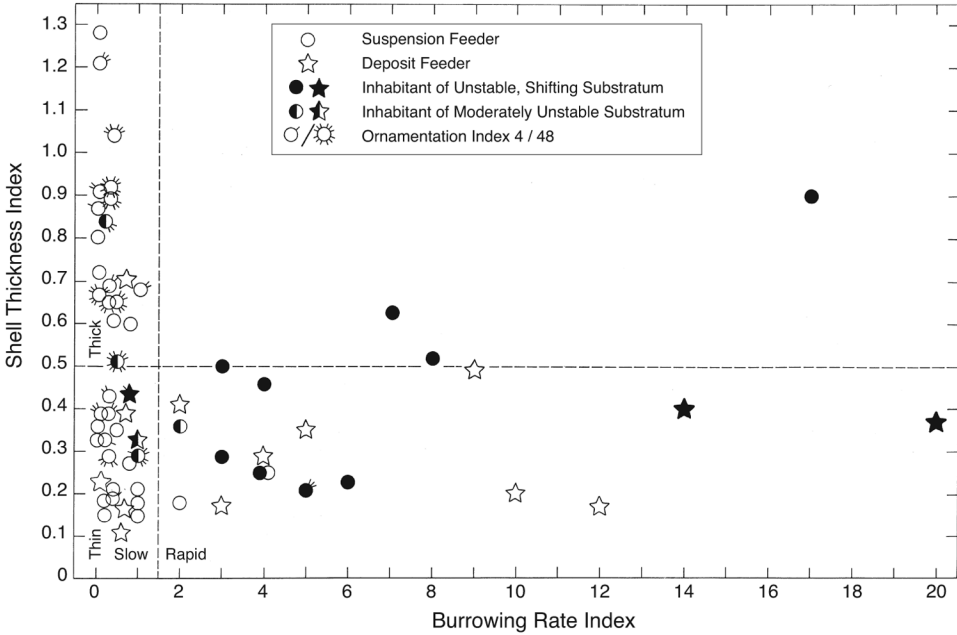


FIG. 13. Relation of burrowing rate to shell thickness, shell ornamentation, feeding type, and substratum character; the shell thickness index is the ratio between the total volume of the shell and the volume of the shell interior (see Fig. 11 for a definition of the ornamentation index); most rapid burrowers are deposit feeders or occupy shifting substrata and do not have ornamentation that stands in strong relief (Stanley, 1970).

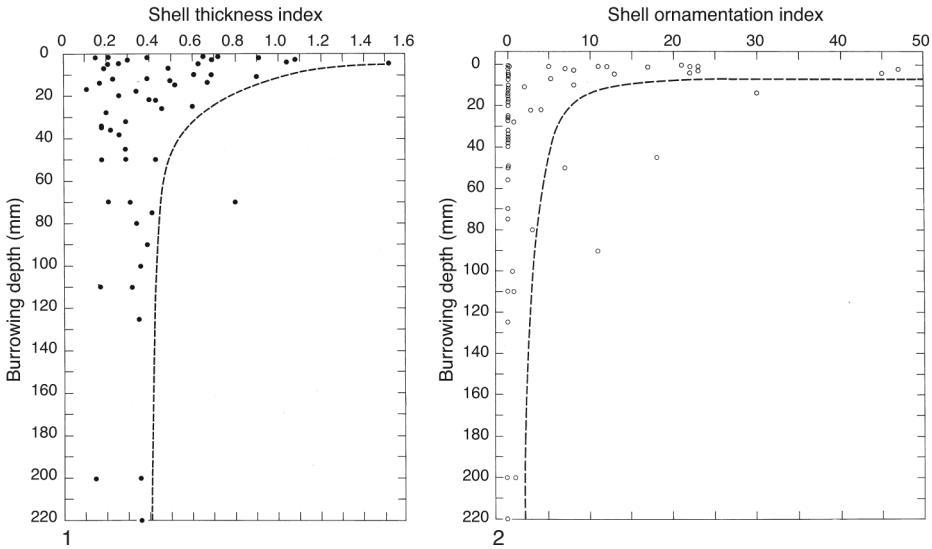


FIG. 14. Relation of bivalve shell morphology to depth of burrowing; 1, a plot showing that deep burrowing species tend to have thin shells; 2, a plot showing that most species with pronounced ornamentation are shallow burrowers; depth of burrowing for a species is defined here as the greatest distance from the sediment surface to the shallowest point on the buried shell that was observed for any member of the species in a study of many individuals (Stanley, 1970).

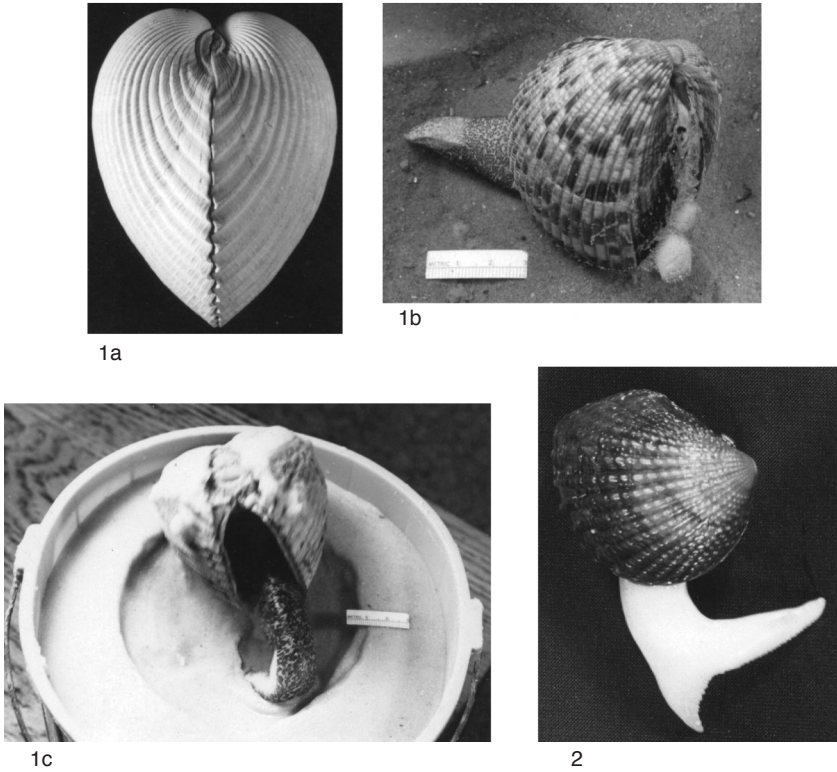


FIG. 15. Bivalves with a thick, muscular foot; 1, *Dinocardium* DALL, 1900; 1a, anterior view showing ribbing and serrated ventral margin, $\times 0.4$; 1b, animal with foot emerging, $\times 0.4$; 1c, animal in the process of leaping with its L-shaped foot, $\times 0.27$ (Stanley, 1970); 2, The T-shaped foot of *Neotrigonia* COSSMAN, 1912b, $\times 0.75$ (Stanley, 1977b).

On the other hand, thick shells provide the advantage of thwarting shell-boring and shell-breaking predators and in stabilizing animals against disruptive water movements. Thus, it is no accident that thick-shelled species tend to be shallow burrowers, whereas, many deep burrowers, such as *Mya*, being less exposed to biological and physical disturbance, are thin shelled (Fig. 14.1).

Bivalves with relatively thick shells would tend to sink deeply into soupy muds and seldom live there; most bivalve burrowers that inhabit fine-grained sediments are thin-shelled (STANLEY, 1970). Chalky deposits, cavities, and vesicles reduced shell density in early, solitary gryphaeids that occupied muddy substrates. In addition, their skeletal calcite reduced shell density relative to aragonite by about 15%, when the buoyancy of water is taken into account (CARTER, 1980a, 1990a).

DENTITION

As noted earlier, the ligament of arcoid bivalves is deficient in being weak (THOMAS, 1976). On the other hand, arcoids' taxodont dentition, extending across a broad cardinal area, is more effective than heterodont dentition in preventing the valves from shearing as they open and close.

For many millions of years, both cardiids and trigonioids have possessed a thick, muscular foot, which accelerates their burrowing and also allows them to leap (Fig. 15). The negative consequence of this type of foot is that its extrusion requires wide gaping of the valves. Cardiid evolution has reduced this problem by producing lateral teeth that project quite far from the plane of commissure and are located far from the hinge axis, where they can keep the valves approximately aligned at a wide

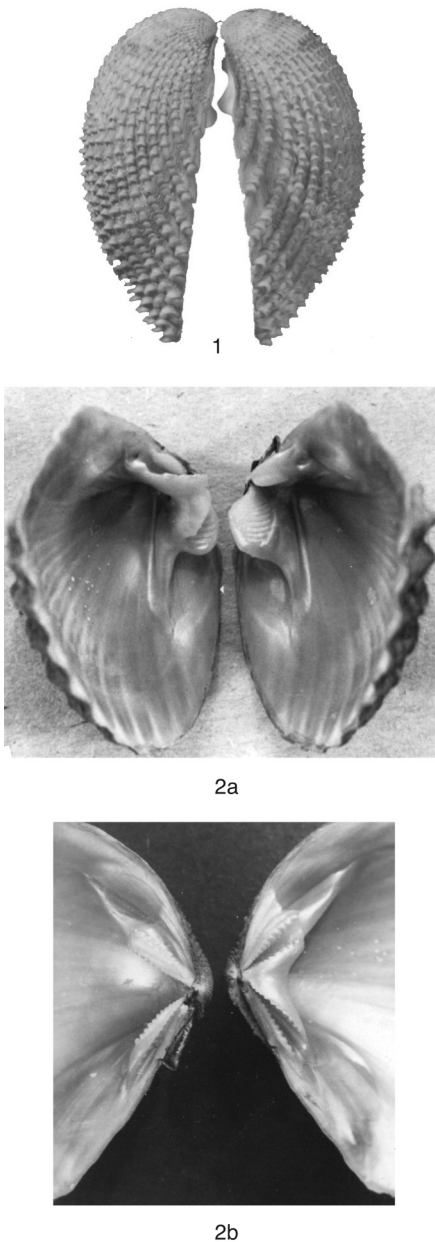


FIG. 16. Hinge teeth that maintain valve alignment at wide angles of gape for cardiids and trigoniids; 1, lateral teeth of *Trachycardium egmontianum* (SHUTTLEWORTH, 1856), which project far across the plane of commissure and are located well ventral of the hinge axis, $\times 1$; 2, *Neotrigonia margaritacea* (LAMARCK, 1804), $\times 0.8$; 2a, large teeth occupy a considerable portion of the umbonal region (right valve on the right); 2b, secondary dentition; a buttress supports the primary anterior tooth, which projects far from the hinge axis (right valve on the left), $\times 2$ (Stanley, 1977b).

angle of gape (Fig. 16.1). Crenulation or denticulation of the shell margins then completes the alignment as the valves come together. Trigonioid evolution provided a very different solution to the problem of valve misalignment (STANLEY, 1977a). Since Permian time, the hinge teeth of trigonioids have displayed two important adaptations. First, they have been very long, projecting quite far in a ventral direction. For a given amount of play between the teeth, this reduces the maximum angle of shear. In addition, the teeth have deep, interlocking striations, which can be viewed as secondary dentition and virtually eliminate sheer (Fig. 16.2). These dental adaptations account for the fact that trigonioids have never evolved marginal denticulation to complete the job of alignment as their valves approach closure.

Hinge teeth have been reduced or eliminated in the evolution of some deep-burrowing and boring bivalve taxa, such *Mya*, *Panopea*, and the Pholadidae. This condition, along with concentration of the ligament in a nymph or chondrophore, has permitted the valves to rock back and forth about a dorsoventral axis. Thus, the anterior and posterior gapes can expand or contract, depending on whether the foot or large siphons are being extruded or withdrawn.

Hinge teeth have also been reduced or eliminated by the evolution of flexible shell margins, which produce a wide band of contact during closure, thereby obviating precise guidance of the margins during closure (CARTER & TEVESZ, 1978). Examples include the Solemyidae and Pinnidae.

ORNAMENTATION OF BURROWERS

Ornamentation on the shell surface of burrowing bivalves performs multiple functions. Two of these relate to the need to maintain a position of burial. Some kinds of ornamentation accelerate burrowing, whereas others reduce the probability of being dislodged to begin with. Other kinds of ornamentation ward off predators that habitually nip off siphons while animals are in their normal life positions.

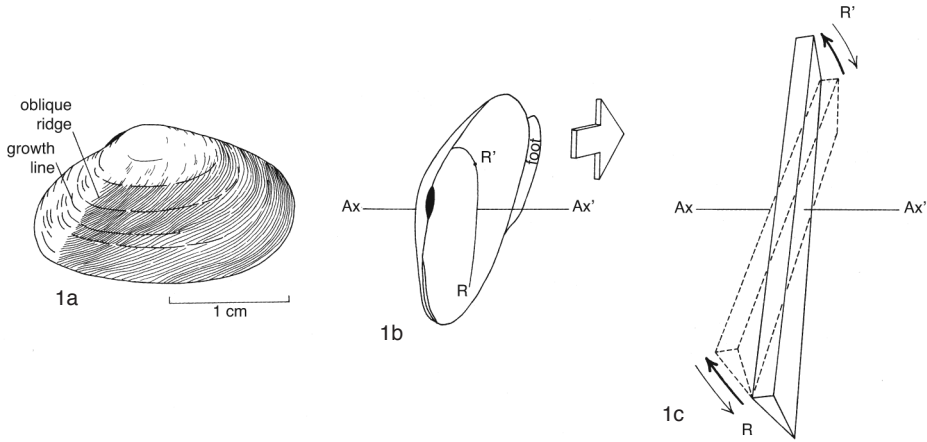


FIG. 17. 1, Function of oblique ridges in assisting the burrowing of *Scissula similis* (J. SOWERBY, 1806); 1a, external view of right valve; 1b, oblique dorsal view of burrowing animal; the large arrow denotes the burrowing direction, and $R-R'$ represents a single rib; 1c, diagrammatic representation of a ridge during a single forward-backward burrowing movement, with the thick arrow indicating strong frictional resistance and the thin arrow indicating weak frictional resistance (Stanley, 1970).

Ornamentation That Accelerates Burrowing

Pronounced ornamentation on the surface of many kinds of bivalve shells impedes burrowing (Fig. 13). On the other hand, certain kinds of ornamentation, most of them more subdued, accelerate burrowing. The most obvious kind of ornamentation of this type consists of asymmetric, cuesta-shaped ridges that have a steep dorsal slope and a gentle ventral slope (STANLEY, 1969, 1970; SEILACHER, 1972; SAVAZZI, 1991). Many such ridges are discordant structures, whose formation was described previously (see Fig. 3). For most species displaying such ridges, as the shell rotates forward during burrowing, posteriorly positioned ridges (or portions of ridges) grip the sediment, while anteriorly positioned ridges slide through the sediment with little resistance; when the shell rotates backward, the frictional disparity for the anterior and posterior ridges is reversed (Fig. 17). Thus, like the blunt end of a bivalve of typical venerid shape, these ridges increase the magnitude of downward burrowing steps by impeding upward slippage of the shell during backward rotation of the shell. As described below for *Divalinga* CHAVAN, 1951, *Divaricella* MARTENS, 1880b,

and a few other lucinids, the ridges instead act as rasps.

Commarginal asymmetric ridges can also assist burrowing, as has been demonstrated for the venerid *Anomalocardia brasiliiana* (GMELIN, 1791) (Fig. 18.1), by filling the valleys between ridges with neutrally buoyant wax and finding that animals required more rotational movements to burrow than control individuals in which the wax was applied to the posterior region of the shell, where it had no influence on burrowing (STANLEY, 1981).

Divalinga and other lucinids possess chevron-shaped, asymmetric ridges (Fig. 3.2). It appears that the forward and backward axes of rotation of *Divalinga*'s circular shell are virtually coincident. This suggests that the ridges do not function primarily to help the animal pry its way downward but instead rasp away sand adjacent to the ventral region of the shell and pass it upward, allowing the shell to descend slightly with every rotational cycle (STANLEY, 1969, 1970); *Divalinga* normally lives in fine sand having a diameter similar to the height of the asymmetric ridges.

In contrast, for the tellinid *Strigilla* TURTON, 1822, another circular shell, asymmetric

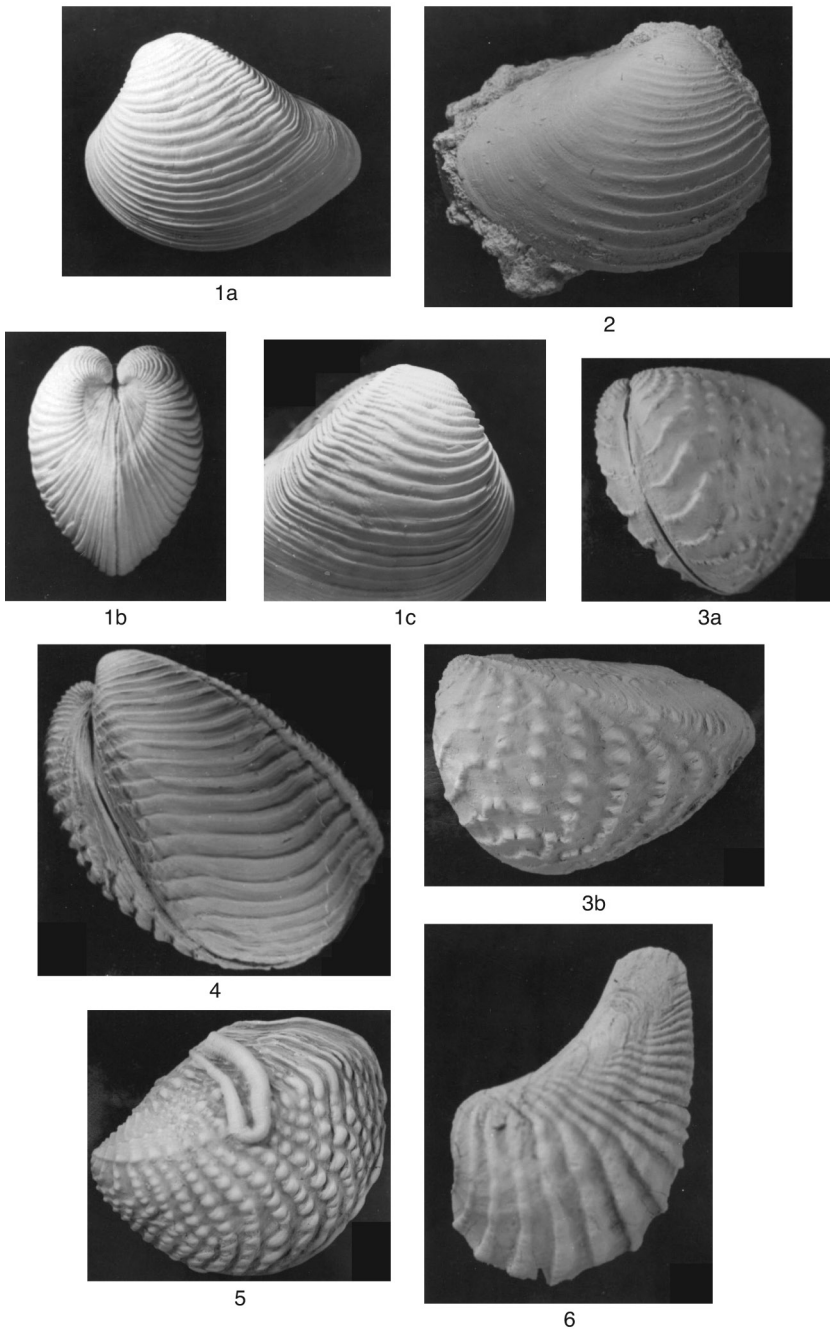


FIG. 18. Ornamentation serving as an aid to burrowing for an extant venerid species (1) (STANLEY, 1981) and five Jurassic trigoniid species (2–6) (STANLEY, 1977b); 1, *Anomalocardia brasiliana* (GMELIN, 1791); 1a, left lateral view, $\times 1.15$; 1b–1c, anterior and oblique posterior-lateral views, showing asymmetry of the comarginal ridges, $\times 1.15$, $\times 1.3$; 2, *Rutitrigonia dunscombensis* (LYCETT, 1872–1873), which displays ridges resembling those of *A. brasiliana*, $\times 1.1$; 3, *Myophorella clavellata* (PARKINSON, 1811); 3a, oblique anterior view, showing ridges that gripped the sediment, $\times 0.5$; 3b, left lateral (Continued on facing page.)

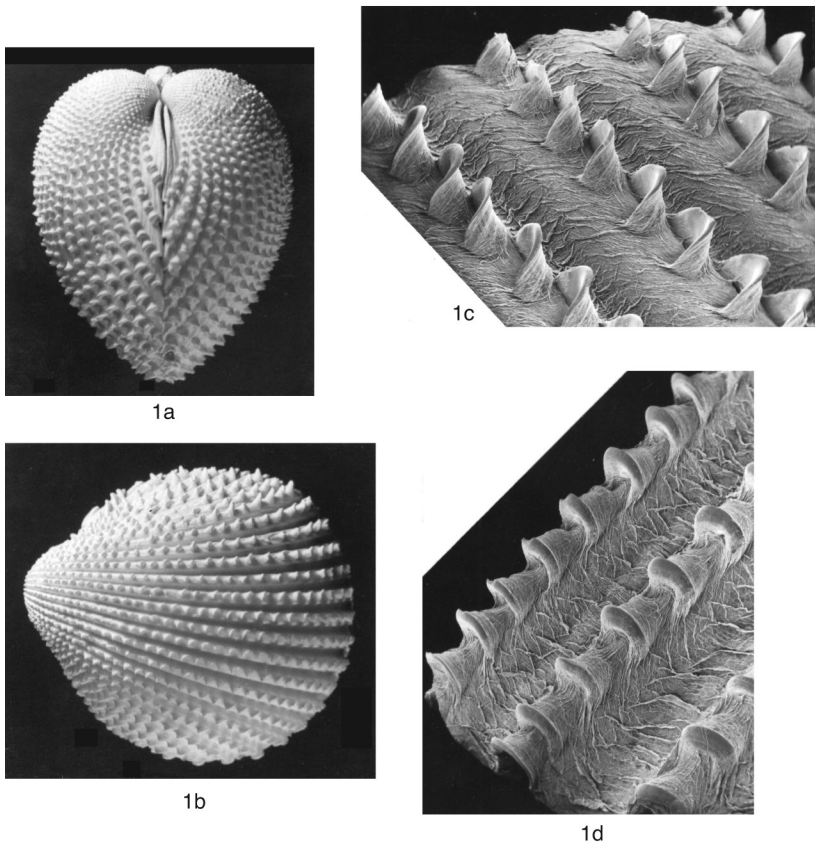


FIG. 19. *Trachycardium egmontianum* (SHUTTLEWORTH, 1856), the ribs of which bear two kinds of spines that perform different functions; *1a*, anterior view, $\times 1.3$; *1b*, left lateral view, $\times 1.3$; *1c*, spines on the posterior of the shell that are cup-shaped, like the ear of a cat, and serve to reduce scour, $\times 5$; *1d*, spines on the anterior region of the shell that are also cup-shaped, but flared dorsally, sliding readily through the sediment during forward shell rotation but gripping it during backward rotation, $\times 4.3$ (Stanley, 1981).

divaricate ridges (Fig. 3.1) appear to serve for prying rather than sawing, because this more laterally compressed species slices rapidly downward into the sediment with very few rotational movements; its forward and backward axes of rotation lie far apart, so that it takes a large step downward with each forward-and-back rotation (STANLEY, 1970).

SEILACHER (1972) interpreted the asymmetric ridges of the elongate genus *Solecirtus* BLAINVILLE, 1824, most of which are roughly perpendicular to the long axis of the shell, as functioning to resist upward slippage of the shell while the foot probes downward.

The cardiid *Trachycardium* MÖRCH, 1853, possesses an entirely different

FIG. 18. *Continued from facing page.*

view, showing rows of knobs that gripped the sediment, $\times 0.5$; *4*, oblique anteroventral view of *Trigonia papillata* (AGASSIZ, 1839), showing ribs that are comarginal on the flanks of the shell but that bend near the anterior to become cuestaslike ridges, $\times 0.6$; *5*, left lateral view of *Yaardia nodosa* (J. DE C. SOWERBY, 1826 in 1812–1846), showing rows of knobs that gripped the sediment; the attached serpulid worm grew downward to the sediment-water interface and reversed itself, demonstrating that the bivalve was only partly buried for a substantial interval of time, $\times 0.5$; *6*, *Megatrigeria conocardiiformis* (KRAUSS, 1843), a form with large, ratchetlike ribs, $\times 0.8$ (Stanley, 1977b).

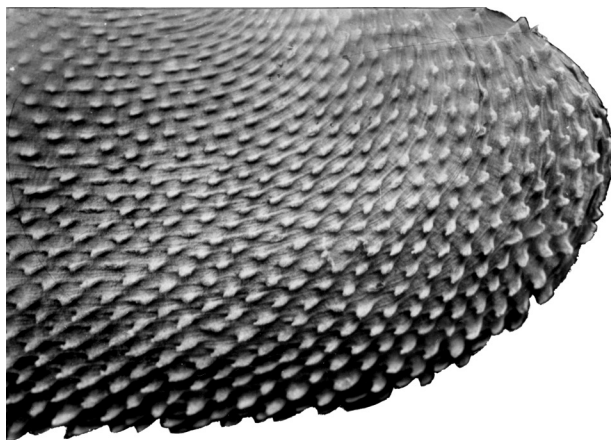


FIG. 20. Hooked spines on the flanks of the extant tellinid *Tellinella asperima* (HANLEY, 1844), which must aid in burrowing during backward rotation of the shell (new).

kind of ornamentation, which accelerates burrowing; cup-shaped spines on the anterior radial ribs of the shell are directed ventrally but flared dorsally, so as to resemble a segment of a trumpet (Fig. 19.1d). A finger runs smoothly toward the umbo over these spines, but encounters considerable friction when run toward the shell margin. Like the asymmetric ridges described above, these spines grip the sediment during backward rotation of the shell and slide easily through it during forward rotation. This effect has been demonstrated via experiments in which individuals from which the anterior spines were removed required more forward-and-back rotations for burial than control individuals from which only posterior spines were removed: spines that have no effect on burrowing but, as will be shown below, have a different function (STANLEY, 1981). The flanks of the tellinid *Tellinella asperima* (HANLEY, 1844) (Fig. 20) bear discordant rows of hooked spines that must function in the same way, as do rasplike scales on the shell of the tellinid *Scutarcopagia scobinata* (LINNAEUS, 1758) (SEILACHER, 1972).

The cardiid *Dinocardium* DALL, 1900, has a plicate shell on which the ribs are approximately symmetrical in cross section

but bear low, rasplike scales. This genus clearly saws its way into the sediment with the ventral portions of the ribs and the crenate margin of the shell (Fig. 15.1). In fact, *Dinocardium* rocks back and forth not once but three times, quite rapidly, at the culmination of each burrowing sequence, with the magnitude of the rotational motion decreasing from the first rocking cycle to the third. *Dinocardium* also makes use of a strong expulsion of water from the mantle cavity to loosen the sediment below (STANLEY, 1970). It resembles *Divaricella* in sawing its way into the sediment, but in contrast to the smooth, slow movements of *Divaricella*, the rapid, powerful movements of *Dinocardium* seem almost violent. SAVAZZI (1982) showed experimentally that the ribs of the cardiid *Acanthocardia tuberculata* (LINNAEUS, 1758) and the arcid *Scapharca inaequivalvis* (BRUGUIÈRE, 1789 in BRUGUIÈRE, DESHAYES, and HWASS, 1789–1832), which are also more or less symmetrical in cross section, aid in burrowing.

Mesozoic species of the Trigoniidae exhibit several kinds of ornamentation that provide assistance in burrowing (STANLEY, 1977b). Experiments with models of shells similar to those employed to study move-



FIG. 21. Reduction of sediment scour by the cuplike spines on the partly exposed shell of *Trachycardium egmontianum* (SHUTTLEWORTH, 1856) in life position; in this flume experiment, regardless of current direction, scour was greater around the shell model from which the spines had been removed (above) than around the shell on which they were intact (below); scale, 5 cm (Stanley, 1981).

ments of *Mercenaria* SCHUMACHER, 1817 (Fig. 5) showed that the discordant rows of knobs on the flanks of *Yaardia nodosa* (J. DE C. SOWERBY, 1826 in 1812–1846) (Fig. 18.5) assisted the animal in burrowing, and that both the asymmetric ridges on the anterior and the symmetric ridges on the flanks of *Trigonia papillata* (AGASSIZ, 1839) (Fig. 18.4) assisted this species in burrowing. The Jurassic trioniid *Rutitrigonia dunscombensis* (LYCETT, 1872–1873) displays ornamentation that resembles the concentric asymmetric ridges of *Anomalocardia brasiliiana* (compare Fig. 18.1 and 18.2) and must have aided burrowing.

Ornamentation That Retards Sediment Scour

Shallow-burrowing bivalves often end up with the posterior ends of their shells poking slightly above the sediment-water interface and, like pebbles or cobbles in a similar

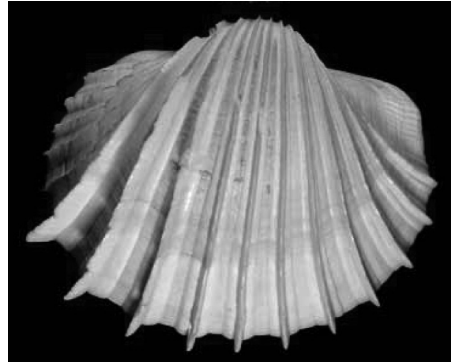


FIG. 22. The shell of *Cardium costatum* (LINNAEUS, 1758), which displays tall, thin keels on the external ridges of the shell (new; photo courtesy of Machiko Yamada).

position, their elevation promotes scour (STANLEY, 1981). This scour is explained by the Bernoulli Principle, according to which momentum must be conserved in a flowing liquid, so that a parcel of water that is deflected around an obstacle must accelerate. As a result, sand is commonly scoured around the margins of an object, such as a pebble, that is only partly buried in the seafloor or a stream bottom, further exposing the object. Ridges or spines on the posterior of a bivalve shell, when exposed above the sediment-water interface, tend to reduce scour by creating turbulence. In effect, a strong, smooth flow that would scour away sediment is broken up into random (multi-directional) motion, the components of which are weak and short-lived. Experiments have shown that the crenulated commarginal costae on the posterior shell region of *Chione cancellata* (LINNAEUS, 1767 in 1766–1767) reduce scour when exposed above the sediment-water interface. Similar experiments have shown that the spines on the posterior shell region of *Trachycardium* perform the same function (Fig. 21). These spines are cuplike, resembling a cat's ear, in contrast to the anterior, flared spines of this species, which aid in burrowing (Fig. 19.1c). Projecting periostracal structures can offer the same advantage with regard to reducing sediment scour around the shell (BOTTJER & CARTER, 1980).

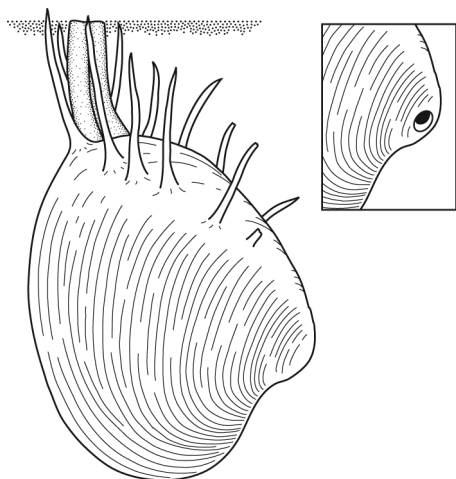


FIG. 23. Long, sharp spines on the dorsoposterior region the shell of the venerid *Hysteroconcha* DALL, 1902, which protect the siphons from siphon nippers; *inset*: umbonal region of the shell used as a model for this drawing, which displays a naticid snail boring that indicates that the animal was killed by a flank attack, which is the norm for naticids, and for which the posterior spines were useless (new).

It is important to understand that some kinds of ornamentation serve more than one function. The highly elevated costae of *Chione cancellata*, for example, may serve not only to reduce scour but also to resist forces that might dislodge partly exposed individuals.

Ornamentation That Aids Flotation in Sediment

Cardium costatum (LINNAEUS, 1758) and *Cardium hians* BROCCHI, 1814, are two cardiids that, unlike most members of their family, live in soft, muddy sediments, which, in general, do not favor suspension feeders because mud can clog their feeding apparatuses. The ribs of these two cardiid species bear thin, highly elevated keels (Fig. 22), which SAVAZZI (1985) interpreted as serving to increase the strength of the animals' thin shells. There is little to break the shell of an animal living in a quiet environment where mud accumulates, however, and smooth-shelled species of *Laevicardium* SWAINSON, 1840, that live in sand are also quite thin shelled. The thin keels

on the surface of *Cardium costatum* would not repulse a shell-snipping crab, which would easily break the thin intervening shell. It seems almost certain that the primary function of the keels of the mud-dwelling species is instead to act like a snowshoe, for flotation in a soupy environment.

Ornamentation That Obstructs Siphon Nippers

Long, sharp spines extend from the siphonal region of the venerid *Hysteroconcha* DALL, 1902 (Fig. 23). CARTER (1967) interpreted these as functioning to ward off predaceous starfishes and gastropods, but starfishes are not major predators on infaunal bivalves and burrowing snail predators (chiefly naticids) make flank attacks (Fig. 23, inset). The spines of *Hysteroconcha* almost certainly represent adaptations that evolved to quite wickedly ward off sublethal siphon nippers (STANLEY, 1988). Siphon-nipping by fishes is well documented in the modern ocean. Bivalves can regrow siphons, but only at the expense of considerable energy. As reviewed by TOMIYAMA and OMORI (2007), siphon nipping reduces the growth rates of bivalves. As *Hysteroconcha* grows, spines become obsolete, only ones close to the posterior shell margin remaining functional. A few venerid species with short siphons, such as *Circomphalus foliaceolamellosa* (DILLWYN, 1817), display flangelike protuberances on the posterior margins of their shells that may also rebuff siphon nippers.

Why, one might ask, is elongate siphon-protecting ornamentation rare among burrowing bivalves? It would clearly benefit many species, but presumably genetic opportunities (mutation and recombination) required for its evolution have arisen only rarely. One of the problems is the age-old issue of the value of incipient features. Very short nubbins presumably cannot ward off predators and be subject to natural selection by serving such a function. It would appear that the unlikely first step upon which selection can operate must be a substantial outgrowth of the shell in the proper position.

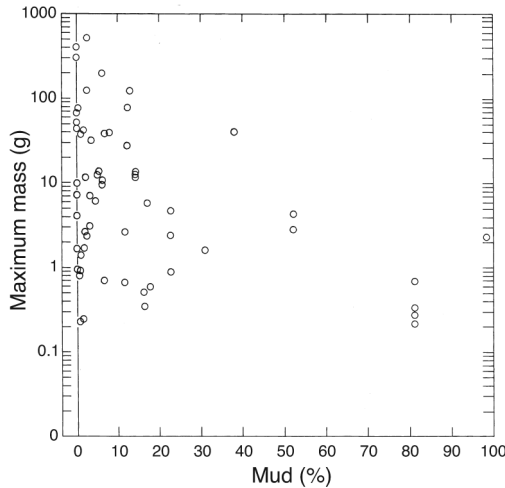


FIG. 24. A plot showing that bivalves that occupy soupy, fine-grained sediments tend to be of small body mass (Stanley, 1970).

Ornamentation and Burrowing Depth

Because pronounced ornamentation is generally valuable only to shallow-burrowing bivalves, most strongly ornamented burrowing species are shallow burrowers (Fig. 14.2).

SHELL SIZE

As noted earlier, there is an inverse relationship for bivalves between body size and the percentage of species that employ nonplanktonic larvae. In addition, bivalve species of small size, including infaunal forms, can easily engage in symbiotic relationships.

As previously noted, bivalves of small size are better adapted to life in soupy mud than large animals, which have a larger weight-to-surface area ratio. Thus, burrowing bivalve species that occupy fine-grained sediments are mostly small (Fig. 24).

THE TRIGONIIDAE: A CASE STUDY OF COADAPTATED TRAITS

The history of the trigonioids exemplifies the evolution of a coadapted complex of features; the group acquired unique evolutionary solutions to adaptive problems imposed by features that evolved earlier (STANLEY, 1977b). *Neotrigonia* COSSMAN,

1912b, the only surviving trigonioid genus, is an exceptional nonsiphonate bivalve in being a relatively rapid burrower because, like a cockle, it possesses a muscular foot, which in the case of *Neotrigonia* is T-shaped to provide anchorage when the animal rocks back and forth in burrowing (Fig. 15.2). This foot, like the similar L-shaped muscular foot of the Cardiidae (Fig. 15.1b–15.1c), can be used to leap in order to escape from a predator. Along with the muscular foot, early trigonioids evolved large teeth, extending far into the shell interior and bearing secondary, serrational dentition (Fig. 16.2). As previously explained, this dentition kept the shell aligned during extrusion of the wide foot. The orthogyrate or opisthogyrate shell form reflects morphological constraints. The anterior adductor of trigoniids is positioned close to the apex of the umbo, and the large anterior hinge tooth is linked to it by attachment to the myophorous buttress; this configuration has left no room for evolution of a prosogyrate shape that would produce a large, blunt anterior end of the shell dorsal to the anterior adductor, where it would have to be located. The absence of a prosogyrate shape would have caused upward slippage of the animal's anterior during



FIG. 25. Evolutionary convergence between the petricolid and pholad borers; 1, the petricolid *Petricolaria* STOLICZKA, 1870 (in 1870–1871), $\times 2.1$; 2, the pholad *Pholas* LINNAEUS, 1758, $\times 0.4$ (Stanley, 1970).

burrowing (see Fig. 5). In compensation for this potential problem, evolution provided various forms of pronounced shell ornamentation that gripped the sediment (Fig. 18). Thus, the trigonioids represent a curious coadapted complex of features. It can also be argued that the columnar prisms comprising the outer shell layer of trigonioids (and unionoids) are biomechanically less suitable for constructing fine, projecting spines and narrow, commarginal ridges than the smaller prisms or CL structures comprising the outer shell layer of most other heteroconchians (J. CARTER, personal communication, 2011).

The cardiids' solution to the problem of shearing along the commissure at wide angles of gape was much less complex than the trigonioids' solution and posed fewer problems: cardiids simply evolved lateral teeth that are well ventral of the hinge axis and project far across the commissure (Fig. 16.1). The trigonioids' coadapted features, though intriguing, would not have been produced by an omnipotent engineer.

ADAPTATIONS FOR BORING

Bivalve taxa bore into hard substrata by mechanical means or chemical means, or both. Most rock-boring and coral-boring bivalves have a relatively elongate shell with

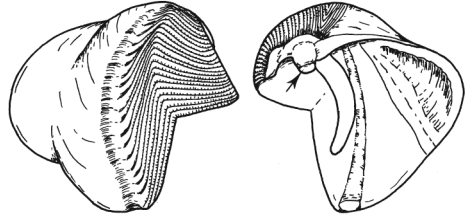


FIG. 26. Morphology of the right valve of the wood-boring Teredinidae; arrow indicates ball joint on the hinge and ventral margin that permits the valves to rotate and apply pressure (Clench & Turner, 1946).

an anterior gape for extrusion of a pluglike, suctorial foot that is used for attachment during the boring process.

Members of the Pholadidae abrade the substratum with cancellate toothlike projections on the surface of the shell that point posteriorly. In typical pholads, the ligament is reduced or absent, and hinge teeth are lacking; these features permit the shell to rotate about a joint formed by the hinge, so that the anterior and posterior gapes can be widened alternately. The pressure resulting from anterior expansion contributes to abrasion of the substrate, and rotational movements contribute to the circular cross section of the burrow. These various movements are produced by complex musculature, with the anterior adductor muscle having shifted to a position dorsal of the hinge, and with some of the pedal muscles inserted on an apophysis. Some boring members of the Petricolidae (Veneroidea) are strikingly convergent with certain pholadids in their external morphology (Fig. 25).

In the Teredinidae, the compact shell is rotated by way of ball joints on the hinge and ventral margin so that sharply serrated ridges on the shell surface apply pressure to abrade a circular boring in a woody substratum (Fig. 26).

Gastrochaenids possess the typical suckerlike foot and pedal gape of bivalve borers, and they appear to use a combination of chemical and mechanical boring mechanisms (CARTER, 1978).

Hiatellids, though remaining byssally attached and exhibiting no special features

for boring, bore mechanically in the manner of pholadids and possibly also engage in chemical boring.

Lithophaginids are chemical borers confined to carbonate substrata. They are approximately cylindrical, which adapts them well to the tubes they occupy, and as noted earlier, their periostracum protects their shell from their own acid. Rarely, as in *Lithophaga antillarum* (D'ORBIGNY, 1853), a file-like exterior surface on the posterior of the shell aids in scraping the boring walls, thereby assisting their predominantly chemical boring mechanism.

ADAPTATIONS OF ENDOBYSSATE FORMS

Endobyssate bivalves live infaunally or semi-infaunally in soft sediment. They attach by a byssus to sedimentary particles, ideally relatively large ones such as shell fragments, but sometimes they also attach to each other or to subsurface portions of marsh grass or seagrass. Endobyssate taxa have evolved polyphyletically from burrowing taxa. The byssus became an adult feature of many groups of bivalves via neoteny, having been present in the postlarval stages of burrowers and subsequently retained into the adult stage (YONGE, 1962). The initial byssate adult descendants were infaunal forms; semi-infaunal taxa evolved from these and gave rise to epibyssate taxa. There have been sporadic reversions from epibyssate to endobyssate habits (STANLEY, 1972).

Epibyssate taxa exhibit more derived morphologic features than endobyssate taxa when compared to their burrowing ancestors. Endobyssate representatives of all taxa characteristically retain a rounded anterior shell region, inherited from ancestral burrowers but reduced in size (Fig. 27). This anterior lobe usually extends slightly beyond the umbos and houses a small anterior adductor muscle, which in epibyssate taxa has been further reduced or eliminated. Many endobyssate species are modioliform in outline and many exhibit a broad byssal sinus.

The extant Mytilidae include both endobyssate and epibyssate species, and the two groups differ from each other morphologically in ways that are instructive for the interpretation of extinct species representing a wide variety of higher taxa. Figure 28 illustrates how the evolution of the triangular shape of *Mytilus* from the ancestral modioliform shape entailed contraction of the anterior region, along with expansion of the posterior region and hypertrophy of the byssal retractor muscles. This configuration provides for firm epifaunal attachment via strong contraction of the retractors in a direction nearly normal to the substratum (Fig. 29.2). In contrast, in the endobyssate *Geukensia* VAN DE POEL, 1959, smaller byssal retractor muscles pull downward at a small angle to the long axis of the shell, which itself is positioned at a high angle and mostly buried in the substratum. The substratum provides support not available to epibyssate species. Downward movement by *Geukensia* is generally limited to episodic steps required by growth that are presumably accomplished by tugging on the byssus. Presumably in reflection of this behavior, the umbos of this genus are commonly abraded.

Burrowing arcids that employ a weak accessory byssus can reasonably be classified as burrowers rather than endobyssate forms. However, a few elongate arcoids are endobyssate, the most interesting from the standpoint of functional morphology being *Trisidos* RÖDING, 1798, whose shell is twisted through about 90°, so that the anteroventral region extends downward, while the posterodorsal region lies flat on the substratum, offering little resistance to water movements (MCGHEE, 1978; THOMAS, 1978b; TEVESZ & CARTER, 1979) (Fig. 30).

Endobyssate pterineids of the Paleozoic were inequivalve and must have lived with the flatter right valve underneath, the commissure at a low angle, and the incurrent and excurrent regions of the shell projecting above the sediment-water interface. This posture would have provided for firm byssal attachment and would also have reduced the

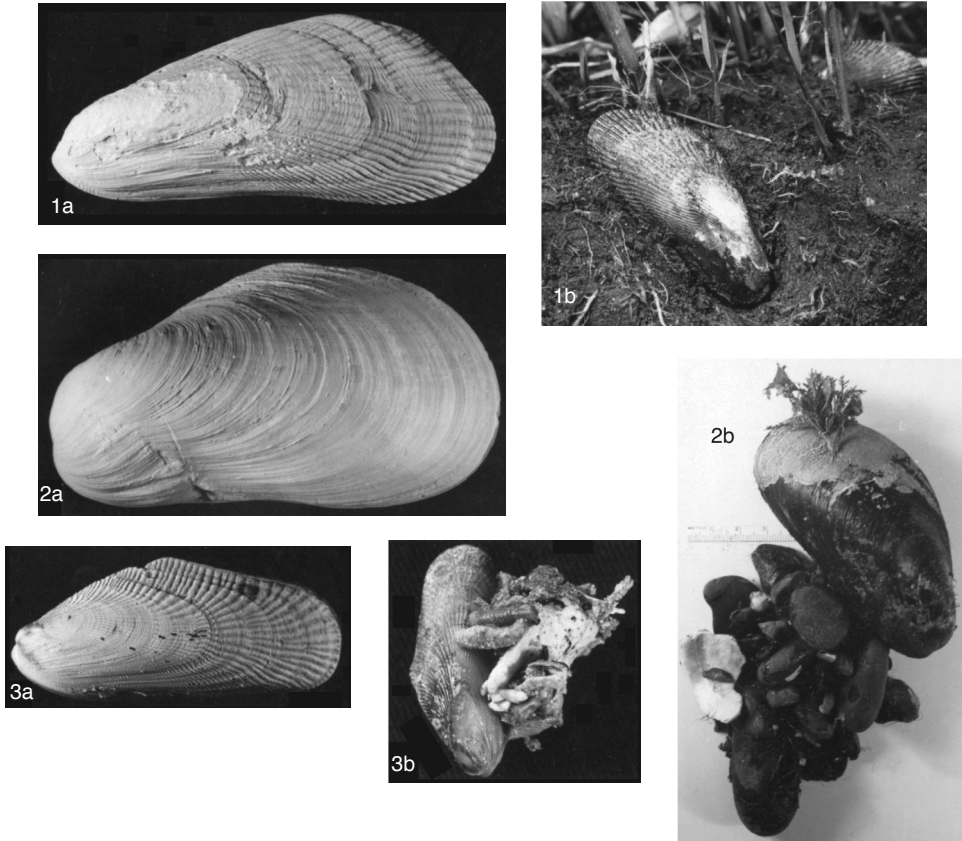


FIG. 27. Morphologies and modes of life of extant endobysate mytilids; all are elongate and possess an anterior lobe; 1, *Geukensia granosissima* (G. B. SOWERBY III, 1914); 1a, left lateral view, $\times 0.7$; 1b, an animal exposed in its normal life position, mostly buried in marsh peat, $\times 1$; 2, *Modiolus modiolus* (LINNAEUS, 1758); 2a, left lateral view, $\times 0.45$; 2b, animal attached to gravel (the sharp boundary between the coralline algae overgrowth and bare shell marks the position of the sediment-water interface when the animal was in life position), $\times 0.75$; 3, *Brachidontes citrinus* (RÖDING, 1798); 3a, left lateral view, $\times 1.5$; 3b, animal removed from a seagrass bed, in which it was almost entirely buried and attached to skeletal debris, $\times 1.35$ (Stanley, 1972).

disruptive force of strong water movements. Some of these forms possessed a posterior wing, which, as will be described below for the epifaunal genus *Pteria* SCOPOLI, 1777, would have sheltered the exhalant current, increasing its trajectory when the direction of external water movements would otherwise have diverted waste water into the inhalant region.

Although the pinnids, which range back to the late Paleozoic, have never been a diverse group, they are the most conspicuous endobysate bivalves of the modern tropics because their adult shells are large and project slightly

above the sediment surface. Their elongate, triangular shape, with the umbos pointing downward and the hinge axis at a high angle, permits them to wedge downward as they grow (see *Treatise Online*, Part N, Revised, Volume 1, Chapter 19, Fig. 15). Their evolution has circumvented a normal geometric constraint of bivalve morphology: restriction of the shell gape near the hinge to a very narrow angle. Pinnids' valves are partly or entirely fused along the hinge axis, but their shell is flexible, gaping when they are pumping water and bending shut when they stop. This flexibility, and the restriction of the viscera to the umbonal

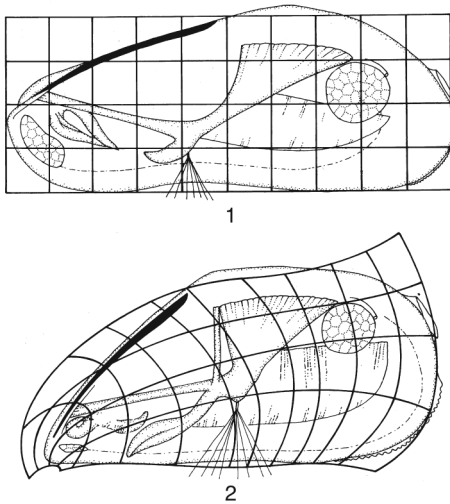


FIG. 28. Illustration, by way of deformation coordinates, of the morphological changes by which epibyssate mytilids were derived from endobyssate mytilids. A grid was plotted on a cutaway view of *Geukensia granosissima* (G. B. SOWERBY III, 1914) (1), and points homologous to line intersections on this grid were located on a cutaway view of *Mytilus edulis* LINNAEUS, 1758 (2), where deformed grid lines were then plotted (Stanley, 1972).

region, greatly reduces the risk of predation. Flexibility also permits complete shell closure, even if the valve margins have been damaged (VERMEIJ, 1987, p. 295).

The shells of early members of some endobyssate taxa were elongate at a high angle to the hinge axis. These taxa could not readily evolve more or less cylindrical shapes, like that of endobyssate mytilids, in which elongation more or less parallels the hinge axis (Fig. 27). The evolution of some of these taxa followed a more likely path: accentuation of their shell curvature. They became, to varying degrees, L-shaped (Fig. 31). This shape offered the advantage of positioning the inhalant and exhalant regions of the shell margin far from the hinge axis, where the gape was wide; thus, they were not required to employ a wide angle of gape to pump water.

ADAPTATIONS OF NESTLERS

Nestlers are forms that attach to hard surfaces in cavities within, between, or beneath rocks or skeletal constructions.

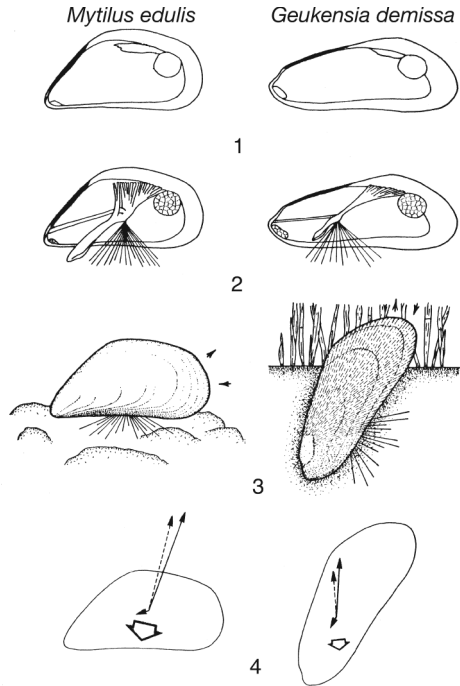


FIG. 29. Ways in which differences in shell morphology relate to mode of life of the mytilids *Mytilus edulis* LINNAEUS, 1758, and *Geukensia granosissima* (G. B. SOWERBY III, 1914); 1, shell morphology, showing anterior reduction and posterior expansion of *M. edulis* relative to *G. granosissima*; 2, musculature, showing hypertrophy of the byssal retractor muscles of *M. edulis*; 3, life positions and feeding currents (arrows) of the two species; 4, byssal retractor forces (thin arrows) and direction of shell force against the substratum, which is much greater for *M. edulis* (thick arrows) (Stanley, 1972).

Most nestling bivalve species are byssate. Some of these are obligate nestlers, but some normally endobyssate species are facultative nestlers. Furthermore, many species normally classified as epibyssate or epifaunal cemented forms often are actually semi-nestlers, living in the protection of depressions or shallow cavities.

Frequent possession of an irregular, xenomorphic shape (as for *Hiatella* BOSCH, 1801; *Cucculæarca* CONRAD, 1865; and some species of *Isognomon* LIGHTFOOT, 1786) is an indication of a nestling habit. Some extinct taxa with endobyssate morphologies normally lived as nestlers, and xenomorphic shapes can reveal their habits.

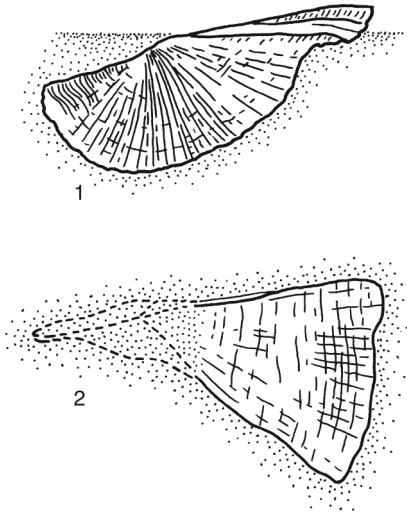


FIG. 30. *Trisidos* RÖDING, 1798, an arcid with a torted shell; 1, lateral cut-away view of animal in semi-infaunal life position; 2, top view, showing the exposed flattened posterior (Tevesz & Carter, 1979).

Many arcids with elongate oval shapes are nestlers (Fig. 32). In general, these are relatively small, somewhat laterally compressed forms that are suited to this habit but would be relatively unstable if living as endobyssate forms in soft sediment.

Nearly all pectinids that are byssally attached as adults are nestlers, avoiding predators in their seclusion, although they can release their byssus and swim awkwardly if disturbed. Although they have been characterized as free swingers (KAUFFMAN, 1969), these forms all attach firmly to the substratum by virtue of their elongate anterior auricle, which in conjunction with the ventral shell margin, provides the shell with two points of contact with the substratum beyond the site of byssal attachment (Fig. 33). This configuration, made even more effective by a narrow umbonal angle compared to that of a free-living pectinid, prevents overturning unless the byssus is ripped loose (STANLEY, 1970). In fact, adult pectinid species that are byssally attached can be distinguished from ones that are free-living by measurement of umbonal angles and auricular asymmetry (Fig. 34). The adaptive value of the shapes of the free-living forms will

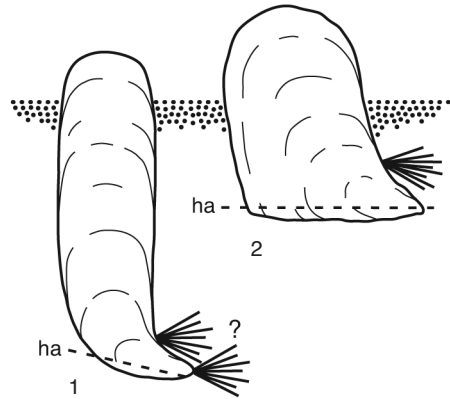


FIG. 31. L-shaped endobyssate species, in which the resulting orientation of the hinge axis (*ha*) relative to the rest of the shell resulted in a large gape for the sector of the commissure exposed above the sediment-water interface; 1, the Triassic myalinid *Novaculaperna* McROBERTS & NEWELL, 1997 (adapted from McRoberts & Newell, 1997); 2, the equivalved form of the taxonomically problematical Jurassic lithitoid *Mytiloperna* IHERING, 1903 (Fraser, Bottjer, & Fischer, 2004).

be discussed below. Also associated with the elongate auricle of pectinids that are byssate as adults is a ctenoleum, a comblike structure that guides and separates the byssal threads where they emerge from the shell (WALLER, 1984).

Nestling pectinids usually occupy spaces large enough not to induce irregular shell growth. The same is true of limids, many which today are nestlers that habitually suspend loosely from a byssus. A notable adaptive feature of the shell of these species is a flared, liplike aperture through which the byssus emerges, permitting the animal to move about easily without abrading its byssus (Fig. 35). Other limids, including *Lima lima* (LINNAEUS, 1758), have flattened ventral regions like those of epibyssate mytilids, and attach firmly (STANLEY, 1970). Like pectinid nestlers, limids enjoy considerable protection from predators but can release the byssus and swim awkwardly.

ADAPTATIONS OF EPIBYSSATE FORMS

Epifaunal bivalves in the modern ocean are highly vulnerable to predation. As previ-

ously noted for endobysate pinnids, many epifaunal periwinkles have flexible shells that permit them to close their valves even when the margins have been damaged by a predator (VERMEIJ, 1987, p. 295). Some epifaunal taxa—notably many oyster species—benefit from occupation of bays and estuaries, where fluctuating temperatures and salinities exclude major predators. Other species, including some mytilids, occupy regions of the rocky intertidal zone that are hostile to most marine predators. *Mytilus edulis* LINNAEUS, 1758, for example, forms dense populations in the intertidal zone of the Western Atlantic, but the lower limit of these colonies is emphatically established by the upper limit of starfish populations (DEXTER, 1947). The fact is that many other bivalve species conventionally regarded as epifaunal are actually nestlers, partial nestlers, or partial borers—and gain protection from these habits.

Although many epifaunal bivalves have been characterized as loosely attached free-swingers (KAUFFMAN, 1969), none actually live in this way in the modern ocean. All epibyssate bivalves that occupy solid substrata are rigidly attached.

Most of the adaptive morphologic features of epifaunal mytilids for firm attachment were reviewed earlier (Fig. 29). It should also be noted that the ventral region of these forms is flattened for the same purpose, contrasting with the ventral region of a typical endobysate mytilid, which resembles the hull of a boat. Similar anterior shell reduction, posterior expansion, and ventral flattening indicate the same kind of hard-substratum attachment for many Paleozoic ambonychiids, as well as such Mesozoic genera as the inoceramids *Parainoceramus* VORONETZ, 1936, and *Retroceramus* KOSCHELKINA, 1957, and the large limid *Regalilima* COX, 1943 (although some of these forms may have been partial nestlers).

Pteriids have been characterized as free-swingers with the posterior wing extending horizontally and functioning like a weather vane, aligning animals with prevailing

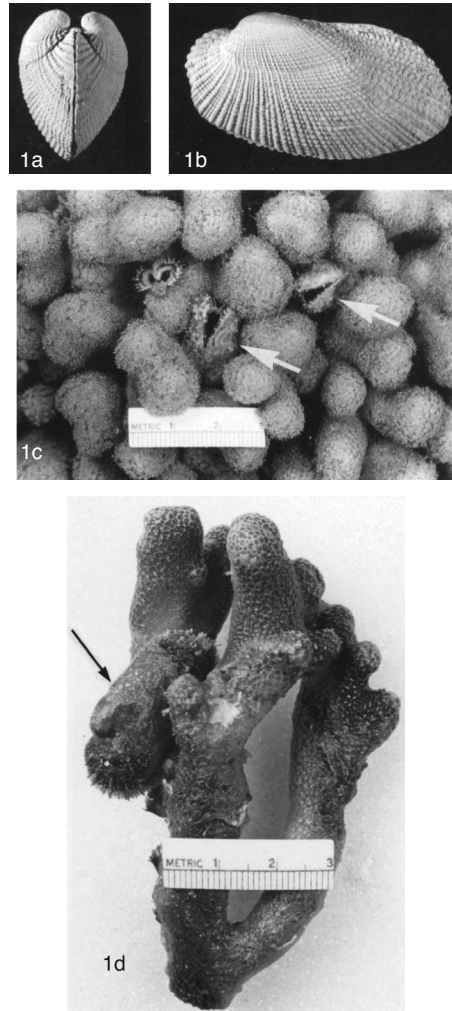


FIG. 32. 1, *Barbatia cancellaria* (LAMARCK, 1819 in 1818–1822), a small, nestling byssate arcid; 1a, anterior view, $\times 1.5$; 1b, left valve, $\times 1.5$; 1c, life position within a colony of the coral *Porites* LINK, 1807 (white arrows); scale, 3 cm; 1d, an individual exposed by breaking up a *Porites* colony; scale, 3 cm (Stanley, 1970).

currents (KAUFFMAN, 1969). Actually, this mode of life is impossible because all bivalves are denser than seawater, and any uncalcified byssus is flexible. If any bivalve with a flexible byssus were held with its byssus extended horizontally and then released, it would flop helplessly downward to dangle at the end of the byssus. Measurements in Bermuda for numerous *Pteria colymbus*

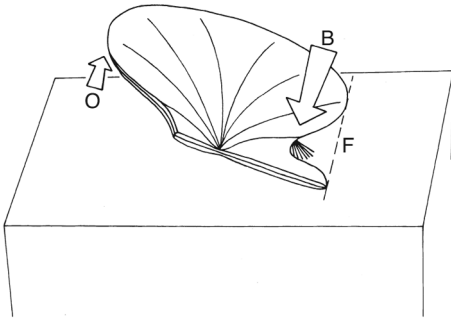


FIG. 33. Function of the elongate anterior auricle of byssally attached pectinids. Given the presence of the auricle, a strong external force (*O*) would be required to overturn the animal about a fulcrum (*F*) against the opposing force of the byssus (*B*) (Stanley, 1970).

(RÖDING, 1798) individuals attached to alcyonarians showed no prevailing compass direction (STANLEY, 1972). In fact, *Pteria colymbus* habitually attaches firmly to alcyonarians, with the shell upside down at an angle and the posterior wing projecting obliquely upward (Fig. 36.1a), and it appears that nearly all extant species of *Pteria* habitually attach to alcyonarians in the same manner. This type of preferred life position, above the sea floor, provides a refuge from benthic predators. The pteriid *Pterelectroma zebra* (REEVE, 1857), though possessing a very short wing, lives in this orientation and

benefits from a color pattern that mimics the branching configuration of its alcyonarian host (Fig. 37).

The upward orientation of the posterior wing of *Pteria* in its normal life position is adaptive and serves as a functional model for the wings of extinct pterioids. The wing extends outward parallel to, and just dorsal to, the exhalant current of *Pteria*. It diverts water currents flowing in the plane of the commissure in a direction that would otherwise send exhalant water back into an animal's inhalant region (water currents coming from other directions present no problem). Experiments with artificial currents have demonstrated this effect of *Pteria's* wing (STANLEY, 1972) (Fig. 36.1b).

Not only for pectinids, but for all epibyssate taxa that live with their sagittal plane at an angle to the substratum, a byssal notch will create stability against overturning by providing the shell with two points of contact beyond the site of byssal attachment (Fig. 33). A byssal sinus performs a similar stabilizing function (STANLEY, 1972) (Fig. 38).

As previously mentioned, most arcid species that are conventionally regarded as epibyssate actually habitually bore part way into calcareous substrata by way of their coarse ribbing (STANLEY, 1970). This leaves exposed only the posterodorsal region, which

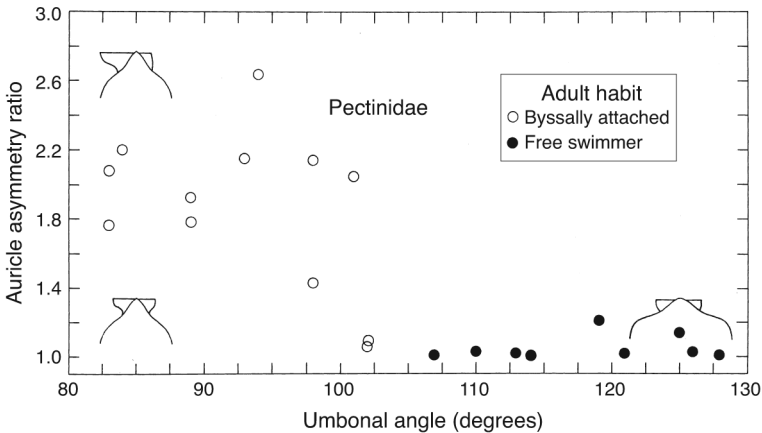


FIG. 34. Relation of umbonal angle to auricle asymmetry ratio (ratio between anterior and posterior auricle lengths) for free-living and byssally attached Pectinidae (Stanley, 1970).

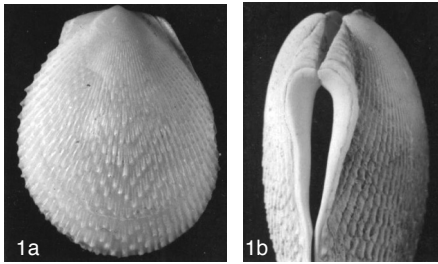


FIG. 35. 1, *Ctenoides scabra* (BORN, 1778), a loosely attached limid nestler; 1a, right valve, $\times 0.6$; 1b, the lip-shaped byssal aperture, $\times 1.2$ (Stanley, 1970).

is broadly triangular in cross section and relatively invulnerable to shell-breaking predators. These arcids are somewhat rectangular in outline and generally have a large byssal gape that accommodates a thick byssus for strong attachment. Byssate arcoids lack the conspicuous anterior reduction of many other byssate taxa. The reason for this is that arcoids employ not only posterior, but also anterior, muscles (modified pedal muscles) as strong byssal retractor muscles. Within the Arcidae, species that attach to hard substrata are more elongate than burrowers; the same relationship is evident for carditids (Fig. 39). Elongation provides a lengthy ventral shell margin for stable fixation to the substratum (STANLEY, 1970).

Anomia LINNAEUS, 1758, which today is quite abundant in shallow seas, attaches to hard substrata in a manner similar to that of a craniid brachiopod, with a flat lower valve pressed against the substratum. It employs a cylindrical, calcified byssus that protrudes through an invagination of the lower shell that amounts to a hole. Crab claws and fish teeth have difficulty gripping the smooth, dome-shaped upper valve of *Anomia*. Interestingly, *Placunanomia* BRODERIP, 1833, an anomiid with a strongly plicated shell that is not fully in contact with the substratum, has been able to survive into the Neogene, perhaps because of having its viscera located far from the margin of the shell and possessing the ability to repair marginal shell damage.

Pseudoplanktonic organisms—ones attached to floating objects—represent a special ecological category of epifauna. It appears that no bivalves live this way today, except rarely and facultatively. Many small, thin-shelled bivalve species that have been considered to have been pseudoplanktonic actually lived on the seafloor under dysaerobic conditions (see *Treatise Online*, Part N, Revised, Volume 1, Chapter 19, p. 3–4). It is not certain that any bivalve species has ever habitually attached to floating objects.

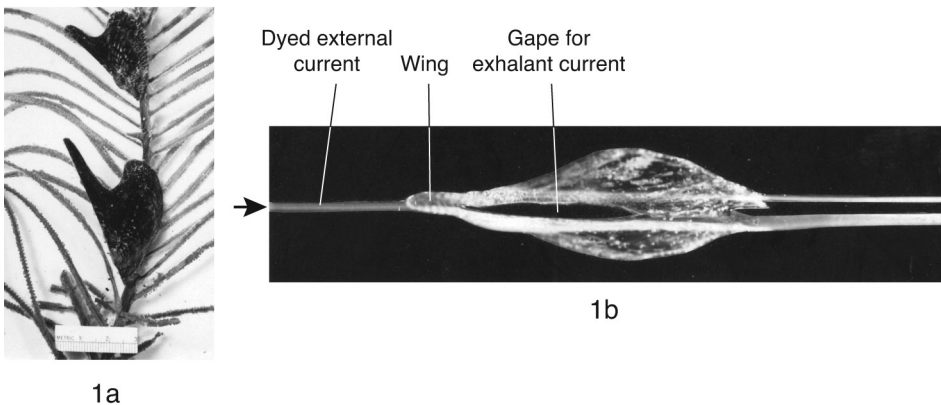


FIG. 36. 1, *Pteria colymbus* (RÖDING, 1798); 1a, an animal in the normal life position of the species, attached upside-down at an angle to the vertical axis of an alcyonarian; 1b, sagittal view of the shell of *P. colymbus* parallel to the wing, which, in an experiment, deflected a dyed current around the region through which the exhalant water current flows, thus permitting a strong exhalant trajectory (Stanley, 1972).



FIG. 37. The extant pteriid *Pterelectroma zebra* (REEVE, 1857), which displays protective coloration that mimics the alcyonarians to which it attaches (Stanley, 1988).

ADAPTATIONS OF RECLINERS

A recliner, as defined here, is a form that rests on the seafloor without attachment or potential for locomotion (this definition differs from that of SEILACHER [1984], who included byssally attached forms that rest on soft sediment). Most recliners have been pleurothetic (resting on one valve), but a few have been orthothetic (living with the plane of commissure vertical).

In the modern ocean there are few reclining bivalve species, almost certainly because such animals are highly vulnerable to modern predators. LABARBERA (1981) reported that fiberglass polyester models of large Mesozoic coiled oysters placed as artificial recliners in modern-day intertidal settings were set upon by voracious crabs, apparently stimulated by no more than their appearance. Early in their initial Mesozoic radiation, crabs presumably made less severe attacks on coiled oysters. In fact, reclining ostreids were well represented in the Mesozoic, the most conspicuous being *Gryphaea* LAMARCK, 1801, and *Exogyra* SAY, 1820.

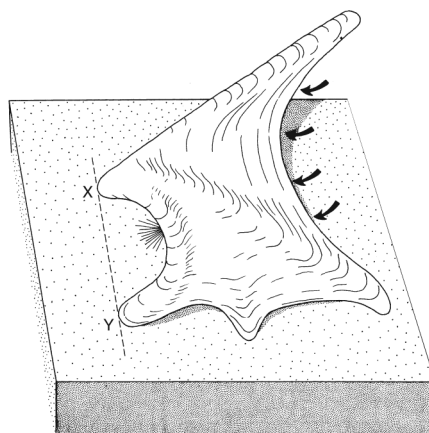


FIG. 38. The Early Cretaceous isogonomid *Mulletia mulleti* (DESHAYES in LEYMERIE, 1842) in life position, illustrating the role of the byssal sinus in stabilizing an epibyssate animal positioned with its sagittal plane at an angle to the substratum by providing the shell with two points of contact (x, y) with the substratum beyond the site of byssal attachment; heavy arrows indicate the direction of a potentially overturning current, $\times 0.25$ (Stanley, 1972).

As noted earlier, bivalves that occupy fine-grained sediment face the potential problem of being denser than the medium they occupy (STANLEY, 1970; THAYER, 1975). This problem is especially acute for large species and species occupying muddy sediments that contain considerable pore water and low-density organic matter. Evolution provided Mesozoic coiled oysters with a solution to this problem for some habitats. Their shells, which in some cases grew quite large, contained chalky layers, vesicular layers, and/or chambers which reduced their density. Their density was further reduced by a mineralogical shift from aragonite to calcite in the middle and inner shell layers (CARTER, 1980, 1990; CHINZEI, 1995); calcite is about 15% more buoyant than aragonite (CARTER, 1980).

Maintenance of a stable life position represents a special problem for reclining bivalves. During the Jurassic in Europe, *Gryphaea* evolved greater breadth and a flatter shape, thus gaining greater stability (HALLAM, 1968). Some modern forms of

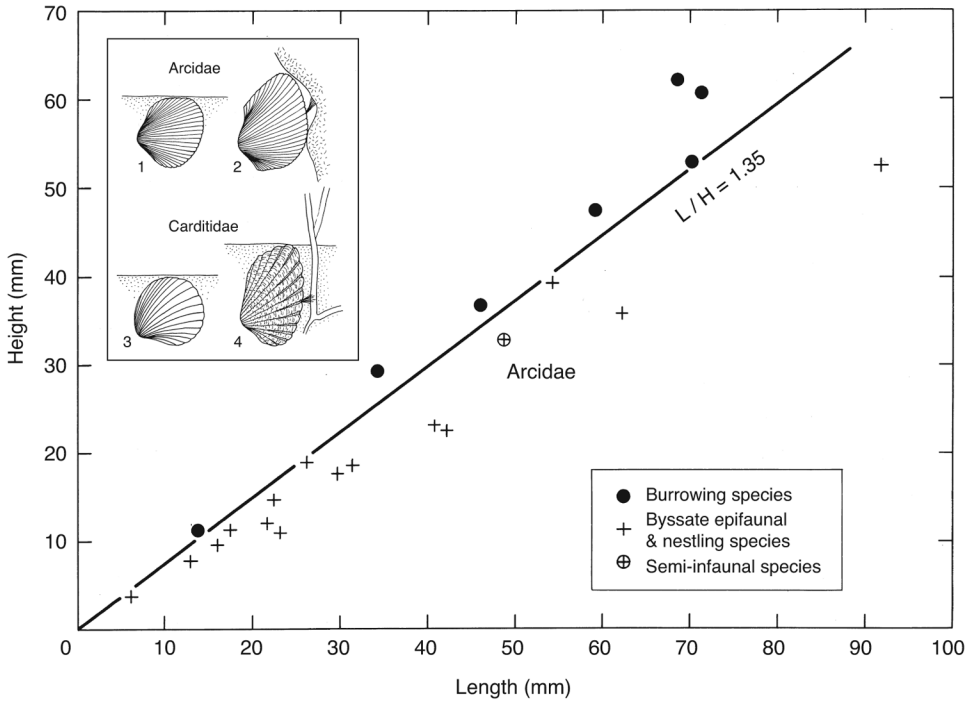


FIG. 39. A plot showing that byssally attached arcids are more elongate than burrowing arcids; inset: the epibyssate arcid *Anadara antiquata* (LINNAEUS, 1758) (2) is more elongate than the burrowing arcid *Lunarca ovalis* (BRUGUIÈRE, 1789 in BRUGUIÈRE, DESHAYES, & HWASS, 1789–1832) (1), and the endobyssate carditid *Carditamera floridana* (CONRAD, 1838 in 1838–1861) (4) is more elongate than the burrowing carditid *Cyclocardia borealis* (CONRAD, 1832 in 1831–1833) (3) (Stanley, 1970).

Ostrea LINNAEUS, 1758 that become recliners following juvenile cementation are also broad and relatively flat. There also existed elongate, relatively flat Mesozoic oysters, some of which possessed flangelike structures that projected laterally to prevent overturn; these are what SEILACHER (1984) termed outrigger recliners. A few similar ostreids persisted into the Plio-Pleistocene (Fig. 40).

For an elongate recliner, the evolution of a lunate shape provides stability (SEILACHER, 1984), reducing the likelihood of being overturned or rolled helplessly along the sea floor. The most notable forms of this type are *Agerostrea* and *Arctostrea*, which were Cretaceous lophinin oysters with zigzag commissures.

Another important function of the lunate shape is that it serves to enhance the strength of the exhalant current. First, it concen-

trates the current in a narrow area so that its velocity is increased. Second, the lunate shape provides shelter for the current so as to keep external water movements from diverting it back into the inhalant region.

Arcinella SCHUMACHER, 1817 (Fig. 41) is a globose extant chamid that reclines in seagrass beds with its commissure vertical. It is covered with spines that must reduce rolling under the influence of strong water movements but that certainly also obstruct some kinds of predators.

Two Eastern Pacific spondylids, the large *Spondylus ursipes* BERRY, 1959 (width approximately 10 cm) and even larger *Spondylus calcifer* CARPENTER, 1855–1857 (width ~15 cm) recline with the commissure horizontal; they probably ward off predators by virtue of their thick shells and, in the case of the latter species, marginal spines. At some

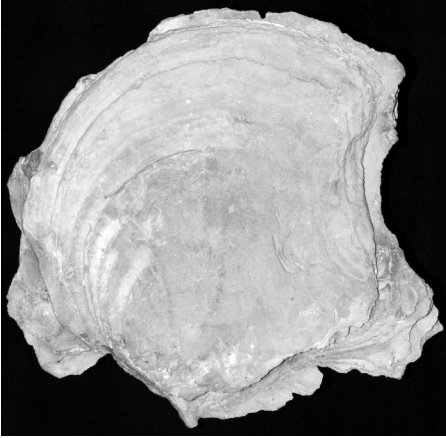


FIG. 40. The Pliocene reclining oyster *Ostrea compressirostra* MORTON, 1834, for which flangelike projections of its lower (left) valve reduce the likelihood of overturning, $\times 0.6$ (new).

point in their growth, these species must experience an escape in size from predators.

When the Pliocene scallop *Fortipecten takahashii* (YOKOYAMA, 1930) grew to 7–10 cm and clearly ceased to swim, not only did its shell thicken markedly, presumably to thwart predators, but its growth eliminated its dorsal gapes; in addition, the lower valve became much more obese, apparently improving the animal's adaptation to an *Exogyra*-like, reclining mode of life (HAYAMI & HOSODA, 1988).

ADAPTATIONS FOR EPIFAUNAL MOBILITY

I have already noted that burrowing trioniids and cardiids are burrowers that can jump if dislodged; so are solenids. As discussed above, the dentitions of trioniids and cardiids provide for alignment of the valves at the large angles of gape required by the large foot that permits these forms to burrow relatively rapidly and also to leap.

The only free-living epifaunal bivalves that can swim are members of the Pectinoidea. *Chlamys* RÖDING, 1798, and some of its relatives, and also limids, are habitual nestlers that can swim awkwardly if disturbed. At



FIG. 41. 1, *Arcinella cornuta* CONRAD, 1866, representing an unusual chamid genus that lives as a recliner in the modern ocean; 1a, oblique anterior view, displaying the portion of the animal that rests on the substratum: the broad anterior, which provides a base, and the spines that help to anchor the animal; 2a, slightly oblique left lateral view, revealing other spines that must thwart predators, $\times 0.9$ (new).

least some solemyids, solenids, and a few cardiids, though habitual burrowers, can swim (STANLEY, 1970, 1977a). All of these taxa with the ability to swim are relatively thin-shelled, a condition that reduces their negative buoyancy. Long ago, VERRILL (1897) noted that the plicated morphology of many pectinoidean shells provides strength that compensates for shell thinness.

Free-living pectinids have obviously evolved more adept swimming behavior than attached, nestling pectinids because they are in greater danger from predators. Pectinoideans that are free living as adults

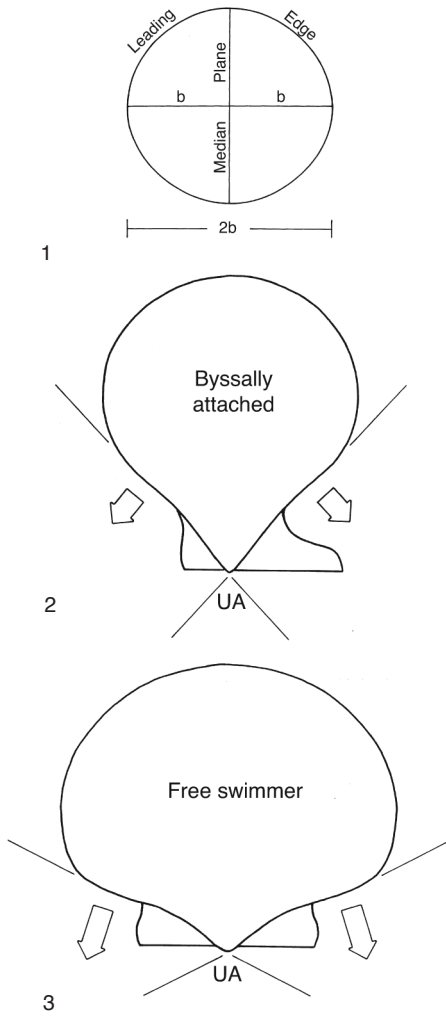


FIG. 42. Morphologic features of free-living pectinids (3) that make them better swimmers than species that are normally attached as adults (2); the large umbonal angle (UA) of free-living forms results in the expulsion of water in a nearly backward direction, and lift is increased by the large aspect ratio of their shell: $2b^2/S$, where b is half the width of the shell perpendicular to the direction of movement (1) and S is the area of the area of the shell in plan view (Stanley, 1970).

are byssally attached as juveniles, and the latter are similar in form to species that are byssally attached as adults. Free-living adults typically have only a small, residual byssal notch; more or less symmetrical valves, including anterior and posterior auricles that are nearly equal in length, a relatively large

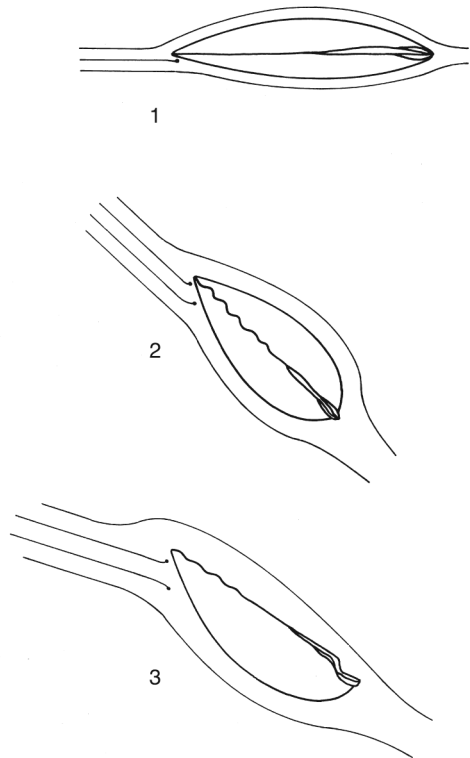


FIG. 43. Swimming orientations and airfoil-like behavior of pectinids; 1, lateral view of the airfoil-like cross-sectional shape of *Placopecten* VERRILL, 1897, which provides lift during horizontal swimming; 2-3, biconvex and planoconvex forms, which gain lift by elevating their ventral regions via downward expulsion of water (Stanley, 1970).

umbonal angle (Fig. 34), and anterior and posterior dorsal gapes for water expulsion.

The value of the approximately symmetrical valves of free-living pectinoideans for swimming by jet propulsion is obvious, because these forms swim in a direction perpendicular to the hinge. Swimming is accomplished by clapping the valves to squirt water from the mantle cavity through the dorsal gapes. The sites of water expulsion account for the typically wide umbonal angle of free-living pectinoideans: water is expelled more directly backward than if the angle were narrower (Fig. 42) (STANLEY, 1970). The relatively narrow umbonal angle of pectinoideans that are byssally attached as adults, although impairing their swimming as noted

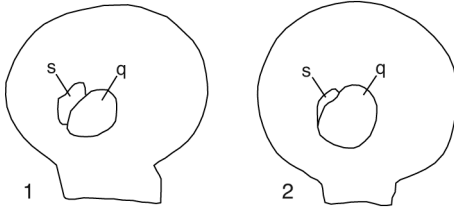


FIG. 44. Relative sizes of the quick and slow portions of the adductor muscle of the swimming pectinid *Amusium balloti* BERNARDI, 1861 (1) and the nonswimming pectinid *Chesapeecten jeffersonius* (SAY, 1824) (2) (Gould, 1971).

above, enhances their ability to attach firmly to the substratum. The special structure of the pectinoidean ligament that provides for rapid clapping of the valves during swimming (TRUEMAN, 1953) was noted earlier.

Pectinoidean valves function like airfoils during swimming; here the wide umbonal angle comes into play, increasing the aspect ratio of the shell: the ratio between the square of the shell width perpendicular to the direction of movement and the area of the shell (Fig. 42). The relatively large aspect ratio of many free-living pectinoideans increases the lift-to-drag ratio (STANLEY, 1970).

Placopecten VERRILL, 1897, a large, discoid scallop, is a particularly adept swimmer. It can make underwater flights of several meters, swimming more or less horizontally after an upward launch. Its cross section is like that of an airplane wing, with the lower valve less convex than the upper valve (Fig. 43.1). The result, in keeping with the Bernoulli

Principle, is lower pressure on the upper valve than on the lower valve, where water follows a shorter path in its movement relative to the shell surface (STANLEY, 1970). *Placopecten* ejects water on both sides of the hinge simultaneously, and the lift provided by its shape is visible to an observer: the shell rises slightly through the water following each ejection and then glides back downward over a greater distance, tracing out a broadly curved path before the next ejection. *Placopecten* benefits in its swimming from having a shell that is not only thin (light weight), but smooth (STANLEY, 1970; GOULD, 1971; HAYAMI, 1991). Its nearly entirely calcitic mineralogy also increases its buoyancy relative to entirely aragonitic shells (CARTER, 1980, 1990).

Many pectinoideans that lack airfoil-shaped cross sections have relatively inflated shells as well. These forms typically undertake short "flights" diagonally upward, at angles as high as 45° from the seafloor. Most of them squirt water alternately from their left and right shell gapes. The result is that they rotate back and forth during their translational movement. They gain lift by employing an angle of attack: by elevating the leading edge of the shell so that the plane of commissure is at an angle to the direction of movement (STANLEY, 1970; HAYAMI, 1991) (Fig. 43.1–2). By causing water to flow in an arcuate path over the upper valve, the angle of attack has the same effect as an airfoil-like shape, although

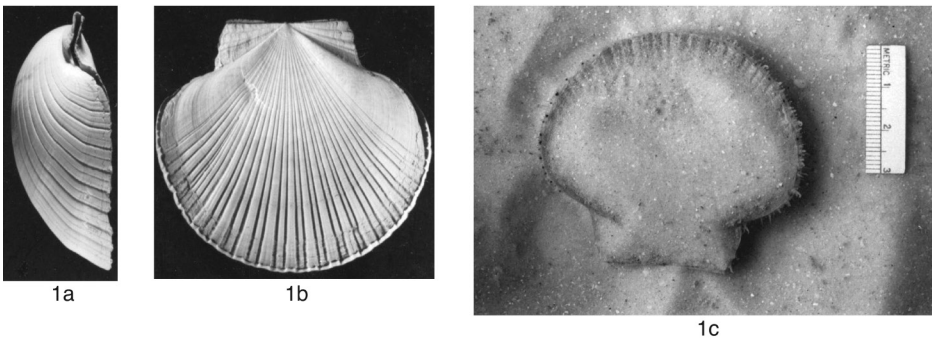


FIG. 45. *Euvola ziczac* (LINNAEUS, 1758); 1a, anterior view; 1b, left valve; 1c, in the act of burying itself and with the concave upper valve almost entirely covered with sand (Stanley, 1970).

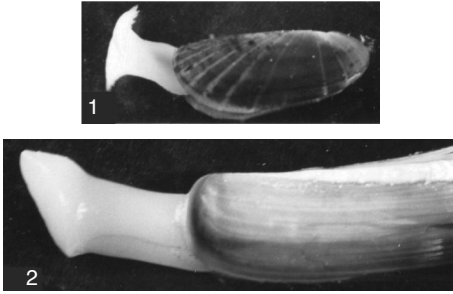


FIG. 46. Cylindrical feet of cylindrical burrowers that swim by jet propulsion; 1, the solemyid *Solemya velum* SAY, 1822, $\times 2$; 2, the solenid *Ensis directus* (CONRAD, 1843), $\times 1.7$ (Stanley, 1970).

the lift-to-drag ratio is relatively low. In addition to strengthening thin shells, the plications of many of these forms probably act like the dimples on a golf ball, reducing pressure drag as the shell rotates back and forth by creating a turbulent boundary layer that results in a low-pressure wake. Short, irregular “flights” serve to separate these forms from relatively slow-moving predators.

In *Amussium* RÖDING, 1798, the lower valve is not less convex than the upper valve, but HAYAMI (1991) showed that even this and other smooth-shelled swimming pectinoideans employ a small angle of attack. He found experimentally that the lift coefficient increases almost linearly with the angle of attack until stalling occurs.

The adductor muscle of a pectinoidean, like other bivalve adductors, is actually two conjoined muscles, the quick muscle, which claps the valves together for swimming, and the slow or “catch” muscle, which holds them shut. Not surprisingly, the quick muscle is larger relative to shell size in swimming scallops than in adult scallops that swim little or not at all (GOULD, 1971). The slow muscle, on the other hand, is larger relative to shell size in nonswimmers, presumably because sedentary habits occasionally necessitate long intervals of tight closure for resistance to tugging starfish or other attackers (Fig. 44).

The quick muscle of swimming pectinoideans passes obliquely between the two valves, causing the valves to shut more quickly for a

given rate of muscle contraction than if the muscle ran straight across (THAYER, 1972). Muscle scar positions on fossils can reveal this condition in extinct species.

The mode of life of concavo-convex pectinoideans is difficult to assign to a particular life habit group, but I will treat this group as mobile epifauna because its members can swim. The issue is that they spend nearly all of their time with their shell almost entirely buried and therefore might be classified as infaunal animals. *Euvola ziczac* (LINNAEUS, 1758) is an example (STANLEY, 1970). If placed on sand, its natural substratum, it claps its valves together, blowing away sand around its margin. Sand spreads away from the shell down the slope thus created, some of it sliding out from beneath the animal, which sinks progressively into the depression that forms beneath it. The concave upper valve of the animal serves a special function: it collects some of the sand blown out by the clapping movements (Fig. 45), and by the time the margin of the plane of commissure is level with the substratum, the upper valve is covered with sand. Presumably, the tentacles at the mantle margin sense the animal’s position at this point, and the valves cease to clap. The animal is then barely visible, but if disturbed, can respond by swimming a short distance. *Pecten maximus* LINNAEUS, 1758, which also has a concave upper valve, has an entirely different way of burying itself (BAIRD, 1958). It ejects water repeatedly from its posterior dorsal gape, directing the jet with its mantle margins. As a hollow excavation forms in the sand, the animal’s anterior tilts progressively upward. Then, when the excavation is of adequate size (presumably as gauged by mantle tentacles), the animal emits an especially large squirt of water that elevates and rotates it. Quite remarkably, it then lands in the excavation. Within a few days, the upper valve accumulates a thin later of protective sand.

Paleozoic stophomenid brachiopods characterized by concave-up upper valves may have lived in a similar way to the *Pecten* species just described, but they lacked the spring-loaded hinge of pectinoideans. They

Deep burrowing in firm, stable substrata

Elongate and tubular:
to minimize siphon length

Siphonal and pedal gapes:
for extrusion of siphons and foot with little danger from predators

Valves thin:
metabolically economical and permitted by a deep life position

Loss of hinge teeth:
for rocking of shell about a dorsoventral axis for extension and contraction of siphons and foot

Shallow burrowing in stable substrata

Posterior elongate:
to minimize siphon length

Center of gravity near anterior:
for stability

Valves thick:
for stability

Rapid burrowing in shifting sand

Anterior triangular:
for easy penetration

Exterior smooth:
to reduce friction during burrowing in the absence of ornamentation that facilitates burrowing

Rapid burrowing in swash zone of sandy beaches

Anterior elongate:
to accommodate large foot

Posterior truncate:
to provide maximum gape at tip of shell for pedal extrusion

Shell compressed, with maximum width near posterior:
to reduce resistance to burrowing

Valves thick (*Spisula*):
for stability

Shallow burrowing in soft, muddy substrata

Small:
to reduce surface/weight ratio for flotation

Valves thin (*Mulinia*):
for flotation

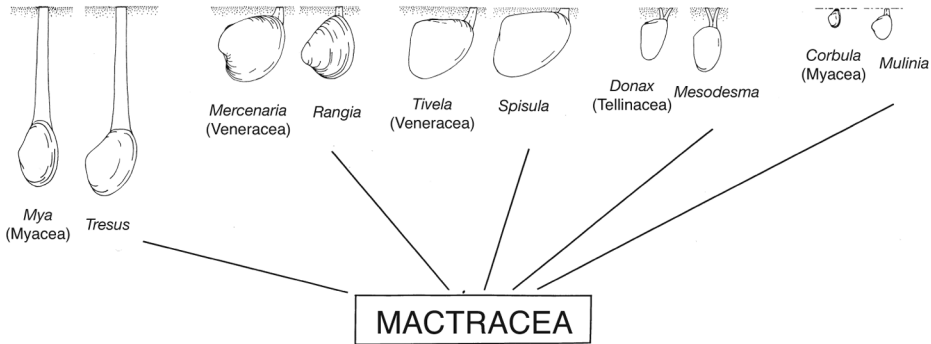


FIG. 47. Adaptive divergence of the Mactroidea and convergence with other taxa (Stanley, 1970).

would not have been as adept at covering themselves with sand, and presumably could not swim, although they may have been able to right themselves when overturned.

Some limids can swim via jet propulsion produced by clapping of their valves, but their plane of commissure remains vertical, their shell provides virtually no lift, and their movements are quite awkward. Also detracting from their swimming ability in comparison to pectinoideans are their relatively thick shells. The cardiid *Laevicardium serratum* (LINNAEUS, 1758) is not only an adept jumper, but this “egg shell cockle,” whose thin shell (see p. 24) enhances its locomotory powers, can also swim short distances with its plane of commissure vertical. It claps its valves for jet propulsion. This is augmented by a rapid kicking of the foot, which thus acts as a kind of oar (STANLEY, 1970).

Solemyids and solenids have independently evolved roughly cylindrical shells and an ability to swim by jet propulsion. For each thrust forward, these forms quickly adduct their valves and withdraw their plungerlike foot (Fig. 46) to expel water posteriorly. Their elongate shape results in the expulsion of a narrow jet of water at high velocity and also stabilizes the animal’s movement parallel to the long axis of the shell.

CONVERGENCE AND THE ADAPTIVE NATURE OF SHELL FORM

The remarkable evolutionary convergence between certain pholadid and petriolid borers has already been noted (Fig. 25). In the course of their diversification, the Mactroidea have converged in general morphology with a variety of other taxa (Fig.

47). Not only can arguments be made for the adaptive nature of the various morphologies here, but the convergences in form and mode of life also constitute an additional kind of powerful evidence for the fundamentally adaptive nature of bivalve shell morphology.

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