Abstract

Study of 95 Western Atlantic bivalve mollusk species representing 29 families has demonstrated that morphologic features of the bivalve shell other than hinge type and microstructure primarily reflect life habits and habitat preferences. Many morphologic features represent potentially powerful tools for paleoecologic and evolutionary interpretation.

Byssally attached groups living with the sagittal plane vertical are characterized by elongation and flattening of the ventral margin. Non-burrowing, byssally attached arcids and carditids, for example, are more elongate than closely related burrowing species. Epifaunal mytilids can be distinguished from related infaunal and semi-infaunal species by cross-sectional shape, degree of anterior reduction, and configuration of the byssal musculature and sinus. Tridacnids show special adaptations for exposure of algae-infested siphonal tissue to sunlight.

Byssally attached groups living with the sagittal plane non-vertical are characteristically inequivalve, with the lower valve flattened for maximum substratum contact. Pectinids and pteriids utilize a special auricle-sinus configuration for firm byssal anchorage. The posterior "wing" of many pteriids apparently shelters the exhalent current to increase its discharge distance.

Epifaunal groups attached by cementation are commonly thick-shelled. The spines of certain cemented groups apparently serve a defensive function.

Many reclining taxa employ a thick shell and a flattened upper valve for stability. The lower valve is commonly convex, if partly buried in life position, and nearly flat, if lying at the substratum surface.

Most swimming species have thin shells. Pectinids with a free-living adult stage differ from those with a byssally attached adult stage in their high degree of auricle symmetry and large umbonal

angle. Their shape is adapted for improved swimming ability; it serves to increase the forward component of propulsive forces, the volume of water expelled, and the aspect ratio of the shell.

For most burrowers in soft substrata, approximate burrowing orientation can be determined from simple geometric relationships. Angle of rocking movement and direction of substratum penetration show a general relationship to degree of shell elongation. Nearly all rapid burrowers are either (1) inhabitants of shifting sand substrata or (2) migratory deposit feeders. Most rapid burrowers have become streamlined by developing shells that are crudely disc-like, blade-like, or cylindrical, rather than spheroidal. Elongate and pointed shell anteriors among burrowing species often coincide with rapid-burrowing habits. Strongly ornamented and thick valves are employed primarily by sluggish shallow burrowers for stability near the sediment-water interface; radial, divaricate, and oblique ornamentation also aid certain species in burrowing. Life orientation of burrowers living with the sagittal plane vertical is often reflected by features of the siphonal region and lateral-view outline. A non-vertical life position is usually associated with an inequivalve condition; in many tellinids, these two features are adaptations for siphonate deposit feeding. Most infaunal species that characteristically inhabit substrata with a mud fraction exceeding 25 percent are small, and many are thin-shelled, for flotation. Tube dwellers and deep burrowing groups with large siphons tend to have distinctive shell forms and are generally confined to cohesive substrata of fine-grained or slightly muddy sand.

Most groups that bore into hard substrata are similar in gross form to *Mya*-like deep burrowers with large siphons, but many possess special shell ornamentation for substratum abrasion. Species that nestle in pre-existing cavities in hard substrata tend to have irregular shell shapes.

Evolutionary divergence, convergence, and homeomorphy support functional interpretations and provide strong arguments for the adaptive nature of shell form in the Bivalvia. Divergent representatives of the Mactracea, for example, show remarkable convergence in form and habit with species belonging to other superfamilies.

Introduction

This study examines the relationships between shell form and life habits in the class Bivalvia (Pelecypoda). Although dealing almost exclusively with living species, it has been undertaken chiefly for application to paleontologic studies of extinct taxa. The phrases "life habits" and "mode of life" will be used synonymously here to represent the essential behavioral attributes of bivalves related to their external requirements for living space, sustenance, and survival. Reproductive activities will not be considered.

It became evident at the outset of this study that the existing literature on bivalve life habits and habitats was too meager to provide a basis for large-scale functional morphologic interpretation. Standardized observations were needed for a variety of species. A program was therefore undertaken to obtain the required ecologic and behavioral information. For convenience, the common Western Atlantic bivalve species were chosen for study, as a sample of the world fauna. Most field and laboratory studies were carried out in three geographic areas: Cape Cod, Massachusetts; southern and western Florida; and southwestern Puerto Rico. Since completing the basic investigation, I have confirmed and extended certain observations through investigations in Bermuda. The region encompassing the study areas extends from the cold-temperate realm to the tropics. The 95 species studied belong to 65 genera, 29 families, and 17 superfamilies, as classified here, and represent a good taxonomic sample of the living shallow-water bivalve taxa of the world.

APPROACHES TO THE STUDY OF FUNCTIONAL MORPHOLOGY

Most previous studies of the functional morphology of invertebrate skeletons have concerned fossil species. Many have been consciously or unconsciously patterned after the philosophic scheme recommended by Rudwick (1964b). Rudwick stresses the fundamental role of mechanical analysis in all functional morphologic interpretation and asserts that the traditional division of functional morphology into inference by "homology" and inference by "analogy" with living forms is philosophically invalid. He believes that both of these allegedly separate methods are ultimately rooted in mechanical analysis. Rudwick's suggested methodology requires first that a function be postulated for a problematical fossil structure. Next, a mechanical model is formulated in such a way as to best serve the postulated function (within the bounds dictated by the materials available to the organism). Rudwick terms this conceptual model a "paradigm." The problematical fossil structure is then tested against the paradigm for morphological similarity, and the likelihood that the postulated function is the true function is thereby assessed.

I would agree with Rudwick that functional inference by analogy ultimately amounts to mechanical analysis. Such is not always the case for inference by homology, however; in this process, the function of a fossil structure is interpreted by its supposed homologous relationship to a very similar structure belonging to a closely related living group. The function of the structure in the living group is sometimes directly observable, obviating the need for mechanical analysis. Interpretation here does not involve direct evaluation of the function itself, but evaluation of the likelihood of homology with the living structure whose function is known. Perhaps Rudwick would exclude this approach from the scope of functional morphology, but it is nonetheless a valid means of interpreting the function of a fossil character.

There is still another approach to functional morphology which is the principal one used in this study. This approach can be undertaken directly only through study of Recent species. Hypothetical functions are proposed for a problematical structure, just as in Rudwick's method. Life habit and habitat data are then gathered for species possessing the structure. These data, in conjunction with mechanical considerations, provide critical tests for evaluation of the working hypotheses. Usually one hypothesis emerges as the most reasonable, the others being inconsistent with the life habit and habitat data. For many fossil groups, the possibility of taking this Recent approach has been eliminated or greatly reduced by extinction. The Bivalvia, however, are unusually well-represented in modern seas. Table 1 lists percentages of fossil bivalve taxa living today. Most major fossil taxa are represented by living species. Furthermore, many extinct taxa are similar in shell form to living taxa, so that most morphologic features of fossil taxa can be found among living groups.

In any study of functional morphology, it is important to recognize the existence of what might be called "multiple-effect

TABLE 1. PERCENTAGES OF MARINE FOSSIL BIVALVE TAXA LIVING TODAY

Geologic Era	Percentage of Super Families Extant	Percentage of Families Extant	Percentage of Genera Extant
Cenozoic	100	97	71
Mesozoic	88	63	33
Paleozoic	88	32	1
Total	88	56	37

(*after* Stanley, 1968)

factors." First, a single gene commonly affects more than one morphologic character (pleiotropy). Second, a single morphologic character is commonly affected by more than one gene. And third, a single morphologic character is commonly related to more than one aspect of an animal's mode of life. As an illustration of the third type of multiple-effect factor, consider the potential usefulness of long, radially arranged external spines to a sand-burrowing bivalve species in providing stability, but the deleterious effect of such spines in slowing burrowing movements and limiting mobility. In fact, only relatively short, less effective spines are employed by burrowing bivalves for increasing stability. The existence of multiple-effect factors makes compromises necessary in evolution. Thus, the correct paradigm in Rudwick's approach may not represent the best possible design for solution of a single problem but the best compromise solution that could evolve from selection pressure in two or more directions.

METHODS

Life habits and habitats of the 95 Western Atlantic species studied in this investigation are discussed in the final section. Live animals were collected in intertidal and shallow subtidal settings by hand and with screen and shovel. In water deeper than about 1 m, specimens were hand-collected by SCUBA diving and dredged from shipboard. Wherever possible, sediment samples were taken at the collection sites of soft-substratum dwellers. As many life habit observations as possible were made in nature, but most species, especially burrowers, were transferred to laboratory aquaria for detailed study. Laboratory techniques used for study of life habits are discussed in detail in the final section. Burrowing, jumping, and swimming movements at or above the sediment-water interface were observed directly. Times required for burrowing were measured for nearly all burrowing species. Many aspects of animal behavior at and above the sediment-water interface were recorded in photographs. Movements within the sediment and life positions of buried species were studied by X-radiography of animals permitted to burrow in narrow, thin-walled aquaria. Photographs and X-radiographs accompany the life habit descriptions given in the final section.

Most bivalve species show tolerance for more than a single type of habitat and exhibit some variation in mode of life. An attempt was made to establish the normal ecologic requirements and behavioral traits for each species studied. Exceptional individuals or populations commonly demonstrate the ecologic flexibility of a species, but the habits and habitats found to be typical for the species are taken to be those for which its morphology is primarily adapted.

In relating shell form to life habits and habitats, certain morphologic features have been emphasized in this study. In the course of bivalve evolution, certain conservative shell features, such as hinge type and shell microstructure, have tended to remain constant within major lineages. These characters represent useful criteria for classification of the Bivalvia in accordance with their evolutionary relationships. Other shell characters have been quite plastic in the course of evolution, altering readily with life habit changes in minor lineages. Because of their adaptive plasticity, these characters represent good ecologic indices. The most important appear to be *gross shell shape, shell thickness,* and *shell ornamentation.* A description of shell morphology, emphasizing these characters and including measurements, where applicable, accompanies the life habit and habitat data for each species in the final section. Each description is supplemented with shell photographs presented alongside those illustrating life habits (Pls. 1-39).

Bivalve Life Habits and Habitats

LIFE HABIT CLASSIFICATION

Virtually all bivalves are aquatic bottom-dwellers. Their life habits, as defined here, fall within three major categories: life position, mode of locomotion or attachment, and feeding type.

Life Position

Any classification of bivalve life habits must be somewhat arbitrary and artificial because of intergradations among categories. For gross classification according to life position, the common division of marine benthos into *epifauna* and *infauna* can be profitably adopted, but some groups, such as certain species of mytilids and pinnids, fall within an intermediate category. The term *semi-infaunal* will be applied to these intermediate groups that live partly buried in the substratum. Animals living between or on the undersides of rocks and coral colonies are regarded here as being epifaunal unless housed within discrete cavities. More detailed discussions of epifaunal, semi-infaunal, and infaunal life positions are presented in subsequent sections.

Mode of Locomotion or Attachment

In discussing locomotion and attachment of bivalves, the nature of the substratum must be considered. The most clear-cut substratum division is between a soft, or fluid, substratum and a hard, or solid, one. A more detailed soft substratum classification will be introduced later for discussion of the adaptations of burrowing species to particular sedimentary regimes. Classification according to mode of locomotion or attachment is very useful for dividing bivalves into meaningful ecologic groups. Seven major categories are recognized here:

Byssally attached. Employing a byssal apparatus for fixation to the substratum, and normally lacking the capacity for pedal burrowing.

Cemented. Attached by secreted shell material to a hard substratum.

Reclining. Occupying a position on or partially buried in a soft substratum and lacking the capacity for attachment.

Swimming. Moving freely through the water by self-propulsion.

Burrowing. Penetrating a soft substratum by means of pedal locomotion and maintaining a life position of at least partial burial.

Boring. Occupying a permanent or semi-permanent, self-made cavity in a hard substratum.

Nestling. Living within a pre-existing cavity in a hard substratum, and lacking the ability to excavate such a cavity.

These 7 life habit groups are defined in order to be as nearly mutually exclusive as possible, but overlapping relationships occur, especially for the "byssally attached" category. Some burrowing species (especially arcids) employ a weak byssus for increased stability in soft substrata, but because their primary adaptations are for burrowing, such species are excluded from the "byssally attached" category. Many byssally attached species (for example, *Isognomon* and *Barbatia* spp.) characteristically live wedged in among coral colonies or rocks like unattached nestlers, such as *Petricola carditoides* (Yonge, 1958). Additional problems arise because certain species characteristically employ two of the listed locomotion-attachment methods as normal alternate activities. For example, many animals that have the ability to swim spend most of their lives reclining on the bottom (many pectinids), attached by a byssus (other pectinids and limids), or living in burrows (*Solemya* and *Ensis*). Representatives of other species may employ either one of two habits throughout life. For example, *Petricola pholadiformis* normally lives as a borer in hard substrata, but some individuals of the species live as burrowers in soft sediment. Several species of pholadaceans may also occupy either hard or soft substrata.

Assignment of certain taxa to locomotion-attachment groups must be somewhat arbitrary, but the majority of species clearly belong to one of the 7 categories listed above.

Feeding Mechanism

Two basic food-gathering methods are employed by shallow-water bivalve species: *suspension feeding* and *deposit feeding.* The huge majority of bivalve species (including all epifaunal forms and hard substratum dwellers) are suspension feeders.

Deposit feeders are restricted to the "burrowing" locomotion-attachment category and belong to only two superfamilies, the Nuculacea and the Tellinacea. Previous suggestions by various authors that the Solemyacea and two families of the Tellinacea (the Donacidae and Sanguinolariidae) are deposit-feeding groups are rejected in this study, on the basis of life habit observations described in the final section. Nuculacean deposit feeders collect food particles from sediment with appendages of the labial palps called proboscides (Yonge, 1939); the two shallow-water families feeding in this way are the Nuculidae and Nuculanidae. Deposit-feeding tellinaceans belong to the Semelidae and Tellinidae; they make use of a specialized, vermiform inhalent siphon for sucking in detritus along the sediment-water interface. Stasek (1965) has suggested that nuculanids obtain a portion of their food by suspension feeding. It is apparent from observations made in the present study that many tellinids make use of both suspension feeding and deposit feeding. It appears that degree of reliance on deposit feeding may vary among members of the shallow-water families in which it is employed.

Taxonomic Abundance of Life Habit Groups

The numerical distribution of most marine bivalve genera among the basic life habit categories recognized here is presented in Table 2. The genera included are all of those listed by Thiele (1935) for which habits are known or could be inferred from personal observation or literature references. They represent nearly 85 percent of Thiele's marine genera, excluding the minute Erycinacea, which are largely symbiotic and cannot be classified within the scheme employed here. (Symbiotic relations of the Erycinacea have been thoroughly reviewed by Boss, 1965.) The majority of bivalve genera are infaunal burrowers. Byssally attached genera rank second, and borers, third. Nestlers, cemented forms, and swimmers follow; recliners are least common. As might be expected, the most highly diversified of the 7 locomotion-attachment groups, in terms of life position and substratum type, is the byssally attached group.

Because they are incomplete and based on a single, outdated classification, *absolute* figures for categories are not strictly meaningful. They do, however, give a reasonably accurate indication of the *relative* abundance of various life habit groups.

ENVIRONMENTAL FACTORS

Salinity and temperature are important limiting factors in bivalve distribution, but appear to have little influence on life habits. Thorson

TABLE 2. DISTRIBUTION OF MARINE BIVALVE GENERA AMONG MAJOR LIFE HABIT CATEGORIES

		Method of Attachment or Locomotion	General Life Position		
			Epifaunal	Semi-Infaunal	Infaunal
Substratum Type	Soft Substrata	Reclining	1	1	• •
		Burrowing	• •	(1)	166(3)
		Byssally Attached	21(4)	3(1)	(3)
	Hard Substrata	Boring	• •	• •	17(1)
		Nestling	• •	• •	7
		Cemented	5	• •	• •
		Swimming	3(2)	• •	• •

Parentheses indicate partial representation.

(1957, p. 463) has made the following generalization for marine benthos: "Increase in numbers of species toward the tropics is very pronounced in epifaunas, while the number of infauna species seems to be roughly the same in Arctic as in temperate or tropical seas."

Many difficulties hamper attempts to meaningfully compare bivalve species diversity at different latitudes. Most of these result from regional climatic anomalies and from differences in sizes of areas studied, depths of bottoms sampled, and intensity of collecting. Nevertheless, a pronounced general increase in bivalve diversity from high latitudes toward the equator is readily apparent. In documenting this increase, Stehli and others (1967) have shown that faunal lists for "particular geographic areas" at 70° to 80° N. lat. tend to contain a maximum of about 50 species, whereas the species total exceeds 500 for some equatorial areas of comparable size.

Ockelman's comprehensive study of the predominantly Arctic bivalve fauna of East Greenland (Ockelman, 1958) is especially useful for considering possible correlation between infaunal-epifaunal percentages and latitude. Ockelman's study is based on collections from numerous stations, most of which were made along a stretch of coastline exceeding 1200 miles in length, and he describes his study collection as "one of the largest ever brought home to a museum from arctic regions." Of 55 East Greenland species, Ockelman states that

74 percent are infaunal and 26 percent are epifaunal. I am in general agreement with his life habit designations. For comparison with Ockelman's percentages, in Table 3, I have estimated similar percentages from faunal lists for non-arctic Atlantic regions (a semi-infaunal species is counted as one-half an infaunal species and one-half an epifaunal species). The anomalously high total species diversity in waters surrounding the British Isles was noted by Stehli and others (1967) and attributed to the influence of the Gulf Stream.

In addition to the problems of measuring total regional diversity, calculated infaunal and epifaunal percentages are subject to minor errors and judgment biases. Still there is no question that both epifaunal and infaunal species diversity increase toward the equator. Thorson's generalization simply does not hold for bivalves. Approximately four times as many infaunal bivalve species are known from Puerto Rican waters alone as from the much more extensive stretch of East Greenland coastline included in Ockelman's study. The Tellinacea, Veneracea, and Lucinacea are the superfamilies that contribute most to this increase of infaunal species diversity toward the equator. The low epifaunal estimate (about 17 percent for the British Isles) suggests that there may, however, be a slight poleward decrease in *relative proportion* of epifaunal bivalve species. I have estimated approximately the same epifaunal percentage for the fauna of Cape Cod, Massachusetts, but from less complete species listings. Ockelman's conclusion that 26 percent of the East Greenland fauna is epifaunal would seem to contradict this idea, but his estimate is subject to especially large errors because of the low total species diversity of this fauna. At any rate, it can be stated that (1) infaunal species diversity increases markedly toward the tropics and (2)

TABLE 3. RELATIVE PROPORTIONS OF INFAUNAL AND EPIFAUNAL BIVALVE SPECIES IN MARINE FAUNAS AT VARIOUS LATITUDES IN THE WESTERN ATLANTIC

Locality	Faunal List	Number of Species	Infaunal Percentage	Epifaunal Percentage
East Greenland	Ockelman (1958)	55	74	26
British Isles	Tebble (1966)	184	83	17
Texas	Pulley (1952)	130	78	22
Southwest Florida	Perry (1940)	150	80	20
Puerto Rico and Virgin Islands	McLean (1951)	211	77	23
Puerto Rico and Virgin Islands	Warmke and Abbott (1961)	233	77	23

regional bivalve faunas consist of approximately 75 to 85 percent infaunal species and 15 to 25 percent epifaunal species, regardless of latitude.

The striking increase toward the equator of epifaunal species attaching by cementation (Nicol, 1967) will be discussed in this study under the heading "Adaptations for Cementation" (p. 33).

Whether they are suspension feeders or deposit feeders, virtually all shallow-water marine bivalve species are primary consumers in short food chains and feed chiefly on small, particulate plant material; except for their position as prey for certain carnivores, their occasional role in commensalism and parasitism and special adaptations to biologic substrata, bivalves are rarely involved in interdependent relationships with other marine animals. For this reason, it is reasonable in relating the life habits of bivalve species to specific aspects of the marine ecosystem to disregard most other nonpredatory elements of the macrofauna.

Predation, however, does influence bivalve life habits and represents an almost universal problem for shallow-water species. It can certainly be argued that the molluscan shell originated primarily as a protective device against predation, but the shell also serves as a supporting structure for muscular systems, and commonly, as a refuge against unfavorable aspects of the physical and chemical environment. Even in the absence of predation, animals like bivalves but lacking a shell could not live in the ways that bivalves live. Many fundamental activities of bivalves are at least partially concerned with survival against predation (for example, secretion of a strong byssus for attachment, and efficient burrowing to seek and maintain protection within the substratum). Carter (1968) has recently summarized the biological literature on bivalve predation and behavioral traits of bivalves concerned with avoiding it. He has also discussed certain morphologic features of the bivalve shell that he believes may represent protective adaptions against predation. I will discuss some of Carter's views in the chapters that follow, but should express at the outset my general conclusion that relatively little of the morphologic variation in the bivalve shell has evolved specifically for protection against predation.

Given the general need of bivalves to avoid predation and their fundamental adaptations serving this need, the most important environmental factors directly influencing *specific* bivalve life habits (and, hence, shell morphology) appear to be *food supply, substratum character,* and *water movement.* (Other minor factors, such as water depth, will be introduced later, where appropriate.)

The relationships of these environmental factors to each other and to bivalve life habits are summarized in Figure 1. Food avail-

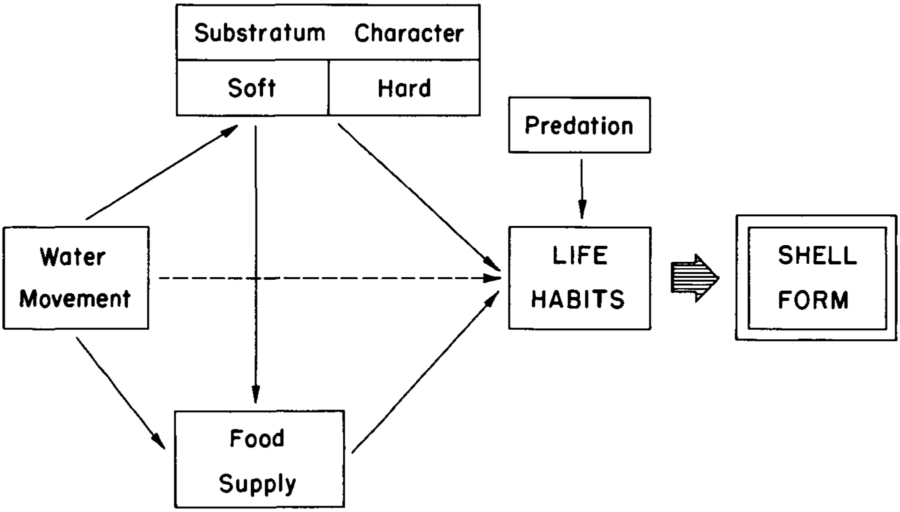


Figure 1. Interrelationships among environmental factors and bivalve life habits. Solid lines indicate major effects; dotted line, minor effect.

ability for both *suspension feeding* and *deposit feeding* is controlled primarily by substratum character and water movement. Deposit feeders are most abundant in fine-grained sediments in quiet water; suspension feeders are most abundant in coarse-grained sediments under more agitated conditions (Davis, 1925; Sanders, 1956) and on hard substrata. For soft bottoms, substratum character itself is primarily controlled by type and degree of water movement. Because of its effect on substratum character and food supply, water movement is ultimately the most important factor determining the distribution of bivalve life habits in soft-bottom, shallow-water habitats. On rocky shores and other hard bottoms, substratum character and water movement are commonly independent of one another and exert separate controls on life habits.

Bivalve Shell Morphology

GEOMETRY AND GROWTH

Much more has been written about bivalve shell geometry and its ontogenetic development than about the functional significance of resulting shell forms. A brief review of shell geometry will serve as a basis for some aspects of the discussion that follows.

The bivalve condition probably arose in the Mollusca through modification of an ancestral form possessing a single, flattened dorsal shell (as outlined by Yonge, 1953). The basic modification involved lateral compression and dorso-ventral elongation of the whole animal, which required folding of the original shell along its longitudinal axis so that the margins of the two shell halves met ventrally. The dorsal folding axis became decalcified to act as an elastic spring (the ligament) tending to open the valves by compression or extension. Anterior and posterior marginal embayments concentrated the ligament in the mid-dorsal region of the shell; through it passed the axis of valve movement. Adductor muscles developed, probably by cross-fusion of pre-existing pallial muscles, to operate against the ligament in closing the two valves.

The bivalve shell halves may be looked upon as a pair of coiled cones that grow by marginal accretion. The geometry of shell coiling has been analyzed by many workers, notably Huxley (1932), Thompson (1942), Lison (1949), Owen (1953), Stasek (1963), and Raup (1966). Long ago, Moseley (1838) proposed a logarithmic spiral model for shell coiling in bivalves and other groups. Thompson (1942) and many other workers have adopted this model, which derives its appeal both from supporting empirical evidence and from the fact that it permits shell growth without shape change (because a logarithmic spiral is equiangular). Natural exceptions to the logarithmic model are known, but the number and magnitude of such discrepancies have not been accurately evaluated. Stasek (1963, p. 216) states that "for those bivalves studied [to date] each spiral radius . . . *resembles* a logarithmic, equiangular spiral although it may not be mathematically precise."

Shape and growth of the logarithmic spiral have been analyzed for bivalves in several ways. Most workers speak of the apertural shape of the spiral (that is, the commissure line) as the *generating curve*. Owen (1953, p. 57) defines the *normal axis* as the sector of the valve that exhibits the greatest concavity. He states that the form of a single valve "should be considered with reference to (a) the outline of the generating curve; (b) the spiral angle of the normal axis; (c) the form (i.e., planospiral or turbinate spiral) of the normal axis." Owen suggests that direction of growth at a given point on the mantle/shell margin of a planispiral form may be resolved into (1) a *radial component*, radiating from the umbo and acting in the plane of the generating curve and (2) a *transverse component* acting at right angles to the plane of the generating curve. For turbinate spirals, a third component, the *tangential component*, acts tangentially to, and in the plane of, the generating curve. It should be understood that Owen's components are abstract directional features used for qualitative description and cannot be measured in reality.

Stasek (1963) has considered the inherent problem posed by juxtaposition of two logarithmic spirals in the bivalve condition: the problem of overlapping umbones. He outlines five mechanisms that have evolved to solve this problem and lists genera that exemplify each mechanism: (1) Penetration of one umbo by the other (*Platyodon, Solen, Ensis,* and *Tellina*), (2) development of offset umbones, one positioned anteriorly and the other posteriorly (*Dualina* of the Silurian and *Corculum* of the Recent), (3) use of valves that represent less than one-half of a spiral revolution (*Pecten*), (4) development of one flattened, lid-like valve (*Caprina, Gryphaea, Corbula*), and (5) use of interumbonal growth, or shell growth along the hinge beneath the umbo (*Arca* and, to a lesser extent, many other bivalve genera).

Raup (1966) has used the logarithmic model for shell growth to make important mathematical comparisons of the shell coiling geometries of several major invertebrate groups. He relates the use of high rates of whorl expansion among bivalves to the umbonal overlap problem discussed by Stasek. Raup also notes that few bivalve mollusks or brachiopods have developed strongly helicoid valves. He suggests that extreme helical coiling may have been avoided in these groups because of the necessity that a large ratio of aperture size to shell weight be maintained to accommodate the required adductor and diductor muscles. Equally important, perhaps, is the use of the mantle cavity for current flow in both bivalves and brachiopods. It would appear that large cul de sac apical spaces of two strongly helical valves would not easily accommodate the basic current system of either group. Most rudistid bivalves of the Mesozoic did employ extreme helical coiling of *one* valve, however, and the family Diceratidae possessed *two* strongly helical valves. Yonge (1967) interprets the mantle cavity of the latter group as having housed elongate ctenidia and labial palps, with food particles being passed distally to the divergent umbonal regions along the ctenidia and proximally to the mouth along the palps.

THE CONCEPT OF INDEPENDENT ENTITIES

In his classic review of the monomyarian condition in the Bivalvia, Yonge (1953) propounded a long-established idea (Blainville, 1825) concerning the body-shell relationships of bivalves; Yonge's arguments have since gained considerable acceptance, particularly among British workers. The basic idea supported by Yonge is that form of the body and form of the mantle/shell are independent of one another. Yonge used two axes to define the configuration of the body and two different axes to define the configuration of the mantle/shell. Representing the basic bivalve body plan with the genus *Glycymeris*, Yonge analyzed the modifications required to produce such divergent forms as solenid razor clams, mussels, scallops, and tridacnids. In *Glycymeris*, the two sets of axes are parallel, but in the other forms, they become offset in a variety of ways, indicating relative dislocations of the mantle/shell with respect to the body (Fig. 2).

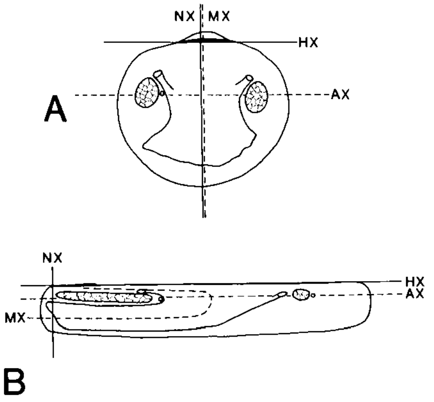


Figure 2. Distortion of *Ensis* (B) relative to *Glycymeris* (A) according to the concept of independent entities. NX (normal axis), HX (hinge axis) = shell axes; AX (antero-postero axis), MX (median axis) = body axes (*after* Yonge, 1953).

Stasek (1963) has criticized Yonge's scheme, which he calls the "concept of independent entities," claiming that the body and the mantle/shell are inseparable and that points along the mantle/shell are related homologically to adjacent points of the underlying body. In place of Yonge's separate axes, he recommends the use of deformation co-ordinates (as described by Thompson, 1942) to represent each species as a single entity. Stasek's comparison of *Solen* and *Clinocardium* using this method is illustrated in Figure 3. Young (1953) deformed

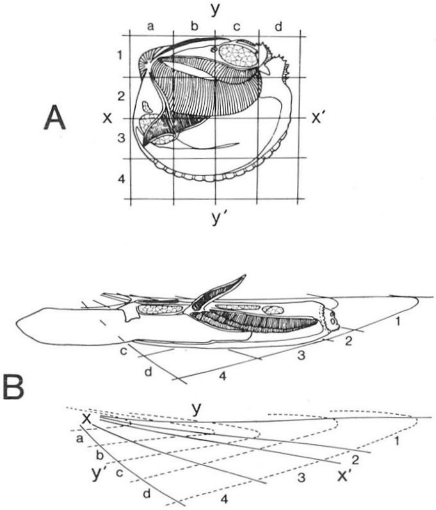


Figure 3. Deformation of *Solen* (B) relative to *Clinocardium* (A) using co-ordinate translocation (*after* Stasek, 1963).

only the body of the similar genus *Ensis* (Fig. 2) in much the same way that Stasek has deformed the whole animal *Solen* (Fig. 3). *Clinocardium,* which forms the basis for Stasek's comparison, is roughly comparable in shape to Yonge's starting point, *Glycymeris.* The difference in the two points of view is shown by the fact that Yonge's shell co-ordinates for *Ensis* do not follow the body deformation. According to Yonge, the *ventral* foot of *Ensis* emerges from the *anterior* end of the shell. Stasek claims that the pedal region of the shell is, by definition, ventral.

I agree with Stasek on this point. In the first place, the axes of Yonge (1953) seem to be somewhat arbitrarily defined. Especially puzzling is the basic anatomical significance of the normal axis of the shell, which appears simply to describe shell coiling geometry, while overlying anatomically dissimilar regions of the mantle in different species (Fig. 2). In addition, it is difficult to make a clear-cut anatomical distinction between the body and the mantle/shell. For example, the adductor muscles, which Yonge used to define the antero-posterior *body* axis, are generally considered to have formed by evolutionary cross-fusion of pallial (*mantle*) muscles (Yonge, 1953).

Unfortunately for the paleontologist, Stasek's use of deformation co-ordinates is not directly applicable to fossil taxa because the bivalve shell alone provides too few homological landmarks for successful comparison of species. Still the technique's utility as a tool for anatomical comparison of living species suggests that its use here may illuminate many basic geometric differences among major taxa that might otherwise go unnoticed.

SHELL MEASUREMENTS

The shell measurement techniques employed in this study are discussed in the final section. Linear measurements of gross shell shape have been standardized morphologically in the manner illustrated in Figure 4. The *antero-posterior axis* of an isomyarian shell is

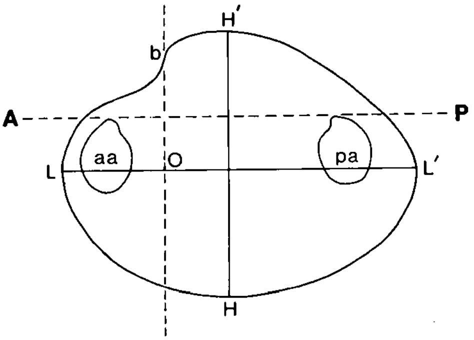


Figure 4. Orientation of shell shape measurements for dimyarian bivalves. aa = anterior adductor scar; pa = posterior adductor scar; AP = antero-posterior axis; LL′= length; HH′= height; LO = anterior length; OL′= posterior length; b = beak.

defined as the line passing across the dorsal margins of the adductor muscle scars. The adductor muscles themselves are mechanically significant in that their centers in isomyarian bivalves normally lie at approximately equal distances from the ligament axis. Because the mouth normally lies near one adductor muscle and the anus near the other, the adductor muscles are, by definition, anterior and posterior. The dorsal margins of the two adductors have special significance in that they mark the sites of shell insertion of the pedal muscles, by which the entire visceral mass and foot are suspended. Use of the dorsal margins, rather than the centers, of adductor scars to define the *antero-posterior axis* also eliminates the problem introduced by special ventral elongation of the anterior adductor (as in the Lucinidae).

Shell length (LL′) is defined as the maximum shell dimension parallel to the *antero-posterior axis* and determines the *long axis* of the shell. *Shell height* (HH′) is defined as the maximum dimension perpendicular to shell length. *Anterior length* (LO) and *posterior length* (OL′) are the segments of the shell length on either side of a line parallel to the shell height and passing through the projection of beak (b) onto the height-length plane. *Shell width* (W) is the maximum dimension of the two valves perpendicular to the plane of commissure (or, in bilaterally asymmetrical species, the maximum dimension of the two valves perpendicular to a plane tangential to the surface of commissure).

Relief on the outer shell surface is termed *ornamentation* when following a special, genetically controlled pattern and *rugosity* when merely representing growth irregularities. The *ornamentation index* (O.I.) for a species is the ratio between the surface relief formed by ornamentation in the mid-ventral region of the shell and the geometric mean of the shell height and shell length:

$$\text{O.I.} = \frac{\text{mid-ventral ornamentation relief}}{\sqrt{\text{H} \times \text{L}}} \times 10^4.$$

Thickness of a pair of valves is represented by the *thickness index* (T.I.), which is the ratio between volume of shell material and internal volume. Because both shell density and internal density (density of flesh plus mantle cavity fluid) are roughly constant throughout the Bivalvia, the thickness index is an approximate measure of whole-animal specific gravity and was chosen for this reason. It is only a crude measure of shell strength, which depends also on shape and can be measured accurately only by breakage experiments, but evidence will be presented indicating that thickening of the shell beyond the mean thickness for bivalves in general is primarily an adaptation for increasing whole-animal specific gravity rather than shell strength.

A special parameter has been measured for members of the Pectinidae (scallops). This is the *umbonal angle,* which is shown in Figure 15. The two lines defining this angle are tangent to the shell margin at the umbo and the dorsal "shoulders." The angle increases slightly in most species during ontogeny and therefore can only be used in an approximate way for morphologic comparison of species.

Adaptations for Byssal Attachment

A byssus is a group of attachment threads, or less commonly a single strand, secreted by the foot and used for fixation to the substratum. Byssus formation has been best studied in *Mytilus edulis* (Field, 1922; White, 1937), in which the byssus is composed of collagen (Mercer, 1952). The byssus of *Mytilus* and other genera is formed from a glandular secretion at the base of the bivalve foot. The liquid secretion is shaped into a thread within a groove along the foot's ventral surface and is tacked to the object of attachment by the tip of the foot. After being released, the thread hardens quickly in sea water. In *Mytilus*, the distal attachment threads radiate from a proximal stalk, which is tightly held by the byssal retractor muscles.

Yonge (1962) has summarized the distribution of byssal fixation among the major Recent bivalve superfamilies. A byssal apparatus is extensively employed by members of the Arcacea, Mytilacea, Pteriacea, Pectinacea, and Anomiacea. Yonge stresses the widespread development of byssal fixation among the young of many groups that are free burrowers, or have other non-byssate habits as adults. He presents a strong argument that the byssus had its evolutionary origin as a post-larval organ of attachment and became established in adult bivalves by neoteny.

The basic bivalve requirement of physical stability is one that will be stressed throughout this study. Commonly, stability is achieved through shell thickening, which increases whole-animal density. The current velocity competent to initiate movement of a shell on the bottom is roughly proportional to the square root of both shell density and shell diameter (Menard and Boucot, 1951). Because very small animals act as unstable particles regardless of their density, juveniles of many species have come to rely on byssal fixation for stabilization.

FIXATION WITH THE SAGITTAL PLANE VERTICAL

Byssally attached marine species that normally live with the sagittal plane vertical (or perpendicular to the substratum surface) include a few members of the Carditidae and Limidae, many members of the Arcidae and Isognomonidae, and all members of the Mytilidae and Pinnidae.

Equivalve Condition

Perhaps the most fundamental geometric feature of species with this mode of life is their equivalve condition. Because the two shell halves face similar environmental conditions, there has been little or no selective pressure for alteration of the bilateral symmetry of the primitive bivalve body plan. If properly classified as pteriaceans (Thiele, 1935), the Pinnidae are unusual in being oriented in life with the sagittal plane vertical; they are also unusual in having retained primitive bilateral symmetry in association with their upright life position, in which the shell anterior is buried in the sediment (Fig. 43C).

Elongation

A second, nearly universal feature uniting epifaunal species living with the sagittal plane vertical is elongation of the body and shell. Elongation is usually accompanied by flattening of the ventral margin and, commonly, by development of a byssal sinus. The most convincing evidence for the association of elongation with upright byssal attachment is provided by families characterized by this mode of life but also containing free-burrowing species. Both the Arcidae and the Carditidae exhibit adaptive divergence of this type.

In Figure 5, shell height is plotted against shell length for arcid species known from the literature or from personal observation to be either free burrowers, in some cases employing a weak, temporary byssus, or forms that attach firmly by a permanent byssus to hard substrata. The two groups are clearly separated by a line representing a L/H ratio of approximately 1.35. *Anadara notabilis* is an unusual species that lacks a byssus as an adult and lives one-third to one-half buried in soft sediment. As shown in Figure 5, it is placed by itself in a semi-infaunal ecologic category. The byssally attached condition in the Arcidae can be seen from the fossil record to have preceded the development of modern, free-burrowing groups, which have apparently originated in the Cretaceous and Cenozoic. Many free burrowers (for example, *Anadara ovalis*, *A. chemnitzi*, and *Noetia ponderosa*, p. 121-123 retain a weak byssus for anchorage in loose sediment. It is likely that certain species which are morphologically intermediate between the

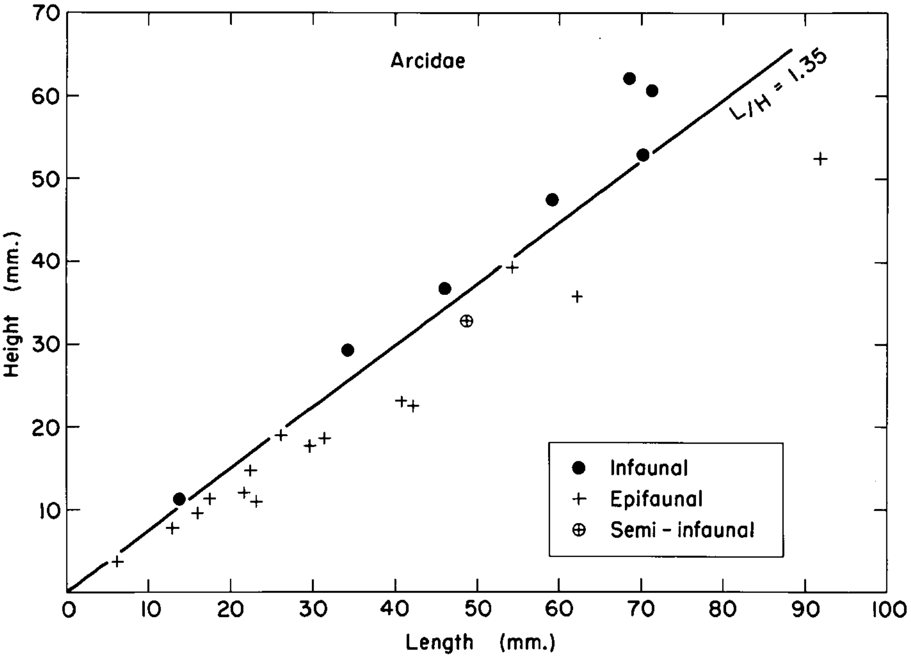


Figure 5. Relation between degree of elongation and mode of life in the Arcidae.

two groups, but which attach to hard substrata by a weak byssus, have partially reverted to the more primitive condition from a free-burrowing state, without entirely losing the morphologic characters of their free-burrowing ancestors. *Anadara antiquata,* described by Lim (1966), is a good example of such a species (Fig. 6B).

Most burrowing arcids are placed in the genus *Anadara,* and most byssally attached species, in such genera as *Arca* and *Barbatia.* It might therefore be argued that the two morphologic groups shown in Figure 5 simply follow taxonomic lines and only incidentally coincide with life habit groups. The elongation of *Anadara antiquata* in association with its reversion to the byssally attached habit argues against this idea and supports the idea of a meaningful correlation between shell form and mode of life.

Less ecologic information is available in the literature for the Carditidae than for the Arcidae, but the two carditid species examined in this study illustrate the same type of adaptive divergence as the arcids. *Cardita floridana* lives infaunally, but is attached along its ventral margin to buried stems of submarine grasses (Pl. 14, fig. 13). *Venericardia borealis,* in contrast, is a free burrower. The L/H ratio for *C. floridana* is approximately 1.45, while that for *V. borealis* is only 0.96.

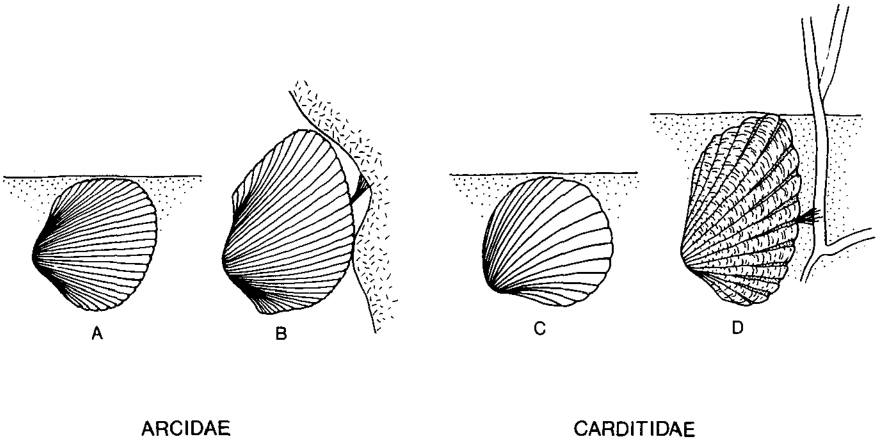


Figure 6. Adaptive convergence between divergent representatives of the Arcidae and Carditidae. A = *Anadara ovalis;* B = *Anadara antiquata* (after Lim, 1966); C = *Venericardia borealis;* D = *Cardita floridana.*

Adaptive divergence within the Arcidae and the Carditidae and adaptive convergence between members of the two families, related to the two basic modes of life, are illustrated in Figure 6. The significance of shell length in burrowing species will be discussed in a later section. The elongate form and flattened ventral margin of byssally attached species provide a broad base for support. A short, rounded ventral margin would provide only a single, tangential point of contact with the hard substratum, offering little stability. Elongation and ventral flattening provide a minimum of two points of contact with the substratum, and a maximum of complete marginal contact, for greatly increased stability.

The Anisomyarian Condition

Yonge (1953) has presented a very thorough and important discussion of the monomyarian and anisomyarian conditions in the Bivalvia. Reduction in the size of the anterior adductor is accompanied by reduction of the entire anterior shell region. Yonge has suggested that anterior reduction in gregarious mytiloid bivalves is an adaptation for elevating the posterior shell region so that the inhalent currents of closely crowded individuals are not obstructed. Stasek (1966) has suggested alternatively that anterior reduction may have evolved in mytiloids in tropical regions where productivity was low, as a means of increasing food intake. Aside from the lack of concrete evidence to support such an idea, I see no reason for a relationship in bivalves between inhalent current area and pumping rate. The size and structure of the pumping organs (the gills) would seem to be far more important in this regard. In fact, Yonge's crowding hypothesis has considerable merit in light of the gregarious habits of such species as *Mytilus edulis* (Pl. 7, fig. 9) and *Brachidontes exustus* (Pl. 8, fig. 6).

From studies of Recent mytilid species, I have concluded that mytiloid shape primarily reflects basic life habits, especially life position and substratum preference. Not only does anterior reduction in gregarious epifaunal mytiloids elevate the inhalent current, but it also brings the byssal retractor muscles into a position more directly above the byssus, where they can pull the ventral shell margin against the substratum with a strong, direct force (Fig. 7). Firm anchorage to the substratum is extremely important for exposed epifaunal species like *Mytilus edulis,* in contrast to infaunal and semi-infaunal forms like *Modiolus demissus* (Fig. 7), which gain stability and protection from the enclosing substratum. Support for the argument that anterior reduction in mytiloids is primarily an adaptation for strong byssal fixation comes from an unrelated family, the Limidae. Limid species that normally live attached by a weak byssus but can readily free themselves to swim, tend to have elliptical valves with curved margins. Examples are *Lima hians* (Yonge, 1953) and *Lima scabra* (Pl. 13, figs. 5-8). *Lima scabra* has a flared, lip-like byssal aperture, reflecting its ability to hang, loosely attached, in a variety of positions (Pl. 13, fig. 8). In contrast, *Lima lima* (Pl. 13, figs. 9-14) attaches by a strong byssus in crevices and cavities on the undersides of rocks. It is apparently unable to swim. *L. lima* has taken on a distinctive triangular, mytiloid shape, with the ventral valve margins flattened to provide a broad surface of contact with the substratum. The ventral margins of the valves are slightly recessed anteriorly along the commissure so that the anterior auri-

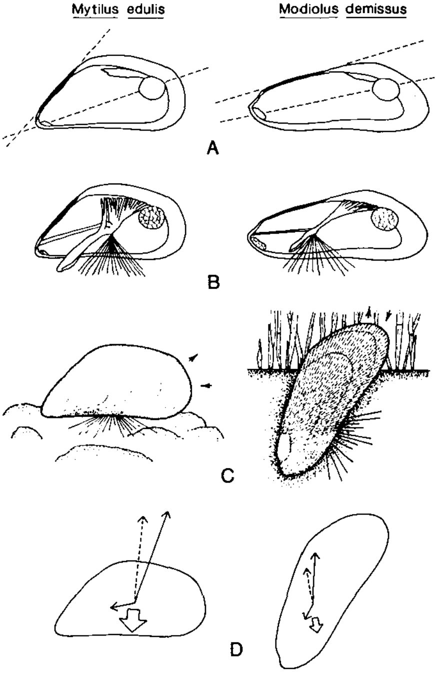


Figure 7. Relation of shell form and musculature to attachment orientation in *Mytilus edulis* and *Modiolus demissus.* A = interior shell morphology; B = musculature; C = life position and feeding curents (arrows); D = byssal retractor forces (fine arrows) and direction of shell force against the substratum (heavy arrows). Vector magnitudes estimated from cross-sectional areas of muscles (small relative magnitudes of anterior retractor vectors make knowledge of exact magnitudes unnecessary).

cles barely project beyond the flattened shoulders on which the shell rests. The byssal retractors exert a strong force perpendicular to the surface of attachment, as in *Mytilus.*

Epifaunal-Infaunal Relationships

Excluding borers of the genus *Lithophaga,* it has commonly been assumed that mytiloid bivalves are, and always have been, characteristically epifaunal in habit. This misconception is probably a consequence of the great abundance of a few species, like *Mytilus edulis,* along intertidal rocky shores. In fact, many Recent mytilid species normally live partly or entirely buried in soft sediment. The habits of four of these(*Modiolus modiolus, M. demissus, M. americanus,* and *Brachidontes citrinus*) are described and illustrated in the final section of the present study (Pl. 9, figs. 1-11). These infaunal and semi-infaunal species possess certain common shell features that reflect their mode of life.

Mytilus edulis and *Modiolus demissus* represent extreme adaptations for the two major mytilid modes of life (excluding the *Lithophaga* boring habit). Interestingly enough, these two species live in adjacent intertidal habitats along much of the Atlantic coast of North America so that their habits can be compared readily in nature. Their habits and major adaptive features are illustrated in Figure 7. *Mytilus* attaches firmly to hard substrata, most commonly to rocky surfaces, in areas of strong wave action. The significance of its anisomyarian condition has been discussed in the previous section. The shell is roughly conical. Anterior reduction has shifted the posterior byssal retractor muscles anteriorly so that they insert into the shell almost directly dorsal to the byssus (Fig. 7B). The posterior byssal retractors are also greatly enlarged. When acting in conjunction with the weak anterior pedal retractors, they produce a strong force that operates at nearly right angles to the ventral margin to clamp the shell securely to the substratum against the strongest waves (Fig. 7D). As suggested by Yonge (1953), elevation of the inhalent current may also be adaptively significant for successful pumping under crowded conditions.

Modiolus demissus normally lives mostly buried, at a high angle, in marsh peat (Pl. 9, fig. 9). It displays several important differences from the body plan of *Mytilus.* The shell is drawn out in an anteroposterior direction, reducing the angle between the hinge line and the line connecting the two adductor muscles. The anterior adductor is large and elongate relative to that of *Mytilus,* to cope with the relatively larger anterior portion of the shell. In short, the shell is roughly cylindrical rather than conical. With the more nearly isomyarian condition and general elongation, the byssal retractor muscles lie well posterior to the byssal stalk, where they cannot exert a direct upward force comparable to that of the *Mytilus*. The resultant force of the anterior and posterior retractor muscle forces in *M. demissus* is instead more nearly parallel to the long axis of the shell and serves to pull the animal downward into the substratum. A slight downward movement can, in fact, be observed in nature when a living "ribbed mussel" is disturbed. (Movements of this type are almost certainly also used for deeper penetration of the substratum as the animal grows during ontogeny.) The retractor muscles of *M. demissus* are smaller and weaker than those of *Mytilus*, reflecting its lesser need for strong byssal anchorage because of the support derived from the enclosing substratum. The relative positions and sizes of the byssal retractor muscles of the two species are quite clearly discernible from corresponding shell muscle scars (Fig. 7A).

Modiolus modiolus, M. americanus, and *Brachidontes citrinus* are less extreme than *Modiolus demissus* in their adaptations for infaunal or semi-infaunal modes of life. Still, they all have relatively weak byssal retractors that exert a force more nearly parallel to the shell's long axis than the corresponding muscles of epifaunal species.

The strong anisomyarian condition, triangular shell outline, and large posterior retractor muscles and muscle scars that characterize the *Mytilus* body plan are also found in other mytilacean species with similar epifaunal habits (*Brachidontes recurvus*, Pl. 7, figs. 5 and 6; *B. exustus*, Pl. 8, figs. 4-6). *B. recurvus* exhibits another shell feature commonly found in the epifaunal group. This is the recurved or hooked shape in lateral view. It facilitates attachment to rounded surfaces, including neighboring mussels. The recurved shape is less pronounced in *B. exustus* and *M. edulis*.

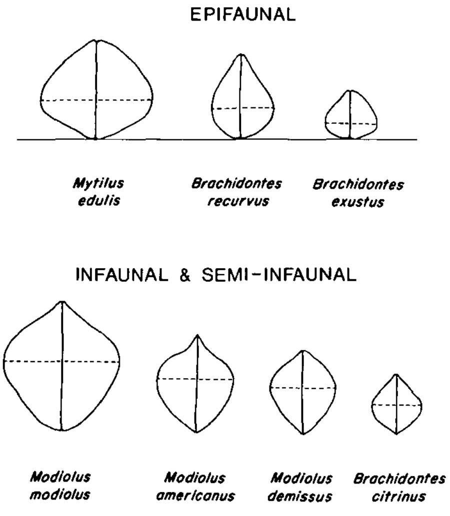


Figure 8. Comparison of cross-sectional shapes of epifaunal mytilids with those of semi-infaunal and infaunal mytilids. Horizontal dotted lines indicate positions of maximum shell width.

Perhaps the most diagnostic shell feature separating the two mytilid life habit groups is cross-sectional shape. In Figure 8, cross sections of all 7 of the mytilid species studied are compared. Shells of infaunal and semi-infaunal species that live in soft substrata have a wedge-shaped ventral region, with the widest portion of the shell located approximately midway between the dorsal and ventral margins. In contrast, epifaunal species are characterized by a much flatter ventral surface, with the widest dimension of the shell lying near the ventral margin. The adaptive significance of this distortion in cross-sectional shape for epifaunal attachment is readily apparent. It lowers the center of gravity of the animal and provides a broad surface of contact with the hard substratum, for increased stability.

The basic morphologic features distinguishing the two mytilid life habit groups can all be fossilized. Of these features, the most easily preserved and discerned is the lateral-view outline, in which degree of anterior reduction and location of the byssal sinus are most significant. Cross-sectional profile is also readily observed for many fossil species, and muscle scar patterns are commonly visible on well-preserved specimens.

It is likely that the infaunal or semi-infaunal habit is the more primitive of the two and that it arose through neotenous retention of a post-larval byssus. *Mytilus*-like forms exhibit a more extreme anisomyarian condition; their secondary epifaunal habit may have had a polyphyletic origin.

If the classification of Thiele (1935) is correct, the Pinnidae represent a divergent pterioid lineage that has evolved to adopt a semi-infaunal mode of life. The anterior has been greatly drawn out along the hinge line to form a point which penetrates the sediment. The byssal sinus is reduced to a broad concavity in the ventral shell margin, if present at all (Pl. 11, fig. 9; Pl. 12, figs. 2, 3). Pinnids apparently move deeper into the sediment during their life history by pulling against the anchored byssus. The triangular streamlining of the shell anterior is an obvious adaptation for facilitating such downward movements. The musculature and byssal apparatus are shown in Figure

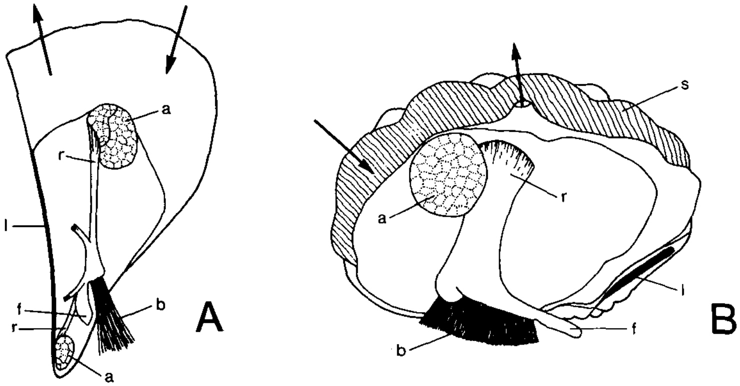


Figure 9. Musculature, byssal apparatus, and life orientation of *Atrina* (A) and *Tridacna* (B). a = adductor muscle; r = retractor muscle; l = ligament; f = foot; b = byssus; s = algae-infested siphonal tissue.

9A. The external spines of the genus *Atrina* (Pl. 12, figs. 1, 2) are oriented perpendicular to the shell surface; they can in no way protect the broad posterior aperture from predation. Instead, they apparently serve to protect the exposed part of the fragile shell itself from physical breakage by bearing the force of external blows. The spines are commonly found to be broken on living animals.

One of the most unusual of byssally attached bivalve groups in which the sagittal plane is oriented vertically is the family Tridacnidae (Cardiacea). The habits and functional morphology of tridacnids have been discussed by Yonge (1936a) and Stasek (1961). Stasek, especially, has analyzed the unusual morphology of the group. The most striking morphologic alterations of the basic cardiacean body plan involve the siphonal region, which is hypertrophied and directed upward in life, while the byssus passes vertically downward to attach firmly to the substratum (Fig. 9B). The siphonal (posterior) and byssal (ventral) regions are brought to these diametrically opposite positions by reduction of the anterior and ventral regions of the shell. The dorsal hinge thus lies on the underside, adjacent to the byssus. Yonge (1953, p. 470) has quite reasonably concluded that the distorted tridacnid form is a consequence of symbiotic association with zooxanthellid algae, which inhabit the expanded siphonal tissues in large numbers. Yonge (1936a) has argued that the tridacnids use zooxanthellae as a food source. Although such a relationship has not been conclusively demonstrated, it is favored by a wealth of circumstantial evidence, including the clams' distorted body plan and their typically large size.

A feature of the tridacnid shell that is of special significance with respect to life habits is its coarsely plicate structure. Yonge (1936a) has described the use of the concentric ridges that intersect the shell plicae for boring into the substratum. Some species do not bore, but live attached at the surface. It seems likely that the plicae increase the abrasive effect of the concentric ridges. At any rate, shell plication serves another function that has not, to my knowledge, been previously brought to light. The plicae interdigitate along the broad posterior commissure. By simple graphic analysis (Fig. 10), it can be shown that for a given angle of shell opening, a simple zig-zag commissure will not affect the area of gape, regardless of the wave length of the zig-zag pattern. Rudwick (1964a) has previously pointed out this relationship in his consideration of the zig-zag commissure in brachiopods. In living tridacnids, the gape is entirely filled by algae-infested siphonal tissue, except for the inhalent and exhalent apertures. Rounding of the zig-zag corners has no effect on area of gape as long as the valve margins exactly meet (Fig. 10). But many species of the genus *Tridacna* have increased the area of gape by sacrificing complete closure. The projections of the valve margins are pointed and therefore narrower than

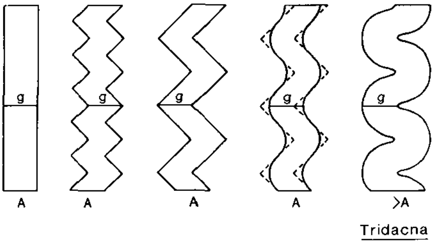


Figure 10. Enlargement of commissure gape in siphonal region of *Tridacna.* A = area of unit size; g = gape of unit width.

the corresponding embayments into which they fit (Fig. 10). The valve surfaces are correspondingly folded into broad external ridges and narrow troughs. With these commissure modifications, tridacnids maximize the area of siphonal tissue exposure. (The siphonal tissues actually overlap the valve margins slightly in life.) These adaptive features are in accord with the general tridacnid body plan, which is chiefly modified for elevation and enlargement of the siphonal region, apparently for exposure to the maximum number of zooxanthellae to sunlight.

FIXATION WITH THE SAGITTAL PLANE NON-VERTICAL

Most living bivalve species that attach by a byssus with the sagittal plane in a non-vertical position belong to the Pteriacea, Anomiacea, and Pectinacea.

Inequivalve Condition

Bivalves that rest on one side, with the sagittal plane horizontal, or at an oblique angle to the vertical, expose their two valves to differing environmental conditions. For this reason, it is understandable that the two valves usually have distinct morphologies. Nearly always, the lower valve is in closer contact with the substratum. If the sagittal plane lies nearly horizontal, the lower valve is usually the less convex (as in most byssally attached anomiids and adult pectinids). This condition increases the area of surface contact with the substratum and provides for increased stability.

Elongation of the Anterior Auricle

A very important functional feature of many non-vertical, byssally attached species is an elongate anterior auricle (in association with a byssal sinus). Figure 11 is a plot of auricle asymmetry against umbonal angle for pectinid species known from the literature to be either free-living or byssally attached as adults. A marked trend toward high asymmetry is evident among byssally attached species, reflecting relative elongation of the anterior auricle.

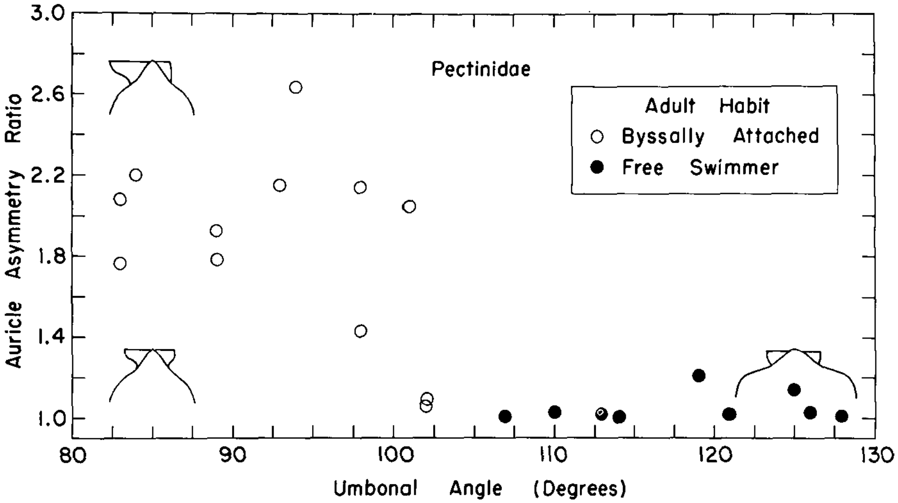


Figure 11. Graph of auricle asymmetry versus umbonal angle for byssally attached and free-swimming members of the Pectinidae. Auricle asymmetry ratio is the ratio between anterior and posterior auricle lengths.

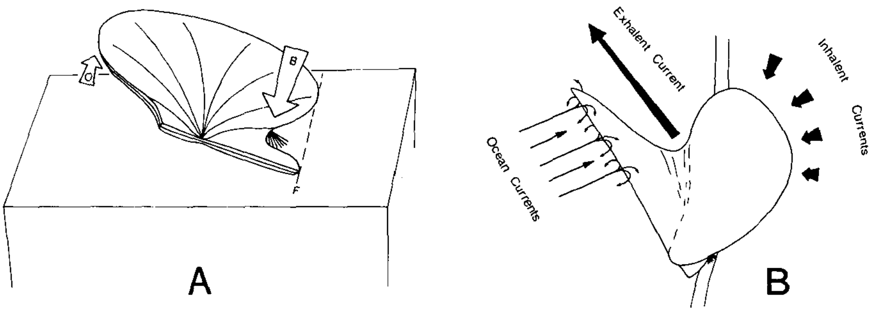


Figure 12. Mechanical functions of auricle elongation. A = support function of the elongate anterior auricle and byssal sinus of attached pectinids (F = fulcrum; large arrow = byssal force; small arrow = overturning force); B = postulated sheltering function of the elongate posterior auricle of *Pteria*.

The auricle-sinus configuration lends itself well to mechanical analysis, but I can find no mention of its adaptive significance in the literature. The elongate anterior auricle acts as a support to prevent overturning of the shell, as shown for an idealized pectinid in Figure 12A. Lacking the auricle and sinus, the shell would be susceptible to overturning along the antero-ventral margin by a weak upward force acting on the posterior part of the shell; the shell margin near the site of emergence of the flexible byssus would act as a fulcrum. With the auricle and sinus present, two points along the shell margin, one on either side of the byssus, act as a fulcrum, and this fulcrum is shifted distally from the byssus: complete overturning is impossible without breakage of the shell or byssus. The greater the distance from byssal sinus to fulcrum for a given shell size, the greater the leverage against an overturning force. A similar auricle-sinus configuration is used for byssal anchorage in the Pteriacea.

In attached anomiids (Pl. 14, figs. 1-3) the byssal sinus is deeply embayed within the lower valve, becoming, functionally, a hole in the valve for passage of the stout, calcified byssus. No projecting auricle is present. This mode of attachment permits the lower valve to lie flat against the hard substratum. The fragile margins of both valves are then supported by the substratum when the valves are closed, and the shell is not easily broken or dislodged.

Posterior Elongation of the Hinge Line

The elongate, wing-like extension of the hinge line of many pteriids (for example, *Pteria colymbus*, Pl. 11, fig. 2) is related to the pattern of the animals' current system. Yonge (1953) has suggested that general elongation of the elliptical portion of the pteriid shell parallel to the hinge axis has served to separate the inhalent and exhalent currents. Certainly, the posterior embayment from which the current issues separates this current from the inhalent current. As shown in Plate 11, figure 4, the exhalent current is a powerful jet, passing for some distance parallel to and beyond the posterior wing (compare Pinctada, Pl. 11, fig. 7).

It is important that pteriids, as immobile forms, expel used water as far as possible. It seems likely that the basic function of the pteriid wing is to shelter the exhalant current to prevent it from being swept back toward the inhalant current regions by external water movements (Fig. 12B). Although the wing is a basic and widespread feature in the Pteriidae, among Recent species, it usually seems to coincide with a habit of attachment to alcyonarians (Pl. 11, fig. 3). In life, the wing tends to be oriented parallel to the branches of the flexible alcyonarian host, which bends with currents. It is possible that this orientation aids the animal in removal of exhalent water currents. The pteriid shell also offers little resistance to water currents in this orientation and may derive some protection from the manner in which the wing resembles an alcyonarian branch.

Adaptations for Cementation

Species that attach to the substratum by cementation have been excluded from the life habit study reported in the final section because they are commonly fossilized *in situ,* rather than in transported death assemblages. Consequently, the basic life habits of many cemented fossil species are directly observable. For example, many species of the highly aberrant Rudistacea of the Mesozoic are commonly found in life position in biohermal deposits of the Tethyan biogeographic realm; although an extinct and unusual group, their life habits are relatively well known (Dechaseau, 1952, p. 323-362).

Still, certain basic features of cemented taxa are worthy of consideration. The foremost cemented groups of the Recent are the Spondylidae (Pectinacea), Ostreidae (Ostreacea), and Chamidae (Chamacea). Shells of both the Chamidae and Spondylidae commonly bear long external spines. Such spines are rare among most other bivalve groups and, as Nicol (1965) has pointed out, are largely restricted to members of the epifauna in tropical regions. Nicol (1964) has also called attention to the rarity of attachment by cementation among bivalve taxa of Arctic and Antarctic waters. Both cementation and long spine formation require carbonate secretion beyond the amount normally required for shell formation. The larger rudists secreted such massive shells that even though their shell structure was porous, their total volume of carbonate secretion was many times that of most bivalve species. It is certainly not coincidental that cementation and spine development have been most widely employed among species living in warm-water areas, where carbonate is more easily secreted than it is in colder waters.

It seems almost certain that the spines of reef-dwelling spondylids, and perhaps chamids, serve a protective function. Except for these spinose groups, there are strikingly few exposed epifaunal bivalve taxa in reef communities, which are otherwise noted for their high species diversity. Most byssally attached reef-dwelling arcids, for example, live largely or entirely within protected crevices. Shelled invertebrates are subjected to more rigorous fish predation in reef habitats than elsewhere. Calcareous chunks of crustacean, echinoid, coral, and algal skeletons are commonly found among the stomach contents of scarids (parrot fish), balistids (trigger fish), monocanthids (file fish), and tetraodontids (puffers) of reef environments (Cloud, 1958). In particular, parrot fish habitually seem to nip off pieces of coral with their powerful jaws and teeth to digest the living tissues. The exposed, spineless commissure region of most bivalve shells would offer little resistance to fish attack in reef habitats. Although commonly encrusted by sponges and other epibionts, the spines of spondylids must still act as rigid spikes guarding the commissure, where they are secreted. It is true that parrot fish and other similarly endowed groups could nibble away spines in order to reach the commissure, but such behavior would require considerable time and energy expenditure, while other more abundant and better exposed animals, such as reef corals, are far easier prey. Certainly the unusual elongate and poisonous spines of the reef-dwelling echinoid *Diadema* offer resistence to attack by many species of shell-crushing fish. Similar spines are virtually unknown among regular echinoids restricted to other environments.

It is impossible to rule out use of the bivalve spines as sensory warning devices, even if they also serve for direct physical defense, as proposed. Spine contact with any sizable object brings about valve closure and, perhaps, safety from potential danger. The only detailed analysis in the literature of the function of long spines in the Bivalvia appears to be Carter's analysis for the infaunal venerid genus *Hysteroconcha* (Carter, 1967). Carter concluded that the spectacular spines of this genus serve to thwart starfish and gastropod predators. It seems likely to me that the spines function primarily to protect the delicate siphons of the species against fish predation. Bivalve siphons are common constituents of the stomach contents of many fish species, and the spines of *Hysteroconcha* are deployed so as to project upward on either side of the siphons, where they may act as physical barriers or warning devices.

A zig-zag commissure has been developed by certain cemented bivalve species, such as the Western Atlantic *Ostrea frons* (Ostreacea, Pl. 14, fig. 4) and *Plicatula gibbosa* (Pectinacea). As concluded by Schmidt (1937) and Rudwick (1964a) for similar structures in the Brachiopoda, the zig-zag commissure probably serves to protect these bivalves against entry into the mantle cavity of large, undesirable particles.

Adaptations for Reclining

Reclining species rest on, or are partly buried in, soft substrata without any means of attachment. Free-living scallops are part-time recliners by this definition, but very few living bivalve groups are full-time recliners. Perhaps the best Recent example described in the literature is the "window pane oyster," *Placuna* (Anomiacea), which is a bay dweller that reclines on its convex left valve on firm mud. The hinge region and the dorsal one-third of the shell may be lightly covered with mud (Hornell, 1909). Reclining species have been more abundant in the geologic past than they are today. The most notable fossil examples are adult coiled oysters of the genera *Gryphaea* (Hallam, 1968) and *Exogyra*, and some inoceramids (Kauffman, 1967). Most reclining species have evolved from cemented or byssally attached groups by simply losing their attachment as adults. Nearly all rest on one valve, rather than maintaining the commissure in a vertical position. Such species, like byssally attached species with similar orientations, are nearly always inequivalve. The lower valve is commonly convex to elevate the commissure above the substratum and free it from sediment clogging; the upper valve is then usually flat and acts as a lid for the lower valve.

One striking feature of reclining forms (*Placuna* being an exception) is their tendency to develop very thick shells. *Gryphaea* and *Exogyra*, for example, commonly employed much thicker shells than those of cemented oysters. Likewise, many inoceramids tended to have thicker shells than those of byssally attached pteriaceans. The reclining groups are no more vunerable to predation by drilling gastropods or attack by boring sponges, or to physical breakage or abrasion than are attached members of their superfamilies. They are, however, more vunerable to disruption by external forces, chiefly water movement. Overturning of forms like *Gryphaea* and *Exogyra* would have meant certain death. Shell thickening among reclining species has almost certainly been a mechanism for increasing whole-animal density to prevent their being dislodged and overturned, or transported to unfavorable habitats. Hallam (1968) has concluded that in the well-known Liassic lineage from *Gryphaea arcuata obliquata* to *G. gigantea,* shell thickness decreased because the thick shells of early representatives served to provide stability, but the need for a thick shell diminished during evolution, as shells became larger, broader, and more evolute. Flattening of the valves of surface recliners, such as certain inoceramids (Kauffman, 1967) and *Placuna,* has also served to increase stability, lowering the center of gravity and offering little cross-sectional area for resistance to currents.

Adaptations for Swimming

Swimming, as defined here, is self-propulsion through water. Jumping movements in which the foot launches the shell by kicking only against the substratum are not included in this category. Swimming is not a full-time way of life for any bivalve group, but a temporary activity, most commonly used as an escape mechanism; no living bivalve species truly belongs to the nekton.

The most adept and best-studied swimmers are members of the Pectinacea. Within this superfamily, the Pectinidae and Amussidae swim in a direction perpendicular to the hinge axis, with the commissure plane lying within approximately 45° of horizontal; swimming members of the Limidae swim with the commissure plane vertical. Other taxa known occasionally to swim are certain members of the Solenidae (for example, *Ensis directus*, p. 184), Solemyidae (for example, *Solemya velum*, p. 116), and Cardiidae (for example, *Laevicardium laevigatum*, p. 153). Like members of the Limidae, all these taxa swim with the commissure plane vertical.

SWIMMING WITH THE COMMISSURE PLANE NON-VERTICAL

Pectinids characteristically swim with the hinge hindmost, in a direction perpendicular to the hinge axis. The commissure plane may lie in a nearly horizontal position or be tilted as much as 45° from the horizontal. The right valve lies undermost in both the swimming and resting or attached positions (except in species that attach in an upside down position to the undersides of rocks).

Pectinid swimming movements, which result from expulsion of water by rapid adduction of the valves, have been described by several authors, the most notable being Buddenbrock (1911). Buddenbrock considered swimming of shallow-water species to result from two types of propulsive forces (Fig. 13). One of these arises from backward expulsion of water from the anterior and posterior flanks of the body disc adjacent to the auricles, and the other, from downward expulsion of water along the margin opposite the hinge. Gravity and water resistance oppose upward and lateral movement. A sudden, short flight in a direction opposite the normal swimming direction is used as an escape response to imminent danger. It is achieved by explusion of a large volume of water opposite the hinge.

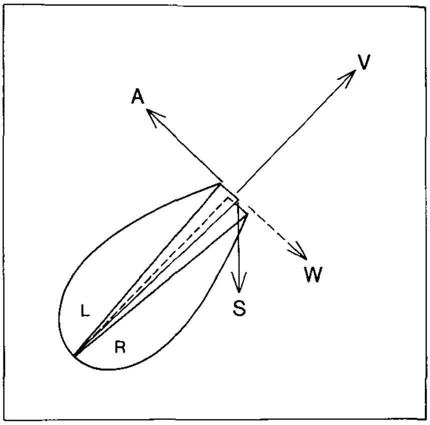


Figure 13. Propulsive forces of pectinid swimming movements according to Buddenbrock (1911). L = left valve; R = right valve; S = downward movement between propulsive movements (due to gravity and water resistance); A = swimming movement due to water expulsion (W); V = swimming movement due to dorsal water expulsion.

Drew (1906) and Yonge (1936-b) have quite reasonably proposed that the swimming habit arose in the Pectinacea through modification of pre-existing cleansing mechanisms in byssally attached monomyarian groups.

There is a gradation among swimming scallops from those that seldom swim to those that swim with considerable frequency. Even many forms that characteristically live attached to a byssus can free themselves and swim when alarmed.

Verrill (1897, p. 42-44) was among the first to conjecture as to the relationship between scallop shell form and swimming habits. He recognized the value of a thin shell to active swimming and the functional significance of plications in adding strength with a minimum of excess weight. Verrill also pointed out that strong radial ribs and plications are best developed in shallow-water species and suggested their importance in strengthening the valves against the force of waves. He contrasted these species to certain smooth-shelled, adept swimmers of the outer shelf. Verrill also suggested that free-living species with a convex lower valve and a flattened upper valve are poorly adapted for swimming because water should emerge from their convex lower valve in an upward, rather than a downward, direction and tend to force the shell toward the bottom.

In fact, direction of water jets used in swimming is largely controlled by the mantle margins rather than by shell form. In the very adept swimmer *Placopecten magellanicus* (p. 138, Pl. 13, figs. 1, 2), the upper valve is more convex than the lower valve. This cross-sectional shape is not so important in producing downward-directed swimming currents as in forming an efficient hydrofoil. *P. magellanicus* is an outer shelf form that frequently undertakes "flights" covering distances of several meters. The commissure plane lies horizontal during movement, and water is ejected from the anterior and posterior flanks of the body disc simultaneously. Apparently there is very little downward expulsion of water along the margin opposite the hinge, as suggested by Buddenbrock (Fig. 13). As shown in Figure 14A, when the shell of *Placopecten* glides through water, the distance of water flow is longer over the more convex upper valve than beneath the less convex lower valve. In accordance with Bornoulli's Theorem, this flow pattern must result in lower water pressure on the upper valve than on the lower valve, to provide lift. Although the amount of lift offered by the shell in this orientation has not been determined in this study, it could be measured experimentally. Because of the thinness of the valves, the effective weight in water of an individual 12 cm in diameter is only about 65 g. Even with the commissure plane horizontal, the lift provided by the hydrofoil shape is apparently adequate to maintain neutral or positive buoyancy (Fig. 14A).

Most swimming pectinids, such as those belonging to the genera *Pecten* and *Aequipecten*, are more strongly inflated than *Placopecten* and possess a lower valve that is more convex than the upper valve. They are also less proficient swimmers. Many inhabit shallow, grassy bays, where long-distance swimming is difficult. Movement is primarily used for escape from predation or other unfavorable environmental conditions. When resting on the bottom, bay-dwelling species commonly lie on muddy sediment or dead submarine grass debris. Extreme convexity of the lower valve almost certainly aids feeding by elevating the commissure above the sediment surface to keep it free from clogging. Commissure elevation is also important in permitting rapid take-off from the

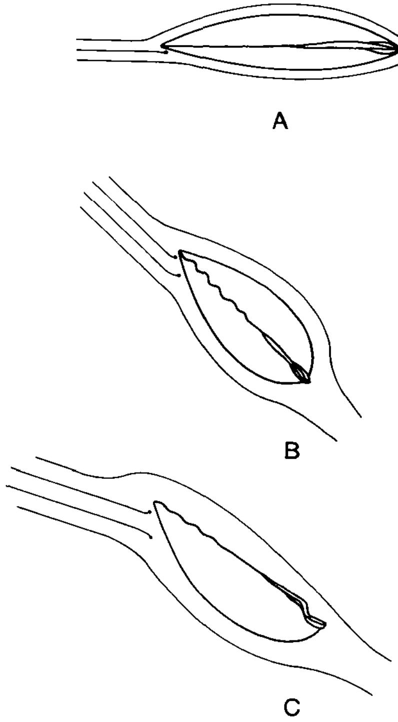


Figure 14. Swimming orientations and possible hydrofoil operation of swimming scallops. A = outer shelf genus *Placopecten;* B, C = biconvex and plano-convex forms. Movement direction indicated by flow lines to the left of each shell. Commissure planes of B and C lie at slight angle to movement direction.

bottom, leaving several millimeters of space below the commissure for water expulsion.

Some clean-sand dwellers, typified by *Pecten ziczac* (p. 137, Pl. 12, figs. 6-8) and *P. maximus* (Baird, 1958), possess a strongly convex lower valve and a slightly concave upper valve. These species are moderately adept swimmers, but spend most of their lives nearly buried in sand. In *P. ziczac,* burial is accomplished by repeated clapping of the valves, to scour sand from beneath the convex lower valve, which slowly sinks into the substratum (Pl. 12, fig. 8). The dish-shaped upper valve collects some of the sand thrown into suspension, eventually becoming covered by a thin layer. In the final life position, only the commissure and tentacled mantle margin are visible at the sediment surface. *P. maximus* uses remarkably well-controlled water expulsion to excavate a cavity in the sand on the ventral side of its shell and then to propel itself into the cavity, where its upper valve eventually becomes covered with sand (Baird, 1958).

Although not nearly so effective hydrofoils as the shell of *Placopecten,* strongly biconvex and plano-convex shells can still provide lift if inclined to the direction of movement at a sufficiently high angle of incidence. It is apparently characteristic of strongly biconvex and plano-convex species that the anterior and posterior water jets operate alternately, rotating the shell back and forth in the plane of commissure. The animal sinks very slightly between water expulsions. Swimming movement usually carries the animal upward at an angle that may be as high as 45° from the horizontal. The net effect of rotational and translational movement is an awkward zig-zag motion. In Figure 14, B and C, direction of movement is represented by lines of water flow, which are deflected around the shells. A slight inclination of the commissure plane relative to movement direction in both diagrams causes water to flow through a longer path over the upper valve than beneath the lower valve; it is possible that strongly biconvex and plano-convex scallops derive lift in this manner. In fact, most of them have thin shells which require little lift. The effective weight in water of an *Aequipecten irradians irradians* individual with a shell diameter of 6 or 7 cm is only about 10 grams. For strongly biconvex and plano-convex species, it is difficult to determine the angle, if any, between commissure plane and swimming direction because of the irregular nature of the swimming movement. The fact that these species swim obliquely upward rather than horizontally suggests that much of their upward movement may be provided simply by the thrust of their water jets. To what extent their shells may act as hydrofoils is uncertain.

Morphologic distinction was made earlier between pectinaceans that normally live byssally attached as adults and those that live free on the bottom (Fig. 11). Unattached forms have no need for an elongate anterior auricle, although they commonly retain a byssal notch from their juvenile period of fixation. In addition to their higher degree of auricle symmetry and (commonly) their strongly convex lower valve, the shells of free-living scallops are broader in a direction parallel to the hinge axis than shells of byssally attached species. This condition is represented in Figures 11 and 15 by the feature called the *umbonal angle.* In several ways, a large umbonal angle increases the swimming ability of free-living species. The currents expelled from the dorsal commissure pass more directly backward, so that the forward-propelling component of force is increased (Fig. 15). The mantle cavity area devoted to water expulsion is also enlarged to increase the volume of water emitted for propulsion. At the same time, the shell dimension perpendicular to movement direction is increased relative to the dimension parallel to movement direction. This serves to increase what, in aerodynamic theory (Kármán and Burgers, 1963), is termed the aspect ratio (λ):

$$\lambda = \frac{(2b)^2}{S}$$

where 2b is the *span* of the hydrofoil (the maximum dimension perpendicular to the median plane), and S is a measure of the hydrofoil surface area in plan view. Increase in the aspect ratio decreases frictional drag

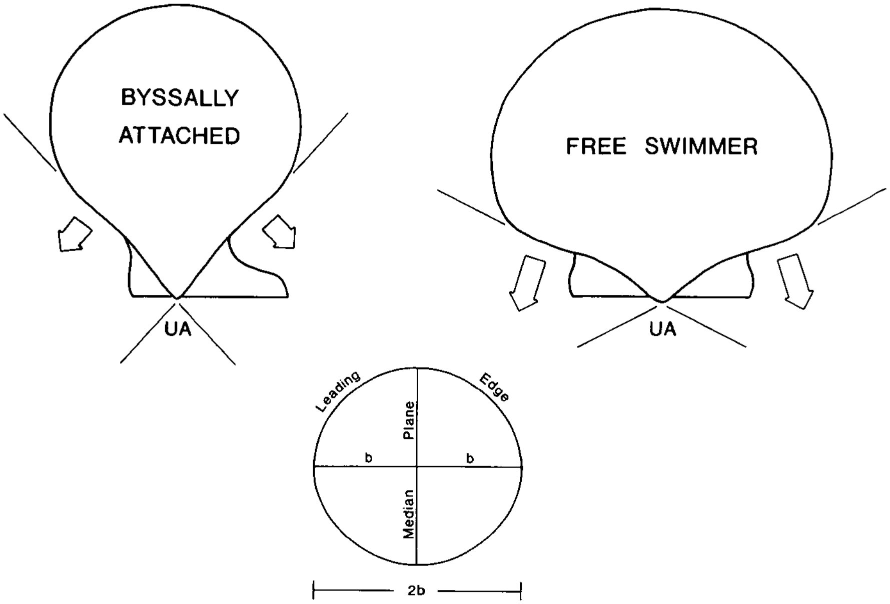


Figure 15. Relation of pectinid valve outline to propulsive forces and lift in swimming. UA = umbonal angle; 2b = span of hydrofoil.

due to lift and increases the resultant upward force on the hydrofoil. The large umbonal angle of swimming pectinids, by increasing the shell dimension perpendicular to movement direction, gives them a greater lift/drag ratio than that of byssally attached forms. A large umbonal angle would also be advantageous to byssally attached species in their less-frequent swimming movements, but this potential advantage has been foregone in deference to the more important need for strong byssal fixation. A small umbonal angle brings the shell margin into a position where it can join the elongate anterior auricle to form half of the support system that prevents overturning (Fig. 12A).

Permanent gapes are present along the valve margins of most swimming species adjacent to the auricles. Such gapes are generally absent or very narrow in byssally attached forms and represent another useful feature for distinguishing between representatives of the two life habit groups.

SWIMMING WITH THE COMMISSURE PLANE VERTICAL

Limids are perhaps the best-studied swimmers in which the commissure plane is maintained in a vertical position. Certain limids possessing adaptations for strong byssal attachment (for example, *Lima lima*, p. 140) are apparently unable to swim. Ovate species lacking a strongly flattened attachment surface spend most of their lives loosely attached by a byssus. They can easily release the byssus to swim when disturbed. Examples are *Lima scabra* (p. 139) and *Lima hians* (Studnitz, 1931). The orientation of swimming limids gives them little surface for resistance to downward movement, and they tend to drop toward the bottom between water expulsions.

Two tubular burrowing groups, the Solemyidae and the Solenidae, contain species that can swim from a resting position at the substratum surface. In the final section of this study, the habits of one species of each family (*Solemya velum*, p. 116) and *Ensis directus* (p. 184) are described. It is significant that both these species are tube-dwellers; the efficient water expulsion systems used in swimming may initially have evolved for the purpose of cleansing their open burrow systems, as suggested by Drew (1900) for *Solemya.*

Another species for which swimming is reported in this study is the cardiid *Laevicardium laevigatum*, in which swimming is accomplished by means of pedal movements (p. 153). Most other cardiids appear to lack the capacity for swimming.

It is notable that all three of these groups of swimming burrowers are thin-shelled. Like swimming pectinids, they benefit from having low whole-animal densities. It is also significant that no disc-like burrower is known to possess the ability to swim. Because burrowers that swim have identical shell halves and move through the water with the commissure plane vertical, a disc shape would provide the smallest planing surface per shell volume of any possible shape (assuming all elongate forms to swim like solemyids and solenids, with the long axis horizontal). The inefficient swimming mechanisms used by burrowing species could not easily counteract such a handicap.

Adaptations for Burrowing in Soft Substrata

INTRODUCTION: THE MECHANICS OF BURROWING

Burrowing physiology in the Bivalvia has been studied by a number of workers, notably Fraenkel (1927), Quayle (1949), Ansell (1962), Trueman (1966), and Trueman and others (1966).

Fraenkel's terms *Grabstufe* and *Grabperiod* will be anglicized here to *burrowing sequence* (each patterned series of muscular movements that produces a downward movement of the animal) and *burrowing period* (the entire series of burrowing sequences, from the one that marks the initiation of burrowing to the one by which the final life position is attained).

Trueman and others (1966, p. 474) have provided the most recent and accurate description of the typical bivalve burrowing sequence:

> (i) The foot makes a major probe downward, tending to raise the shell if pedal penetration is not easily achieved, followed by dilation of the foot.
>
> (ii) Siphons close, preventing water passing out through them during the next stage.
>
> (iii) Adduction of the valves, which occurs rapidly in 0.1 sec and corresponds with (a) maximum pedal dilation, and (b) ejection of water from the ventral mantle margins.
>
> (iv) Contraction of retractor muscles, the anterior being immediately followed by posterior, resulting in movement downward into the substrate.
>
> (v) Adductor muscles relax, gape of valves increases.
>
> (vi) Static period until the next cycle commences at (i). During this period, protrusion of the foot and slight lifting of the shell occur, repetitively.

Ansell (1962) has observed that the siphon tips maintain contact with the substratum surface throughout burrowing, and that depth of burrowing may be sensed by degree of siphon extension. Cessation of burrowing at the life position depth may be a response to this tactile stimulus. Ansell has also shown that as an animal penetrates more deeply during its burrowing period, the time required for individual burrowing sequences increases and depth of penetration per sequence decreases.

Most of each burrowing sequence is spent in pedal probing activity (stages vi and i of Trueman's description). In most species, the shell is lifted from its initial horizontal position to an upright position (with the plane of commissure vertical) by a single burrowing sequence, but commonly, this sequence is preceded by one or more preliminary sequences that fail to erect the shell but succeed in anchoring the foot deeply within the substratum. Once upright, the shell occupies an orientation characteristic for its species. All activities of subsequent burrowing sequences, except those of stage iv, normally take place with the shell in this position, which will be referred to as the *erect probing orientation.* A few species, however, rotate progressively farther forward as they enter the substratum.

In most species, downward shell movement in each burrowing sequence (stage iv of the description of Trueman and others) takes place by contraction first of the anterior, and then of the posterior, pedal retractor muscles. This contraction pattern usually produces a forward-backward rocking motion of the shell for downward penetration. The angle through which the posterior dorsal shell margin rotates will be referred to here as the *angle of rotation.* The final, backward phase of rocking movement returns the shell to its erect probing orientation, and the probing activity of the next burrowing sequence begins. (Many cardiids rock back and forth more than once at the end of each burrowing sequence, with the angle of rotation decreasing in successive rocking cycles.)

Downward probing of the foot (stages vi and i) is largely muscular and prepares the foot for anchorage before each downward movement of the shell. Trueman (1966) has made an important contribution to our knowledge of bivalve burrowing physiology by demonstrating the important function of pressure increase within the mantle cavity in producing maximum pedal dilation and ejection of water from the ventral margin (stage iii). With the extended foot partly dilated and siphonal openings closed, adduction of the valves increases pressure in the mantle cavity, pericardium, and throughout the body enclosed by the shell, to force blood into the pedal haemocoel. Trueman has shown that maximum mantle cavity fluid pressures are maintained longer in groups with fused mantle margins, which effectively seal the mantle cavity, than in groups with free mantle margins. It is my observation that ventral expulsion of water is also strongest among species with fused mantle margins. Mantle fusion in heterodont bivalves has led to improved burrowing ability, which has been a major factor in their post-Paleozoic adaptive radiation (Stanley, 1968).

Burrowing Orientation

There is a useful geometric relationship in bivalves between shell form and site of pedal emergence. The hinge axis of a shell passes through the ligament (not the hinge teeth) and is readily determined for most fossil shells from the orientation of the ligament groove or pit. In the absence of a permanent marginal gape, the maximum ventral separation of the valves for any angle of opening will be located at the point along the ventral margin that lies farthest from the hinge axis. This ventral point (M) is shown for several shell types in Figure 16. Normally the foot emerges with its central axis coinciding with this point of maximum separation. Usually point M falls in the center of a convex segment of the shell margin which borders the portion of the mantle cavity that houses the retracted foot. The tangent to the shell margin at point M will therefore lie nearly parallel to the hinge axis (Fig. 16). In the initial erect probing orientation, with the extended foot anchoring the shell in place, the shell will then be positioned so that the substratum is tangent to it at point M. The hinge axis will therefore lie nearly parallel to the substratum (that is, be nearly horizontal). This erect probing orientation will usually be maintained throughout the burrowing period, as described in the previous section. As documented in the final section of this study, the great majority of burrowing bivalves that lack pedal gapes are, in fact, oriented with the hinge axis approximately horizontal in the erect probing orientation.

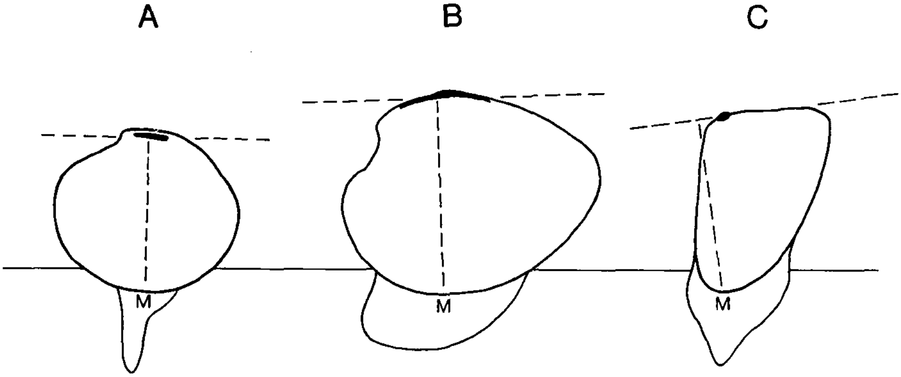


Figure 16. Site of pedal emergence at maximum shell gape (M) and erect probing orientation. A = lucinid; B = venerid; C = donacid.

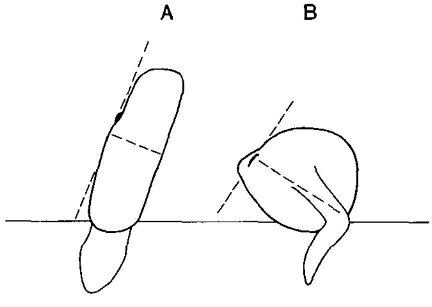


Figure 17. Methods of avoiding pedal emergence at right angles to the hinge axis. A = *Tagelus* (pedal gape); B = cardiid (L-shaped foot).

There are exceptions to the above rule that are worthy of consideration. One widely adopted means of avoiding pedal emergence at point M is employment of a pedal gape elsewhere along the shell margin. Most pedal gapes are positioned so as to allow pedal emergence in a direction nearly parallel to the long axis of elongate shells (as in *Yoldia, Solemya, Mactra, Tagelus, Ensis,* and *Mya*). The terminal pedal gape of most cylindrical and blade-shaped shells thus permits penetration of the substratum in a direction parallel to the shell's long axis (Fig. 17A). This manner of elongation has special functional significance. In the Lucinidae, in which the dominant inhalent current enters anteriorly and the posterior current exits posteriorly, the shell's long axis is normally horizontal in life position. The erect probing orientation and life orientation are nearly identical (Figs. 16A, 18A). In contrast, nearly all more advanced burrowing bivalves employ posterior inhalent and exhalent current apertures (Fig. 18B-E). By definition, these posterior apertures are located approximately 90° from the pedal (ventral) region in the primitive condition. The foot must, of course, be directed downward for penetration of the substratum. If the shell were to become enlongate in the simplest geometric manner (in a dorso-ventral direction), the animal would be required to rotate 90° from its burrowing orientation after burial to assume the normal posterior-up life position for ready communication with the overlying water mass. This rotation would be very difficult to accomplish in light of the shell's elongate shape. The alternative would be to maintain the burrowing orientation as the life position by bending the siphons upward after their horizontal emergence from the shell. Such a disposition of the siphons would be inefficient in requiring especially long siphons for a given depth of burial and in producing more frictional resistance to water flow than would exist in straight siphons (Fig. 18B).

Very few elongate shells rotate from their burrowing orientation to a markedly different life position; for most, the two positions are nearly identical. By distorting the primitive symmetrical shape (Fig. 18A) in a way that brings the ventral (pedal) region closer to the anterior region, the foot becomes located nearly or exactly opposite the siphonal region and the burrowing orientation can approach or become the life orientation, with the siphons passing directly upward (Fig. 18D, E). In very elongate species, a pedal gape is commonly required to accommodate this distortion by permitting the foot to emerge near

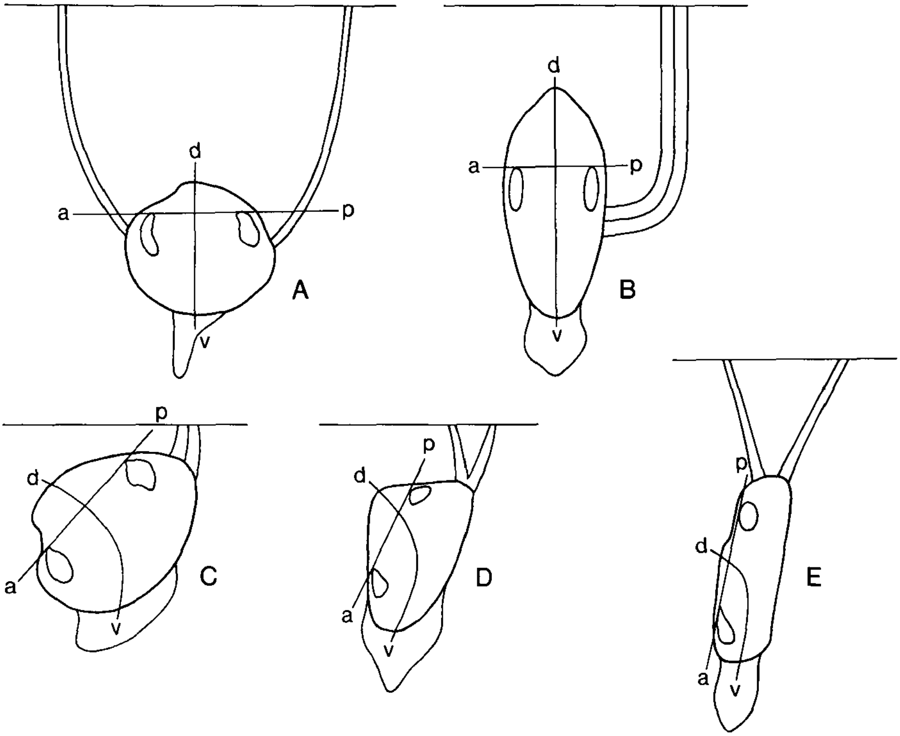


Figure 18. Shell elongation, pedal emergence, and life position. A = lucinid; B = hypothetical form illustrating dorso-ventral elongation; C = venerid; D = donacid; E = sanguinolariid (*Tagelus*). Antero-posterior and dorso-ventral axes shown as crossed lines (ap and dv).

the anterior, at a location that opens very little when the valves are spread (Fig. 17A, 18E).

The Cardiidae exhibit a different type of deviation from the hinge-axis-horizontal rule. Cardiids typically possess a muscular, L-shaped foot (Pl. 19, fig. 5; Pl. 21, fig. 5). When this unusual foot is extended, the proximal portion passes between the valves at point M, but the distal portion bends sharply in an anterior direction (Fig. 17B). The result is that the hinge axis is tilted forward of horizontal in the erect probing position. Most cardiid shells (for example, Pl. 21, figs. 3, 4) are drawn out dorso-ventrally, shell height often exceeding shell length. Ventral expansion of the shell is required to accommodate the L-shaped foot, when withdrawn (Pl. 21, fig. 5).

Rocking Movement

The rocking movement that carries the shell forward and back from the erect probing orientation for downward penetration varies from 0°

to about 45°. My data for this angle are only approximate for the species studied but suggest a distinct relationship to shell form.

Trueman and others (1966) have claimed that the angle of rotation during rocking is greatest for obese species, which penetrate the substratum with difficulty, and least in compressed species, which require very little rocking for penetration. From my data, it appears to be degree of elongation (L/H) rather than obesity (H/W) that is best correlated with angle of rotation. In Figure 19, approximate angle of shell rotation in burrowing is plotted against shell obesity and elongation. There is no apparent relationship between angle of rotation and obesity (Fig. 19A). But in 14 of the 15 very elongate species (L/H >1.60) the approximate angle of rotation is 15° or less, markedly smaller than the average value for less elongate forms (Fig. 19B).

Species with relatively low L/H values (approaching 1.0) are usually nearly circular in ventral outline. Whether slender or inflated,

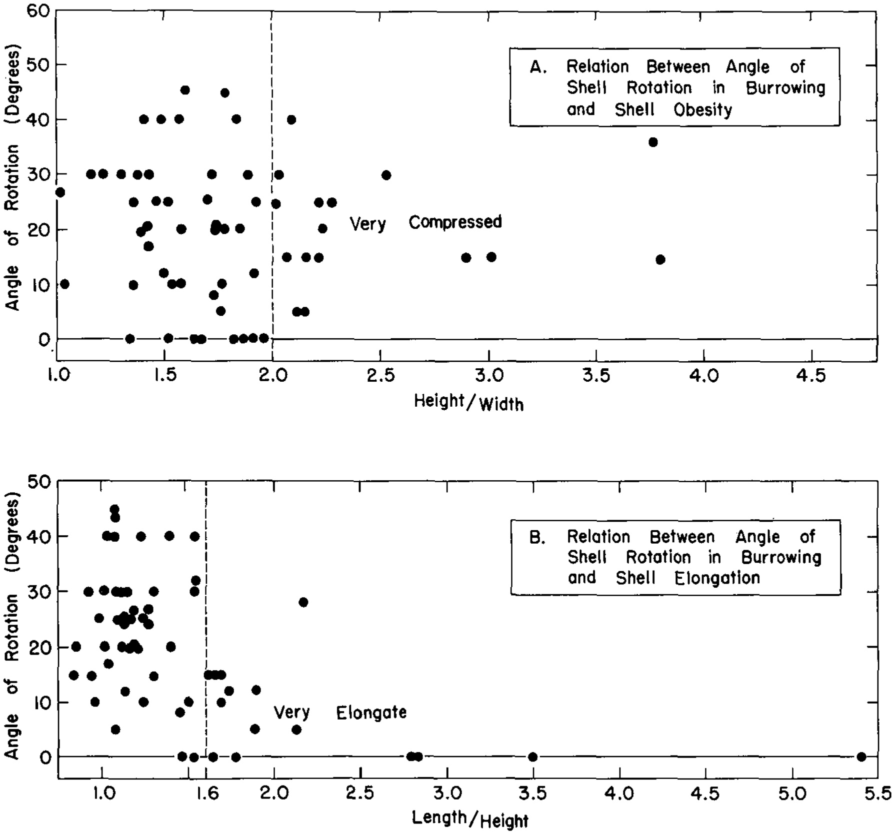


Figure 19. Relation between angle of shell rotation in burrowing and gross shell shape. A = relation to obesity; B = relation to elongation.

most use a pronounced rocking motion to saw or slice their way into the sediment. Examples belong to diverse taxonomic groups: Lucinidae (many genera), Cardiidae (*Trachycardium, Laevicardium*), Veneridae (*Dosinia, Cyclinella*), Semelidae (*Semele*), Tellinidae (*Macoma balthica, Strigilla*).

In contrast, very elongate forms use very little or no rocking movement. As discussed in the preceding section, the foot of such forms usually emerges in a direction nearly parallel to the shell's long axis (often through a pedal gape). The shell opposes the substratum with a very small surface area for its volume and can penetrate the sediment without the need for appreciable rocking movement. In fact, the ventral and dorsal shell surface areas are large for the shell volume, and rocking movement is virtually impossible in such genera as *Solemya, Ensis,* and *Tagelus,* once partial burial is achieved. Examples of elongate taxa employing little or no rocking movement are found in many families: Solemyidae (*Solemya*), Veneridae (*Macrocallista*), Mesodesmatidae (*Mesodesma*), Donacidae (*Donax*), Sanguinolariidae (*Tagelus*), Tellinidae (*Macoma tenta, Tellina listeri, T. radiata*), Solenidae (*Ensis*), and Myidae (*Mya*). The only very elongate species shown in Figure 19B that employs a large angle of rotation is *Yoldia limatula,* which inhabits soft, muddy sediments.

Direction of movement during sediment penetration is also correlated with shell form. For many bivalve species that use rocking movement, downward penetration is not vertical, but has a forward component. Allen (1958) has postulated that the presence of such a forward component among lucinids is related to the presence of a heel in the lucinid foot; diplodontids and thyasirids, which lack a heel, also lack a forward component. Ansell (1962) has stated that all five venerid species he studied, including a species of *Dosinia,* have a forward component of movement and that this component is correlated with their possession of a pedal heel. I have studied burrowing movements of 2 species of *Dosinia* (p. 162), 1 species of the closely related genus *Cyclinella* (p. 163), and 6 lucinid species. All 9 of these species possess pedal heels, yet all have been observed directly and by X-radiography to habitually burrow vertically downward, with no forward component (for example, Pl. 18, figs. 1, 2). They are all distinctly circular in outline (H/L 1.04 to 1.12). Circular shell outline is, in fact, the shell feature that is best correlated with their common habit of burrowing vertically downward. Other nearly circular species that lack a forward component in burrowing are the two tellinaceans *Semele proficua* (p. 173) and *Strigilla* spp. (p. 183-184), and most cardiids. In circular forms, the axis of rotation for rocking movement is usually very near the center of the circular shell, and rocking motion involves a smooth slicing motion of the shell margin against the substratum (Fig. 20A).

As Quayle (1949) has pointed out, when an ordinarily adept bivalve burrower has difficulty penetrating the substratum, its burrowing sequences may produce horizontal forward movement along the substratum surface. This type of movement is very common for species that characteristically have difficulty penetrating the substratum, including a few circular species. For example, members of the disc-like genus *Glycymeris* are sluggish burrowers that tend to crawl for considerable distances before achieving burial (Pl. 7, fig. 3). Likewise, the unusually obese and slow-burrowing arcid *Americardia* (p. 155) commonly moves forward as it penetrates the substratum.

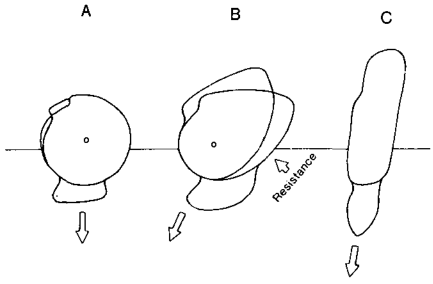


Figure 20. Relation of shell rocking movement and direction of penetration to shell elongation.

In contrast, species with moderately elongate shells (L/H 1.2 to 1.39) nearly always have a forward component of movement. This rule applies to typical venerids, such as *Mercenaria* and *Chione,* and to other taxa with comparable shapes. The axis of rotation for rocking movement is eccentric in these forms, nearly always lying toward the rounded anterior end of the shell. The posterior ventral region of the shell is then forced against the substratum during the backward phase of rocking movement, meeting with considerable resistance (Fig. 20B). The shell therefore tends to move forward as well as downward.

Very elongate species, which tend to use little or no rocking movement, penetrate the substratum in a direction nearly parallel to the shell's long axis (Fig. 20C). If pedal emergence is terminal, movement is usually nearly vertically downward, or in a direction within 45° of vertical, as in *Solemya, Mesodesma, Donax, Tagelus,* and *Ensis.* If pedal emergence is oblique to the shell's long axis, the shell penetrates at a lower angle from the vertical as in *Yoldia* and *Macrocallista* (Pl. 2, figs. 1-7; Pl. 24, figs. 1-6).

In summary, most species with circular shell outlines rock through a large angle of rotation and penetrate vertically downward in burrowing. Moderately elongate forms tend also to use large angles of rotation, but usually move forward somewhat as they penetrate the substratum. Both circular and moderately elongate species that are extremely sluggish burrowers commonly travel horizontally for considerable distances before achieving burial. Very elongate forms tend to rock very little, if at all, and penetrate the sediment in a direction nearly parallel to the long axis of the shell.

Burrowing Rate

Rate of burrowing among bivalves has special ecologic significance. Shell form is an important adaptive feature associated with burrowing rate, but is only one of several factors controlling it; anatomical and physiological factors sometimes override shell form as the prime determinant of burrowing rate.

Measurement of burrowing rate presents special problems. It is possible, first of all, to use either of two basic measurements. The first of these is mean shell *velocity* during burrowing movement through a fixed distance. The second is simply the *time* required for movement over a given morphologic interval, such as the maximum shell dimension parallel to shell movement. It will be shown in subsequent discussions that rapid burrowing is nearly always associated with either (1) occupation of shifting substrata, where re-burrowing is commonly necessary, or (2) deposit feeding, where movement to new food supplies is frequently required. The time necessary for burial of the shell is the more meaningful measurement for the first of these associations and mean velocity of movement, for the second. Because a larger number of rapid burrowers live in shifting substrata than the number that deposit feed, *burrowing time,* rather than velocity of burrowing, has been chosen for correlation with ecologic and morphologic features in this study. *Burrowing time* is defined as the time interval between elevation of the shell above the substratum (to a position where it is supported by the foot) and complete burial. This choice decreases the relative values assigned to animals that have relatively large shell dimensions parallel to the direction of burrowing movement. The effect is not great, however, because for a given mass, shell shape is much less variable than burrowing time.

The chief problem in comparing burrowing times for animals of different shapes is one of relative size. Even within a single species exhibiting no ontogenetic change in shell shape, large animals burrow more slowly than small animals. Burrowing times of large and small species therefore cannot be compared directly. This increase in burrowing time with an increase in size is explained in large part by the fact that the contraction time of a muscle is directly proportional to its length. Therefore, an animal double the size of another similar animal should move a given distance in an equal time, but only half as far in proportion to its size. This means that a burrowing bivalve twice the size of another of the same species should take twice as long as the other to accomplish a given muscle contraction sequence and twice as long to achieve burial. There are additional considerations, however. According to the Principle of Similitude propounded by Thompson (1942), as an organism grows, its weight (proportional to volume) increases with the cube of any given linear dimension, whereas its strength (proportional to cross-sectional area of muscles) increases with the square of the linear dimension. The animal therefore becomes relatively weaker for its weight as it grows, and movements unaided by gravity may become slower. Trueman and others (1966) have shown experimentally that for a given species being pushed directly into the sediment, resistance to shell penetration is inversely proportional to surface area (or the square of the linear dimension). This relationship may not hold for all shell shapes or all types of burrowing movement, however.

An approximate relationship between size and burrowing time for a given species showing no ontogenetic shape change might be predicted mathematically from the above relationships except for added complexities. The Cube-Square Rule applies not just to muscle strength, but also to such surface-dependent processes as respiration and ciliary feeding. In a recent summary article on molluscan growth, Wilbur and Owen (1964, p. 231-2) have stated:

> The efficiency of feeding in bivalves decreases as the individual becomes larger. Measurements using suspended material or radioactively labelled microorganisms have shown that rate of filtration [in three species] expressed in terms of unit weight or unit tissue is reduced with increased size. . . . But we do not know the cause, whether from a decrease in efficiency of the filtration mechanism or from entrapment of particulates by mucus. In any case, the result is a reduced intake of food per unit tissue. To what degree the observed decrease in relative growth rate with increase in size and age is due to this factor is also unknown.

In fact, physiological aging unrelated to size *per se* may occur. But, if so, it is probably a relatively minor factor in causing ontogenetic growth-rate decrease. Certainly the principal factors are decrease in respiratory and food-collecting capacity per unit volume of tissue. These and similar surface-dependent growth effects are unavoidable without ontogenetic changes to offset them. There is no evidence for such changes in most bivalve species. Growth is therefore a self-limiting process in the Bivalvia. It must also be self-limiting in other taxonomic groups, but the surface-dependence of ciliary feeding in bivalves makes the problem especially evident for them. The complex interaction of surface-dependent physiological processes renders mathematical consideration of a single process, such as muscle contraction time, unfeasible.

In considering the relationship between burrowing time and animal size, the question is really whether size-dependent factors like sediment resistance to shell movement and muscle strength per unit weight invalidate the basic prediction that burrowing time within a species should be approximately proportional to linear dimensions. This question can be resolved empirically. Rapid-burrowing species are especially useful here because they tend to commence burrowing readily and continue without interruption. They can therefore be timed easily in large numbers. Many individuals of the rapid burrower *Donax denticulatus* were carefully timed with a stop-watch. The results are plotted in Figure 21 which shows a nearly linear relationship between burrowing time required for shell burial and shell length. (Any other linear shell measurement could be substituted for length.) It is significant (Fig. 22)

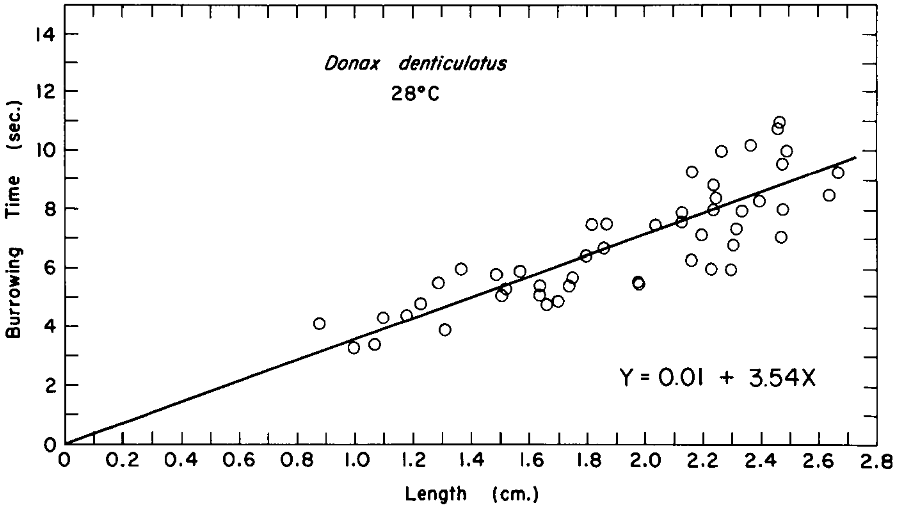


Figure 21. Plot of burrowing time versus shell length for *Donax denticulatus* (sediment 36). Regression equation calculated by least squares method.

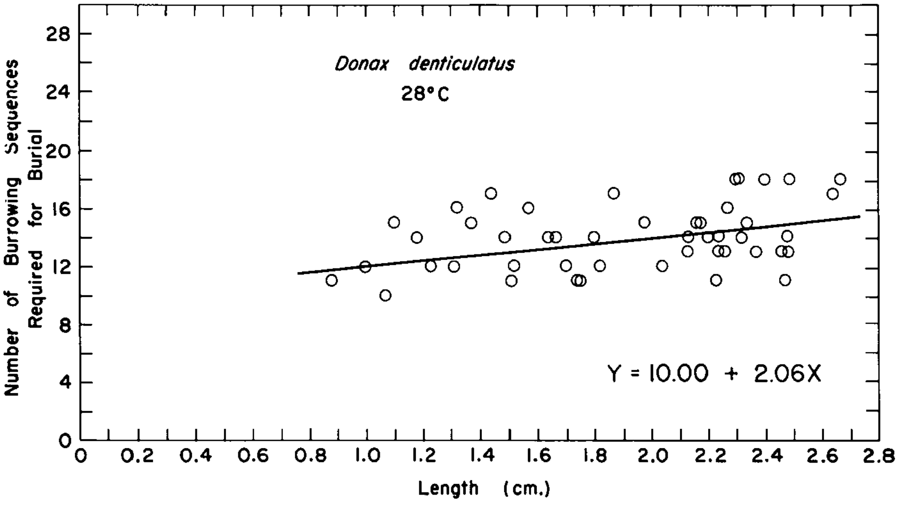


Figure 22. Plot of number of burrowing sequences required for burial versus shell length for *Donax denticulatus* (sediment 36). Regression equation calculated by least squares method.

that there is only a slight increase in number of burrowing sequences required for burial (about 30 percent) over the entire size range. Yet the increase in burrowing time is approximately 300 percent. Clearly the principal factor causing the time increase is a marked increase in the time required for *individual* burrowing sequences, as one would predict from the simple linear relationship between muscle length and contraction time. The effects of other size-related factors appear either to be relatively minor or to cancel each other out.

One can reason that if the linear relationship of Figure 22 holds in an approximate way for all species, it can be used as a means of comparing burrowing times for diverse species regardless of size. For species comparison, a plot of shell length versus burrowing time makes the slope of the resulting curve nearly equivalent to mean velocity for species such as *Donax*, in which movement direction is approximately parallel to shell length.

But use of any linear dimension, whether oriented parallel to direction of movement or not, makes comparison of species in part dependent on shell shape. What we are really concerned with in comparing species is time required for burial of a given *mass*. To make use of the linear relationship suggested in Figure 21, it is desirable to substitute for length a measure of mass that is proportional to linear shell dimensions. This will be the cube root of the mass. In summary, the following proportionalities should hold in an approximate way:

$$\begin{aligned} \text{Length} &\propto \text{Burrowing time} \\ \text{Mass} &\propto \text{Volume} \\ \text{Length} &\propto \sqrt[3]{\text{Volume}} \propto \sqrt[3]{\text{Mass}} \\ \sqrt[3]{\text{Mass}} &\propto \text{Burrowing time} \end{aligned}$$

The validity of the linear relationship observed for *D. denticulatus* has been tested by plotting burrowing time for several species against cube root of mass, which has been multiplied by 100 to reduce the number of decimal places in the numbers representing slopes of lines radiating from the origin (Fig. 23). The species represented are all those for which several times had been taken for animals over a large enough size range to produce a meaningful pattern. The species were objectively selected on this basis without consideration of calculated data. The only suitable species for which data were not plotted is *Mercenaria mercenaria,* whose mass was too great in its larger range to be easily accommodated on a graph with the other species. All times represent uninterrupted burrowing periods.

Figure 23 attests to the crude utility of the linear relationship suggested by the *D. denticulatus* plot (Fig. 21). Deviations from perfect linearity are apparent for some species, but they are minor compared to

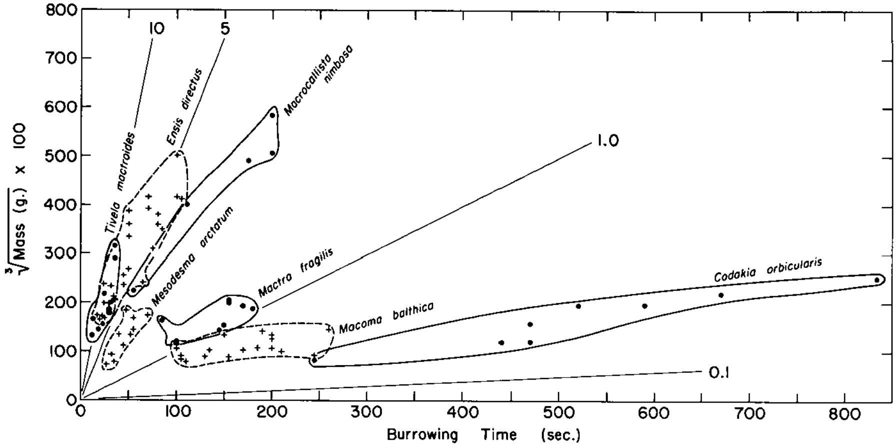


Figure 23. Graph of burrowing time versus cube root of mass. Species included are all those for which measured times were numerous enough and spread over a large enough size range to show a meaningful trend.

differences between species. Data for a species can therefore be used to calculate what is termed a *burrowing rate index*:

$$\text{B.R.I.} = \frac{\sqrt[3]{\text{Mass (g.)}}}{\text{Burrowing time}} \times 100$$

The burrowing rate index is approximately constant throughout the size range of a given species. For nearly all burrowing species of the final section, a burrowing rate index has been calculated from all times obtained in the laboratory and in nature. Timing methods are discussed in the final section of this study. Mean values for the species studied range from 0.01 to 20. The two thousand-fold difference between the extremes and the large spread of intermediate values makes the slight deviations from linearity insignificant for the purposes of this study, where only crude comparisons are required. Descriptive terms for burrowing rate index are listed in Table 4.

TABLE 4. DESCRIPTIVE TERMS FOR BURROWING RATE INDEX VALUES

Very rapid	$\geqq 6$
Rapid	2 to 5
Moderately rapid	0.6 to 1
Slow	0.1 to 0.5
Very slow	$\leqq 0.09$

Relation of Morphology to Burrowing Rate

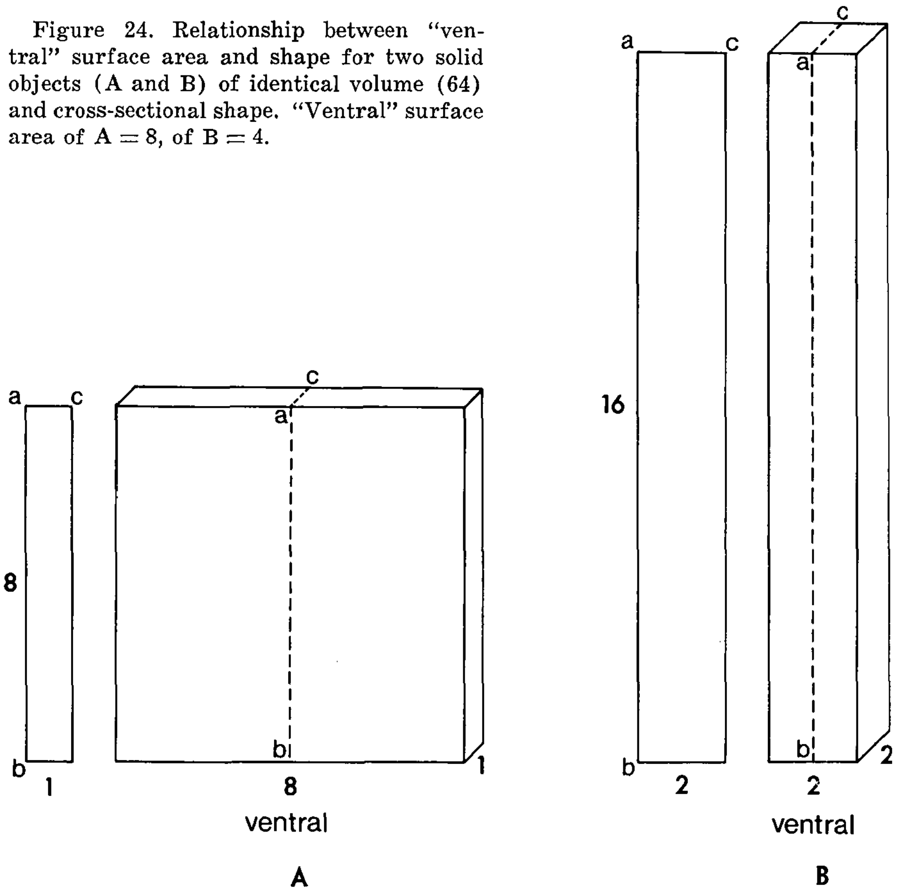
Size reduction is among the simplest adaptations that serve to decrease burrowing time. It has been shown that small animals can bury themselves more rapidly than large animals of the same shape and anatomy. If disinterment is relatively frequent, the need to reburrow often puts a premium on rapid burrowing, and small size may be advantageous. But decrease in size has the disadventage of lowering the animal's mass-to-surface area ratio and raising its center of gravity in life position, thereby rendering it more susceptible to disinterment. The relative advantages and disadvantages of small size must be weighed against each other in the evolution of groups inhabiting shifting substrata.

For deposit feeding, small size is of little value with regard to burrowing efficiency. Although small animals will be able to bury themselves more rapidly than similar large animals, burrowing *velocity* for all sizes will be nearly constant; migration to fresh food supplies will not be facilitated by small size, except perhaps in enabling species to avoid obstacles as they move through the sediment.

Trueman and others (1966) have studied relationships between shell shape and rate of burrowing by subjecting empty shells of four British intertidal species to downward forces and relating force to depth of penetration for each species in a variety of sediment types. Their principal morphologic conclusion is that penetration is easiest for slender species. As a measure of shell inflation, they use the shell profile parallel to the direction of movement and perpendicular to the commissure plane. This measure of shell streamlining is a useful one, but the shell dimension perpendicular to the plane in which it is made is also significant. For example, a disc-like shell will oppose the substratum with a greater surface area than will a cylindrical shell possessing the same volume and cross-sectional shape parallel to the direction of movement (and moving in the direction of its long axis). This relationship is shown diagrammatically in Figure 24, using rectangular solids for simplicity. The same argument can be made for shells of other three-dimensional shapes with identical cross sections. Clearly, a three-dimensional picture of shell shape is necessary for correlation with burrowing rate.

The measure of streamlining adopted by Trueman and others requires precise knowledge of direction of movement in burrowing and is therefore not readily applicable to studies of fossil taxa, even if coupled with a measurement in the third dimension. In the present study, simple shell height, length, and width measurements are employed for correlation of gross form with burrowing speed. For some species, especially those that are nearly circular or very elongate in outline, height and

Figure 24. Relationship between "ventral" surface area and shape for two solid objects (A and B) of identical volume (64) and cross-sectional shape. "Ventral" surface area of A = 8, of B = 4.



width or length may lie in the plane of the profile used by Trueman and others; for other species, they represent components of his measurements. Simple linear measurements such as height, length, and width provide only a crude description of shell shape. With their use, the effective assumption is that shells are rectangular solids. But the chosen measurements have the advantage of being applicable directly to undeformed fossils without knowledge of life habits.

Height, length, and width measurements have been used to construct a 3-dimensional shell shape diagram for burrowing species (Fig. 25). Rapid (and very rapid) burrowers (B.R.I. $\geqslant 2$) are represented by solid dots, to distinguish them from slower burrowers. Few species in the spherical region are rapid burrowers. Most rapid burrowers are streamlined, in being cylindrical, blade-like, or disc-like. An empirical line has been drawn to separate the spherical region of slower burrowers from the region of rapid burrowers. Only 3 of 34 species in the spherical region are rapid burrowers, compared with 18 of 29 in the non-spherical region.

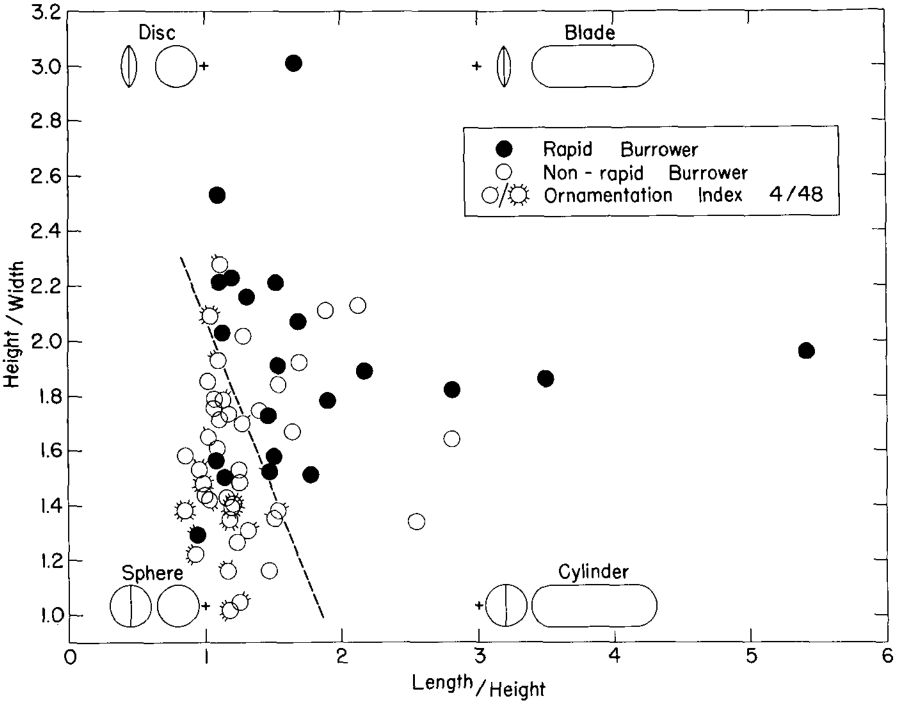


Figure 25. Relation of burrowing rate to gross shell shape and shell ornamentation. Empirical dashed line separates rapid-burrowing region from slow-burrowing region.

Previously, it was shown (Fig. 5) that within the Arcidae, burrowing species tend to be compact (spheroidal) and byssate epifaunal species tend to be elongate. This situation might at first appear to contradict the conclusions drawn from Figure 25. The explanation is that in elongate (non-arcid) burrowers, the ventral (pedal) region is invariably rotated toward the anterior, so that the foot emerges obliquely, or even parallel, to the long axis of the body and shell (Fig. 18). In both burrowing arcids and byssate, epifaunal arcids, however, the primitive bivalve symmetry is retained (the hatchet-like foot of burrowers emerges perpendicular to the antero-posterior axis). Because of this basic feature of arcid symmetry, elongate shells of this group offer more resistance to sediment penetration than compact shells.

Burrowing rate can also be related to shell thickness. Such a relationship is predictable from the simple fact that whole-animal density must increase with an increase in shell thickness. (Both shell density and internal density are relatively constant among the Bivalvia.) High density might be expected to aid burrowing by adding weight for downward penetration. However, animal weight is a minor force com-

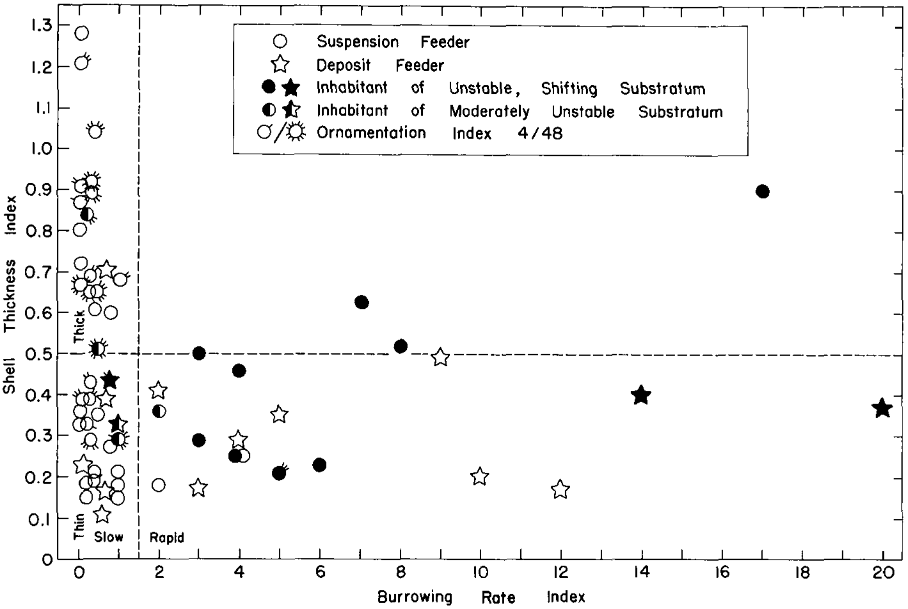


Figure 26. Relation of burrowing rate to shell thickness, shell ornamentation, feeding type, and substratum character:

(1) Nearly all (19 of 22) thick-shelled species are slow burrowers.

(2) Nearly all (18 of 21) rapid burrowers have very thin to moderately thick shells.

(3) Nearly all (19 of 21) rapid burrowers are either (A) deposit feeders, or (B) inhabitants of moderately unstable or unstable shifting substrata.

(4) Only one of 16 deposit feeders is a slow burrower (B.R.I. ⩽0.5).

(5) Nearly all (12 of 13) species with moderately coarse or very coarse ornamentation (O.I. ⩾10) are slow burrowers.

pared to that exerted by the pedal retractor muscles. Furthermore, burrowing is usually accomplished by rocking movement, which requires that the animal's inertia be overcome. If rotation is excentric, gravity must also be overcome. Very elongate species that use little rocking movement nonetheless face the problem of erecting a shell whose center of gravity lies far from the ventral margin, which acts as a rotational axis for shell erection. For nearly all species, a thick shell therefore acts as a hinderance to burrowing.

The *shell thickness index*, as defined in the Introduction, is the ratio of shell volume to internal volume. The methods used to obtain these measurements are discussed in the final section. The relationship of shell thickness to burrowing rate is shown in Figure 26. Nearly all thick-shelled species are slow burrowers. The only two major exceptions are two species of *Donax*, which have other obvious morphologic adaptations for rapid burrowing (p. 67, 81). Similarly, nearly all rapid burrowers are thin-shelled. Again, the only major exceptions are the two *Donax* species. There are, of course, many thin-shelled forms that are slow burrowers. One would expect that a thick shell would not be neccessary, or even desirable, for all slow-burrowing species; for certain ecologic groups, secretion of a thick shell should simply be a waste of metabolic energy.

Burrowing rate can also be related to shell ornamentation. The *ornamentation index* is defined in the Introduction. Nearly all strongly ornamented forms are slow burrowers, while ornamentation is weak or absent in nearly all rapid burrowers (Figs. 25, 26). There are, however, slow burrowers that have little or no ornamentation. They either have no need for it or their need is not strong enough to warrant expenditure of the metabolic energy required for its secretion. Trueman and others have shown that removal of the ribs of *Cardium edule* makes penetration of the substratum easier for an empty shell forced directly downward into the sediment. The obvious conclusion, and the one which Trueman and others have suggested, is that ornamentation adds friction to burrowing movements and increases burrowing time. Rapid burrowers should be expected to lack it for this reason. Slow burrowers might employ it for purposes unrelated to burrowing and tolerate its effect of adding drag to burrowing movements. An argument that can be formulated against this one stems from the fact that strong ornamentation is almost entirely restricted to species in or near the spherical shape region shown on Figure 25. Perhaps ornamentation actually aids burrowing and is used in spherical species for sawing into the substratum to partially offset the adverse effect of shell shape. (It could not be used for this purpose by elongate forms that employ little or no rocking movement.)

To evaluate the effect of ornamentation on burrowing rate, it is useful to consider the distribution of simple, rigid ornamentation among major bivalve taxa, as summarized in Table 5.

Concentric ornamentation is especially common in the Astartacea and Veneracea. Concentric ridges present resistant surfaces to downward movement. During shell rocking movement, these surfaces rotate with the shell margin and cannot perform a sawing or slicing function. They can only hinder penetration and increase burrowing time (*see* Pl. 22, fig. 5).

Radial ribbing is characteristically employed by burrowing members of the Arcacea, Carditacea, and Cardiacea. In the Cardiacea, ribs commonly bear short spines. Nearly always, radial ribbing produces a serrated ventral shell margin. It is possible that this margin may aid burrowing in some species by acting as a saw edge at the margin or an abrasive surface on the valve exterior. The cardiids are, in fact, unusually rapid burrowers for their nearly spherical shape, although

TABLE 5. DISTRIBUTION OF SIMPLE RIDGED ORNAMENTATION AMONG BURROWING REPRESENTATIVES OF MAJOR RECENT BIVALVE SUPERFAMILIES

Superfamily	Concentric	Radial	Cancellate
Arcacea	• •	nearly all	• •
Trigoniacea	• •	nearly all	• •
Astartacea	most	• •	• •
Carditacea	• •	most	• •
Lucinacea	few	few	few
Cardiacea	• •	nearly all	• •
Veneracea	many	• •	many
Tellinacea	few	few	• •

this is in part due to their powerful L-shaped foot discussed earlier. In observing cardiids burrow, I have become convinced that radial ribbing serves as an aid rather than a hindrance, especially to the species *Dinocardium robustum,* which is a rapid burrower that has a thin shell and moderately strong ribbing but no spines. The ribs form a sharp, serrated edge along each valve margin. The margins, which are separated slightly during burrowing, appear to saw into the sand in a more efficient manner than the straight valve margins of the smooth-shelled cockle *Laevicardium laevigatum.* In addition to being smooth-shelled, *L. laevigatum* is both thinner shelled and more slender than *D. robustum,* and yet for burial, it requires more burrowing sequences (approximately 10 versus 7 or 8) and is a considerably slower burrower (B.R.I. 1 versus 5). Laboratory experiments will be necessary to further evaluate the effects of radial ribbing on the burrowing rates of cockles.

A strong case can be made that divaricate ornamentation serves as an aid to burrowing. Divaricate ornamentation is generally of low relief, as opposed to both radial ribbing and concentric ridges, which may be strongly developed. The lucinid species *Divaricella quadrisulcata* (Pl. 15, figs. 6, 7) and two tellinid species belonging to the genus *Strigilla* (Pl. 36, figs. 1-8; Pl. 37, figs. 1, 2) exhibit divaricate ornamentation. The three species show additional morphologic similarities. All three are approximately circular in outline, and in all three, the break between the anterior and posterior ornamentation occurs anterior to the normal axis of the shell. Also in all three, the ornamentation consists of cuesta-like ridges and valleys; the ventral slope of each ridge is the gentle back slope, and the dorsal slope is the abrupt slope. The three species are also united by ecologic and behavioral features. They live in fine or medium sand with little or no mud admixture, and they burrow vertically downward with a pronounced rocking motion.

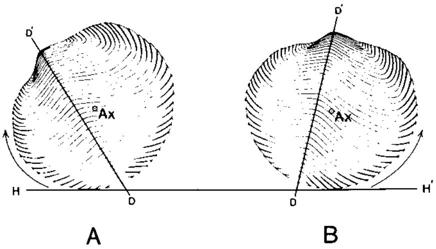


Figure 27. Function of divaricate ornamentation in aiding burrowing of *Divaricella quadrisulcata.* A = shell orientation at maximum forward rotation; B = shell orientation in erect probing orientation. Arrows show displacement of ridges during rotation from each orientation; HH' = horizontal reference line ; DD' = line of demarcation between anterior and posterior ridges; Ax = axis of shell rotation. Location of the demarcation line anterior to the shell midline is related to the forward direction of rocking movement.

The mechanical function of the divaricate ornamentation in aiding burrowing is illustrated for *Divaricella quadrisulcata* in Figure 27. A similar diagram could be constructed for *Strigilla.* If the animal pulled directly downward with little rocking motion, it would gain little from divaricate ornamentation. The key to the function of the unusual ridges is the pronounced rocking motion used by forms possessing them. *Divaricella,* in which the angle of rotation is about 45°, revolves extremely smoothly about a central axis as it penetrates the sediment. As shown in Figure 27, forward rotation from the erect probing orientation permits the posterior ridges to act as a rasp, carrying sand dorsally along the shell surface and margin. The anterior ridges slip through the sand with little friction. Backward rotation to the erect probing orientation reverses the situation; the anterior ridges carry sand dorsally and the posterior ridges slip through the sand. The animal saws its way into the sediment in this fashion. The average back-and-forth rocking movement carries the animal downward a distance equal to only 2 to 5 percent of the shell diameter. Little penetration is accomplished through direct pedal contraction and downward pressure of the shell against the substratum. Though a slow burrower, *Divaricella quadrisulcata* was found to have the highest burrowing rate index of the six lucinid species studied. It is also unusual among lucinids in inhabiting clean sands with little or no mud or gravel admixture and little or no submarine grass cover. In such sandy environments, the special burrowing mechanism of *Divaricella* is effective and also useful (because of the need to reburrow or move deeper within the sediment to offset the effects of current scour).

Divaricella quadrisulcata inhabits very fine to medium sand, but *Strigilla carnaria* and *S. mirabilis* are apparently largely restricted to fine sand just seaward of the breaker zone of sandy beaches. The divaricate ornamentation of these tellinids is correspondingly weaker than that of *Divaricella quadrisulcata,* but is used in much the same way. It is notable that all three species are inhabitants of sands; it is doubtful that their rigid ornamentation could grip mud effectively. All three species are also nearly circular in outline and employ a pronounced rocking movement in burrowing.

Divaricate ornamentation is not common among bivalves, but shows widespread taxonomic distribution, brought about through adaptive convergence. One prominent genus that exhibits it is *Acila,* which is unusual among deposit-feeding nuculids in commonly inhabiting sands. Whether the ornamentation of *Acila* operates in a manner similar to that described for *Divaricella* and *Strigilla* is difficult to predict without observation because in *Acila,* individual ridges are not asymmetrical (cuesta-like).

The oblique ornamentation exhibited by *Tellina similis* (Pl. 32, figs. 1-7) bears a strong resemblance to the divaricate ornamentation just described. The ridges have a cuesta-like form, but run obliquely across the lateral valve surface, where they are oriented nearly parallel to the posterior dorsal shell margin and perpendicular to the central axis of the emergent foot (and to the direction of movement of the shell through the sediment). The gentle back slope of each ridge faces anteriorly, and the steep slope, posteriorly. This means that as the very elongate shell rocks rapidly back and forth through a few degrees during each burrowing sequence, the dorsal and ventral portions of the ridges alternately grip and slide past the surrounding sediment to aid the

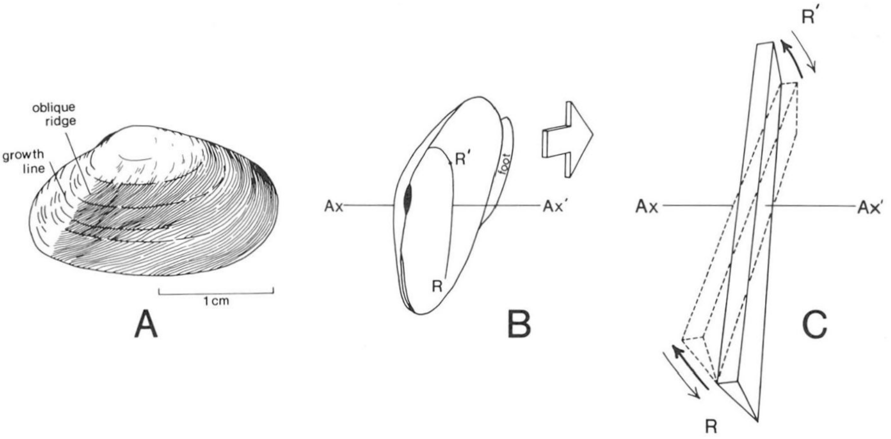


Figure 28. Function of oblique ridges in aiding burrowing of *Tellina similis.* A = external of right value; B = oblique dorsal view of burrowing animal; C = diagrammatic representation of a single ridge; Ax-Ax' = axis of rotation; RR' = single ridge ornamentation. Large arrow in B denotes direction of animal movement. Heavy arrows in C represent rotational burrowing movement involving large frictional resistance between the steep ridge slope and sand, aiding downward shell movement; light arrows represent small frictional resistance.

animal in moving in a direction perpendicular to them (Fig. 28). Again the rocking movement of the shell is the key to the ridges' function.

There is no question that the best morphologic adaptations for rapid burrowing include a smooth, streamlined shell. Radial ribbing and divaricate and oblique ridges may be used to increase burrowing rates of poorly streamlined shells, but can seldom offset the great resistance of the basic shell shape. Certainly, strong radial ribbing also functions like concentric ornamentation in stabilizing shallow burrowers in life positions of shallow burial.

Rugosity is not easily measured because of its variability within species. In general, however, strongly rugose shells seldom belong to rapid burrowers. In addition to lacking strong patterned ornamentation, most rapid burrowers have smooth shells with few strong growth "checks." The shells of many have shiny or glossy exterior surfaces. Examples described in the final section of this study are: *Yoldia* spp., *Macrocallista nimbosa, Dosinia elegans, Tivela mactroides, Donax variabilis, Tagelus divisus, Tellina* spp., and *Ensis directus*. Relatively few slow burrowers have shells with the polished exterior appearance exhibited by these species.

The correlations between morphology and burrowing rate index that have been presented graphically are especially striking in light of the fact that they represent clear-cut bivariate relationships in a multivariate system. In other words, the goal of rapid burrowing is only rarely achieved through a single morphologic adaptation (representing one measured character).

Of the features found to be related to burrowing rate index, shell shape has been the most crudely measured (using only shell height, length, and width). A more detailed picture of shape is needed for accurate burrowing rate analysis of certain species.

The ventral expansion of the cardiid shell to accommodate the large, L-shaped foot has already been described. This expansion is unusual in producing a low L/H value and yet indirectly allowing for increased burrowing speed. In contrast, ventral expansion in most groups (where the foot is not folded) is directed anteriorly so that the foot emerges more nearly opposite the siphons. For this reason, pedal enlargement usually produces an increase in *anterior length* (Fig. 18D). The ratio AL/L has been determined for all species, but because its importance depends on the relative positions of the ventral (pedal) and anterior regions, it cannot be very meaningfully plotted against burrowing rate index. Where present, however, anterior expansion usually indicates an enlarged foot and a rapid-burrowing habit. It is important to note that anterior expansion is usually accompanied by some degree of posterior truncation, which orients the hinge axis so that the maximum marginal gape is shifted anteriorly along with the foot (Fig. 15C). The families in which anterior length commonly exceeds 0.50 are the Nuculidae, Nuculanidae, Mesodesmatidae, Donacidae and Tellinidae. Nuculids are not rapid burrowers, but their relatively large foot partly compensates for their lack of a streamlined shell; they are moderately rapid burrowers. The other four families characteristically contain rapid-burrowing species with smooth, streamlined shells. Anterior reduction is not necessarily correlated with a slow-burrowing habit. The most striking example from the final section of this study illustrating this point is *Ensis directus* (AL/L 0.06; B.R.I. 6).

A triangular anterior-ventral shell margin usually indicates a rapid-burrowing habit. Some donacids (*Iphigenia*, Pl. 29, fig. 2), venerids (*Tivela*, Pl. 24, fig. 9), and many mactrids (*Spisula*, Pl. 26, fig 5) exhibit this feature. All are rapid burrowers (*see* Fig. 39). The pointed, rather than blunt, anterior shape represents an obvious advantage for substratum penetration.

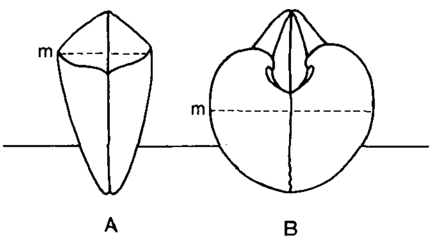


Figure 29. Location of maximum shell width and burrowing rate. A = *Donax* (rapid burrower); B = *Anadara notabilis* (sluggish, partial burrower).

The position of maximum shell width can also be an important indicator of burrowing rate. For most burrowing species, maximum shell width occurs nearer the dorsal than the ventral margin, to effectively reduce the angle of the ventral cross section and improve streamlining. In Figure 29, *Donax*, which provides an extreme example of a shift of maximum width away from the ventral margin, is compared to the semi-infaunal burrower *Anadara notabilis*.

MORPHOLOGY AND LIFE POSITION

The *life position* of a burrowing bivalve species is the normal feeding position assumed by the animal at the conclusion of its burrowing period. In this study, life position is described by two features, depth of shell burial and shell orientation.

Depth of Burial

Throughout this study, *depth of burial* is measured as distance from the sediment surface to the shallowest point on a buried shell. As a convention, shallow burrowers are considered to be those for which depth of burial is less than 2 to 3 cm; deep burrowers are those for which it is greater. Depths of burial used to represent species in this study are the maximum depths measured in nature or the laboratory for individuals of the species.

One of the most striking relationships between bivalve shell form and depth of burial concerns shell thickness. As shown in Figure 30, virtually all thick-shelled forms are shallow burrowers.

One hypothesis that might explain this correlation is that increased shell thickness has evolved in shallow-burrowing species to thwart predation by such carnivores as shell-breaking and boring gastropods. This hypothesis has been mentioned by Carter (1968). A similar hypothesis would be that increased thickness is an adaptation to avoid physical abrasion or breakage of shells lying at or near the sediment surface. One argument against the latter hypothesis stems from the fact that many thin-shelled shallow burrowers (for example, *Spisula* and *Ensis*) inhabit high-energy environments without suffering noticeably from physical shell destruction in life.

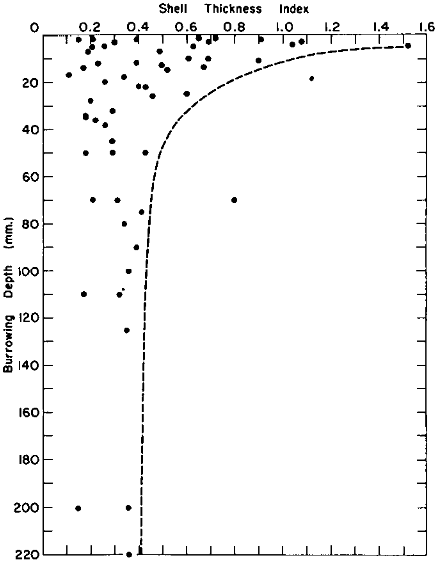


Figure 30. Graph of shell thickness index versus depth of burial. Depths are to the uppermost point of the shell in life position. Depths are the maximum recorded for species in nature or the laboratory.

To further test both shell-durability hypotheses, it is instructive to consider epifaunal species, which are even more vulnerable to shell damage by both physical and organic agents than are shallow burrowers. Byssally attached epifaunal species tend to employ thin shells. Many inhabit rigorous environments and yet fail to exhibit shell thickening. A prominent example is *Mytilus edulis*, which occupies wave-battered rocky shores and current-swept tidal channels. Epifaunal mussels and oysters are also commonly the victims of boring gastropods, such as *Urosalpinx*. The arcids once again represent a useful test case. Figure 31 shows that epifaunal arcids, which are anchored by a strong byssus, tend to have markedly thinner shells than infaunal species, in which a byssus is weak or absent. The only thick-shelled epifaunal species appear to be those that attach to the undersides of rocks and coral heads, where crushing must be avoided. The fact that cemented epifaunal species commonly possess thick shells has also been discussed above. But increased shell secretion by cemented forms is used for attachment and, commonly, for contributing support to the structural framework to which attachment is made. The argument has been advanced above that unattached reclining taxa employ unusually thick shells for stability

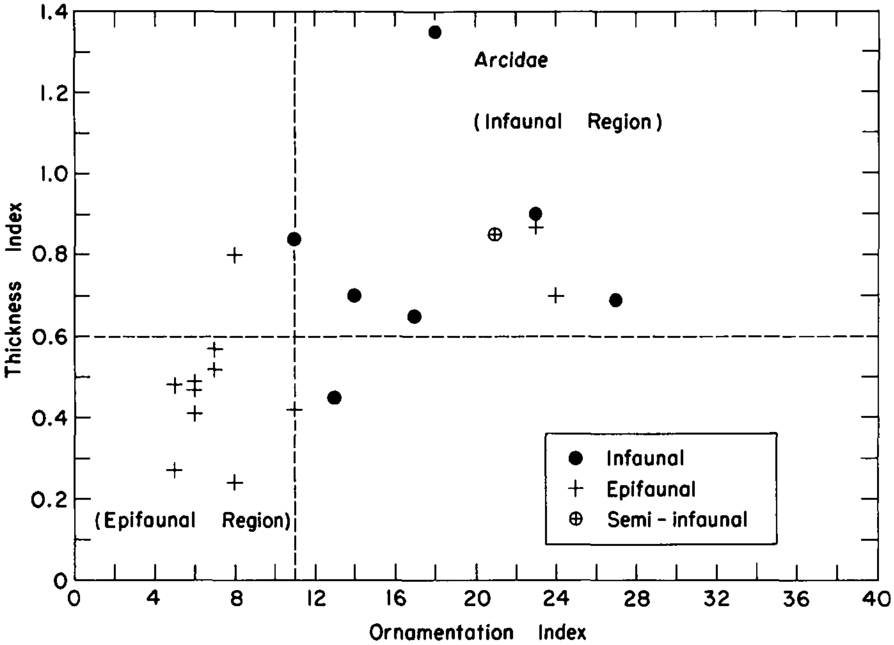


Figure 31. Relation of shell thickness and ornamentation to mode of life in the Arcidae.

rather than durability, for these species are no more exposed to agents of shell destruction than are their byssally attached or cemented relatives, which typically have much thinner shells.

Cemented forms excluded, the virtual restriction of thick shells to unattached shallow burrowers and recliners is strong evidence that shell thickening in the Bivalvia serves a stabilizing function; attached epifauna and deep burrowers are less vulnerable to disruption and transport by waves and currents and can forego the energy expenditure required for secretion of a thick shell. Additional support for these arguments is presented in the discussion of relationships between morphology and sedimentary regime. The few rapid-burrowing bivalve taxa that employ thick shells are ones that inhabit wave-swept, shifting sand, where they are much more vulnerable to disinterment than are infaunal taxa of other habitats. All other factors being equal, the current velocity competent to move an object such as a bivalve is proportional to the square root of its density. Menard and Boucot (1951) found effective density in water to be the most important factor controlling the current velocity required to initiate movement of brachiopod shells on the surface of sediment.

Ornamentation is a second morphologic feature showing a marked relationship to depth of burial among burrowing bivalves. Nearly all strongly ornamented infaunal species are shallow burrowers (Fig. 32). The ornamentation of certain pholad species that burrow deeply in soft sediment (for example, *Cyrtopleura costata*) is a vestigial adaptation from the group's basic boring habit. Other pertinent facts about ornamentation have already been discussed. Most strongly ornamented infaunal species are relatively slow burrowers (Fig. 26), whose shapes lie in the spherical region of Figure 25. Furthermore, strong ribbing (except among pectinids; *see* above) and strong concentric ridges are uncommon among epifaunal taxa. Figure 29 shows that within the Arcidae, strong ornamentation is largely restricted to infaunal species. The chief exceptions among epifaunal arcids are the same species that possess unusually thick shells, namely small forms that attach to the undersides of rocks and coral heads where shell strength is advantageous. The high incidence of coarse, non-spinose ornamentation among infaunal species suggests a physical interaction between ornamentation and substratum. Its general restriction to shallow burrowers suggests a connection with the surface characteristics of the substratum, the most important of which is physical instability. Furthermore, ribs and ridges are found largely in species inhabiting sandy substrata, which are not too fluid for significant friction to exist between sediment and shell at low velocities. While radial ornamentation in some species may aid burrowing, concentric ornamentation can only be a hindrance as discussed above. The resistance of concentric ornamentation to movement, and the ecologic restrictions cited for the distribution of ornamentation among bivalves in general, suggest that concentric ridges serve to increase stability, once the life position is attained, by adding drag. Lack of ornamentation in nearly all deeply buried species supports such an argument.

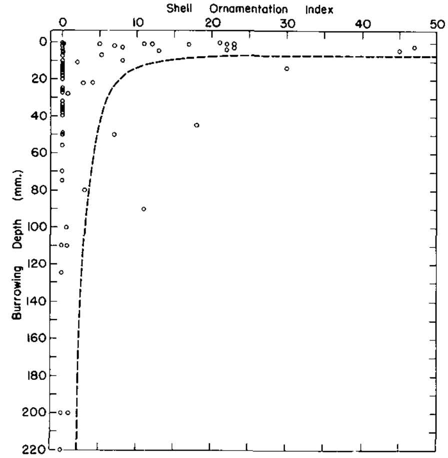


Figure 32. Graph of shell ornamentation index versus depth of burial for burrowing species.

It is especially notable that among certain large venerids having nearly smooth adult shells, the surface of the juvenile shell bears strong concentric ridges. An example is the common species *Mercenaria mercenaria*, in which the juvenile shell crudely resembles the small, strongly ridged venerid *Chione cancellata* (Pl. 22, figs. 3-5), but is more circular in outline. As *Mercenaria* grows, the thick-shelled animal's weight increases more rapidly than its surface area, to provide increased stability against wave and current scour, and the need for stabilizing ridges is apparently lost. Juvenile ridges are entirely worn from the umbonal regions of most adult animals. The greater potential danger of sediment scour to *Mercenaria* juveniles is also reflected by their tendency to assume deeper life positions within the sediment than adults of the same species.

Whether aiding burrowing movements or not, radial ornamentation also almost certainly functions to increase stability once a shell is in place. Most radial ribbing also produces interdigitation along the ventral shell margin. In the absence of radial ribbing, interdigitation may be accomplished on a smaller scale by fine denticulation along the interior ventral margin. Interdigitation of both types is largely restricted to shallow burrowers. Carter (1968) has argued that interdigitation serves a protective function in thwarting predators, especially starfish. A starfish digests a bivalve within its shell by slipping its everted stomach between the slightly separated valves, which it pries apart with its tube feet. Carter attempts to explain the deployment of radial ribbing and marginal interdigitation among bivalves on this basis. I cannot accept this argument. In the first place, the stomach of a starfish is so thin and flexible that it seems unlikely that interdigitation can effectively exclude it. In the second place, one of the bivalve families that most characteristically displays coarse radial ribbing is the Cardiidae, and in most ribbed cardiids there are gaps between the valves, even when closed as tightly as possible, that will permit penetration of a starfish stomach. Also complex spinose ribbing, as in *Trachycardium* (Pl. 21, figs. 3, 4), cannot be explained on this simple basis. Finally, the same argument can be presented that was directed against the hypothesis that thick shells have evolved primarily to thwart predators: Why is interdigitation largely absent from epifaunal species, which are even more vulnerable to predation than are shallow burrowers? Extensive starfish predation on mussels and oysters, in fact, represents a well-known economic problem.

Not only is marginal denticulation almost entirely restricted to shallow burrowers, it is also largely restricted to species in the spherical region shown on Figure 25. It seems evident that it must serve a special mechanical function related to shell shape and habit. Without interdigitation along the ventral margin, the only structures preventing rotational shearing of the valves in the plane of commissure are the ligament and hinge teeth. Obese, shallow burrowers would seem to be especially susceptible to shear because of their broad peripheral shell region (especially the dorsal surface near the sediment-water interface) on which forces can act parallel to the commissure plane. It seems most likely that interdigitation along the ventral margin functions to increase resistance to such shearing forces. Where ribs are present, their ventral terminations offer a ready solution to the problem. Where ribs are absent, minute denticulation along the inner ventral margin serves the same purpose.

A corallary of the foregoing interpretations is the deep-burrowing bivalve species, which are protected from disinterment, should have thin shells with little or no ornamentation. Figures 30 and 32 bear out this prediction. Many deep burrowers are species that live in the intertidal zone, where their deep burial enables them to avoid unfavorable conditions near the sediment surface when the tide is out.

As shown in Figure 33, there is no simple correlation between burrowing rate and depth of burial. In general, the very shallowest burrowers (those in the upper 4 to 5 mm of sediment) lack siphons and extensive mantle fusion and are slow burrowers (Stanley, 1968). Examples are members of the Arcidae, Astartidae, and Carditidae. Cardiids

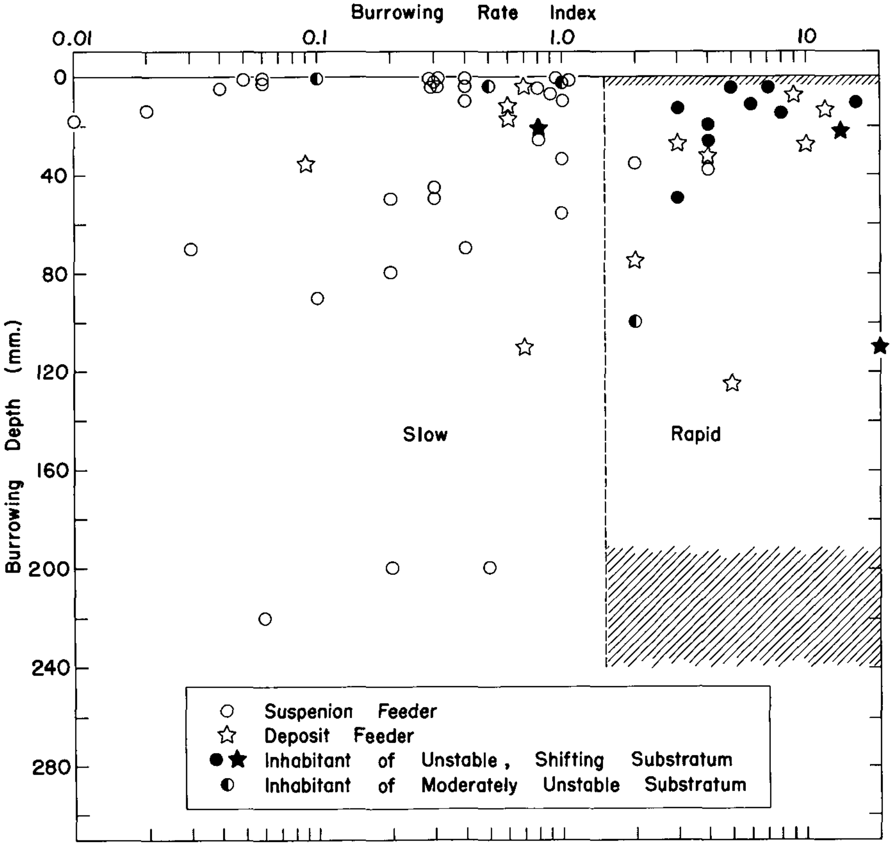


Figure 33. Plot of burrowing rate index versus depth of burial, showing no simple relationship. Feeding type and substratum character also shown. Shaded areas indicate vacant portions of the graph.

have very short siphons and live at very shallow depths, but some species are moderately rapid or even rapid burrowers.

Extremely deep burrowers also tend to be very sluggish. Examples described in the final section are *Anodontia alba* (p. 148), *Divaricella quadrisulcata* (p. 150), and *Mya arenaria* (p. 186). Others are *Tresus* (Pohlo, 1964), *Panope* (Weymouth, 1920), and *Cyrtopleura costata* (Abbott, 1954). These deeply buried genera, except perhaps for *Divaricella*, are seldom entirely disinterred by natural agents and therefore seldom need to reburrow. Most of their burrowing activity is simply that required to accommodate growth during ontogeny or to offset surface scour. Some deep-burrowing species virtually lose the ability to reburrow when very large.

Species living at intermediate depths (5 to 200 mm) exhibit a variety of burrowing rates. Especially in the shallower part of this depth range, rapid burrowing has evolved among inhabitants of unstable, shifting substrata. Most of the remaining rapid burrowers of this intermediate depth range are migratory deposit feeders.

A long-recognized feature indicating approximate depth of burial for bivalves is the pallial sinus, which permits siphons to be accommodated within the shell when withdrawn. No precise measurement of sinus length or area can be used as an index of siphon length, however, because of the variation in siphon proportions among diverse taxa. Most tellinids, for example, have extremely slender siphons compared to suspension-feeding taxa; when withdrawn, they occupy a relatively small space compared to their length when extended.

Life Orientation

Normal orientation after burial may or may not coincide with the erect probing orientation. Where it differs, the change of position usually involves forward rotation after final depth of burial has been reached so that the posterior, current-bearing region is uppermost. There are certain key morphologic features of the bivalve shell that are related to infaunal life orientation.

Very elongate species (L/H 1.6) are unable to rotate their buried shells with ease. As discussed earlier, the foot in such species tends to emerge in a direction parallel, or nearly parallel, to the shell's long axis by anterior displacement of the ventral region. Often a permanent gape provides adequate shell separation for pedal emergence near the shell anterior. The erect probing orientation becomes the life orientation, and the need for post-burial rotation is averted. Therefore, if the burrowing orientation of a very elongate species can be determined (as from the location of a pedal gape), the approximate life orientation will also be known.

Certain very elongate, deep-burrowing forms exhibit a characteristic shell form that illustrates adaptive convergence among several families (*see* Fig. 34, *Tresus* and *Mya*). Typically the valves are thin and approximately oval in outline. Large siphonal and pedal gapes open approximately parallel to the shell's long axis. The ligament is concentrated in a small area and hinge teeth are reduced or absent. As discussed by Trueman (1964), this hinge condition permits rocking of the valves about a dorso-ventral axis during extension and withdrawal of the siphons and foot. Shells of this type belong to deep burrowers that occupy more-or-less permanent burrows. The life position is with the long axis vertical, or nearly vertical. The siphons are long and fused and frequently cannot be withdrawn entirely into the shell. Burrowing capacity is often reduced in adult animals. Examples are *Mya arenaria,* Myidae (Pl. 39, figs 1-3), *Panope generosa,* Hiatellidae (Weymouth, 1920), *Cyrtopleura costata,* Pholadidae (Abbott, 1954), and *Tresus nutalli,* Mactridae (Weymouth, 1920; Pohlo, 1964). *Mactra fragilis* (Pl.

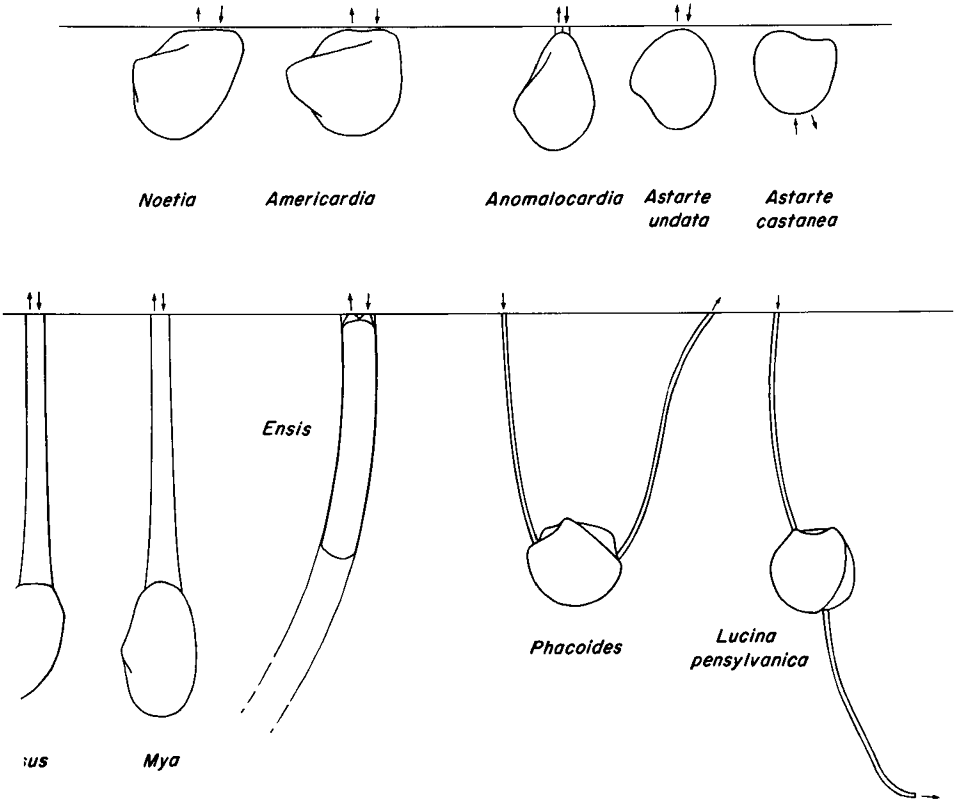


Figure 34. Relation of lateral-view shell outline to life position. Explanations in text.

27, figs. 3-6) approaches this condition. When disturbed, these animals do not retreat rapidly into the sediment, as sometimes suggested, but simply withdraw their siphons very rapidly to the lower portion of the burrow. In mactrids, such as *Mactra fragilis* (Pl. 27, figs. 3-6) and *Tresus nutalli* (Pohlo, 1964), the siphonal gape is oriented slightly closer to the dorsal region than in most other genera, reflecting the life orientation, in which the shell's long axis lies at a slight angle from the vertical, while the siphons pass directly upward.

A second important type of elongate shell is cylindrical and usually truncate at both ends, with large siphonal and pedal gapes. Shells of this type belong to tube-dwellers; their shape reflects the cross-sectional shape of the burrow they occupy. Tube-dwellers can move very rapidly backward and forward through their burrows by means of a plunger-like foot emerging from the ventral gape. Examples from the final section of this report are *Ensis directus* (Solenidae), *Solemya velum* (Solemyidae), and *Tagelus* spp. (Sanguinolariidae). The "Y" shape of the burrow of *Solemya velum* (Pl. 3, fig. 6) is unrelated to the shell form of this species. Burrows of the other two genera, however, commonly reflect shell form. The shell of *Ensis directus* is curved in lateral view, the anterior and posterior being bent dorsally. The animal's burrow has approximately the same radius of curvature as the shell (Pl. 38, figs. 2-5; Fig. 34). The animal lives only in the upper part of the burrow, but descends rapidly when disturbed. The function of shell and burrow curvature is probably to bring the animal to the sediment surface when pursued by a predator. An active burrower, *Ensis* continues burrowing even after being grasped by a human hand. Without following a curved path when pursued, it would burrow to a great depth, from which it might never extricate itself. (Once buried, the elongate shell cannot rotate in the plane of commissure.) The direction of curvature is such that the dorsal margin remains uppermost as the animal burrows to the surface. The shell of *Tagelus divisus* is curved in the opposite direction, but the curvature is less pronounced. The burrow that is formed is corrrespondingly curved in the opposite direction from that of *Ensis*, but in a less consistent and less pronounced fashion. *Tagelus* has long, separate siphons and is somewhat similar to deep-burrowing species described in the previous paragraph in maintaining a relatively deep life position. The siphons pass to the surface through divergent, narrow extensions of the main burrow. Like *Ensis*, the animal descends rapidly to the lower part of its burrow when disturbed.

Many short, robust shallow burrowers (especially arcids and cardiids) have a flattened posterior margin that lies at, or just beneath, the sediment surface in life position. It is flattened because it bears the very short siphons or current openings, which must be brought to the level of the sediment surface (Fig. 34, *Noetia* and *Americardia*). This flattened surface is an excellent indicator of life position. Seilacher (1954) has previously noted the significance of this relationship.

The development of a rostrate posterior, as in *Anomalocardia* (Fig. 34), generally indicates a life position with the long axis vertical. The rostrate structure projects directly upward to the sediment surface. It accompanies very short siphons and, in a sense, takes the place of longer ones.

A pointed, triangular shell posterior normally indicates a life position in which the shell's long axis lies vertical or at an oblique angle from the horizontal. The pointed posterior, although not necessarily directed vertically upward, serves to elevate the region of current flow or siphon emergence to a position nearer the sediment surface. Many nuculanids, astartids, venerids, mactrids, and corbulids illustrate this shape-orientation relationship. The two *Astarte* species described in the final section of this study show contrasting shapes and life positions that support the validity of this relationship. *A. undata* has a typical heterodont shape and lives in a common orientation for shallow burrowers, with the long axis vertical (Fig. 34). *A. castanea* normally assumes an unusual upside-down life position, with the current-flow region undermost (Fig. 34). Because the animal simply filters water through a coarse gravelly substratum, it has no need to elevate the shell posterior. (Whether the use of interstitial water has any special nutritional significance is uncertain.) *A. castanea* also has an unusual shape compared to other heterodonts. It is unusually equant in lateral view (L/H 1.02), and the posterior is round rather than pointed. *A. castanea* has lost the need for a typical pointed and elongate heterodont posterior in adopting its unusual upside-down life position.

Thick-shelled shallow burrowers in which the shell is not strongly inflated and siphons are short or absent are characterized by unusually variable life positions. Examples from the final section are *Glycymeris pectinata, Astarte* spp., *Venericardia borealis*, and *Chione cancellata.* Each of these species has a characteristic life position, but deviations from the norm are much greater than in other species (Figs. 42, 44, 45). Elongate siphons of other groups are usually disposed in a characteristic orientation relative to the substratum surface, which seems to account for the consistent shell orientation of taxa with long siphons.

Deep-burrowing species that live with the commissure plane vertical but the long axis horizontal have no need for elongation, which would not elevate the siphonal region. As a group, the Lucinidae are the best representatives of this habit. The lucinids have almost certainly adopted this life position because of their use of an anterior mucus tube, in conjunction with the single posterior siphon. Emerging at opposite ends of the shell, the mucus tube and siphon have a balancing effect on life orientation. Directing either one toward the sediment surface by rotation of the shell would direct the other downward. An interesting exception is *Lucina pensylvanica,* which is able to extend the mucus tube directly upward because the posterior siphon passes downward, to discharge into the sediment (Fig. 34; Pl. 18, figs. 1, 2). This orentation is reflected in the shell outline. The anterior region of the shell, where the mucus tube emerges, is produced into a bluntly pointed projection, and the entire anterior dorsal region is compressed, to elevate this projection to a position closer to the sediment surface (Pl. 18, fig. 4).

It has been suggested by Ansell (1961) that the venerid genus *Dosinia* has adopted a life position similar to that of most lucinids, with the antero-posterior axis horizontal and the siphons emerging horizontally before bending upward to the surface. The disc-like shell outline of *Dosinia,* lacking a triangular posterior, is not inconsistent with such a habit. My observations for *D. elegans* and *D. discus,* however, have indicated that these two species live with the antero-posterior axis vertical and the siphons passing directly upward (Pl. 25, fig 6). The related genus *Cyclinella* has a similar life orientation (Pl. 25, fig. 3). These observations prevent me from relating the characteristic, disc-like dosinid shape to the life orientation reported by Ansell.

Perhaps the most well-known relationship between shell form and life orientation in the Bivalvia concerns inequivalve species. In nearly all species whose left and right valves differ markedly in shape, the commissure plane normally lies at some angle (usually 45° or more) from the vertical. The reason for this loss of bilateral symmetry is that there are slight functional differences between the two valves.

Two exceptional groups to the above rule with representatives described in the final section of this study are the Corbulidae and members of the arcid genus *Anadara.* Yonge (1946) has pointed out that *Corbula* is unusual in being inequivalve and yet living with the commissure vertical. He suggests that overlap of the right valve by the larger left valve may improve the animal's ability to eject pseudofeces in a muddy environment by clapping the valves together. A border of periostracum along the left valve margin effectively makes this valve the same size as the right valve when the two are separated slightly. Closure of the valves seals the calcareous margin of the right valve against the inner surface of the left, and greatly reduces the mantle cavity volume. No such function can be ascribed to the very slight overlap of the right valve by the left in the posterior ventral region of certain species of *Anadara* (Pl. 5, fig. 7). The significance of this condition in *Anadara* remains a mystery. Nicol (1958) has listed other vertically oriented species in a survey of inequivalve bivalves, but most have valves that are nearly alike.

The principal burrowing superfamilies in which an inequivalve condition is associated with a non-vertical life orientation are the Tellinacea (Holme, 1961) and the Pandoracea (Allen and Allen, 1955).

The majority of species belonging to the Tellinidae and a few species of the less diversified, but closely related Semelidae possess shells in which the plane of commissure is curved to the right. Usually the bend is restricted to the posterior region. For four British tellinid species, Holme (1961) has correlated the bent-commissure condition with a life position on the left side and the long axis within 30° of horizontal. All ten tellinids and semelids of the final section that are inequivalve have non-vertical life positions, lying on the left side. The remaining species (*Cuminga tellinoides, Macoma balthica, Strigilla carnaria,* and *S. mirabilis*) are so nearly equivalve that their shell posteriors cannot be said to bend consistently either to the left or the right. All but one of these (*S. carnaria*) have vertical life positions.

Holme (1961, p. 703) has suggested that the tendency of tellinids to lie on one side may facilitate horizontal migrations for "fuller exploitation of the soil . . . " or "finding more favorable areas or for migrations up and down the shore." The uniqueness of the tellinaceans' deposit feeding habit and the unusual nature of their life orientation indeed suggest that there may be a relationship between the two.

The first question that arises concerns what advantage the horizontal or near-horizontal orientation might offer for the siphonate deposit feeding habit. Nearly all tellinaceans that lie on one side migrate laterally in the course of feeding. Rapid burrowing for lateral movement calls for a streamlined shell. Most deposit feeding tellinaceans are blade-like, but a few are disc-like. Virtually none is cylindrical. Some species lie with the long axis horizontal, others with their long axes at angles of up to 45°. The simplest means of traveling laterally would be to move in a straight line. One method of achieving this goal would be to employ an elongate, cylindrical shell, which would tend to produce linear movement; the shell would then require a terminal gape and lie in the sediment with the long axis at a low angle. The chief difficulty imposed by such a form is that it would permit rotation of the shell about its long axis, even if the axis itself maintained a nearly constant orientation.

Even if linear travel cannot be attained, it is desirable that movement between feeding stations, especially for species lying at low angles, be within a single plane so that depth of burial will be controlled and standard life position maintained. The compressed shell that typifies deposit feeding tellinaceans, whether elongate or disc-like, does not easily rotate about its long axis. The shell tends to hold the animal in a single plane (the plane of commissure). If such a shell were oriented with the long axis nearly horizontal but the plane of commissure vertical, the shell would be of little aid in controlling vertical position in the sediment; the flattened valve surfaces would effectively oppose only lateral movement (Fig. 35A). In the typical tellinid life position, however, the flattened valves lie more nearly horizontal and tend to prevent

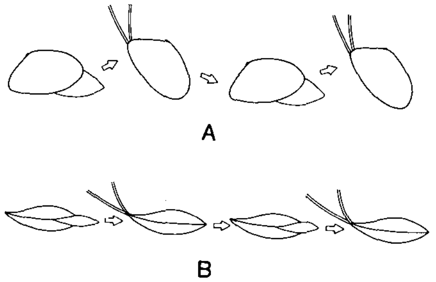


Figure 35. Lateral burrowing movements of the Tellinidae. A = burrowing and feeding orientations of a hypothetical tellinid-like form living with the commissure surface vertical; B = a typical deposit-feeding tellinid, not requiring rotation from its burrowing orientation to attain its feeding orientation.

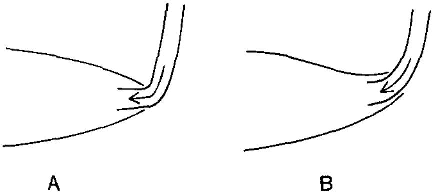
upward or downward movement (Fig. 35B). The horizontal or nearly horizontal life position and compressed shell thus aid the animal in maintaining a fixed orientation and a constant, or controlled, depth of burial. I know of no tellinid species in which the foot emerges parallel to the shell's long axis. Movement direction in burrowing is therefore not parallel to the long axis, but the need for such movement is unnecessary because of the restriction of movement to a single plane. The rocking motion of burrowing, when present, takes place within this plane.

Of the three deposit feeding tellinacean species of the final section that live with the commissure plane vertical, at least one (*Cumingia tellinoides*) moves very little after assuming its life position. Brafield and Newell (1961) report migratory deposit feeding movements in *Macoma balthica* living intertidally in England; subtidal representatives of this species seem to remain largely stationary, once buried.

Given the advantage of the low-angle life position for lateral movement, what is the significance of the inequivalve condition in tellinids? If its function were to produce a curved burrowing path, one would expect shell curvature to involve the entire commissure line or be restricted to the shell anterior. Yet it is most frequently restricted to the shell posterior and, often, to the narrow region of siphon emergence. Furthermore, I have observed by X-radiography that feeding movements of most species tend to be restricted to a single plane, rather than following a curved path.

Feeding capacity is one of the most important features upon which selection pressure acts in animal species. In the Bivalvia, pumping rate for food intake must be primarily controlled by the effectiveness of the ctenidial ciliary mechanism and by frictional resistance to current flow within the mantle cavity and siphons. The upward bend or twist in the region of siphonal emergence of tellinids serves to broaden the radius of curvature where a siphon turns upward. This condition streamlines the flow of water while allowing the siphon to pass nearly directly upward to seek a short route to the surface (Fig. 36). In most species, the inhalent siphon passes nearly vertically to the surface; the exhalent siphon may pass upward, horizontally, or downward. Commonly, it discharges into

Figure 36. Function of the bent posterior in the Tellinidae. A = current flow constriction in a hypothetical form lacking a bent posterior; B = streamlined flow in a typical tellinid.



the sediment. A striking example of a sharp deflection of the shell margin permitting upward turning of only the inhalent siphon is seen in the shell of *Tellina listeri* (Pl. 33, figs. 9, 10). As would be predicted from shell form, the exhalent siphon of this species discharges downward into the sediment at a low angle (Pl. 33, fig. 11).

Of the Pandoracea, the genus *Pandora* is inequivalve and lies on one side very close to the sediment surface. Allen and Allen (1955) have presented convincing experimental data indicating that the British species *P. inaequivalvis* favors a life position with the curved left valve undermost. Having been unable to determine a preferred life position for *P. gouldiana* (p. 188, Fig. 48), I hesitate to draw definite conclusions concerning the functional significance of the inequivalve condition in *Pandora*. From the data of Allen and Allen (1955), it would appear that the convex valve may normally lie undermost to permit a gentle upward bend in the short siphons, such as that described for tellinaceans.

MORPHOLOGY AND SEDIMENTARY REGIME

The term *sedimentary regime* refers to the physical environment in which sedimentation occurs. It includes the physical characteristics of the water mass and the nature of the sediment being deposited. As discussed in the Introduction, sedimentary regime is the most important environmental factor controlling morphologic adaptations of bivalves.

Shifting, Coarse-Grained Substrata

In areas of the marine realm where strong currents or waves act upon the bottom, fine-grained particles are winnowed out and only coarse-grained sediment remains. The surface of the remaining sediment is physically unstable; particles move laterally in traction or suspension. Most nearshore environments of this type are under the influence of wave action or tidal currents; exposed sandy beaches and tidal channels are the most common examples of such "high energy" environments. There are very few marine species that inhabit these unstable sedimentary regimes. Yonge (1950) has discussed the problems of survival on sandy shores. Very similar problems are encountered in and along the margins of tidal channels. Very few epifaunal taxa inhabit either environment. (Banks of *Mytilus* along European tidal channels represent a notable exception.) It is doubtful that many infaunal Paleozoic macro-invertebrates were able to dwell in such environments, where the premium is generally on rapid burrowing to maintain a buried life position. Judging from shell form, very few Paleozoic bivalve taxa, except mud-dwelling protobranchs, were rapid burrowers. The rigors of shifting, coarse-grained substrata exclude all but a few living bivalve genera.

Interrelationships among burrowing speed, shell thickness, ornamentation index, feeding mechanism, and sedimentary regime are presented graphically in Figure 26, which has been referred to earlier. Use of a single graph permits visual inspection of relationships among all five features simultaneously. Furthermore, individual species would lose their identities if several graphs were used. The major conclusions that can be drawn from the graph are listed in its caption. Figure 26 shows that 11 of 12 animals judged typically to inhabit unstable, shifting substrata are rapid (or very rapid) burrowers. Most have thin, smooth shells whose shapes fall within the non-spherical region of Figure 25.

Among the rapid-burrowing shell forms associated with extreme high-energy regimes are two that stand out as classic examples of adaptive convergence. They are illustrated in Figure 39. One is the "wedge-clam" shape of *Mesodesma* (Mesodesmatidae) and *Donax* (Donacidae), which is characterized by posterior truncation and extreme anterior-ventral elongation, which reflects the large foot (Pl. 26, figs. 7-9; Pl. 28, figs. 1-9). The maximum shell width is near the posterior margin. The other is the "surf-clam" shape of *Tivela* (Veneridae) and *Spisula* (Mactridae), which is characterized by a triangular outline, the anterior being pointed for ready penetration of the substratum (Pl. 24, figs. 7-9; Pl. 26, figs. 4-6). *Iphigenia* (Donacidae) is morphologically intermediate between the two groups (Pl. 29, figs. 1-4).

It is extremely significant that 5 species belonging to these genera represent 5 of the 6 thickest-shelled rapid burrowers studied (Fig. 26). They are *Donax denticulatus*, *D. variabilis*, *Tivela mactroides*, *Mesodesma arctatum*, and *Iphigenia brasiliensis*. Obviously special metabolic effort is expended by these species to develop thick shells, despite the sacrifice of burrowing rate that must accompany increase in whole-animal density. Special shell form and pedal adaptations largely counteract the burrowing rate loss resulting from increased shell thickness.

The most obvious interpretation of extreme shell thickening among these few inhabitants of shifting substrata would be that increased shell strength is required to prevent shell destruction by physical abrasion or breakage. Arguments have been directed against such a hypothesis, based on the presence of thin-shelled infaunal species like *Spisula* and *Ensis* in similar environments and the preference of such thin-shelled epifaunal species as *Mytilus* for exposed, wave-battered rocky shores and current-swept tidal channels. A shell thickness index of about 0.25 (depending on morphology) renders most shells strong enough to withstand physical forces encountered in any normal benthic situation.

A more reasonable argument concerning the significance of shell thickening among certain rapid burrowers in shifting substrata is similar to the arguments presented to explain the significance of shell thickening among reclining species and shallow burrowers in general: namely, that shell thickening serves to increase physical stability. Maintaining a stable life position is perhaps the most difficult problem facing species that inhabit high-energy regimes. Ability to reburrow rapidly is only one solution to this problem. A more direct partial solution is to avoid disinterment in the first place by increasing whole-animal density. Once dislodged, a high-density animal is also less likely to be carried to an unfavorable or lethal environment, such as the upper wash zone of a beach.

It is evident, however, that increased shell thickness is of itself an inadequate adaptation for coping with strongly shifting substrata. While some thin-shelled species (for example, *Spisula solidissima* and *Ensis directus*) have been able to adapt to such regimes by becoming rapid burrowers, only those thick-shelled species that have also evolved rapid burrowing mechanisms are found here in abundance. Clearly, rapid burrowing is the key bivalve adaptation to life in coarse, shifting substrata.

Soft, Fine-Grained Substrata

Fine-grained sediments, where available, settle to the bottom in marine environments where water movements are weak and restricted. When the percentage of mud reaches about 25 percent (depending on silt/clay ratio, organic fraction, and so on) the viscosity and density of sediment are lowered to levels that permit large, dense-shelled animals to sink below the sediment-water interface. In some environments, a low-density layer of clay-sized sediment and organic matter up to about 1 cm thick carpets the denser material below. In the shallow-water marine realm, soft, muddy substrata are found chiefly in restricted bays and lagoons. They also occur in marginal marine estuaries.

As discussed in the Introduction, Davis (1925) and Sanders (1956) have emphasized the higher relative abundance of deposit feeders in muddy substrata than in sandy substrata. Among the Bivalvia, deposit feeders belong only to four shallow-water families, the protobranch Nuculidae and Nuculanidae (Nuculacea) and the heterodont Semelidae and Tellinidae (Tellinacea). Most intertidal deposit feeders are siphon-feeding tellinaceans that burrow deeply to avoid unfavorable conditions at low tide. Other tellinacean deposit feeders live subtidally, as do nearly all nuculaceans.

Suspension feeders living in soupy muds face the problem of clogging by loose, fine-grained sediment. A problem that confronts all species, but suspension feeders in particular, in soupy mud substrata is maintenance of negative bouyancy. One method of at least partly solving this problem is to employ a thin shell, thereby maintaining a low whole-animal density. Another way is to remain small, thereby keeping the surface/volume ratio as large as possible to maximize support from the substratum per unit animal weight.

The second course, rather than the first, has been followed by most bivalve inhabitants of soupy substrata, although many are also thin-shelled. (The thinnest-shelled species described in the final section of this study is *Macoma tenta,* a mud dweller with a thickness index of 0.11.) Figure 37 is a plot of whole-animal mass versus percentage of mud

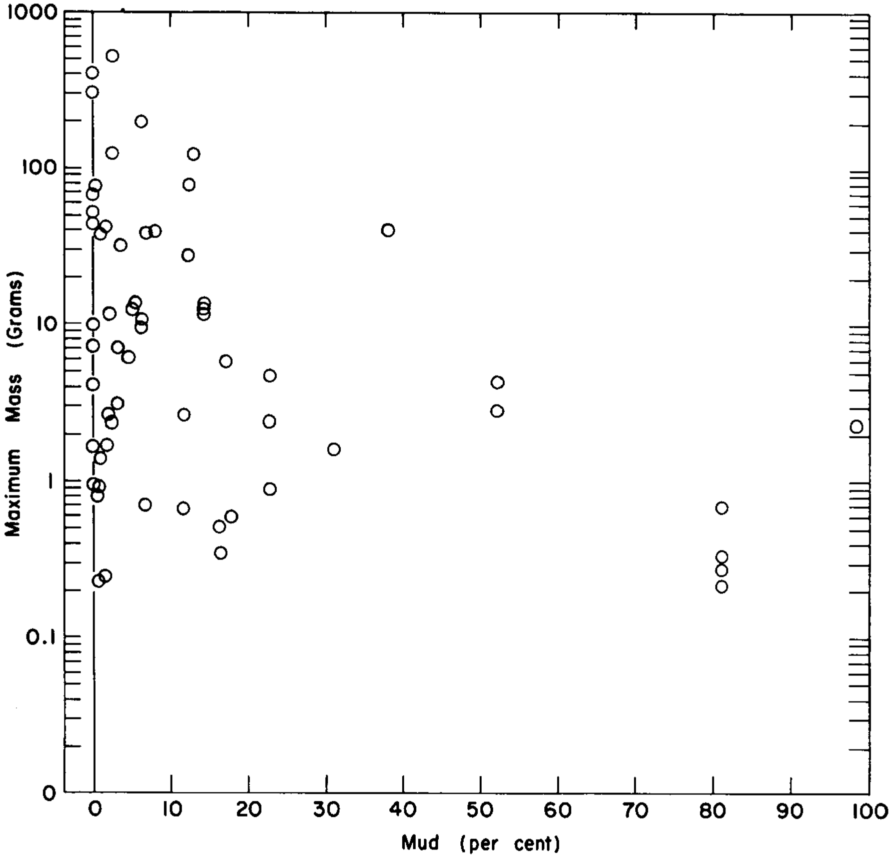


Figure 37. Graph for burrowing species of whole-animal mass versus percentage of mud in the substratum where encountered in greatest abundance.

in the native substratum, for all burrowing species of this study. (Whole animal mass represents the mass of the largest individual encountered, and the sediment sample used for each species represents the habitat where the species was found in greatest abundance.) A logarithmic scale is used for the ordinate. Although relatively few points are present in the high-mud region, all represent small animals. The few typically large filter-feeding species encountered in muddy bay habitats (for example, *Pitar morrhuana* in Buzzards Bay, Massachusetts, and *Dosinia discus* in Biscayne Bay, Florida) were juveniles or stunted forms.

Stable, Firm Substrata

Most marine sedimentary regimes are intermediate between the shifting sand and soupy mud regimes described in the previous sections. They are not so protected and quiescent as basins where extensive mud deposition occurs, and not so strongly agitated by waves and currents as exposed beaches and tidal channels. They are characterized by clean sand, or more commonly, sand containing a small admixture of mud, which renders it more cohesive. Because of their cohesive nature or infrequent exposure to strong currents and waves, such substrata tend to be relatively firm and stable.

Yonge (1950) has stressed the importance of cohesive substrata to permanent burrow dwellers. Both the deep-burrowing *Mya*-like forms and the tube dwellers are restricted to cohesive substrata of muddy sand or, rarely, compact fine sand. *Mya*-like forms must maintain an open tube through which their long siphons can be withdrawn and re-extended following a disturbance. Tube dwellers must maintain an open burrow system for rapid downward escape (and, in *Solemya*, for current flow). The relatively few *Ensis directus* individuals that inhabit large medium-sand megaripples in tidal channels at Barnstable Harbor, Massachusetts, are unable to maintain permanent burrows. The species is much more abundant on adjacent fine-sand tidal flats. Small representatives of *Mya arenaria* living in soft mud are similarly unable to maintain permanent tubes for their siphons. The species is better represented where the substratum is more cohesive.

Many types of bivalve species, in addition to those comprising the *Mya*-like group and the tube dwellers, characterize environments with stable, firm substrata. Their adaptations are too numerous and varied to enumerate. Most are more closely linked to life habits than to the general nature of the sedimentary regime. This intermediate regime is both easier to become adapted to than those described in the preceding sections and represented in a wider variety of shallow marine settings.

Perhaps the most widespread shell form associated with stable, firm substrata is the typical venerid form represented by *Mercenaria* (Pl. 21, figs. 6, 7) and *Chione* (Pl. 22, figs. 1-4, 6, 7). Its diagnostic features are thick valves, an elongate, often pointed posterior, and a rounded anterior. Most commonly, the shell is at least moderately inflated. It is adapted for stability, having a large whole-animal density and a low center of gravity, at the expense of burrowing speed. As suspension feeders in stable substrata, taxa of this type are not frequently troubled by the need to shift locations or reburrow.

MORPHOLOGY AND FEEDING MECHANISM

As discussed in the Introduction, shallow-water bivalve species employ both deposit feeding and suspension feeding mechanisms. Suspension feeding animals have little need to change locations for feeding. Most remain stationary unless disinterred and forced to reburrow. Suspension feeding, as the predominant habit among bivalve species, accounts for little variation in shell form.

Deposit feeders, in contrast, deplete sediment of nutriment, and many species undertake frequent shifts of location in order to obtain fresh food supplies. As discussed in the previous section, the only two bivalve superfamilies known to contain deposit feeders are the Nuculacea and Tellinacea. Because it tends to place a premium on active burrowing, the deposit-feeding habit tends to be associated with specific shell forms. Most deposit feeders that migrate in the course of feeding are rapid burrowers with streamlined shells. Figure 26 shows relationships between the deposit feeding habit and burrowing speed, sedimentary regime, shell thickness, and shell ornamentation. Because most deposit feeding species are restricted to substrata that are relatively rich in organic matter, few live in shifting sands. Even so, most have thin, smooth shells and are moderately rapid or rapid burrowers. Even *Nucula*, which lacks a streamlined shell, has an enormous foot, reflected by the pronounced anterior expansion of its shell (AL/L 0.76), and is a moderately rapid burrower. Significance of the unusual life position and inequivalve condition of most tellinids has already been discussed. It has also been pointed out by Owen (1959) that only deposit feeders that live in very muddy substrata, where food is plentiful, are sluggish. *Cumingia tellinoides*, which lives in a stationary position with its long axis vertical (Pl. 31, fig. 1), is the most notable example described in the final section of this study. The unusually short, wide tellinid *Tellina martinicensis* (Pl. 32, figs. 8-10) is another mud dweller that migrates very little.

Many deposit feeders apparently derive part of their food supply from suspension feeding. According to my observations, this is especially true of tellinid species. Stasek (1965) has stressed the possibility that it may also be true of the nuculids and nuculanids, although so many of their basic adaptations are associated with deposit feeding that suspension feeding, if undertaken, certainly represents only a secondary food-gathering mechanism.

Adaptations for Life in Hard Substrata

Shell adaptations for life in hard substrata, especially for excavating cavities for habitation as reviewed by Yonge (1963), are relatively well known in the Bivalvia and will not be emphasized here. The highly aberrant Pholadacean "shipworms" will not be considered. Dr. Ruth Turner of Harvard University is currently undertaking a thorough study of their biology (Turner, 1966).

The basic ecologic division of hard substratum dwellers that is recognized here is between *boring* forms, that excavate their own cavities, and *nestling* forms, that passively occupy pre-existing cavities. Yonge (1958, 1963) has previously made this important distinction. There is a gradation between the byssally attached category recognized in this study and the boring and nestling categories. Some borers and nestlers (for example, *Lithophaga* and *Hiatella*) retain a byssus.

ADAPTATIONS FOR BORING

The most characteristic shell feature of boring bivalve species is their similarity in gross morphology to deep-burrowing species with long siphons and a life orientation with the long axis vertical (*Mya, Tresus, Panope,* and the like). In fact, some pholadaceans have become facultative or obligate deep burrowers in soft sediment, while retaining most of the basic pholad skeletal features for boring. *Cyrtopleura costata* of the southern United States is such a species, living in cohesive sediments of the intertidal zone. Nearly all borers are cylindrical in gross form and produce tubular borings. Many have shells with short, external spines, which are commonly most prominent on the anterior portion of the shell. In some species, the spines are fluted so that they may pick up small fragments of the substratum, which acts as tools for excavation.

One of the most striking examples of adaptive convergence in the Bivalvia involves boring species of the Pholadidae (Pholadacea) and Petricolidae (Veneracea). As shown in Plate 40, figures 1 to 4, shells of both types are extremely thin, with large siphonal and pedal gapes, and are characterized by short external spines, which are best-developed anteriorly.

The thinness of the valves of mechanical borers is especially significant. It demonstrates the resistance of the bivalve shell to physical abrasion and the importance of thin, light valves to species that must move their shell frequently.

ADAPTATIONS FOR NESTLING

Animals that nestle passively in cavities in hard substrata and lack the capacity for enlarging these cavities commonly have distorted shells that conform to the shape of the constricting cavity. Byssally attached groups sometimes display this feature. *Isognomon radiata* (Pl. 10, figs. 5-8) is a good example, as are some species of the genus *Hiatella* (Hunter, 1949). Yonge (1958) has discussed the marked contrast in shape between the boring species *Petricola pholadiformis* (Pl. 40, figs. 1, 2) and the nestling species *Petricola carditoides,* which lacks ornamentation and tends to conform to the shape of its cavity.

Summary and Conclusions

In the previous sections, ecologic categories have been used as a framework for discussion of morphologic adaptations in the Bivalvia. The organization is reversed in this concluding chapter. Morphologic characters and their adaptive significance are considered individually.

CROSS-SECTIONAL SHAPE

Obesity

Degree of obesity, measured by shell height/width ratio, is one control of streamlining in burrowing species. Very few species in which this ratio is less than 1.5 are rapid burrowers. The most rapid pectinid swimmers also have a compressed cross-sectional shape.

Position of Maximum Shell Width

Among burrowers, maximum shell width in cross-sectional outline commonly occurs in the dorsal or posterior region, opposite the site of pedal emergence. This condition tends to minimize the cross-sectional angle of the leading edge of the shell in burrowing. The very rapid burrower *Donax* exhibits extreme modification of this type. Among epifaunal species that live byssally attached to hard substrata, maximum width is commonly nearer the ventral than the dorsal margin, serving to lower the center of gravity and provide a wide attachment surface. This character distinguishes epifaunal mytilids from those that live partly or entirely buried in soft sediment.

The Inequivalve Condition

An inequivalve condition in byssally attached forms nearly always indicates a life position with the commissure plane lying at some angle from the vertical. Usually the lower valve, which is in closer contact with the substratum, is nearly flat, as in the Pteriacea, Pectinacea, and Anomiacea. This condition provides a broad area of contact with the substratum, for increased stability.

Among reclining species that rest on one valve at the substratum surface, a convex lower valve is often employed to maintain the commissure above the substratum and free from clogging (for example, *Placuna*, *Volviceramus* (Kauffman, 1967), *Gryphaea*, and *Exogyra*). The upper valve of reclining species is nearly always flattened to reduce its resistance to currents, for increased stability.

In life position, the commissure of nearly all inequivalve burrowers lies at some angle from the vertical. Exceptions are some species of *Anadara*, *Corbula*, and a few other genera in which the left valve slightly overlaps the right. The most highly diversified inequivalve burrowers are the tellinids, in which a horizontal or low-angle life position helps to restrict lateral deposit-feeding movement to a single plane. In nearly all such species, the shell posterior is twisted to the right, allowing one or both siphons to pass nearly vertically to the surface without severe constriction where they emerge from the shell and bend upward.

Among free-living pectinids, the most adept swimmers have an effective hydrofoil shape, the upper valve being more convex than the lower valve. Most swimming pectinids (especially shallow-water groups) employ a more convex lower valve for elevating the commissure region above the substratum surface when at rest, to avoid sediment clogging and permit a rapid take-off. A few sand dwellers employ a concave upper valve for holding a disguising layer of sand, while the convex lower valve remains entirely buried.

LATERAL-VIEW OUTLINE

Elongation

Degree of elongation, measured by shell length/height ratio, can be used to distinguish between byssally attached and free-burrowing members of the Arcidae and Carditidae. (Some free-burrowing arcids employ a weak byssus.) In the Arcidae, the two ecologic groups are separated by a L/H ratio of approximately 1.35. Elongation provides a broad ventral surface for stable byssal attachment. Shortening of the shell among burrowers reduces the ventral surface area opposing sediment penetration.

Burrowing bivalve species that are nearly circular in lateral view nearly always employ a large angle of rotation in burrowing and penetrate vertically downward. Deep-burrowing lucinid species are characterized by this shape because of their life orientation with the long axis horizontal (and commissure plane vertical), which is a consequence of the balancing effect of their anterior mucus tube and posterior siphon;

they cannot make use of shell elongation, which is employed by other groups to elevate the posterior region of current flow.

Moderately elongate burrowing species commonly used a large angle of rotation. Usually, there is a strong forward component in their burrowing movement because of their eccentric axis of rotation and the resulting resistance of the posterior margin to penetration.

Very elongate burrowers are characterized by displacement of the ventral region so that the foot emerges anteriorly, opposite the siphons. They often employ a pedal gape to accommodate pedal emergence near the hinge axis. Most of them use little or no rocking movement in burrowing and penetrate the sediment in a direction nearly parallel to the shell's long axis, making use of their slender form for rapid burrowing.

Among the Pectinidae, the maximum shell dimension parallel to the hinge axis above is relatively larger among swimmers than among byssally attached species. This increase enlarges the aspect ratio of the elliptical shell to increase the lift/drag ratio. It also increases the volume of water expelled for jet propulsion and directs the propulsive forces at nearly right angles to the movement direction.

Anterior Shape

Anterior reduction associated with the anisomyarian condition in mytilids is accentuated in epifaunal species. It elevates the posterior region to avoid blockage of current flow and brings the byssal retractor muscles into a position directly above the byssus for exerting a force nearly perpendicular to the ventral margin. In contrast, mytilids living partly or entirely buried at a high angle in soft sediment exhibit less anterior reduction and their byssal retractors are situated so as to exert a force more nearly parallel to the shell's long axis for downward movement.

The elongate anterior auricle of byssally attached pectinids and pteriids is used to prevent shell overturning. The auricle and the shell margin on the opposite side of the byssal sinus contact the substratum at two points distal to the site of byssal attachment to form a rigid support system.

Anterior elongation among burrowing groups, such as the mesodesmatids and donacids, usually reflects enlargement of the foot and a capacity for rapid burrowing.

A triangular shell anterior in burrowing taxa like *Tivela* and *Spisula* is usually an adaptation for easy penetration of the substratum in association with a rapid-burrowing habit.

Posterior Shape

The posterior wing and marginal embayment of many pteriid shells appear to isolate and protect the exhalent current so that it can be expelled as a coherent stream to travel the maximum possible distance from the areas of water intake.

A truncate posterior is used by such burrowing groups as the donacids and mesodesmatids for shifting the region of maximum shell separation anteriorly, for pedal emergence opposite the siphons and movement in a direction parallel to the shell's long axis.

A broad, flattened shell margin posterior to the ligament usually lies parallel to, and very near, the sediment surface in life position, as in the Arcidae and Cardiidae. It brings the broad region of current flow into a position close to the overlying water mass.

A rostrate posterior, as in *Anomalocardia,* is usually directed vertically upward and indicates a shallow-burrowing life position with the long axis vertical. It elevates the posterior region of current flow with a minimal increase in shell material, while permitting the center of gravity to remain relatively deep (at the sacrifice of streamlining).

A pointed, or triangular, shell posterior in equivalve species nearly always indicates a life orientation with the long axis at some angle from the horizontal. Like a rostrate structure, but in a less extreme manner, it serves to raise the posterior region of current flow with a minimum of shell secretion.

COMMISSURE GAPES

Byssal Gape

A permanent byssal gape is present in at least some species of nearly every bivalve family in which adult byssal attachment is widely employed. Location of the byssal gape is an obvious key to life orientation relative to the substratum surface. *Lima scabra* has an unusual, flared byssal aperture, indicating loose, suspended attachment and variable orientation.

Pedal Gape

A pedal gape serves, in nearly all cases, to permit pedal emergence near the anterior shell region. It is nearly always associated with displacement of the ventral region anteriorly in elongate shells, which permits rapid burrowing in a direction more nearly parallel to the shell's long axis. A gape is required because of the shift of pedal emergence to a site near the hinge axis, where little separation is effected by spreading of the valves.

Siphonal Gape

A siphonal gape is used most commonly by tube-dwelling genera with cylindrical shells (for example, *Solemya, Tagelus,* and *Ensis*) and by deep-burrowing genera with elliptical shells (for example, *Mya, Panope, Cyrtopleura* and *Tresus*). In the former, the need for complete valve closure is averted by possession of ability to escape into the lower region of a permanent burrow. In the latter, it is averted by the use of a deep life position and long siphons. Among cylindrical species, terminal gapes are a natural consequence of shell geometry. Among species with elliptical shells, the siphonal gape permits rapid extension and withdrawal of the large siphons without appreciable valve movement.

Gapes for Water Expulsion

Swimming pectinids employ slit-like gapes for water expulsion adjacent to the auricles. Similar gapes are poorly developed or absent among species that are byssally attached as adults.

SHELL THICKNESS

Thick Shells

A shell with a thickness index as low as 0.25, depending on morphology, is generally strong enough to withstand abrasion or breakage in rigorous wave or current-dominated benthic settings. *Mytilus, Spisula,* and *Ensis* illustrate this point. Further thickening, especially beyond a thickness of 0.5, serves primarily to stabilize a shell by increasing whole-animal density.

Pronounced thickening is characteristic of unattached reclining and shallow-burrowing groups, which are vulnerable to disruption by waves and currents, and cemented groups, in which increased shell secretion is associated with attachment and, commonly, formation of a communal organic framework.

Among burrowers, shell thickening is adopted at the expense of burrowing speed. Generally the only rapid burrowers with thick shells are genera that occupy coarse, shifting substrata, where stability is essential (for example, *Tivela, Mesodesma,* and *Donax*). These taxa have developed special morphologic and physiologic adaptations that offset the burden of increased shell thickness.

Thin Shells

Thin shells (T. I. $\leqslant 0.30$) are employed by the majority of rapid burrowers, including most of those adapted for frequent reburrowing in shifting substrata and nearly all those adapted for frequent shifts of location associated with deposit feeding.

Very thin shells (T. I. $\leqslant 0.20$) are used by some mud dwellers for flotation in a substratum of low density and viscosity. A few of these (for example, *Macoma tenta*) are too fragile to survive in a coarse, shifting substratum.

Nearly all swimming taxa (for example, pectinids, limids, *Solemya, Laevicardium,* and *Ensis*) have thin shells, which reduce negative buoyancy.

SHELL SURFACE FEATURES

Long Spines

Long spines are largely restricted to members of the epifauna of tropical regions. *Hysteroconcha,* an infaunal venerid, is an exception (Carter, 1967). In nearly all cases, long spines appear to serve a defensive function against predation. In *Atrina,* they probably serve to protect the exposed portion of the fragile shell from breakage, rather than from predation.

Linear Ornamentation

Prominent external ribs sometimes associated with short spines, are largely restricted to shells of borers and shallow burrowers. In boring taxa, they are often best developed on regions of the shell that are used for mechanical excavation of hard substrata. Strong ornamentation among shallow burrowing taxa serves as a stabilizing function. It is largely restricted to species that are more nearly spherical in shape than disc-like, blade-like, or cylindrical. Most species that are strongly ornamented are slow burrowers. Concentric ornamentation resists burrowing movement. Radial ornamentation may, in some cases, aid burrowing of poorly streamlined forms by producing a serrated ventral margin. Divaricate and oblique ridged ornamentation are special adaptations that aid burrowing by rasping or gripping surrounding sediment during rocking movements of the shell.

Plicae involving the entire shell thickness are largely restricted in the Bivalvia to swimming scallops, in which they provide strength, while permitting the shell to remain thin for low negative buoyancy. *Tridacna* uses coarse shell plication to create a modified zig-zag commissure for increasing the area of siphonal tissue exposure to light, which permits increase in the biomass of symbiotic zooxanthellae.

Non-Genetic Irregularities

Pronounced, irregular rugosity among burrowers is largely restricted to slow burrowers (*Rangia, Mya,* and the like). In contrast, shells with extremely smooth, polished surfaces most commonly belong to rapid-burrowing taxa (for example, *Yoldia, Macrocallista, Dosinia, Tivela, Donax, Tagelus, Tellina,* and *Ensis*).

Irregular shell forms belong chiefly to unattached nestling taxa, such as *Hiatella* (Hunter, 1949) and *Petricola carditoides* (Yonge, 1958), and byssally attached species that occupy crevices in rocks or corals, such as certain isognomonids and arcids. In all these taxa, the shell tends to conform to the shape of the enclosing cavity.

INTERIOR SHELL FEATURES

Ligament Type

Internal ligaments housed in spoon-shaped chondrophores have evolved primarily in deep-burrowing taxa with long siphons, where they permit rocking of the valves about a dorso-ventral axis for siphonal and pedal extension and withdrawal. Most of the other ligament types have been utilized by a variety of life habit groups.

Hinge Type

In general, hinge structure has been a conservative feature in bivalve evolution and is therefore more useful in taxonomy than in functional morphology. The taxodont hinge, for example, has spread to a wide variety of life habit groups. The heterodont hinge is generally limited to burrowing species, especially to shallow burrowers, where it may facilitate rapid valve movements because of its low-friction mechanism (as compared to the taxodont hinge, for example). Most chondrophore-bearing deep burrowers are desmodont forms, in which hinge teeth are reduced or absent, their shells being removed from shearing forces near the sediment-water interface.

Pallial Sinus

It has long been recognized that size of pallial sinus is a crude measure of siphon length. No simple size correlation exists, however, because of variation in siphon shape among diverse taxa.

Marginal Denticulation

Denticulation along the ventral shell margin may be developed as distinct, fine teeth along the inner valve borders or may simply represent the termination of radial ornamentation. It is largely restricted to nearly spherical shells, rather than elongate or compressed forms and also occurs chiefly in shallow burrowers, rather than in deep burrowers or epifaunal groups. It apparently functions to prevent shearing of the valves parallel to the commissure plane.

ADAPTIVE DIVERGENCE, CONVERGENCE, AND HOMEOMORPHY

As implied in the previous sections, shell adaptations associated with various burrowing modes of life transgress taxonomic boundaries. Adaptive divergence and convergence have led to several instances of homeomorphy among unrelated, but ecologically similar taxa.

A striking example of homeomorphy on a small taxonomic scale is provided by the Mytilacea (Fig. 8). The genus *Brachidontes* contains both *Mytilus*-like epifaunal representatives (*B. exustus* and *B. recurvus*) and *Modiolus*-like infaunal representatives (*B. citrinus*).

Though possibly homologous, the auricle-sinus configuration associated with byssal attachment in the Pteriidae and Pectinidae is probably homeomorphic.

Divergence of both the Arcidae and Carditidae into byssally attached and free-burrowing groups has produced adaptive convergence between members of the two families, the compact species being free burrowers; the elongate species being attached by a strong byssus (Fig. 6.)

The unusually sluggish cardiid *Americardia* is strikingly similar in form and habits to shallow-burrowing arcids; it possesses an inflated, ribbed shell and a broad, flattened posterior dorsal surface where the very short siphons emerge near the sediment-water interface (Fig. 38).

Divaricate ornamentation serving as an aid to burrowing in sand has developed convergently in the lucinid *Divaricella* (Pl. 15, figs. 6, 7) and the tellinid *Strigilla* (Pls. 36, 37).

Homeomorphy between *Petricola* (Veneracea) and pholadaceans (Pl. 40, figs. 1-4), in association with a boring habit, represents a truly remarkable example of adaptive convergence.

One of the most highly diversified burrowing superfamilies is the Mactracea, which embodies many of the adaptive features described for bivalves that burrow in soft substrata. The most important of these are illustrated in Figure 39, which shows convergence of mactracean genera with unrelated genera having similar life habits.

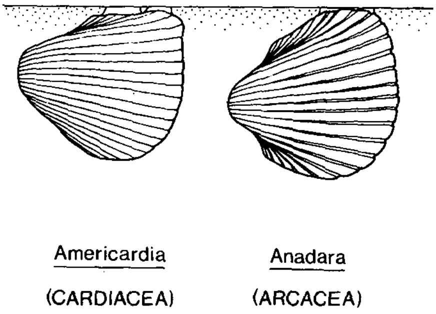


Figure 38. Convergence between the cardiid *Americardia media* and the Arcidae (represented by *Anadara chemnitzi*).

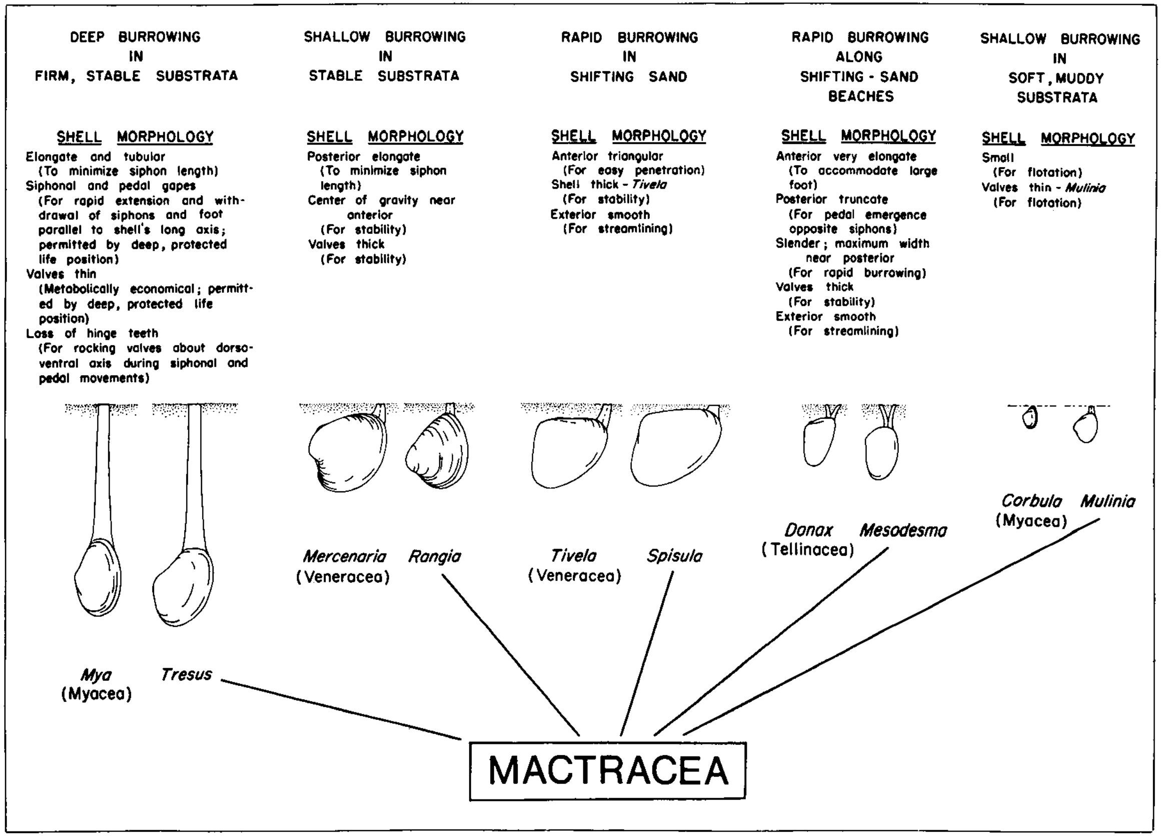


Figure 39. Adaptive divergence of the Mactracea and convergence in form and habit with unrelated burrowing taxa.

As described by Weymouth (1920) and Pohlo (1964), *Tresus* has the typical *Mya*-like adaptations of sedentary deep burrowers that live in cohesive substrata with their long axes vertical. *Mactra fragilis* (Pl. 27, figs. 3-6) approaches this condition, but is only a moderately deep burrower.

Rangia is similar in form to sluggish, shallow-burrowing venerids, astartids, and arcticaceans. Their common adaptations are for an immobile existence in stable substrata.

As an occupant of shifting-sand habitats, *Spisula* is specialized for rapid burrowing. Its venerid homeomorph *Tivela* has been able to retain its capacity for rapid burrowing, while evolving a thick shell for stability. The species represented in Figure 39 is *Tivela stultorum,* the "pismo clam" of the eastern Pacific; it more closely resembles *Spisula* than does *T. mactroides* described in the final section.

Mesodesma is strikingly similar to the wedge clam *Donax.* Their common adaptations are for mobility in shifting sand. Like *Tivela,* both have found it possible to offset the effects of thick shells, which they use for stability in life position, by evolving other special adaptations for rapid burrowing.

Finally, *Mulinia* is a small, thin-shelled genus that commonly inhabits the soft, muddy bottoms of restricted bays and lagoons. As a filter feeder in such habitats, its adaptations are for increased buoyancy, to avoid clogging by mud. The myid *Corbula* is a comparable genus in form and habit, although it has a thicker shell; apparently most mud-dwelling *Corbula* species are small enough so that shell thickness has become a relatively unimportant factor in their buoyancy.

The many instances of convergence in form and habit of unrelated taxonomic groups provide one of the strongest arguments for the adaptive significance of morphology in the Bivalvia. Aside perhaps from hinge structure and shell microstructure, basic taxonomic variation in shell form within the class primarily reflects life habits and habitat preferences. It is hoped that paleontologic application of the relationships discussed in this study, and others as yet undiscovered, will lead to accurate interpretation of the ecology of extinct forms and, ultimately, to a better understanding of the evolutionary history of the Bivalvia.

Observations on Western Atlantic Species

The morphology, habitat preferences, and life habits of 95 Western Atlantic bivalve species studied in life are described in this section. The data presented here form the primary basis for the functional interpretations of previous sections.

TECHNIQUES

A number of observational and measurement techniques were developed specially for gathering data in this investigation. These techniques will be described briefly before presentation of the information they have yielded.

Life Habits of Burrowing Species

Life positions of burrowing species were observed directly in nature by digging, wherever possible, but for most species more detailed information was obtained in the laboratory. Several shallow-burrowing species, such as *Glycymeris* sp., *Astarte* spp., and *Venericardia* sp., were permitted to burrow in the laboratory in large containers filled with their native sediment. The sea water was then drained from their containers, and the overlying sediment was removed, to expose each animal in life position. A large pair of tweezers was clamped around an exposed shell with a constricting ring. The tweezers were attached to a rod which slid up and down through a support, so that animals could be lifted from the substratum in life position; shell orientation relative to the sediment surface was then measured with a protractor and pendulum.

Life positions of most infaunal species, especially siphonate forms, were studied by means of X-radiography. Animals were placed in their normal erect probing orientation in thin aquaria partly filled with sediment and were allowed to burrow. The aquaria used were chosen so as to be as thin as possible without introducing boundary effects that might alter animals' burrowing behavior. Aquaria ranged in internal width from 0.5 to 5 cm; their walls were made of one-eighth-inch glass or plexiglass. The aquaria were immersed in sea-water tanks and removed periodically for X-raying with medical and dental X-ray units. A film sheet placed against the exterior surface of the aquarium wall opposite the X-ray source was exposed to produce a negative X-radiograph of the animals and enclosing sediment. The maximum amperage used was 50 milliamperes and the maximum voltage, 65 kilovolts. Many animals were studied by time-lapse X-radiography and suffered no apparent adverse effects. The behavior of nearly all species was studied first in their native sediment. Fine quartz sand was found, however, to provide the most revealing X-radiographs for most species. Many species were transferred to it after observation of their behavior in native sediment. Fine quartz sand has several advantages as a medium for X-ray study: (1) It can be easily introduced to a thin aquarium to form a homogeneous substratum with few air or water bubbles. (2) It is moderately cohesive and tends to hold pedal or siphonal cavities for a long period of time after the soft organs have been withdrawn. (3) Its fine-grained texture produces good resolution of linear features on film. (4) Its optical density differs from that of a calcium carbonate shell. Aside from very minor changes in life position or depth of burial, substratum type was found to have little effect on life position among the many species studied. For nearly all species, X-radiographs were compared with direct observations on burrowing behavior and were found to correspond quite closely.

Burrowing movements were studied in nature and in the laboratory. Sixty-three species were timed in a standardized fashion. The measured times were for the time period from initial erection of the shell (to a position in which the foot supported it against gravity and did not permit it to fall again to a reclining position) to disappearance, or virtual disappearance, of the shell beneath the sediment surface. The number of burrowing sequences in this portion of the burrowing period (including the sequence used to erect the shell) were counted. Burrowing rate indices were calculated as described on p. 57. Table 6 lists mean burrowing rate index and burrowing sequence number for each species that was timed. An average of more than 5 individuals was timed for each species. In all, well over 300 individuals were timed, making presentation of all burrowing time data impractical. Instead, the mean burrowing rate index and burrowing sequence number for each species are listed, along with raw data for the individual of that species whose calculated burrowing rate index was nearest the mean value for the species. The data included for this single individual are shell length, whole animal mass, and the time and number of burrowing sequences required for burial. The reason for listing these data is that they provide a tangible description of size and burrowing time which are obscured in the burrowing rate index calculation.

The validity of the burrowing rate index for individual species is discussed (on p. 56) and illustrated in Figure 23. Comparison of species on the basis of this index requires that the index be determined with reasonable accuracy for each species. Only uninterrupted burrowing periods were timed. Interruptions were noted by timing the intervals between burrowing sequences. It was found in repeated experiments with single animals that burrowing time varied little from trial to trial. Variation in burrowing rate index within a species was found to be greater than that for repeated trials using a single individual. For this reason, individuals were generally timed only once. Excluding *Donax denticulatus, Macoma balthica,* and *Ensis directus,* for which many individuals were timed, the average number of individuals timed was nearly 4 per species. Nine of the 63 timed species were represented by a single individual; most of these were slow burrowers. Statistical treatment of burrowing rate indices for each species was unwarranted because of the relatively small number of individuals timed. For species in which more than one individual was timed, the maximum burrowing rate index exceeded the minimum burrowing rate index by a factor of 1.9, on the average. Variation among individuals of a given species was caused by such factors as physiologic and morphologic variation and substratum inhomogeneity.

Two other major factors may affect the validity of the burrowing rate index as a means of comparing species. One of these is temperature and the other is substratum type. Temperature affects metabolic rates of bivalves as it does other poikilotherms. Rhoads (1963), for example, has shown that the rate of reworking of sediment by *Yoldia limatula* is at a maximum at temperatures in the neighborhood of 22° to 23°C and decreases rapidly at temperatures approaching 30°C and at temperatures below about 15°C. I found that most species, regardless of their geographic distribution, tended to burrow at rates markedly slower than their maximum rates at temperatures below about 15°C. *Mesodesma arctatum,* a boreal Western Atlantic species seldom found in shallow water south of Cape Cod, burrowed 40 to 80 percent faster at 21°C than at 11°C, although the species would not survive long in nature at the higher temperature. *Macoma balthica,* whose range extends from Arctic seas as far south as waters offshore from Georgia, was found to burrow roughly three times as rapidly at 18°C as at 11°C. *Tivela mactroides* and *Donax denticulatus,* two tropical species, however, were found to burrow virtually as rapidly at 21°C as at 28°C. No detailed plots of burrowing speed versus temperature were made, but it is evident from the data cited here, and from additional observations, that the optimum burrowing temperature for most species falls in the

TABLE 6. BURROWING RATE DATA

	Data for All Individuals Timed					Data for Individual with Burrowing Rate Index Nearest Species Mean			
Species	(°C)	Sediment Number	Number of Individuals Timed	Mean Rate Index Burrowing	Mean Burrowing Sequence Number	Length (cm)	Mass (g)	Burrowing Sequence Number	Time (sec)
NUCULACEA									
Nucula proxima	21	4	5	0.7	8	0.45	0.02	7	36
Yoldia limatula	21	6	8	12	8	1.7	0.47	8	6
Yoldia perprotracta	28	33	4	9	9	2.1	0.23	8	7
SOLEMYACEA									
Solemya velum	21	4	2	1	8	1.3	0.15	8	35
ARCACEA									
Anadara ovalis	18	29	1	0.3	11	4.5	18.2	11	780
Anadara chemnitzi	28	34	2	0.3	27	1.7	2.3	25	390
Noetia ponderosa	21	19	3	0.1	....	5.8	65	....	3680
ASTARTACEA									
Astarte undata	11	5	1	0.06	....	2.2	4.5	....	3000
Astarte castanea	21	5	5	0.04	....	2.3	5.1	....	4500
CARDITACEA									
Venericardia borealis	21	8	6	0.06	....	1.7	2.1	....	2160

TABLE 6. BURROWING RATE DATA—CONTINUED

	Data for All Individuals Timed					Data for Individual with Burrowing Rate Index Nearest Species Mean			
Species	(°C)	Sediment Number	Number of Individuals Timed	Mean Burrowing Rate Index	Mean Burrowing Sequence Number	Length (cm)	Mass (g)	Burrowing Sequence Number	Time (sec)
				LUCINACEA					
Diplodonta notata	28	33	2	0.01	....	0.84	0.16	....	2280
Codakia orbicularis	20	14	8	0.3	8	3.3	7.6	7	600
Phacoides pectinatus	20	14	4	0.1	17	2.5	4.3	17	1320
Phacoides muricatus	28	33	3	0.02	16	1.1	0.34	17	1640
Anodontia alba	21	14	3	0.06	19	2.3	3.0	19	2160
Lucina pensylvanica	21	21	1	0.03	....	2.5	4.9	....	5700
Divaricella quadrisulcata	18	29	4	0.5	27	1.4	10.5	20	405
				CARDIACEA					
Dinocardium robustum	18	19	3	5	7	4.0	23.5	7	60
Trachycardium egmontianum	21	18	3	0.5	20	3.0	16.0	19	625
Trachycardium muricatum	21	19	2	1	11	2.1	4.0	7	132
Laevicardium mortoni	20	1	3	1	5	1.3	0.74	5	91
Laevicardium laevigatum	21	19	4	1	10	2.7	8.1	11	175
Papyridea soleniformis	28	1	2	0.9	8	2.9	3.3	6	130
Americardia media	28	1	1	0.4	6	2.0	3.4	6	420
				VENERACEA					
Mercenaria mercenaria	20	1	6	0.8	14	6.8	108	15	560
Antigona listeri	21	25	1	0.3	14	5.8	52	14	1425
Chione cancellata	21	14	4	0.3	12	2.0	2.8	6	290
Chione granulata	28	34	5	1	12	2.6	5.9	11	175
Chione paphia	28	1	2	0.4	11	2.4	5.7	9	340
Anomalocardia cuneimeris	21	28	5	0.3	12	1.4	0.51	12	260

TABLE 6. BURROWING RATE DATA — CONTINUED

	Data for All Individuals Timed					Data for Individual with Burrowing Rate Index Nearest Species Mean			
Species	(°C)	Sediment Number	Number of Individuals Timed	Mean Burrowing Rate Index	Mean Burrowing Sequence Number	Length (cm)	Mass (g)	Burrowing Sequence Number	Time (sec)
			VENERACEA — continued						
Anomalocardia brasiliana	28	34	1	0.3	30	3.2	10.8	30	865
Macrocallista nimbosa	20	23	5	3	13	13.9	199	13	200
Dosinia elegans	21	27	2	2	8	6.1	41	7	190
Cyclinella tenuis	21	20	4	0.2	8	1.7	1.25	7	540
Tivela mactroides	28	32	9	8	8	4.2	23	9	35
			MACTRACEA						
Mesodesma arctatum	21	10	10	3	15	3.1	4.7	17	55
Spisula solidissima	19	46	11	4	14	12.9	265	14	165
Rangia cuneata	27	47	8	0.4	13	5.3	40	11	840
Mactra fragilis	21	1	8	1	8	3.2	3.5	8	150
Mulinia lateralis	20	42	3	0.8	13	1.3	0.53	12	105
			TELLINACEA						
Donax denticulatus	28	37	50	17	14	2.1	2.2	13	8
Donax variabilis	20	19	3	7	14	1.9	10.3	14	14
Iphigenia brasiliensis	21	17	4	4	13	5.9	28.9	13	80
Tagelus plebeius	24	12	2	0.4	• •	6.5	18.8	• •	680

TABLE 6. BURROWING RATE DATA — CONTINUED

	Data for All Individuals Timed					Data for Individual with Burrowing Speed Index Nearest Species Mean			
Species	(°C)	Sediment Number	Number of Individuals Timed	Mean Burrowing Rate Index	Mean Burrowing Sequence Number	Length (cm)	Mass (g)	Burrowing Sequence Number	Time (sec)
Tagelus divisus	21	1	9	2	7	2.8	1.17	7	50
Asaphis deflorata	21	26	3	0.2	23	6.4	4.9	22	810
Semele proficua	28	1	3	4	7	2.1	2.4	7	30
Cumingia tellinoides	20	3	6	0.09	25	1.4	0.37	26	1005
Tellina tampaensis	20	18	9	2	9	1.3	0.31	8	20
Tellina similis	28	38	3	10	7	1.8	0.52	6	8
Tellina agilis	20	1	3	3	10	1.4	0.23	9	23
Tellina alternata	21	20	5	4	4	3.8	3.8	5	35
Tellina listeri	21	30	1	0.8	6	3.9	3.1	6	175
Tellina radiata	28	40	1	1	12	1.2	0.14	12	46
Tellina martinicensis	20	20	5	0.6	4	1.0	0.20	4	90
Arcopagia fausta	20	14	2	5	6	5.6	31.0	6	60
Macoma tenta	20	6	3	0.6	8	1.3	0.20	8	95
Macoma balthica	16	2	18	0.7	10	2.5	2.4	13	200
Strigilla carnaria	28	32	5	20	6	1.1	0.28	6	4
Strigilla mirabilis	28	32	5	14	7	0.8	0.17	7	4
			SOLENACEA						
Ensis directus	19	1	31	6	14	15.2	62.3	13	70
			MYACEA						
Mya arenaria	21	13	4	0.2	17	6.4	33.5	24	1770
			PANDORACEA						
Pandora gouldiana	20	43	1	0.05	20	2.9	2.7	20	2760

20° to 30°C range. Inasmuch as nearly all species were timed in the 18° to 28°C range in this study, temperature differences are judged to account for relatively little interspecific variation in burrowing rate indices. Summer shallow-water temperatures at Woods Hole, Massachusetts, and winter temperatures at Miami, Florida, for the time periods of the study, were nearly identical (18° to 21°). Spring shallow-water temperatures in southwestern Puerto Rico were somewhat high (about 28°C), which may have produced a slight increase in the burrowing rate indices determined for Puerto Rico species relative to those studied at the more northern localities. However, the fact that numerous individuals of *Donax* and *Tivela* showed no apparent tendency to burrow more slowly when conditioned and timed at 21°C than at 28°C suggests that the temperature difference between Puerto Rico and the northern localities had only a minor effect on the values of burrowing rate indices determined for Puerto Rican species.

Substratum type unquestionably affects burrowing rate for individual species, but its effect varies from species to species. Sediment type not only affects substratum resistance to shell penetration, it also affects substratum resistance to pedal probing and substratum support for pedal anchorage. Trueman and others (1966) have shown experimentally that cohesive mixtures of fine sand offer more physical resistance to bivalve shell penetration than mixtures of medium sand. They suggest that pedal anchorage is firmer in fine sand, however, and that this effect may offset its greater resistance to penetration. I independently arrived at the same conclusion from observations on the burrowing activity of various species; while cohesive fine sand and sand-mud mixtures offer more resistance to shell penetration than medium sand or mud, they also permit stronger pedal anchorage.

Substratum type affects burrowing behavior as well as the mechanics of burrowing. Most mactrids, for example, have a pointed triangular foot that is very effective for locomotion in their native sandy sediment, but less effective in mud. Many mactrids temporarily cease their burrowing activity after partial burial in mud, largely as a behavioral response to the unfamiliar medium. The flared protobranch foot, in contrast, is primarily adapted for movement in muddy substrata. Pedal probing is difficult and the slender terminal flanges of the foot do not spread easily or grip well in a sandy medium; for most protobranch species, burrowing is hampered by the presence of a high proportion of sand. *Yoldia limatula*, a normally active burrower, was found to delay its burrowing period in medium sand to the extent of requiring several hours, instead of a few seconds, to complete the burrowing process.

Obviously, no simple rule can be established to describe the effects of substratum on burrowing rates because of variation among species in pedal morphology and physiology and in burrowing behavior. Although many species were timed in a variety of sediment types, few species were found to burrow normally without delays in a full spectrum of sediment types (muds, mud-sand mixtures, and sands). Two tellinid species, *Tellina agilis* and *Macoma tenta*, were found to burrow normally in a variety of sediment types, and their burrowing rates are compared in Figure 40, which is based on mean burrowing rate index data for three individuals of each species. *Macoma tenta*, which inhabits muddy substrata, was found to burrow most rapidly in sediments containing large mud fractions. *Tellina agilis*, which inhabits sands, was found to burrow most rapidly in sediments containing very little mud. In gross shell morphology, the two species are rather similar. Their differing response to identical substrata is probably a function of behavior and pedal anatomy rather than shell form. Maximum or near maximum burrowing rates were obtained for most species in their native substrata. Burrowing rate indices for most species were calculated from measurements using native sediment. Where this was impossible, fine sand (sed. 1 or 19) was employed because most animals burrow normally in it. Some

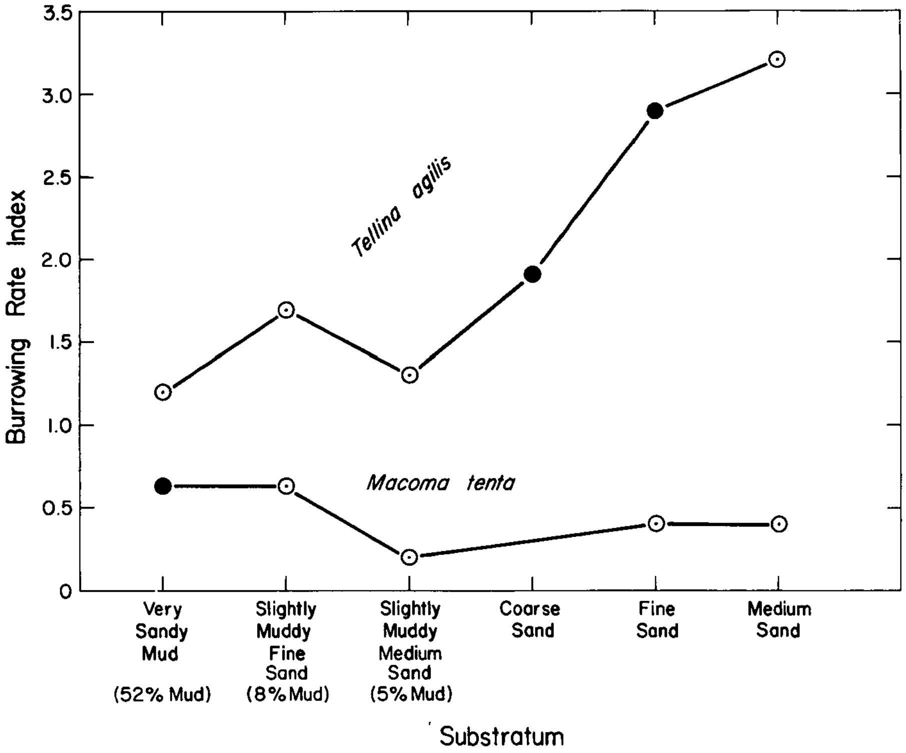


Figure 40. Variation of burrowing rate indices for two tellinid species in a variety of substrata. Each burrowing rate index represents the mean for three individuals. Solid dots represent native substrata.

species have *difficulty* burrowing in medium sand or muddy sand, both of which are less compact than fine sand.

There is no easy way to evaluate the sizes of error that characterize calculated burrowing rate indices. In general, it is judged that sample size (number of individuals timed per species) and variation in substratum and temperature have not invalidated burrowing rate index comparisons at the level of accuracy required for the present study. A three- or four-fold difference between the calculated indices of two species is meaningful in nearly every case, and a two-fold difference is probably significant in the majority of cases. There is a two thousand-fold difference between the largest and smallest indices calculated for species in this study.

Sediment Analyses

Native sediment samples were collected for nearly all soft-stratum dwellers. They were treated with sodium hypochlorite solution to remove organic matter and were then washed thoroughly in distilled water. It was observed that clay-sized particles were not flocculated following organic matter removal. The organic-free samples were wet-seived to separate them into gravel, mud, and 5 sand grades. Silt and clay percentages were determined for mud fractions by pipette analysis, as described by Krumbein and Pettijohn (1938, p. 166-176).

Terminology traditionally employed by sedimentologists to describe sediment texture (for example, Pettijohn, 1957, p. 21-27) is poorly suited for use in benthic ecology. Most sedimentologic schemes describe a predominantly sandy sediment as "muddy," "silty," or "clayey," only if more than 20 or 25 percent of its constituents are in the mud size range. However, an admixture of mud as small as 5 percent renders most sands considerably more cohesive than clean sand of the same grain size and commonly alters their character enough to affect their faunal content. The terminology used here to describe grain size has been adopted especially for this study. The standard Wentworth size scale is employed (Fig. 41). A sediment is called a "gravel," "sand," or "mud," depending on which of the three constituents is most abundant. The adjective "gravelly," "sandy," or "muddy" is added if the proportion of a secondary constituent exceeds 5 percent. The modifier "slightly" is added to this adjective if the minor constituent forms 5 to 15 percent of the sample, and "very," if it comprises 30 to 49 percent. A sand may be both "muddy" and "gravelly" by this scheme. If the proportion of clay exceeds that of silt by a factor of 5, the word "clay" or "clayey" is substituted for "mud" or "muddy"; if the relative proportions of silt and clay are reversed, the word "silt" or "silty" is used. The adjective "clean" is used if the percentage of mud is less than 0.1.

Size distribution histograms for analyzed sediment samples are presented in Figure 41. Constituent composition of sediments was not determined, but the textural names applied to sediments in which calcium carbonate predominates are modified by the word "carbonate."

Shell Morphology

Most measurements of morphologic features were made on specimens representing populations whose life habits and habitats were studied. In a few instances, these specimens were supplemented with ones from other localities borrowed from museums. Morphologic variation at the population, species, and inter-species level was estimated in order to determine the degree of accuracy and precision to be sought for various measurements. Height, length, width, and anterior and posterior length measurements were made in a standardized fashion according to the conventions described earlier. In general, the value used to represent a species is the mean of 10 measurements. Shells were not measured directly. With the aid of an opaque optical projector, their images were projected onto a translucent surface, where their outlines were traced. This technique facilitated accurate measurement by projecting all morphologic features onto a plane surface and by permitting enlargement of small species.

Ornamentation indices were calculated from shell surface relief measurements made with an indicator gauge fitted with a special pointed stylus (Pl. 40, fig. 5). The relief value recorded for each specimen represented the mean of 3 measurements taken near the mid-ventral shell margin. The ornamentation index used to represent a species is the mean of the indices determined in this manner for three shells.

Shell thickness indices were measured by making internal molds of shells with a silicone cold molding compound. If thick or prominent, the periostracum was removed. The mold and shell were weighed in air and water to determine their specific gravities. Their volumes were then calculated from their respective weights and specific gravities. The shell thickness index used to represent most species is the mean of indices determined for 5 specimens.

MORPHOLOGIC, BEHAVIORAL, AND ECOLOGIC DATA

Habitat preferences listed below for individual species are based on personal observation, which was largely restricted to shallow-water environments. Some species may therefore occur in deeper settings than those described.

Inasmuch as this is not a taxonomic study, species identifications have been made from Abbott (1954) and Warmke and Abbott (1961),

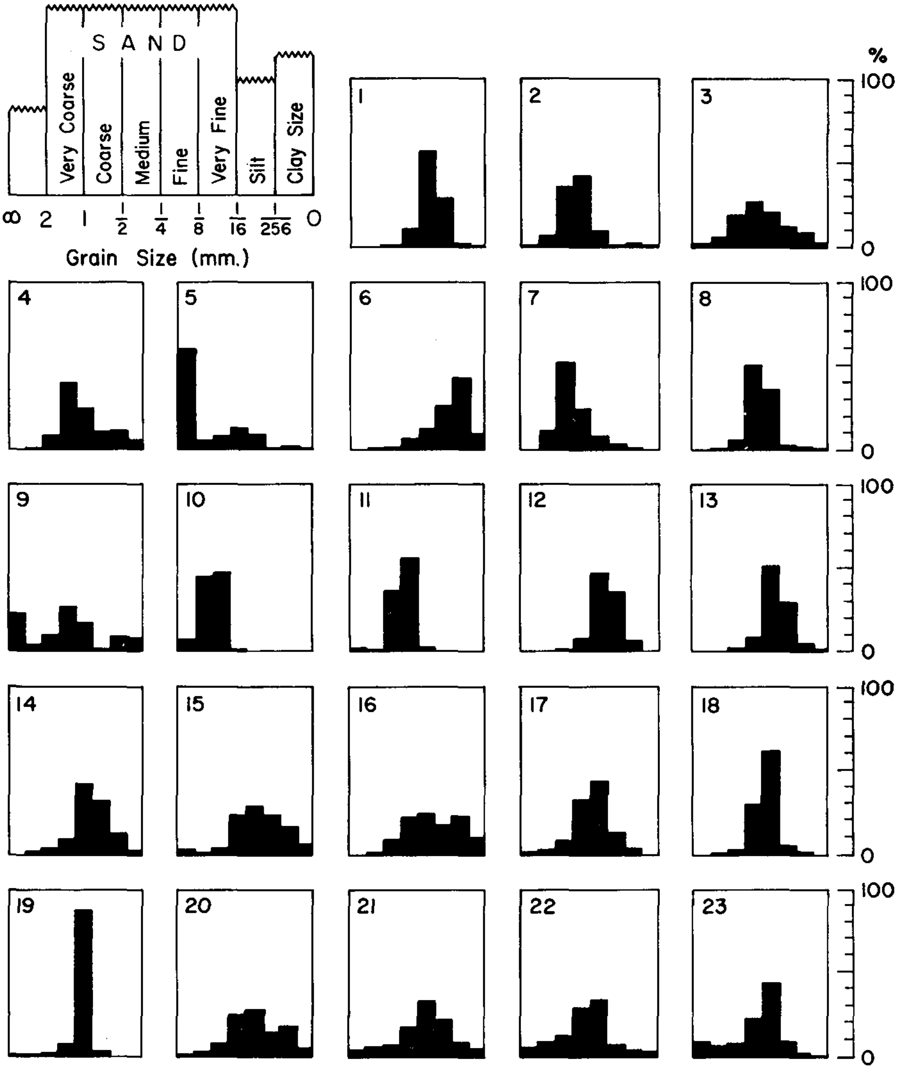
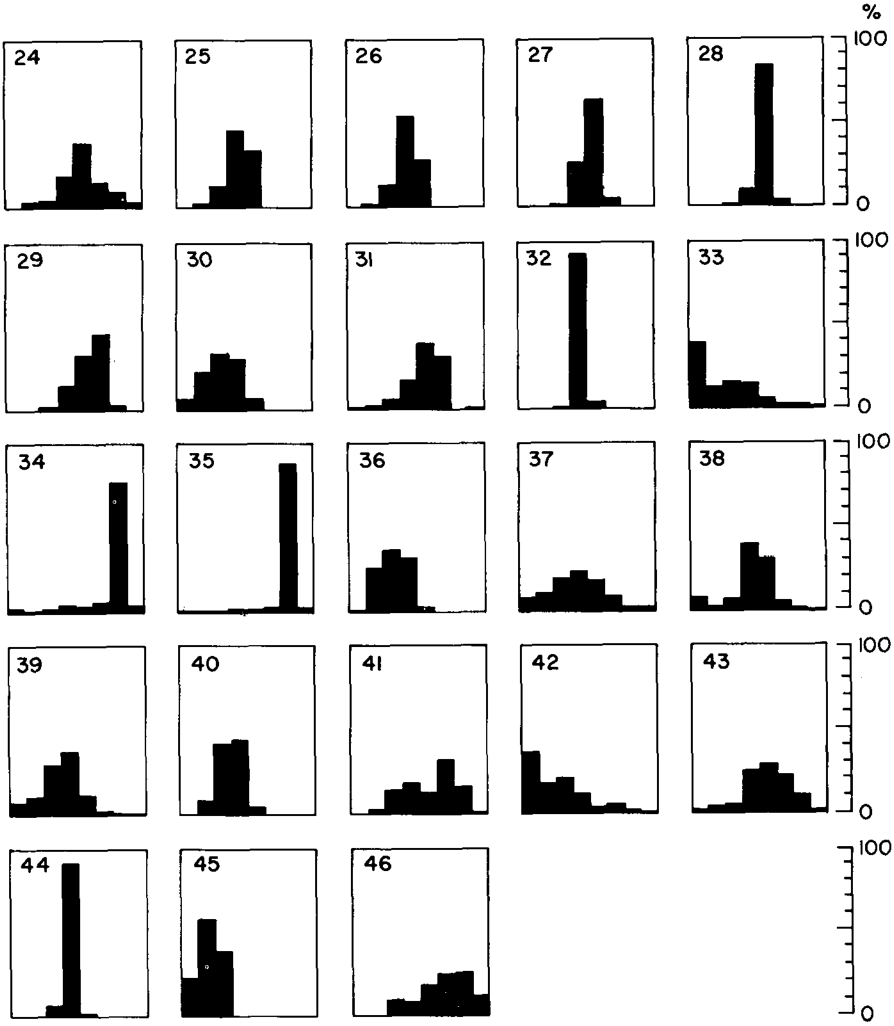


Figure 41. Sediment grain size analyses. 1 = near Huckins Island, Barnstable Harbor, Massachusetts (intertidal flat); 2 = ponded portion of Squeteague Harbor, Massachusetts (< 1 m); 3 = Quisset Harbor, Massachusetts (1 m); 4 = Quisset Harbor, Massachusetts (2 m); 5 = near Quicks Hole, Buzzards Bay, Massachusetts (35 m); 6 = Quisset Harbor, Massachusetts (6 m); 7 = Bass River Mouth, Massachusetts (intertidal); 8 = 1 mi west of Penikese Island, Buzzards Bay, Massachusetts (15 m); 9 = near Quicks Hole, Buzzards Bay, Massachusetts (25 m); 10 = beach in front of Coast Guard Station, Plum Island, Massachusetts (intertidal); 11 = tidal channel, Great Harbor, E. Falmouth, Massachusetts (1 m); 12 = Bass River Mouth, Massachusetts (intertidal); 13 = tidal marsh, Huckins Island, Barnstable Harbor, Massachusetts; 14 = Rickenbacker Causeway (near Miami Seaquarium), Biscayne Bay, Florida (intertidal); 15 = Rickenbacker Causeway (near Miami Seaquarium), Biscayne Bay, Florida (intertidal); 16 = Norris Cut, Biscayne Bay, Florida (intertidal); 17 = Norris Cut, Biscayne Bay, Florida (intertidal); 18 = Matheson Hammock Wading Beach, Biscayne Bay, Florida (< 1 m.); 19 = exposed beach, Marco Island, Florida (intertidal); 20 = north of Southwest Point, Biscayne Bay, Florida (3 m); 21 = southwest side of Soldier Key, Biscayne Bay, Florida (< 1 m); 22 = sandy shoal south of Cape Florida, Biscayne Bay, Florida (< 1 m); 23 = north



of Terra Ceia Island, Tampa Bay, Florida (< 1 m); 24 = Rickenbacker Causeway, (near Miami Seaquarium) Biscayne Bay, Florida (< 1 m); 25 = Bear Cut, Biscayne Bay, Florida (intertidal); 26 = in limestone cavities, Bear Cut, Biscayne Bay, Florida (intertidal); 27 = Norris Cut, Biscayne Bay, Florida (intertidal); 28 = pond, northwest end of Marco Island, Florida (< 1 m); 29 = intertidal flats behind North Point, near Salerno, Florida; 30 = southwest of Rodriguez Key, Hawk Channel, Florida (6 m); 31 = Mani Beach, north of Mayaguez, Puerto Rico (1 m); 32 = near sewage outflow, Mayaguez Harbor, Puerto Rico (6 m); 33 = mouth of Salinas El Papayo, La Parguera, Puerto Rico (intertidal); 34 = Boqueron Bay, Puerto Rico (6 m); 35 = Boqueron Bay, Puerto Rico (8 m); 36 = Mani Beach, north of Mayaguez, Puerto Rico (intertidal); 37 = behind Cayo Caracoles, La Parguera, Puerto Rico (1 m); 38 = Guanica, Puerto Rico (< 1 m); 39 = northwest side of Sandy Point, St. Croix, Virgin Islands (8 m); 40 = intertidal flats behind North Point, near Salerno, Florida; 41 = south side of Sandy Point, New Haven Harbor, Connecticut (intertidal); 42 = near yacht club, south shore Barnstable Harbor, Massachusetts (intertidal); 43 = Quahog Pond, West Falmouth, Massachusetts (intertidal); (1 m); 44 = Gansett Beach, Woods Hole, Massachusetts (2 m); 45 = beach, Menemsha Bight, Marthas Vineyard, Massachusetts (2 m); 46 = Upper Cedar Point, Potomac River, Maryland (1 m).

and the generic and specific nomenclature of these authors has been adopted. Shells representing the populations studied have been deposited in the Peabody Museum of Yale University in the event of future taxonomic confusion. Morphologic descriptions provided here are not intended to be taxonomically definitive; they are intended to supplement photographs in the presentation of important adaptive shell features. Descriptive terms used to represent values of measured morphologic characters are listed in Table 7. For photography, the periostracum was removed from most species in which it alters the shell surface configuration in life. The periostracum was left intact for species in which it overlaps the ostracum to form a large percentage of the shell (as in *Solemya* and members of the Pteriidae). Most shells were coated with ammonium chloride for photographing, to cover color patterns and accentuate morphologic features. In plate captions, Yale Peabody Museum is abbreviated as YPM and Harvard Museum of Comparative Zoology as MCZ.

Species List

Superfamily NUCULACEA
- Family NUCULIDAE
  - *Nucula proxima* (Say) 115
- Family NUCULANIDAE
  - *Yoldia limatula* (Say) 117
  - *Yoldia perprotracta* Dall 118

Superfamily SOLEMYACEA
- Family SOLEMYIDAE
  - *Solemya velum* Say 119

Superfamily ARCACEA
- Family ARCIDAE
  - *Arca zebra* Swainson 121
  - *Arca imbricata* Bruguière 121
  - *Barbatia cancellaria* (Lamarck) 122
  - *Barbatia tenera* (C. B. Adams) 122
  - *Barbatia domingensis* (Lamarck) 123
  - *Arcopsis adamsi* (Dall) 123
  - *Anadara ovalis* (Bruguière 124
  - *Anadara notabilis* (Röding) 125
  - *Anadara chemnitzi* (Philippi) 125
  - *Noetia ponderosa* (Say) 126
- Family GLYCYMERIDAE
  - *Glycymeris pectinata* (Gmelin) 127

Superfamily MYTILACAE
- Family MYTILIDAE
  - *Mytilus edulis* Linné 129

Superfamily PTERIACEA
Family ISOGNOMONIDAE

Family PTERIIDAE

Family PINNIDAE

Superfamily PECTINACEA
Family PECTINIDAE

Family LIMIDAE

Superfamily ANOMIACEA
Family ANOMIIDAE

Superfamily ASTARTACEA
Family ASTARTIDAE

Superfamily CARDITACEA
Family CARDITIDAE

Superfamily LUCINACEA
Family DIPLODONTIDAE

Family LUCINIDAE

Superfamily CARDIACEA
Family CARDIIDAE

Superfamily VENERACEA
Family VENERIDAE

Superfamily MACTRACEA
Family MESODESMATIDAE

Family MACTRIDAE

Superfamily TELLINACEA
Family DONACIDAE

Family SANGUINOLARIIDAE

Family SEMELIDAE

Family TELLINIDAE

Superfamily SOLENACEA
Family SOLENIDAE

Superfamily MYACEA
Family CORBULIDAE

Family MYIDAE

Superfamily PANDORACEA
Family LYONSIIDAE

Family PANDORADAE

Species Morphology, Habitats, and Life Habits

Nucula proxima (Say)
(Pl. 1, figs. 1-7)

SHELL DESCRIPTION: The shell is very small (maximum length 1 cm), ovate, and inflated. The anterior is greatly extended. The valves are thick. The exterior is generally smooth but commonly eroded slightly in the umbonal regions.

L/H 1.18, H/W 1.42, AL/L 0.76, T.I. 0.70

LOCALITIES: Large numbers of individuals were collected from organic-rich, muddy medium sand (sed. 4) at depths of 0.5 to 3 m below mean low tide in Quisset Harbor, Cape Cod, Massachusetts (amid sparse grass).

HABITAT: *N. proxima* prefers muddy substrata and sheltered subtidal conditions; smaller forms that abound in less sandy sediments in Buzzards Bay and Long Island Sound (Sanders, 1956, 1960) may represent a separate species (G. E. Hampson, 1965, personal commun.).

TABLE 7. DESCRIPTIVE TERMS FOR VALUES OF MEASURED MORPHOLOGIC CHARACTERS

Character Value	Descriptive Term
	SIZE (Length)
≦ 1.5 cm.	very small
1.6 - 3.5 cm	small
3.6 - 5.0 cm	moderately small
5.1 - 7.0 cm	moderately large
7.1 - 10 cm	large
≧10.1 cm.	very large
	ELONGATION (L/H)
≦ 1.19	equant
1.20 - 1.39	moderately elongate
1.40 - 1.59	elongate
≧ 1.60	very elongate
	OBESITY (H/W)
≦ 1.29	strongly inflated
1.30 - 1.49	inflated
1.50 - 1.69	moderately inflated
1.70 - 1.99	compressed
≧ 2.00	very compressed
	ANTERIOR ELONGATION (AL/L)
0.51 - 0.60	anterior extended (expanded)
≧ 0.61	anterior greatly extended (expanded)
	THICKNESS (T.I.)
≦ 0.20	very (extremely) thin
0.21 - 0.30	thin
0.31 - 0.40	moderately thin
0.41 - 0.50	moderately thick
0.51 - 0.70	thick
≧ 0.71	very (extremely) thick
	ORNAMENTATION (O.I.)
≦ 4	very weak (very fine)
5 - 9	weak (fine)
10 - 14	moderately strong (moderately coarse)
15 - 19	strong (coarse)
≧20	very strong (very coarse)

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 0.7), but is considerably slower and less active than *Yoldia* spp. Burrowing mechanics of the protobranch foot are not as regularly patterned as those of higher forms so that burrowing times of *N. proxima* are unusually variable. Mean burrowing rate index for a variety of sediment types was found to vary only modestly, however.

Members of this species have never been observed to kick or jump in the manner of *Yoldia*. Individuals do move about continually in the course of feeding (Pl. 1, figs. 1-3) but slowly and sporadically. The animal probes with difficulty at the surface, with the bifurcate foot extending, flaring, and withdrawing in attempts to grip the substratum (Pl. 1, figs. 6, 7), and finally moves into the sediment at a steep angle. Once buried, the animal rotates its anterior end upward to assume a position for lateral migration just beneath the sediment surface. The resulting position is the life position that Yonge (1939) has ascribed to the genus (with the plane of commissure vertical and the anterior dorsal margin approximately horizontal). But *N. proxima,* in the course of its subsequent movements, shows considerable deviation from this initial orientation (Pl. 1, figs. 1-3). In X-ray aquaria with no boundary effects, it is not uncommon for individuals to assume an attitude with the plane of commissure horizontal or the ventral region uppermost. Animals are seldom found at depths of burial greater than 1 cm. They show a marked tendency to migrate toward areas of current flow, moving from one end of a thin aquarium to the other with transfer of the water-supply hose.

Yoldia limatula (Say)
(Pl. 2, figs. 1-4)

SHELL DESCRIPTION: The shell is moderately large (its length may exceed 6 cm). It is compressed and very elongate, with a pointed posterior and distinct siphonal and pedal gapes. The valves are very thin. The exterior is very smooth but is commonly eroded in the umbonal regions.

L/H 2.17, H/W 1.89, AL/L 0.48, T.I. 0.17

LOCALITIES: This species was collected in large numbers from soft, black, very sandy mud containing fragments of dead eel grass (sed. 6) at depths of 3 to 8 m, Quisset Harbor, Cape Cod, Massachusetts. It was also collected from Sanders' (1960) station "R" in Buzzards Bay.

HABITAT: *Y. limatula* prefers muddy substrata and sheltered subtidal conditions. Sanders (1956) found it to be restricted to muddy sediments in Long Island Sound, reaching its greatest abundance in sediments containing about 40 percent silt-clay.

LIFE HABITS: This species is a very rapid and active burrower (B.R.I. 12). The bifurcate foot (Pl. 2, fig. 3) is quite mobile and may emerge at nearly right angles to the shell's long axis, but normally emerges more anteriorly, through the pedal gape. The distal flanges of the foot spread while contraction of the anterior pedal retractors pulls the foot dorsally, to be withdrawn into the shell in a direction nearly parallel to the shell's long axis. Rapid pedal movements of this type are commonly used by unburied animals in kicking to change position; they are also used for burrowing. An animal disturbed in the act of burrowing normally persists, in an attempt to escape, rather than ceasing its activity and withdrawing its foot. Initial probing by the foot is much more difficult in sandy substrata than in mud. Once the foot is implanted, the animal erects itself with a single burrowing sequence and enters the substratum with a series of very rapid burrowing sequences (about one per second). The shell rocks through an angle of about 30°.

The life position of partial burial figured by Drew (1899) for *Y. limatula* and commonly refigured in the literature is erroneous. This and other species of the genus live with the shell completely buried, and proboscidial feeding takes place entirely beneath the sediment surface. The life position of *Y. limatula* is with the shell's long axis 30° to 40° from the horizontal (Pl. 2, fig. 4). The posterior tip of the shell of an adult animal normally lies 1 to 2 cm beneath the sediment surface. The siphons project upward at an angle of about 50° from the horizontal. The tips of the siphons normally stand 2 to 3 mm above the soupy sediment surface. Periodically, small cloud-like puffs of pseudofeces are discharged from the siphonal openings. An individual migrates laterally in the course of its normal activity to reach fresh food supplies; periodic lateral movements of this type require that the long axis of the buried shell be rotated to a roughly horizontal position for movement parallel to the sediment surface.

X-radiographs of some animals in thin aquaria have revealed cavities excavated by the feeding process and supported by adhesion of the surrounding sediment to aquarium walls. One animal burrowed to a considerable depth, leaving an open pit 3.5 cm deep in its wake. Excavation of this sort was never observed in larger containers (lacking boundary effects) and appears to have been a laboratory artifact, but demonstrates the great efficiency of the proboscidial feeding mechanism in processing sediment. Rhoads (1963) found the average rate of sediment reworking by an adult *Y. limatula* to be about 0.165 ml/hr at 20° to 21°C.

Yoldia perprotracta Dall
(Pl. 2, figs. 5-7)

SHELL DESCRIPTION: The shell is small (seldom longer than 3 cm), compressed, and extremely elongate, with a relatively shorter anterior than *Y. limatula.* There are distinct siphonal and pedal gapes. The ventral valve margins are slightly recessed where the foot emerges, producing a shallow anterior sinus in the valve surfaces. The valves are moderately thick. The exterior is very smooth.

L/H 3.50, H/W 1.86, AL/L 0.37, T.I. 0.49

LOCALITIES: Numerous individuals were dredged in Mayaguéz Harbor, Puerto Rico, from slightly clayey carbonate silt (sed. 32) and in Boquerón Bay, Puerto Rico, from sandy carbonate silt (sed. 34), at depths of about 6 m.

HABITAT: Warmke and Abbott (1953) confirm my observations in their report of the occurrence of this species on muddy bottoms between Mayaguéz and the Añasco River Mouth, Puerto Rico. It prefers muddy substrata and sheltered subtidal conditions.

LIFE HABITS: This species is a very rapid burrower (B.R.I. 9). Initial penetration of the flared foot is difficult, as in other protobranchs. *Y. perprotracta* is very active and can kick and jump in a posterior direction when not buried. The angle of rotation is very small. As shown in Plate 2, figure 7, the angle of penetration and final life position are less vertical than *Y. limatula* (the long axis of the shell lying 20° to 30° from the horizontal). As in *Y. limatula,* lateral migration is a normal activity associated with deposit feeding. The siphons are long and very slender and project 1 to 2 mm above the sediment surface.

Solemya velum Say
(Pl. 3, figs. 1-6)

SHELL DESCRIPTION: The shell is small (maximum length 2.5 cm) and cylindrical, with a greatly extended anterior (where the maximum shell height occurs). There are large pedal and posterior gapes. The calcareous shells are small and elliptical in lateral view but are overlapped by extensive periostracum (folded inward along the ventral margins in life). The valves are very thin, and the exterior is very smooth.

L/H 2.55, H/W 1.34, AL/L 0.71, T.I. not determined.

LOCALITIES: This species was collected in large numbers from the western shore of Quisset Harbor in organic-rich, muddy medium sand (sed. 4) at depths of 2 to 4 m. It is most common in bare patches in eel grass meadows but is occasionally found living intertidally in fine sand at Barnstable Harbor, Massachusetts (sed. 1).

HABITAT: As suggested by the Quisset Harbor occurrence, sandy mud in shallow subtidal environments is the preferred substratum. This observation is supported by the statements of Drew (1900) and Morse (1913). Sandy mud is also the common substratum of *S. togata* (Yonge, 1939) and *S. parkinsoni* (Owen, 1961).

LIFE HABITS: *S. velum* is a moderately rapid burrower (B.R.I. 1) that normally enters the substratum at an angle of 45° or 50° from the horizontal. Movement is in a direction parallel to the shell's long axis, with no rocking motion. At a depth of up to 6 to 7 cm (depending on its size), the animal's burrowing direction flattens out and very quickly turns upward, so that the animal moves toward the sediment surface along a path that is nearly a mirror-image of its downward path. The animal emerges at the surface, having formed a U-shaped tube in the cohesive substratum. (Time-lapse X-radiography has shown that this process normally requires at least one hour, but less than 4 hours, for an animal about 1.7 cm long.) The animal then propels itself backward to the lowest portion of the U-shaped tube and burrows downward to form a deep vertical extension of the tube (Pl. 3, fig. 6). The length of this extension may exceed 20 cm, but the maximum length is unknown. It is generally deepened and its course altered periodically after initial formation. Movement within the burrow system is accomplished by means of the flared foot, which is provided with numerous marginal digitations that grip the burrow walls (Pl. 3, figs. 3-5).

Both Drew (1900) and Morse (1913) noted that *S. velum* seemed to form a more-or-less open burrow, but neither worker observed the shape or mode of formation of this burrow. Later workers (Yonge, 1939; Owen, 1961) have observed no such burrow for other species of the genus and have apparently discounted the earlier reports.

As documented by X-radiography, *S. velum* normally lives in the lowest portion of the upper U-shaped segment of the burrow, with its long axis horizontal. This orientation and the animal's basic body plan and current system indicate that *S. velum* is without question a suspension feeder. The animal draws water in through its anterior inhalent opening from the anterior arm of the upper burrow and expels it posteriorly through the other arm.

The function of the deep vertical extension of the burrow has not been determined with certainty. The animal posesses, in addition to its anterior inhalent opening, a ventral inhalent opening through which it might conceivably draw nutrients (for example, bacteria) from the deep burrow extension. The extension may also serve as a refugium, allowing the animal to escape from predation or adverse physical or chemical conditions. And it may serve as a sump that receives waste or loose sediment that would otherwise accumulate at the base of the U-shaped burrow. Frequently, the animal slightly enlarges the anterior entrance to the burrow with its foot to form a shelf in the tube 3 to 4 mm below the surface. This structure apparently serves to catch loose sediment washed into the opening.

The ability of *Solemya* to swim is well documented (Drew, 1900; Morse, 1913). By suddenly clapping its valves together and retracting its foot, the animal ejects water posteriorly and swims in an anterior direction. Repeated movements of this type may carry the animal a distance of several centimeters. Discovery of the open burrow system in this study suggests, as Drew (1900) postulated, that swimming is a secondary function of the posterior water jet in solemyid evolution. The jet may initially have evolved for clearing the upper burrow of undesirable sediment or excrement. It is also possible that jet propulsion is sometimes used for locomotion within the burrow system.

Arca zebra Swainson
(Pl. 4, figs. 1, 2)

SHELL DESCRIPTION: The shell is large (its length may reach 7 to 8 cm). The shape is variable, but very elongate and generally quadrate in lateral view, with the maximum height near the posterior. The shell is strongly inflated. The posterior of each valve is traversed by a distinct furrow emanating from the beak. The umbones are separated by an extensive ligament area, and the byssal gape is small. The valves are moderately thick, with fine ribs of two sizes.

L/H 1.86, H/W 0.91, T.I. 0.47, O.I. 6

LOCALITIES: This species was observed and collected in many shallow-water areas in southern Florida and Puerto Rico.

HABITAT: *A. zebra* lives attached to rocks and coral colonies, from just below the low tide mark to depths of several meters; it is not commonly intertidal.

LIFE HABITS: This species is nearly always found on exposed surfaces of rocks and coral colonies, partly nestled in shallow crevices and depressions with the dorsal and posterior regions of the shell exposed. It seldom lives on the undersides of rocks. It attaches by a stout, ribbon-like byssus that flares at the distal end to form a broad attachment surface. The animal can, to a limited extent, enlarge the depression housing its anterior end; it uses the coarse anterior ribbing of the shell for abrasion by contraction of the byssal muscles. Exposed portions of the shell are frequently encrusted by epibionts that serve as camouflage. A feeding animal abruptly closes its valves and contracts (a few millimeters) against the substratum when a shadow passes over it.

Arca imbricata (Bruguière)
(Pl. 4, figs. 3, 4)

SHELL DESCRIPTION: The shell is very similar to that of *A. zebra*, but with fine, beaded ribs of a single size and a large byssal gape.

L/H 1.80, H/W 0.97, T.I. 0.49, 0.I. 6

LOCALITIES: This species was observed and collected in many shallow-water areas in southern Florida and Puerto Rico.

HABITAT: *A. imbricata* was found living with *A. zebra*, or in its absence, but in similar habitats (attached to rocks and coral colonies in shallow subtidal settings).

LIFE HABITS: No distinction could be made between the habits of this species and those of *A. zebra,* although *A. imbricata* possesses a thicker and stronger byssus.

Barbatia cancellaria (Lamarck)
(Pl. 4, figs. 5-8)

SHELL DESCRIPTION: The shell is moderately small (its length seldom exceeds 4 cm). The shape is variable, but most shells are very elongate and moderately inflated (but considerably more compressed than most byssally attached arcids). The anterior and posterior margins are rounded. The umbones are nearly in contact, and a byssal gape is small or lacking. The valves are moderately thick to thick. The exterior is ornamented with fine, beaded, cancellate ridges.

L/H 1.83, H/W 1.30, T.I. 0.52, O.I. 7

LOCALITIES: This species was found at many localities in southern Florida and Puerto Rico. Large numbers of individuals were collected from patch reefs of *Porites porites* in the vicinity of La Parguera, Puerto Rico, and from clumps of *P. porites* along the eastern margin of Rodriguez Key, Florida.

HABITAT: *B. cancellaria* most commonly occurs in shallow subtidal settings among the finger-like branches of the colonial coral *Porites porites.* It is less commonly found attached to the undersides of rocks and massive coral colonies.

LIFE HABITS: When in their favored habitat, nestled among the branches of *P. porites,* the animals are usually positioned in the upper (living) parts of the colony with their posterior ends directed upward (Pl. 4, figs. 7, 8). The byssus is slender and rather weak. The animal is loosely attached and, when disturbed, frequently releases its byssus and drops from the object of attachment. When detached and placed in an aquarium, animals frequently crawl about extensively before attaching to solid objects.

Barbatia tenera (C. B. Adams)
(Pl. 5, figs. 1, 2)

SHELL DESCRIPTION: The shell is moderately small (maximum length approximately 4 cm). It is similar in gross form to that of *B. cancellaria,* but slightly less elongate, more inflated, and with a more triangular posterior margin. The valves are moderately thick and possess moderately strong radial ribs.

L/H 1.54, H/W 1.19, T.I. 0.42, O.I. 11

LOCALITIES: This species is less common than many of the West Indian arcids. Several animals were found attached to the undersides of rocks just below the low tide mark along the western shore of the mouth of Phosphorescent Bay, La Parguera, Puerto Rico.

HABITAT: The Phosphorescent Bay locality is apparently typical for the species, which favors sheltered habitats.

LIFE HABITS: This species is attached by a weak byssus in a manner similar to *B. cancellaria.*

Barbatia domingensis (Lamarck)
(Pl. 5, figs. 3, 4)

SHELL DESCRIPTION: This is a small species (its shell length is usually less than 2 cm). Shell shape is extremely variable, but generally quadrate, with a strongly triangular posterior. The shell is very elongate and strongly inflated, with a shoulder-like ridge extending from each umbo to the pointed posterior margin. The valves are very thick, often rugose, and bear very strong cancellate ornamentation.

L/H 1.68, H/W 1.15, T.I. 0.87, O.I. 23

LOCALITIES: This species was found at many locations in Biscayne Bay, Florida, and along the southern coast of Puerto Rico.

HABITAT: *B. domingensis* is most common under rocks and coral heads below the low tide mark; it also lives among branches of *Porites porites* coral colonies, but nearly always in protected microhabitats. Bretsky (1967) concluded that in Bermuda this species is attached almost exclusively to coral colonies; I have observed many individuals beneath rocks in Bermuda.

LIFE HABITS: This species is most commonly attached to the undersides of rocks and massive coral colonies with the ventral shell margin uppermost. Often, many individuals live in close proximity to one another; the species is gregarious. When living on *P. porites* colonies, it is usually found among the dead lower portions of branches, below *B. cancellaria;* the long axis of the animal is usually vertical, with the posterior end uppermost. When disturbed, an animal often releases its byssus and drops from the surface of attachment. If detached and placed in an aquarium, animals commonly crawl about extensively before attaching to hard objects.

Arcopsis adamsi (Dall)
(Pl. 5, figs. 5, 6)

SHELL DESCRIPTION: The shell is small (its length seldom exceeds 1.5 cm but occasionally reaches 2 cm). It is markedly quadrate, very elongate, and strongly inflated. The valves are thick and bear cancellate ornamentation.

L/H 1.67, H/W 1.09, T.I. 0.56

LOCALITIES: This species was collected at many locations in Biscayne Bay, Florida, and southern Puerto Rico.

HABITAT: *A. adamsi* usually lives in close association with *Barbatia domingensis*, attached to the undersides of rocks just below the low tide mark. Less commonly it attaches to the undersides of coral colonies.

LIFE HABITS: This small species attaches to the undersides of rocks and corals in the manner of *Barbatia domingensis*, with its ventral margin uppermost. Like the latter, it is gregarious and often present in large numbers on a single attachment surface. Byssal release following disturbance and extensive crawling activity when free in an aquarium also characterize *A. adamsi.*

Anadara ovalis (Bruguière)
(Pl. 5, figs. 7-10)

SHELL DESCRIPTION: The shell is moderately large (may attain a length of 6 cm), ovate, and strongly inflated. The left valve commonly overlaps the right valve slightly along the ventral margin. The posterior is expanded. The umbones nearly touch. The valves are thick and ornamented with coarse radial ribs; the furrows between ribs are partly filled in life by bristle-like growths of periostracum.

L/H 1.17, H/W 1.16, A1/L 0.29, T.I. 0.65, O.I. 17

LOCALITIES: Three individuals were collected (where previously abundant) along the eastern shore of Bass River, Massachusetts, near the mouth, from coarse sand (sed. 7) at water depths of about 1 m. The bottom here is swept by moderately strong tidal currents. One individual was observed in Squeteague Harbor in a more protected setting, in slightly muddy sand. Numerous individuals were collected in fine sand (sed. 29) on moderately protected, intertidal sand flats at Salerno, Florida.

HABITAT: *A. ovalis* apparently prefers predominantly sandy substrata where there are moderately strong current movements but is tolerant of a variety of habitats.

LIFE HABITS: This species is a slow burrower (B.R.I. 0.3). Large animals tend to burrow sporadically and may take several days to attain their final life position. Smaller animals (up to 4.5 cm) were observed to complete their burrowing periods without delays. The broad foot, with its posterior heel, emerges opposite the hinge. Four or five burrowing sequences are commonly required to erect the shell. Downward penetration begins with the hinge axis tilted forward a few degrees from horizontal (Pl. 5, fig. 9). The rocking movement of each burrowing sequence rotates the shell through an angle of about 30°. The entire shell tilts progressively forward in the course of downward movement.

When the shell is almost completely buried, the animal tilts even farther forward to the life position, with the flattened posterior margin horizontal. Usually this margin remains exposed at, or slightly above, the sediment surface (Pl. 5, fig. 10). Individuals can frequently be collected by uprooting tufts of red algae that attach to the exposed portions of shells, just as they attach to pebbles and shell debris. Large animals may remain half-buried indefinitely and are more readily discovered than small animals.

Animals of all sizes are apparently capable of secreting a weak byssus (consisting of several fine threads) which aids the animal in maintaining a secure position at the sediment surface. Small individuals can climb vertical surfaces by fastening byssal threads above their shells and pulling upward by contraction of the pedal muscles.

Anadara notabilis (Röding)
(Pl. 5, figs. 11, 12)

SHELL DESCRIPTION: The shell is large (may reach a length of 9 cm) and grossly quadrate, but with a rounded ventral margin. It is elongate (L/H increasing during ontogeny) and very strongly inflated. The umbones are separated by an extensive ligament area; the valves are very thick and traversed by very strong radial ribs; the ventral furrows between ribs are partly filled in life by bristle-like growths of periostracum.

L/H 1.49 H/W 0.91, PL/L 0.24, T.I. 0.85, 0.I. 21

LOCALITIES: Numerous individuals were collected intertidally at Bear Cut, Key Biscayne, Florida, from a clean, medium to fine carbonate sand substratum carpeted with *Thalassia* grass (sed. 25). One large animal was found along the southwest shore of Rickenbacker Causeway near Virginia Key, Florida, in intertidal muddy sand covered with fine grass. A large population was also observed in both grassy and clean sand near Trunk Island, Harrington Sound, Bermuda.

HABITAT: *A. notabilis* prefers intertidal and shallow subtidal environments and grass-covered, sandy substrata.

LIFE HABITS: This species is a very sluggish burrower which was not timed in the laboratory. Only small individuals achieve nearly complete burial; large animals seldom live with more than one third of the shell buried beneath the sediment surface. The long axis of the shell normally lies tilted forward about 30° from the horizontal, this angle being slightly greater for more deeply buried, small forms. Some animals were observed to possess a weak byssus.

Anadara chemnitzi (Philippi)
(Pl. 6, figs. 1-4)

SHELL DESCRIPTION: The shell is small (length usually less than 2.5 cm) and both quadrate and equant in lateral view. It is strongly inflated. The left valve commonly overlaps the right valve along ventral margin. The valves are very thick and bear very strong, tuberculate radial ribs.

L/H 1.19, H/W 1.02, AL/L 0.29, T.I. 0.90, O. I. 23

LOCALITY: Numerous individuals were dredged in Mayaguëz Harbor, Puerto Rico, from slightly clayey carbonate silt (sed. 32) at depths of about 6 m.

HABITAT: *A. chemnitzi* prefers somewhat muddy substrata and sheltered subtidal conditions.

LIFE HABITS: This species is a slow burrower (B.R.I. 0.3). The erect probing orientation is with the posterior dorsal area horizontal or tilted backward a few degrees. In a manner similar to many cardiids, the animal rises up slightly and rocks backward a few degrees before slowly rocking forward. The angle of forward rotation is 25° to 30°. Penetration of both the native muddy sediment and fine sand is difficult, and complete burial often requires more than 20 burrowing sequences.

In life position, the shell lies just beneath the sediment surface, and the mantle forms the large inhalent and smaller exhalent openings (Pl. 6, fig. 4). All animals studied in the laboratory secreted an unusual byssus, consisting of a single thread about twice the length of the animal. The thread was not fixed to any inanimate object, but was anchored in the sediment by a sheet-like byssal pad, whose center was attached to the distal end of the thread (Pl. 6, fig. 3). Apparently, this unusual byssal apparatus represents a special adaptation for life in fine-grained substrata, where there are few large sedimentary particles for conventional byssal fixation.

Noetia ponderosa (Say)
(Pl. 6, figs. 5-9)

SHELL DESCRIPTION: The shell is moderately large (maximum length approximately 6 cm). The anterior is rounded and the posterior is triangular, with a flattened dorsal area. The shell is slightly opisthogyre, moderately elongate, and strongly inflated. The valves are very thick with moderately coarse radial ribbing (obscured ventrally in life by thick, rough periostracum).

L/H 1.25, H/W 1.04, AL/L 0.43, T.I. 0.48, O.I. 11

LOCALITIES: This species was collected in moderate abundance from a sand bar about 10 m offshore from the mean high water strand line at Marco Island, Florida, where it was exposed at extreme low tide. It is apparently much more common slightly farther offshore, being periodically washed in by storm waves. On the sand bar, it lives in clean fine sand (sed. 19). Several individuals were also collected from fine to very fine sand on moderately exposed intertidal flats near Salerno, Florida (sed. 29).

HABITAT: *N. ponderosa* prefers clean sand substrata and considerable wave or current agitation.

LIFE HABITS: This species is a slow burrower (B.R.I. 0.1). The animal erects itself slowly, using several burrowing sequences. Burrowing movements are very regular and deliberate, and the shell rocks through a very small angle (about 10°) during each burrowing sequence. The animal moves almost directly downward into the substratum, the large umbones butting against the sediment anteriorly to resist forward movement. The hinge line is tilted slightly forward of horizontal at the start of burrowing (Pl. 6, fig. 7), but the shell rotates progressively forward in the course of the burrowing period to assume the life position, in which the flat posterior shell margin is horizontal. This posterior margin is commonly exposed at the surface of the sediment in life (Pl. 6, fig. 9) and may become encrusted with alcyonarians, madreporarian corals, or other epibionts. Nearly all animals secret a ribbon-like byssus (Pl. 6, fig. 8) as an aid in maintaining a stable position in the substratum. What object, if any, this structure may attach to has not been observed.

Glycymeris pectinata (Gmelin)
(Pl. 7, figs. 1-4)

SHELL DESCRIPTION: The shell is small (seldom attaining a length of more than 2.5 cm). It is equant and slightly triangular in lateral view; the anterior and posterior halves of the shell are nearly symmetrical. The shell is moderately inflated. The valves are very thick and bear weak, rounded radial ribs.

L/H 1.03, H/W 1.64, AL/L 0.50, T.I. 0.87, O.I. 5

LOCALITIES: This species was collected in considerable numbers from Biscayne Bay, Florida, just below mean low tide in slightly muddy and gravelly carbonate sand amid dense *Thalassia* grass. It was also collected at Soldier Key (sed. 21) and just south of Cape Florida (sed. 22). It was commonly found lying free on the substratum or resting on the backs of regular sea urchins, which pick up live animals as well as empty shells and shell fragments for camouflage. Unburied animals were probably hampered in efforts to reburrow by the coarse nature of the substratum and the extremely dense meshwork of *Thalassia* roots and runners. Three individuals were dredged from gravelly sand in about 20 m of water off Media Luna Reef, La Parguera, Puerto Rico.

HABITAT: *G. pectinata* prefers coarse, often grass-covered substrata in subtidal environments.

LIFE HABITS: This species is a very sluggish burrower, not timed in the laboratory. The hatchet-shaped foot emerges opposite the broad hinge, as in other arcaceans. The animal burrows with the hinge line horizontal and does not penetrate the substratum easily. The angle of rotation is small. The burrowing period is characterized by long delays. Individuals commonly crawl considerable distances along the substratum surface in the process of burying themselves, leaving a visible furrow in their wake (Pl. 7, fig. 3). Animals about 2.5 cm in length perform approximately one burrowing sequence per minute; each sequence accomplishes little downward penetration but moves an animal about 0.5 cm forward. Individuals were observed to form sinuous trails as long as 0.5 m in the laboratory. Left for several days in an aquarium, nearly every one of 20 animals buried itself in native sediment (without *Thalassia*). Even after burial, many animals emerged to crawl about on the sediment surface and eventually reburrowed at new locations.

Atkins (1936, p. 217) has reported that the species *G. glycymeris* "when buried appears to lie indifferently on the right or left valves, and has been found occasionally more or less vertical." In the present study, 15 individuals of the species *G. pectinata* were placed left-valve down on their native sediment and permitted to burrow. Their life orientations were measured as described on p. 99 and are presented graphically in Figure 42. Eleven of the 15 lay with the plane of commissure between 55° and 75° from the vertical. (The slight predominance of animals lying on the left side probably reflects the initial placement of individuals left-side-down on the substratum.) The orientation of the shell within the commissure plane is with the posterior region uppermost. This orientation requires that the animal rotate anteriorly from the burrowing position after burial is achieved. Although individuals tend to lie on one valve or the other at a low angle, they seldom lie with the commissure plane closer than 25° to the horizontal because of the need to keep the posterior current openings exposed at the sediment surface (Pl. 7, fig. 4). Sometimes the posterior shell margin also remains exposed. The strong tendency to lie on one side may be an adaptation for permitting the small, anterior inhalent current to draw water from the overlying water mass through a minimum thickness of sediment. Employment of this anterior current apparently restricts members of the genus to coarse, permeable substrata.

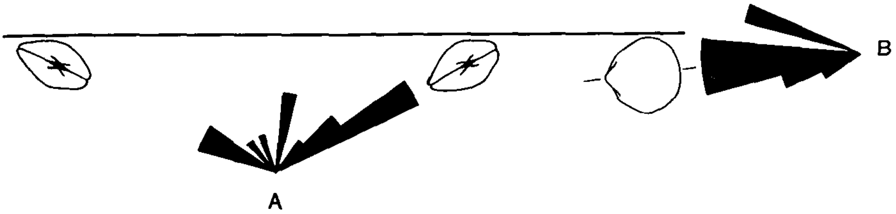


Figure 42. Life orientations of 15 *Glycymeris pectinata* individuals placed on their left valves and permitted to burrow in their native sediment (no. 22) in the laboratory.

Mytilus edulis Linné
(Pl. 7, figs. 7-9; Pl. 8, figs. 1-3)

SHELL DESCRIPTION: The shell is moderately large (sometimes attaining a length of 9 to 10 cm). It is triangular in lateral view with a reduced and bluntly pointed anterior. The umbonal ridge is nearer the ventral than the dorsal margin; the ventral margin is generally straight or slightly concave, with a shallow byssal sinus. The valves are thin. The exterior is smooth or slightly rugose.

LOCALITIES: This species is common along western Atlantic shorelines from the Arctic Ocean to North Carolina. It has been much studied in Europe because of its economic value, which remains largely unexploited in the United States. Field (1922) and White (1937) have provided thorough biological treatments of the species. Colonies of the species were observed on many shores during this study; its depth distribution was measured in detail at a locality in Woodmont, Connecticut.

HABITAT: Rocky intertidal surfaces are the favored substratum, but shells or stones may serve as nuclei for the formation of large clumps or banks of individuals on firm sand. At the Woodmont, Connecticut, locality, where *Modiolus demissus* also occurs, the mean tidal amplitude is 6.2 ft. *M. Edulis* is restricted to the lower 3.5 ft of this zone and extends subtidally in abundance only to a depth of about 0.3 ft. It is abundant only on rocky surfaces. These observations are in close agreement with those of Dexter (1947), who studied the species at Cape Ann, Massachusetts, where it occurs abundantly only from spring low tide through the lower 5 ft of the 8.5 to 8.7 ft intertidal zone.

Individuals preferentially occupy crannies and crevices on rocky shores (Pl. 8, fig. 1), apparently because of the tendency of spat to settle in protected areas. Rocky shores exposed to strong wave action are most commonly colonized, however, and it is only on a smaller scale that limited protection for firm anchorage is sought.

Clumps of individuals were observed on a broad sand flat at Barnstable Harbor, Massachusetts, just north of Bonehill Road (Pl. 8, figs. 2, 3). True mussel banks are uncommon in North America but are spectacularly developed along tidal channels in the Dutch Wadden Sea, where they have been described by many workers (Kuenen, 1942; Geesteranus, 1942; Verwey, 1952). Verwey notes the unusually deep lower limit of mussel distribution in the Wadden Sea (6-17 m below the low tide mark).

In a meter or so of water at Gansett Beach and Black Beach, Falmouth Township, Massachusetts, clumps of mussels bind together clusters of pebbles and cobbles with a network of byssal threads. Although strong water currents are present at both localities, the stone clusters serve as anchors for colonies on shifting sand substrata.

In general, fixation in this species is to hard objects, whether broad rocky surfaces, small rocks, shell fragments, or shells of neighboring individuals. The species is largely restricted to the intertidal realm, and prefers exposure to strong wave or current action.

LIFE HABITS: *M. edulis* fixes itself to the substratum by means of a strong byssus. Byssus formation has been described by Field (1922). Each byssal thread is formed individually in a groove along the ventral margin of the foot. The byssal liquid, of which the thread is formed, hardens immediately upon contact with seawater when released from the pedal groove. The byssal threads radiate from a byssal stalk at the base of the foot. In addition to anchoring the animal against the substratum, they serve as guy wires holding the animal's sagittal plane at approximately right angles to the attachment surface. Commonly many individuals become so closely crowded together that the ventral margins of some animals are no longer in contact with the substratum. The anterior tips of shells are then lowermost, and the posterior regions, with the inhalent and exhalent currents, project upward (Pl. 7, fig. 9). Clumps are formed as some individuals become attached to neighboring shells, rather than to the underlying substratum. An individual can release its byssus and, to a limited extent, creep about with its narrow, finger-like foot. Young animals are more active in this locomotory activity than adults.

On soft substrata, mussels tend to attach to each other in an effort to elevate themselves above the loose substratum (Pl. 8, fig. 3). Almost never is the anterior or ventral region of a live animal buried beneath the sediment surface. Once a single spatfall has colonized an isolated solid object on a sandy bottom, successive yearly spatfalls attach to living and dead individuals of this spatfall to enlarge the clump. A large bank may eventually form by accretion and coalescence of clumps. Rocky shores offer broad, solid surfaces for colonization so that vertical growth of local clusters is unnecessary and accretion is primarily lateral. On sandy substrata, the general restriction of large mussel banks to the margins of tidal channels reflects the mussels' need for strong currents of sufficient vertical dimensions to permit vertical accretion of mussel colonies. On broad sand flats, small mussel clumps may accrete and coalesce laterally to form extensive beds, but little vertical growth can take place (Pl. 8, fig. 2).

Modiolus modiolus (Linné)
(Pl. 9, figs. 4-6)

SHELL DESCRIPTION: The shell is very large (its length may exceed 12 cm) and oblong, with a moderately reduced anterior. The umbonal ridge is located about halfway between the dorsal and ventral margins and is strongly curved in the anterior region. There is a prominent byssal sinus, sometimes present as a sharp marginal inflection. The anterior ventral margin is flared ventral to umbo. The anterior adductor scar is elongate and relatively larger than in *Mytilus*. The valves are thin and rugose exteriorly; the juvenile shell is very similar to adult shells of *M. americanus*.

LOCALITIES: Numerous individuals were observed and hand-collected at Nahant, Massachusetts, in 6 to 10 m of water, where the species lives in gravelly sand. Mr. John Valois kindly provided several specimens dredged from depths of 40 m at a locality a short distance northeast of Cape Cod Canal, Cape Cod Bay, Massachusetts. These specimens were also attached to pebbles and cobbles.

HABITAT: The so-called "horse mussel" occurs from spring low water to depths of 280 m. (Wiborg, 1946, *from* Haas). The species prefers a gravel substratum, or a sandy substratum containing a large admixture of coarse debris. At the Nahant locality, where hundreds of individuals occur, the submarine setting offers a variety of substrata for potential colonization: coarse, shifting sand; rocky surfaces of many types; and gravel-sand mixtures in semi-protected enclosures among rocky prominences. Horse mussels are almost exclusively restricted to the gravel-sand areas, apparently being unable to become established in shifting sands and not favoring attachment to bare rocky surfaces.

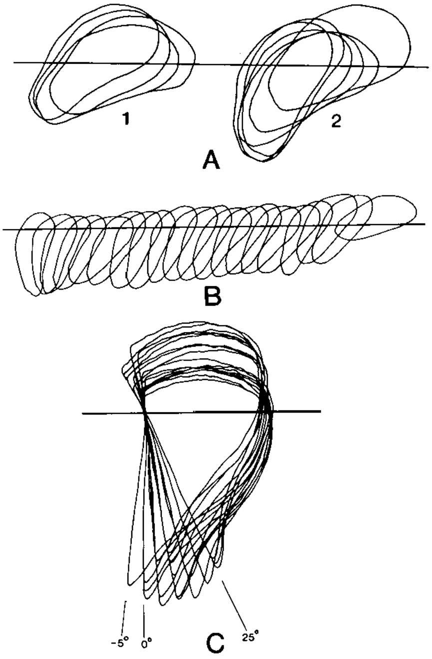


Figure 43. Life positions of: A = *Modiolus modiolus* from gravelly sand of (1) Cape Cod Bay, Massachusetts, and (2) Nahant, Massachusetts; B = *Modiolus demissus* from marsh peat at Woodmont, Connecticut; C = *Atrina rigida* from Biscayne Bay, Florida (sediment 24). Individual outlines reduced to a standard size for each species.

LIFE HABITS: The species is apparently gregarious; animals typically live in groups of 30 or 40, occupying approximately half a square meter of the bottom. Nearly every animal observed in life position in this study had only the posterior portion of its shell exposed above the sediment surface. The exposed region is usually encrusted by coraline algae and commonly bears other types of epibionts as well (Pl. 9, fig. 6). The life orientations of individuals collected from both localities mentioned above were reconstructed using the line between bare shell and algal encrustation as a marker of the sediment-water interface; these orientations are plotted in Figure 43A. Normally, the shell is half or more buried in the sediment and the longest dimension of the shell lies at an angle of 25° to 40° from the vertical. The common occurrence of similar algal encrustation patterns on shells in museum collections supports the validity of this general life position and mode of attachment. Wiborg (1946) has previously implied that a substantial proportion of *M. modiolus* individuals live in a semi-infaunal position, but his general statement (in Danish) is difficult to interpret.

Modiolus demissus (Dillwyn)
(Pl. 9, figs. 7-9)

SHELL DESCRIPTION: The shell is moderately large to large (occasionally reaching 8 to 10 cm in length). It is generally elongate and cylindrical, with a slightly reduced anterior. The umbonal ridge is located about halfway between the dorsal and ventral margins and is curved anteriorly; the umbones are commonly eroded. The byssal sinus is broad and shallow. The anterior adductor scar is elongate and relatively larger than in *Mytilus*. The valves are thin and traversed by radial ribs that enlarge posteriorly to form finely serrated valve margins; the ornamentation is reduced in the anterior ventral region.

LOCALITIES: Thousands of individuals have been observed living in intertidal marshes along the coasts of Connecticut, Massachusetts, and New Jersey.

HABITAT: The "ribbed mussel" occurs in great numbers in peat substrata of marsh environments along most of the Atlantic coastline of the United States. The normal habitat is the low intertidal marsh (which extends from slightly above mean low tide to a level somewhat above the uppermost limit of *Mytilus edulis* in most areas). Only scattered individuals are found attached to rocky surfaces or living subtidally. The typical marsh-dwelling habit is described briefly by Kuenzler (1961) for a locality near Sapelo Island, Georgia; by Moore (1961) for the Mississippi (state) region; and by Allen (1954) for a Chesapeake Bay locality. Dexter (1947) has used the species (along with *Spartina* and *Littorina* spp.) to name the low marsh community at Cape Ann, Massachusetts, and has discussed the semi-infaunal habit discussed below. McDougall (1943) has described the great abundance of the species in "reed beds" adjoining Beaufort Harbor, North Carolina, but mentions that it is also found intertidally on wharf piles.

LIFE HABITS: *M. demissus* most commonly attaches to buried stems and roots of marsh grass, and less commonly to buried pebbles or shells, by a byssus that is weak relative to those of unprotected epifaunal mussels like *Mytilus* spp. or *Brachidontes recurvus*. *M. demissus* gains support from the peat surrounding the shell, which is mostly buried. Orientation of 20 individuals from a marsh at Woodmont, Connecticut, were measured and are represented in Figure 43B. A point in the marsh was randomly chosen from a distance, and the 20 mussels closest to it were selected for measurement. The average orientation agrees with my general observations for the species; the longest dimension of the shell lies at an angle of about 30° from the vertical and is about 75 percent buried in the substratum. A typical individual, but one living at a slightly lower angle than average, is shown in Plate 9, figure 6. The exposed posterior region of the shell commonly becomes encrusted with barnacles. During its life history, an individual must move progressively deeper into the substratum to maintain its normal life position relative to the substratum surface. Net rate of downward movement is very slow (a few millimeters per year). This movement has not been observed, but is apparently accomplished by contraction against anteriorly placed byssal threads, rather than by normal pedal burrowing.

Modiolus americanus Leach
(Pl. 9, figs. 10, 11)

SHELL DESCRIPTION: The shell is moderately large to large (sometimes attaining a length of 8 to 10 cm). Its shape is similar to *M. modiolus* but with the umbonal ridge straighter, the byssal sinus less distinct, and the dorsal margin flared in the region of the posterior ligament area. The rough periostracum on the posterior dorsal shell surface is commonly coated with particles of sediment.

LOCALITIES: The species was collected in considerable numbers on the very shallow subtidal grass flats south of Cape Florida, Key Biscayne, Florida, and from similar grass flats at Guánica, Puerto Rico (sed. 22; 38), and Harrington Sound, Bermuda.

HABITAT: *M. americanus* is predominantly subtidal; it lives primarily amid dense networks of *Thalassia* roots and runners in sandy substrata, but also inhabits clean sand.

LIFE HABITS: Most members of this species collected in this study were found living completely buried in the sediment, with the posterior shell margin at the sediment surface; large individuals and individuals living in clean sand are often partly exposed, however. Attachment by the moderately strong byssus is to buried portions of *Thalassia* or coarse sediment particles. The orientation is highly variable; orientation of the longest dimension of the shell usually ranges from roughly vertical to 45° from vertical, depending on the constricting effects of neighboring plant structures and coarse sedimentary debris.

Brachidontes exustus (Linné)
(Pl. 8, figs. 4-6)

SHELL DESCRIPTION: The shell is small (less than 2 cm in length) and similar in form to *Mytilus edulis*, but more compressed and more strongly hooked anteriorly. The valves are thin, and are ornamented with fine radial ribs.

LOCALITIES: This species was observed in large numbers at many localities along the south coast of Puerto Rico and the north shore of Bermuda.

HABITAT: *B. exustus* lives intertidally on hard substrata, usually rocks. It is generally restricted to exposed portions of rocks, but favors shallow crevices and crannies rather than smooth surfaces.

LIFE HABITS: This species attaches firmly by means of a strong byssus, which is not normally released when the animal is disturbed. It is similar in habits and habitat preferences to the larger northern species *Mytilus edulis.* Animals often wedge tightly together in clusters, so that the posterior ends of their shells are directed upward (Pl. 8, fig. 6).

Brachidontes recurvus (Rafinesque)
(Pl. 7, figs. 5, 6)

SHELL DESCRIPTION: The shell is moderately small (seldom exceeding 5 cm in length). It is triangular in outline with a reduced and pointed anterior. The umbonal ridge lies near the ventral margin. The long axis is broadly curved and the ventral margin is concave. A distinct byssal gape and sinus are usually present. The valves are thin, with distinct, fine radial ribs.

LOCALITIES: This species was not observed as a part of this study but was encountered previously along the Texas Gulf Coast.

HABITAT: A common inhabitant of oyster banks in the Gulf Coast and Chesapeake Bay regions, it is also found attached to mangrove roots and rocky surfaces intertidally and in shallow subtidal settings.

LIFE HABITS: Individuals attach to hard substrata in crowded clusters, or partially imbed themselves in crevices or cavities, usually with the posterior portions of their shells exposed. This species employs a strong byssus, which is not readily broken.

Brachidontes citrinus (Röding)
(Pl. 9, figs. 1-3)

SHELL DESCRIPTION: The shell is small (length seldom exceeding 3 cm) and generally elongate and cylindrical. The umbonal ridge is relatively straight and a byssal sinus is shallow or lacking. The dorsal margin is flared slightly in the region of the posterior ligament area; the anterior ventral margin is slightly flared ventral to the umbo. The anterior adductor scar is relatively larger than in *Mytilus edulis.* The valves are thin and ornamented with five radial ribs that coarsen posteriorly to produce finely serrated valve margins.

LOCALITIES: This species was collected in life position from a *Thalassia* bed in sand (sed. 38) just below the low tide mark, southeast of Guánica, Puerto Rico. It was also found dead, but in large numbers, washed up on a beach with dense masses of *Thalassia* at Sandy Point, St. Croix, Virgin Islands; the shells were apparently derived from a shallow setting much like that at Guánica.

HABITAT: *B. citrinus* is most common in subtidal grass flats.

LIFE HABITS: Animals collected at Guánica were entirely buried in the sediment except for the posterior tips of their shells. Although living among dense *Thalassia* roots and runners, nearly all individuals were byssally attached to coarse sand, rock, and coral debris (Pl. 9, fig. 3). The byssus is weak and readily released when the animal is disturbed. The life position is with the long axis of the shell at an angle greater than 40° from the horizontal (often it is nearly vertical). It is possible that individuals of this species may not always live in the way described here, but the consistency of habits among the individuals observed and the fact that the species is not commonly observed as an epifaunal element in the West Indies strongly suggest that the infaunal mode of life observed at Guánica is normal for the species.

Isognomon alata (Gmelin)
(Pl. 10, figs. 1-4)

SHELL DESCRIPTION: The shell is moderately large (the diameter sometimes exceeding 7 cm) and fan-shaped, with the region opposite the hinge broadly rounded and flared posteriorly. The hinge line is straight but there is a distinct byssal sinus. The shell is extremely compressed; its surface is finely rugose, with an imbricate texture.

LOCALITIES: This species was observed and collected at many locations in South Florida and Puerto Rico.

HABITAT: *I. alata* most commonly attaches to the prop roots of mangroves. It colonizes hard substrata of other types, as well, but is largely restricted to intertidal and shallow subtidal environments.

LIFE HABITS: This is a gregarious species. Clusters of individuals commonly fill the upside-down forks of mangrove prop roots (Pl. 10, figs. 3, 4). Attachment to the substratum is accomplished by a moderately strong byssus; the plane of commissure of the shell may lie parallel to the substratum surface or at any angle up to 90°, depending on crowding conditions; for isolated individuals this angle is normally less than 45°.

Isognomon radiata (Anton)
(Pl. 10, figs. 5-8)

SHELL DESCRIPTION: The shell is moderately small (the maximum dimension is approximately 5 cm). The gross morphology is extremely variable. The shell is generally enlongate and bent to conform to the confines of a cavity; it is strongly compressed. The valves are thin and smooth, but commonly encrusted by epibionts.

LOCALITIES: This species was observed and collected at many locations in South Florida, Puerto Rico, and Bermuda.

HABITAT: *I. radiata* normally lives beneath rocks or within branching coral colonies, especially those belonging to the genus *Porites.* It is apparently restricted to shallow-water settings.

LIFE HABITS: The shell of this species is seldom exposed above the substratum. Individuals are usually nestled between or beneath rocks or coral rubble. Commonly, they live wedged in among the lower, dead branches of ramose coral colonies of the genus *Porites* (Pl. 10, figs. 7, 8). Byssal attachment is very weak, and animals may live in a variety of orientations relative to the attachment surface.

Pteria colymbus (Röding)

(Pl. 11, figs. 1-4)

SHELL DESCRIPTION: The shell is moderately large (may reach 7 to 8 cm in maximum dimension) and obliquely oval, with a long posterior auricle, which forms an angle of about 40° with long axis of the oval portion and commonly exceeds it in length. The anterior auricle is short and bounded by a distinct byssal notch on the right valve. The left valve is inflated and the right valve, compressed; both valves are thin, attenuating toward all margins except those forming the hinge axis. The surface is smooth, but covered with periostracum that forms radiating marginal projections.

LOCALITIES: This species was collected in various shallow-water areas in South Florida and in the vicinity of La Parguera, Puerto Rico.

HABITAT: *P. colymbus* attaches almost exclusively to the upper portions of whip-like alcyonarians in shallow subtidal areas. Individuals occasionally attach to inanimate objects, but there is apparently a strong tendency of the spat to settle on alcyonarians.

LIFE HABITS: This species is apparently gregarious. As many as 5 or 6 individuals commonly inhabit a single alcyonarian colony. The animals are usually found attached to the central alcyonarian stalk, with their elongate posterior auricles directed upward at angles often comparable to those formed by the lateral branches of the alcyonarian colony (Pt. 11, fig. 3). The animal normally attaches by a strong byssus but can alter its posture to a limited extent by contraction of its byssal muscles. A strong exhalent current issues from the marginal sinus ventral to the elongate posterior auricle (Pl. 11, fig. 4).

Pinctada radiata (Leach)

(Pl. 11, figs. 5-7)

SHELL DESCRIPTION: The shell is moderately large (the maximum dimension may exceed 6 to 7 cm) and obliquely oval, with a straight hinge line. There is a shallow posterior sinus where the valves gape in the siphonal region and a distinct byssal sinus on the right valve. The margins opposite the hinge bear blunt radial projections. The left valve is moderately compressed; the right valve is strongly compressed. The valves are thin; their exteriors are generally smooth but with a slight crenulate rugosity.

LOCALITIES: Previous to undertaking this study, I observed representatives of this species in a variety of habitats in South Florida. A. C. Johnson provided a single large specimen for laboratory study (collected from a clump of *Porites* coral near La Parguera, Puerto Rico). I have since observed dozens of individuals in Harrington Sound, Bermuda.

HABITAT: This "pearl oyster" attaches to a wide variety of hard substrata in shallow water settings in South Florida and the Caribbean.

LIFE HABITS: The species is to some extent gregarious. It is commonly represented by clumps of individuals that attach by a moderately strong byssus to a hard substratum or to each other. An individual collected at La Parguera, Puerto Rico, was allowed to exist in a laboratory tank without the benefit of foreign objects for attachment. It somehow climbed nearly 20 cm up a vertical cement wall of the aquarium and attached near the surface of the water. The angle formed between the animal's plane of commissure and the flat aquarium wall was almost exactly 45°; this would appear to represent the normal orientation for the animal when attached to a flat surface with no boundary effects. The exhalent current (Pl. 11, fig. 7) issues from the shell at an angle of 35° to 40° from the hinge line (in a more dorsal direction than the current of *Pteria colymbus*).

Pinna carnea Gmelin
(Pl. 11, figs. 8, 9)

SHELL DESCRIPTION: The shell is very large (may reach a length of 25 cm but usually grows no longer than 15 to 20 cm). It is triangular in lateral view and elongate posteriorly. The posterior margin is rounded and often uneven from breakage; the anterior is pointed. The hinge axis is commonly curved dorsally in the posterior region. There are large posterior and byssal gapes. The valves are very thin. Rounded plicae radiate from umbo, usually bearing short, hollow spines in the posterior region.

LOCALITIES: This species was collected from shallow subtidal grass flats (on sand bottoms) at Bear Cut, Key Biscayne, Florida, and in back-reef areas in the vicinity of La Parguera, Puerto Rico; it was also observed in abundance in Ferry Reach, Bermuda.

HABITAT: This "pen shell" seldom occurs in more than a few meters of water. It lives most commonly in sandy sediment amid growths of *Thalassia.*

LIFE HABITS: This species attaches by a byssus to coarse debris in the substratum. It is normally neither as deeply buried nor as strongly attached as *Atrina rigida.* The longest dimension of the shell is usually about one-half buried in the sediment and oriented in a vertical position. Occasional specimens are found living epifaunally and attached to hard substrata.

Atrina rigida (Solander)
(Pl. 12, figs. 1-3)

SHELL DESCRIPTION: The shell is very large (the length frequently exceeding 20 cm) and is similar in gross shape to *Pinna carnea,* but possesses a relatively shorter hinge line and a broad byssal sinus. The shell is substantially thicker than that of *P. carnea* and the posterior spines are more strongly developed.

LOCALITIES: This species was observed and collected in large numbers along the southwest side of Rickenbacker Causeway, Biscayne Bay, Florida, amid dense *Thalassia* in slightly muddy fine sand (sed. 24). It was also found at other, similar settings in South Florida.

HABITAT: *A. rigida* is most common in low intertidal and shallow subtidal areas that are moderately protected from strong waves and currents; it prefers muddy or clean sand bottoms carpeted by eel grass.

LIFE HABITS: This species attaches by a strong byssus to coarse debris in the sediment (Pl. 12, fig. 3). Animals are firmly anchored and difficult to uproot. Life positions of 20 randomly selected individuals were measured at the Rickenbacker Causeway locality. The plane of commissure was approximately vertical for all animals. Shell orientation (within the commissure plane) relative to the sediment-water interface is diagrammatically presented in Figure 43C. On the average, 83 percent of the hinge line was buried in the sediment and the hinge line was tilted 10° from the vertical. The mean orientation for this locality is, according to my observations, typical for the species in general.

Downward penetration of the substratum during ontogeny is apparently accomplished by periodic muscular contraction against the anchored byssus and attachment of byssal threads at progressively deeper levels within the sediment.

Aequipecten irradians irradians (Lamarck)
(Pl. 12, figs. 4, 5)

SHELL DESCRIPTION: The shell is large (sometimes reaching a diameter of 8 cm) and nearly circular in lateral view. The umbonal angle is about 114°; the maximum dimension parallel to the hinge line exceeds the maximum dimension perpendicular to hinge line. The auricles are of approximately equal length. The valves are moderately convex, the right valve being slightly more inflated than the left; both valves are thin and folded into coarse, rectangular plicae.

LOCALITIES: Large numbers of animals have been observed in Squeteague Harbor and other marginal marine bays of Cape Cod, Massachusetts.

HABITAT: This species is a common subtidal inhabitant of shallow, protected bays and lagoons, where it most frequently occupies areas of the bottom covered by eel grass.

LIFE HABITS: When small, this species lives attached by a byssus, usually to eel grass. In the laboratory, animals as large as 6 cm in diameter secreted a byssus for attachment to the surface of a water table. Especially in larger animals, the byssus is relatively weak and easily broken. Animals 7 cm in diameter or larger seldom, if ever, secrete a byssus but spend most of their time reclining on the substratum, right valve undermost. In nature, reclining animals are commonly surrounded by organic debris, chiefly dead eel grass, which helps to camouflage them.

Swimming in *A. irradians* is an escape response rather than a way of life. When disturbed, an animal relaxes its adductor muscle, allowing its ligament to spread the two valves apart. This initial gaping process normally requires 2 or 3 seconds for completion. The valves are then clapped violently together by a rapid contraction of the adductor and swimming begins. Repetition of the process at short intervals lifts the animal into the water by jet propulsion, with the plane of commissure approximately parallel to the direction of movement. Water is squirted from the anterior and posterior dorsal regions (on either side of the hinge), but not simultaneously. The mantle margins control water discharge so that water is squirted alternately from one side and then the other. The animal rotates through an angle of 30° or so in the plane of commissure with each pair of contractions. The net effect of rotational and translational movement is a clumsy zig-zag motion. An animal claps its way upward at an angle of about 45° and for a distance seldom exceeding 1 m. It then ceases activity, closes its valves, and sinks vertically downward once again to rest on the bottom. When disturbed suddenly, as by a chemical stimulus from a nearby starfish, a reclining animal commonly claps its valves together violently to eject water ventrally and jumps hinge-foremost a distance of a few centimeters. This reverse movement appears to be a special escape response for avoiding imminent danger.

Aequipecten gibbus nucleus (Born)

(Pl. 12, figs. 9, 10)

SHELL DESCRIPTION: The shell is smaller than that of *A. irradians* (seldom attaining a diameter greater than 4 cm); it is similar in form to the latter, but more strongly inflated.

LOCALITY: Large numbers of individuals were collected from the nets of a shrimp boat dredging in 3 to 4 m of water in grassy sand areas of Biscayne Bay, just southwest of Key Biscayne, Florida. A large population was also observed at Trunk Island, Harrington Sound, Bermuda.

HABITAT: Like *A. irradians, A. gibbus nucleus* is apparently largely restricted to shallow, grassy bays.

LIFE HABITS: Large animals normally live resting right-valve-down on the substratum, with the valves gaping about 20°; the mantle velum largely fills the space between the valve margins, the eyes are exposed, and the tentacles are extended. Only small individuals normally attach by a byssus. Of about 30 animals observed in the laboratory, only individuals 3.5 cm in diameter or smaller were observed to secrete byssal threads.

Swimming movements are almost identical to those of *A. irradians*, but being smaller, individuals of *A. gibbus* seldom swim as far in a single "flight."

When overturned on the substratum (left valve down), animals righted themselves, but not by rotating about the hinge line as an axis, as described by Buddenbrock (1911). Instead, they turned on the anterior or posterior valve margin by squirting water from the opposite side (where water is normally discharged during swimming).

Pecten ziczac (Linné)
(Pl. 12, figs. 6-8)

SHELL DESCRIPTION: The shell is very large (the diameter may exceed 10 cm) and circular in lateral view, but the maximum dimension parallel to hinge line exceeds the maximum dimension perpendicular to hinge line. The umbonal angle in adults averages about 121°. The auricles are of nearly equal length. The right valve is strongly convex and the left valve, slightly concave. The valves are thin and traversed externally by shallow radial grooves, each of which is expressed interiorly as a double ridge on the right valve and single ridge on the left valve.

LOCALITY: Robert C. Work kindly provided several specimens from Biscayne Bay, Florida, for laboratory study. I have since observed a sparse population near Trunk Island, Harrington Sound, Bermuda.

HABITAT: This species lives on sandy bottoms in shallow, moderately protected subtidal settings.

LIFE HABITS: The animal normally lives buried in the sediment to the level of the surface of commissure of the valves. When placed with the convex right valve undermost on the substratum the animal attains its life position by clapping its valves together at brief intervals, to scour the sand from around its margins and form a horseshoe-shaped depression (Pl. 12, fig. 8). Sand from beneath the center of the lower valve falls into the depression and is blasted away so that the animal gradually sinks into the sand. Some of the sand thrown into suspension settles on the surface of the concave upper valve so that it has been completely covered by the time the life position is attained; only the circular line of commissure, with its tentacled mantle margins, remains exposed. The animal is a moderately efficient swimmer. As in *Aequipecten,* water is alternately ejected from the anterior and posterior exhalent areas.

Placopecten magellanicus (Gmelin)
(Pl. 13, figs. 1, 2)

SHELL DESCRIPTION: The shell is very large (the diameter may exceed 20 cm) and circular in outline. The maximum dimension parallel to the hinge line is shorter than the maximum dimension perpendicular to the hinge line in small individuals, but for large animals, the reverse is true. The umbonal angle of large animals averages about 125°. The auricles are of approximately equal length. The shell is compressed, the left valve being more convex than the right valve. The valves are thin and relatively smooth, but scored externally by very fine radial grooves.

HABITAT: Unlike the above-mentioned species of the genus *Aequipecten, Placopecten magellanicus* lives in the open sea. It is commonly referred to as the "sea scallop" and has considerable economic importance. I have not personally collected members of this species, but quote from the literature as to its habitat preferences: "Sea scallops generally live on firm sand or gravel bottom although they do occur on muddy bottom. . . . They are also found on rocky bottom and I have seen them tucked away in crevices between rocks" (Bourne, 1964, p. 13). Bourne states that in the northern part of their range, sea scallops may live just below the intertidal zone, but in the southern part of their range, they live at 30 to 60 fathoms.

LIFE HABITS: Several animals kept in a long tank by J. A. Posgay were observed. The following comments are based on these observations and on discussions with Dr. Posgay.

Young individuals are byssally attached, like the young of other scallop species, and the byssus is readily released. Animals larger than 7 to 8 cm seldom secrete a byssus. The species is a much more adept swimmer than the other scallop species studied. Large animals are less active than small ones, but individuals in general swim more frequently and travel farther in a single "flight" than do species of *Aequipecten.* An animal rises from the substratum at an angle of about 45° and then, unlike *Aequipecten* spp., levels off to travel horizontally for several meters. Bourne (1964, p. 16) describes laboratory observations of "scallops swimming continuously for more than 15 or 20 sec., or higher than 2 ft. off the bottom" and underwater observations in nature of "continuous movements of more than 20 ft. horizontally during one swimming period." During swimming, water is drawn into the mantle cavity through an anterior and a posterior inhalent opening and is discharged perpendicular to the dorsal shell margins through smaller openings on either side of the hinge. The anterior and posterior currents are expelled simultaneously so that movement is much smoother and straighter than in *Aequipecten,* in addition to carrying the animal over much greater horizontal distances. The type of swimming movement exhibited by *Placopecten* is apparently an adaptation for life on extensive, bare regions of the open sea floor and would be virtually useless in the restricted bay habitat of *Aequipecten* spp.

Chlamys sentis (Reeve)
(Pl. 13, figs. 3, 4)

SHELL DESCRIPTION: The shell is moderately small (the maximum dimension generally being 4 cm or less); it is obliquely elliptical with a narrow umbonal angle (averaging about 84° in adults). The anterior auricle is 2.2 times as long as the posterior auricle and is bordered by a well-defined byssal notch on the left valve. The valves are thin and are covered with fine radial ribs bearing very short, fluted spines.

LOCALITIES: Several specimens were collected from the undersides of rocks 1 to 2 m below mean low water level along causeway embankments and rocky shores in the vicinity of Miami, Biscayne Bay, Florida.

HABITAT: *C. sentis* occurs beneath rocks and corals in shallow subtidal settings.

LIFE HABITS: This species attaches by a rather strong byssus. Although the right valve is anchored to the substratum, this valve is normally uppermost because of the upside-down life position. The animal can release its byssus and swim with moderate facility, but in a choppy, irregular manner (comparable to the swimming of *Aequipecten*).

Lima scabra (Born)
(Pl. 13, figs. 5-8)

SHELL DESCRIPTION: The shell is moderately large (sometimes attaining a height of 7 cm), elliptical, and slightly oblique. The anterior auricles and adjacent shell margins are flared to form a large, lip-like byssal gape. The shell is moderately thick, with fine radial ribs bearing short blunt spines. The so-called "form" *tenera* Sowerby has thinner valves and finer ornamentation.

LOCALITIES: I have observed both *Lima scabra* s.s. and the "form" *tenera* at Bear Cut, Biscayne Bay, Florida, and in the vicinity of La Parguera, Puerto Rico. They commonly live in close association with one another.

HABITAT: *L. scabra* is found beneath rocks and in crevices in coral colonies (especially branching colonies of the genus *Porites*).

LIFE HABITS: This species spends most of its life loosely suspended by a weak byssus beneath or between rocks or coral colonies. Attachment orientation is inconsistent. Many individuals are completely obscured from view in life position, but others are partially or wholly visible from an external vantage point. The valves normally gape about 20° during feeding. The species is gregarious. A single rock or crevice commonly houses two or more individuals. When its object of attachment is disturbed in nature, an individual usually releases its byssus and escapes by swimming.

Swimming movement is inefficient compared to that of most pectinids. Swimming orientation is with the plane of commissure vertical and the hinge undermost and horizontal. The animal moves anteriorly by a series of shell clapping movements that discharge water posteriorly. Between adductor contractions, the animal sinks downward, lacking the broad planing surface of a pectinid in swimming position. The result is a series of swooping movements that seldom carry the animal more than 30 to 40 cm above the substratum.

Lima lima (Linné)
(Pl. 13, figs. 9-14)

SHELL DESCRIPTION: The shell is small (the maximum dimension seldom exceeding 3 to 4 cm) and obliquely elliptical in lateral view, with a flattened ventral margin and slit-like byssal gape. The auricles are small. The valves are moderately thick, with radial ribbing; the ribs bear short fluted spines.

LOCALITIES: This species was collected in considerable numbers from rocks in shallow subtidal settings around the margins of Biscayne Bay, Florida; it is especially abundant along the southern shore of Norris Cut.

HABITAT: *L. lima* is common within pits and crevices on the undersides of rocks and coral colonies in shallow subtidal environments.

LIFE HABITS: This species attaches firmly to the substratum by a byssus which is quite strong for the size of the animal. The flattened ventral surface of the shell is in close contact with the substratum. The animal is often so tightly lodged in a crevice or cavity that it can only be removed by breaking the object of attachment. Animals released in aquaria crawl into corners or accessible crevices, where they preferentially attach themselves. Never having observed this species in the act of swimming, I concluded that it lacks the capacity to swim.

Individuals can climb vertical surfaces, including glass walls of aquaria, by using byssal threads. The climbing procedure is shown in Plate 13, figures 11 to 14. The animal tacks a thread to the surface above the shell with its extended foot and pulls upward by contraction of the byssal retractors. Holding its new position, it extends the foot to fasten another thread higher on the surface and pulls upward again. Repetition of the process permits the animal to climb a considerable distance, with its ventral margin uppermost.

Anomia simplex Orbigny
(Pl. 14, figs. 1-3)

SHELL DESCRIPTION: The shell is moderately small (the maximum diameter being about 5 cm); its shape is highly variable, but is generally circular in lateral view. The right valve is generally flat but tends to conform to the object of attachment. A discrete byssal opening is formed within the right valve by deep marginal embayment near the umbo; the left valve is of variable convexity and is commonly encrusted by epibionts. The valves are thin and irregularly rugose.

LOCALITIES: Numerous individuals were collected along the southern margin of Barnstable Harbor, Massachusetts, just below the spring low tide level in very gravelly coarse sand (sed. 42).

HABITAT: *A. simplex* attaches principally to pebbles, cobbles, and shell debris lying on the surface of firm substrata; it seldom attaches to broad rocky surfaces. It is generally restricted to shallow subtidal settings where there is moderate current flow.

LIFE HABITS: This species attaches with the flattened right valve undermost by means of a stout, calcified byssus. Individuals appear to grow in such a manner as to seldom overlap the object of attachment. Growth on broad, flat attachment surfaces (such as large mollusk shells) is primarily lateral, producing broad, flattened valves. On a small pebble, the lower valve commonly grows more slowly and the upper valve becomes extremely convex, to accommodate body-size increase without overgrowing the object of attachment. By growing in this manner, the animal avoids exposing its fragile shell margins to breakage.

Astarte undata Gould
(Pl. 14, figs. 5, 6)

SHELL DESCRIPTION: The shell is small (seldom longer than 3 cm), elliptical, and very slightly elongate in lateral view. It is prosogyre and compressed. The valves are very thick. The exterior is ornamented with broad, rounded concentric ridges, and the ventral interior margin is finely denticulate.

L/H 1.12, H/W 1.78, AL/L 0.39, T.I. 0.91, O.I. 8

LOCALITIES: This species was dredged in moderate abundance from muddy, gravelly medium sand (sed. 9) in 25 m of water on the northwest side of Quicks Hole, Buzzards Bay, Massachusetts. The bottom here is scoured by tidal currents that winnow out fine-grained material and leave a much coarser residue of sediments than the sediments of nearby

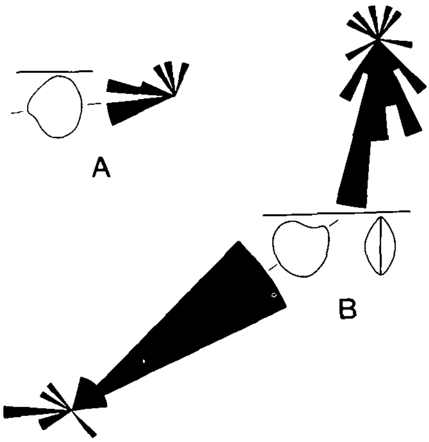


Figure 44. Life orientations of two *Astarte* species permitted to burrow in their native sediment. A = *A. undata* (10 animals from northwest of Quicks Hole, Massachusetts); B = *A. castanea* (26 animals from the same area).

areas of the bay. This species was also dredged from the medium to fine sand (sed. 8) in 15 m of water, 1 mile west of Penikese Island in Buzzards Bay.

HABITAT: *A. undata* prefers coarse, often gravelly substrata and moderate water movement.

LIFE HABITS: This species is a slow burrower (B.R.I. 0.06). Burrowing movements are sluggish and deliberate. Several burrowing sequences are usually required to erect the shell. The erect probing orientation is with the hinge axis approximately horizontal, and the angle of rotation is about 20°.

Measured life orientation of 10 animals allowed to burrow in the laboratory are represented in Figure 44A. Just as for other non-siphonate burrowers, the life orientation of this species is somewhat variable. Commonly, the posterior tip of the shell, with the minute inhalent and exhalent apertures, projects above the substratum surface a few millimeters; often it becomes encrusted with such epizoans as serpulid worms and bryozoans, which probably benefit from the currents produced by the clam. Plane of commissure orientation was not measured but often deviates several degrees from the vertical, as in *A. castanea* (Fig. 44B). Buried animals frequently emerge at night to crawl about at the sediment surface and then reburrow. The function of this nocturnal behavior is unknown.

Astarte castanea (Say)
(Pl. 14, figs. 7, 8)

SHELL DESCRIPTION: The shell is small (seldom exceeding 3 cm in length) and elliptical in lateral view, but relatively higher than *A. undata* and with an elevated and strongly hooked umbo; the shell is also compressed. The valves are extremely thick and lack ornamentation. The exterior is smooth or slightly rugose.

L/H 1.02, H/W 1.85, AL/L 0.40, T.I. 1.28

LOCALITY: Large numbers of individuals were dredged from the Quicks Hole, Massachusetts, locality described for *A. undata*, but *A.*

castanea was found to be more common in coarser sediment (very sandy gravel—sed. 5) occurring at greater depths (35 m).

HABITAT: The favored habitat is apparently much like that of *A. undata,* but *A. castanea* may require a more gravelly substratum.

LIFE HABITS: This species is a very slow burrower (B.R.I. 0.04), and its burrowing behavior is very similar to that of *A. undata.* The striking life habit difference between the two species is in their life positions. *A. castanea* departs from the conventional posterior-up orientation employed by *A. undata.* Life position measurements made in the laboratory for 28 *A. castanea* animals are represented in Figure 44B. As would be expected, the commissure plane often deviates substantially from the vertical, but within this plane, the shell is normally oriented with the *anterior* region uppermost. (Note the very strong mode in Figure 44B.) After burial, the animal rotates the ventral shell margin forward to attain this position, from which it draws water in through the porous, gravelly substratum, rather than directly from the overlying watermass.

Like *A. undata,* this species commonly emerges at night to crawl about. Randomly distributed epizoan patches on shells of some live animals indicate that a moderate number of animals spend part of their lives at the surface of the gravelly substratum.

Venericardia borealis (Conrad)
(Pl. 14, figs. 9, 10)

SHELL DESCRIPTION: The shell is small (largest dimension seldom greater than 3 cm); equant in lateral view, strongly prosogyre, and moderately inflated. The valves are extremely thick. The shell exterior bears moderately strong radial ribs, obscured ventrally in life by thick periostracum. The ribs form interlocking digitations along the interior of the ventral valve margins.

L/H 0.96, H/W 1.54, AL/L 0.32, T.I. 1.22, O.I. 12

LOCALITIES: This species was dredged in great abundance one mile west of Penikese Island, Buzzards Bay, Massachusetts, in about 15 m of water, where it lives in medium to fine sand (sed. 8).

HABITAT: In general, *V. borealis* is an inhabitant of coarse-grained subtidal sediments where moderately strong currents flow.

LIFE HABITS: This species is a very slow burrower (B.R.I. 0.06) that lives unattached within the sediment. Rocking movements during each burrowing sequence are sluggish and methodical and carry the shell through a very small angle of rotation. Erection of the shell is not accomplished by a few preliminary contraction sequences, as in most bivalves, but takes place gradually during movement into the sediment. The erect probing orientation is with the hinge axis tilted forward about 30° from horizontal.

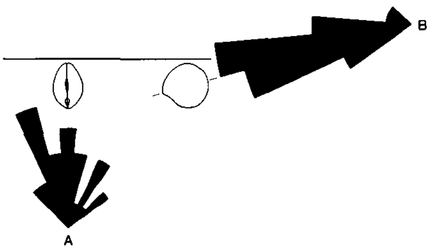


Figure 45. Life orientations of 24 *Venericardia borealis* individuals permitted to burrow in their native sediment (no. 8).

Lacking siphons, *V. borealis* lives with the posterior shell margin at or just below the sediment surface. Life positions measured for 26 animals allowed to burrow in the laboratory are represented in Figure 45. Just as for many other nonsiphonate burrowers, the plane of commissure orientation is somewhat variable, but usually is within 45° of vertical. Orientation of the shell within the commissure plane is more consistent, with the small inhalent and exhalent apertures uppermost and lying just beneath the sediment surface, or barely exposed. Shallowly buried animals are apparently able to draw a weak water current through 1 to 2 mm of sand.

Cardita floridana Conrad
(Pl. 14, figs. 11-13)

SHELL DESCRIPTION: The shell is small (maximum length 3 to 4 cm), quadrate, and elongate. The posterior is greatly extended and slightly triangular. The valves are thick, with coarse radial ribs that bear blunt tubercles; the ribs interdigitate ventrally.

LOCALITIES: This species was collected in large numbers intertidally from grass-covered, muddy carbonate sand (sed. 14, 15) along the southwest side of Rickenbacker Causeway, Biscayne Bay, Florida; it was also found about 1 m below mean low tide at Matheson Hammock, Biscayne Bay, in grass-covered sand (sed. 18).

HABITAT: *C. floridana* inhabits moderately protected intertidal and subtidal environments and shows tolerance for a variety of sediment types but is largely restricted to grass-covered bottoms.

LIFE HABITS: Unlike *Venericardia borealis,* this species is attached by a byssus throughout life. It shows a marked preference for submarine grasses as objects of attachment and normally fixes itself to the buried vertical stems of *Thalassia* or finer grass (Pl. 14, fig. 13).

Burrowing is extremely slow and inconsistent and therefore was not timed. It is undertaken with the hinge axis tilted forward slightly from horizontal, and rocking movements are not pronounced. Animals normally have great difficulty penetrating the substratum and tend to move forward large distances in the act of burrowing. When placed free in an aquarium floored by their native, grass-covered substratum, animals crawl about extensively by means of the small, finger-like foot. Crawling movements are similar to burrowing movements, but little or no penetration of the substratum takes place. Burrowing and byssal attachment to grass stems may be delayed for some time during crawling activity.

Once burial is achieved, attachment takes place with the shell's long axis approximately vertical and the posterior shell margin level with the sediment surface.

Diplodonta notata Dall and Simpson
(Pl. 15, figs. 1-5)

SHELL DESCRIPTION: The shell is very small (seldom longer than 1.3 cm) and circular in lateral view, with a slightly reduced anterior. It is compressed, and the valves are moderately thin and very smooth.

L/H 1.07, H/W 1.76, AL/L 0.47, T.I. 0.34

LOCALITY: A few live animals and many empty shells were dredged in Mayaguëz Harbor and Boquerón Bay, Puerto Rico, from carbonate silt (sed. 32, 34) at depths of 6 m.

HABITAT: *D. notata* prefers muddy substrata and sheltered subtidal conditions. I have collected the similar species *D. punctata* in Biscayne Bay, Florida (sed. 22), but have not studied its habits; unlike *D. notata,* it inhabits poorly sorted carbonate sand amid dense growths of *Thalassia.*

LIFE HABITS: This species is the slowest burrower encountered in this study (B.R.I. 0.01). When extended for burrowing, the foot (Pl. 15, fig. 3) is relatively thicker than in the Lucinidae. It probes extensively before obtaining a purchase. Rocking motion is very slow, and individual burrowing sequences are barely discernible. With each sequence, the animal rises slightly and pulls itself directly into the sediment without the aid of appreciable rocking motion. The angle of rotation is 10° or less. The animal begins burrowing with its hinge line nearly horizontal but revolves slowly forward as it moves into the sediment, finally assuming an unusual upside-down life position (Pl. 15, figs. 4, 5). Two animals studied with X-radiography assumed the final orientation in each of two experiments. The mucus tube follows a broad, arcuate path to the sediment surface, instead of passing directly upward. Other probing marks of the foot may mark footholds used for rotation to the final life position.

Codakia orbicularis (Linné)
(Pl. 17, figs. 1-6)

SHELL DESCRIPTION: The shell is moderately large to large (sometimes attaining length of 8 to 9 cm, but usually smaller). It is circular and slightly longer than high. The beak is centrally located, and the posterior margin is flattened slightly in the siphonal region. The anterior adductor scar is elongate, and the shell is very compressed. The valves are moderately thick and bear fine cancelate ornamentation in which radial ribs predominate.

L/H 1.11, H/W 2.28, AL/L 0.43, T.I. 0.43, O.I. 7

LOCALITIES: This is one of the most abundant and widespread bivalve species of the Caribbean region and was encountered at dozens of localities in this investigation. Individuals for laboratory study were collected from the lower intertidal zone just west of the Miami Seaquarium, Rickenbacker Causeway, Biscayne Bay, Florida, where the species inhabit grass-covered, slightly silty, fine to very fine carbonate sand (sed. 14).

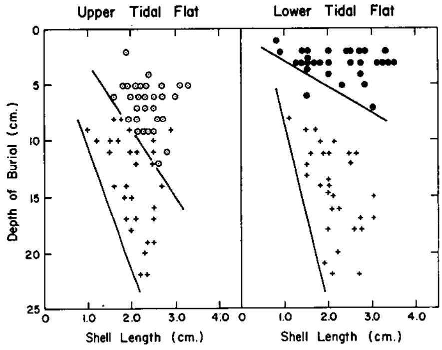


Figure 46. Depths of burial of three lucinid species in an intertidal flat just west of Miami Seaquarium, Rickenbacker Causeway, Biscayne Bay, Florida (sediment 14). Open circles = *Phacoides pectinatus*; solid circles = *Codakia orbicularis*; crosses = *Anodontia alba*. Depths measured to uppermost points on shells.

HABITAT: *C. orbicularis* is an inhabitant of low intertidal and shallow subtidal areas; it is largely restricted to grass-covered sandy bottoms.

LIFE HABITS: This species is a slow burrower (B.R.I. 0.3). An individual generally requires 3 or 4 burrowing sequences to erect its shell at the start of burrowing. Once erect, the shell slices into the sediment with a pronounced rocking motion (Pl. 17, figs. 3-5). Movement is vertically downward. Life position is with the long axis of the shell horizontal (Pl. 17, fig. 6). Assumption of this typical lucinid position involves backward rather than forward rotation of the shell from the burrowing orientation. The inhalent mucus tube, formed by the tubular foot, passes more-or-less vertically from the anterior shell margin to the sediment surface; the single posterior siphon extends upward at a slight angle away from the shell. X-radiographs reveal numerous probing marks of the foot radiating from the ventral shell margin. Depths of burial for 30 animals in nature are presented in Figure 46. Animals of all sizes are generally buried in the sediment at depths of 2 to 5 cm. Large animals are commonly buried more deeply than small animals.

Phacoides pectinatus (Gmelin)
(Pl. 16, figs. 1-3)

SHELL DESCRIPTION: The shell is moderately large (sometimes reaching a length of 6 to 7 cm); it is elliptical, but nearly circular, and the lunule flares to form a small anterior dorsal ridge. A distinct groove passes from the beak to the posterior shell margin, forming a strong marginal inflection in the siphonal region. The anterior adductor is extremely elongate. The shell is moderately thin, and is ornamented by thin concentric ridges.

L/H 1.10, H/W 1.93, AL/L 0.36, T.I. 0.39, O.I. 11

LOCALITIES: This species was collected in large numbers in Florida at the Rickenbacker Causeway locality described for *Codakia orbicularis* (sed. 14), where it lives higher in the intertidal zone, and in Puerto Rico from a protected marine pond in a mangrove forest near La Parguera, where it lives in muddy peat in less than 1 m of water.

HABITAT: *P. pectinatus* is an inhabitant of intertidal and shallow subtidal (often grassy) environments; it apparently prefers finer-grained sediments and quieter conditions than *Codakia* and is more tolerant of stressful nearshore conditions.

LIFE HABITS: This species is a slow burrower (B.R.I. 0.1); as in other lucinids, the foot emerges mid-ventrally. Erection of the shell requires several burrowing sequences and movements are sluggish. The erect probing orientation is with the hinge axis approximately horizontal. Rocking movements carry the shell through an angle of rotation of about 25°, and the animal moves directly downward.

The life position is with the long axis of the shell approximately horizontal. The anterior mucus tube and the posterior siphon diverge slightly as they pass upward to the sediment surface (Pl. 16, fig. 3). Pedal probing marks radiating from the ventral shell margin are evident in X-radiographs. Depths of burial in nature are presented in Figure 46 for 30 small to medium-sized animals. Burial depths are greater than for *C. orbicularis;* for nearly all animals measured depths were between 5 and 12 cm. In the Puerto Rican pond, larger *P. pectinatus* individuals (5 to 7 cm in length) were found buried at depths of up to 50 cm in muddy peat.

Phacoides muricatus (Spengler)
(Pl. 15, figs. 10-12)

SHELL DESCRIPTION: The shell is very small (maximum length slightly more than 1 cm). The gross shape is very similar to that of *P. pectinatus,* but the valves are thick and ornamented with radial ribs bearing relatively long spines.

L/H 1.04, H/W 2.09, AL/L 0.42, T.I. 0.67, O.I. 30

LOCALITIES: Numerous individuals were dredged in Mayaguéz Harbor and Boquerón Bay, Puerto Rico from carbonate silt (sed. 32, 34) at depths of about 6 m.

HABITAT: *P. muricatus* prefers muddy substrata and sheltered subtidal conditions.

LIFE HABITS: This species is a very slow, methodical burrower (B.R.I. 0.02). The vermiform foot emerges mid-ventrally (Pl. 15, fig. 12) but may be directed anteriorly or posteriorly. The erect probing orientation is with the hinge line approximately horizontal; the angle of rotation is 35° to 45° at the start of the burrowing period, but decreases as the animal nears complete burial. Normally the animal burrows vertically downward, but moves forward to some extent if it finds difficulty in penetrating the sediment. The life position is similar to that of the larger *P. pectinatus*, but the average depth of burial is only 1 to 2 cm. The opening of the mucus tube at the sediment surface is constructed with a narrow shelf at a depth of 1 to 2 mm, which apparently serves to catch any material that falls from the perimeter.

Anodontia alba Link
(Pl. 15, figs. 8, 9)

SHELL DESCRIPTION: The shell is moderately small (maximum length 4 to 5 cm) and circular in lateral view, with a flared anterior dorsal margin. A poorly defined groove passes from the umbo to the posterior margin. The shell is compressed, but more inflated than many lucinid species. The valves are moderately thin and very finely rugose.

L/H 1.12, H/W 1.72, AL/L 0.42, T.I. 0.36.

LOCALITY: This species was collected in large numbers with *Codakia orbicularis* and *Phacoides pectinatus* at the Rickenbacker Causeway locality described for the former (sed. 14); high in the intertidal zone, it lives with *Phacoides*, and low in the intertidal zone, with *Codakia*.

HABITAT: *A. alba* is usually found in protected grassy intertidal areas.

LIFE HABITS: This species is a sluggish burrower (B.R.I. 0.06). Individuals erect themselves slowly, using several sluggish burrowing sequences. The erect probing orientation is with the hinge axis approximately horizontal, and the angle of rotation is about 30°. A strong jet of water vented just anterior to the foot before contraction of the pedal muscles loosens the underlying sediment. The heel of the foot (described by Allen, 1958) is apparently used for pedal anchorage during pedal muscle contraction. Penetration is vertically downward. Life position is with the shell's long axis approximately horizontal. The anterior mucus tube and posterior siphon both pass nearly vertical upward to the sediment surface. Depth of burial is greater than for the associated lucinid species *C. orbicularis* and *P.*

pectinatus. Buried depths for two groups of 30 individuals were measured in nature, one group high and one group low in the intertidal zone. The two groups showed almost identical depth distributions (Fig. 46). Animals as small as 2 cm in length are commonly found buried as deeply as 20 cm.

Lucina pensylvanica (Linné)
(Pl. 18, figs. 1-4)

SHELL DESCRIPTION: The shell is moderately small (seldom longer than 4 to 5 cm), circular in lateral view, and more strongly prosogyre than most lucinid species. The anterior margin ventral to the lunule is produced into a blunt point. The shell is inflated, and its surface is scored by a deep groove extending from the beak to the posterior margin, forming a small marginal notch. The valves are very thick. The exterior is covered with very fine concentric ridges that bear fringes of periostracum in life. The interior ventral shell margins are very finely denticulate.

L/H 1.04, H/W 1.43, AL/L 0.33, T.I. 0.80, 0.1. <1

LOCALITIES: This species was collected along the southwest side of Soldier Key, Florida (sed. 21), and nearby, on shoals just south of Cape Florida (sed. 22), and at Bear Cut (sed. 25). At all three localities, the species lives in poorly sorted carbonate sand just below the low tide mark and is restricted to grassy areas.

HABITAT: *L. pensylvanica* occurs predominantly in shallow subtidal environments characterized by grass-covered sandy substrata.

LIFE HABITS: The animal is a very slow burrower (B.R.I. 0.03). The foot emerges at right angles to the hinge axis for burrowing. As in *Anodontia,* a heel is present. Several burrowing sequences are required to erect the shell. The erect probing orientation is with the hinge axis approximately horizontal, and the sluggish rocking movement is less pronounced than in most other lucinids, the angle of rotation being only about 15° to 20°. Penetration is directly downward.

The life orientation is unique among the lucinid species studied. The animal rotates posteriorly from its burrowing orientation (Pl. 18, fig. 1) to adopt a position with its anterior region uppermost and its lunule surface approximately horizontal (Pl. 18, fig. 2). The anterior mucus tube passes almost vertically upward from the small marginal projection of the shell just ventral of the lunule. The posterior siphon passes downward, at a variable angle, to discharge into the coarse sediment. The X-radiograph of Plate 18, figure 2, shows that a disturbance of the aquarium apparently caused both animals to retract their siphons. The siphons were extended at a later time along different paths. Depth of burial in nature was observed to vary somewhat, depending on the restricting effects of *Thalassia* roots and runners. In general, *L. pensylvanica* lives at depths intermediate between those of *Codakia* spp.

and deeper lucinid burrowers such as *Anodontia alba* and *Divaricella quadrisulcata.*

Divaricella quadrisulcata (Orbigny)
(Pl. 15, figs. 6, 7)

SHELL DESCRIPTION: The shell is small (seldom exceeding 2 cm in length), circular, and nearly symmetrical in lateral view. It is moderately inflated. The valves are moderately thin, and the exterior is scored by very fine, divaricate ridges with steep dorsal slopes. The interial ventral valve margins bear extremely fine denticulation.

L/H 1.08, H/W 1.60, AL/L 0.45, T.I. 0.36, O.I. <2

LOCALITIES: This species was collected in great numbers near Salerno, Florida, where it lives on moderately exposed intertidal flats in very fine to fine sand (sed. 29), often amid sparse, fine grass. It was also found in coarser carbonate sands behind Enrique Reef at La Parguera, Puerto Rico, in considerable abundance.

HABITAT: *D. quadrisulcata* is not as strongly restricted to grassy bottoms as are most Caribbean lucinid species; it prefers cleaner sands than most.

LIFE HABITS: This species is a slow burrower, but faster than most other lucinids (B.R.I. 0.5). An individual erects itself in the process of entering the substratum, rather than with a few initial burrowing sequences. The erect probing orientation is with the hinge axis approximately horizontal. Rocking movements are extremely smooth and markedly pronounced, the angle of rotation being about 45°. The animal pulls downward very little during pedal contraction. Instead, the shell is rotated in an almost circular motion about a central axis. The result is a clean slicing or sawing action by the ventral margin. Movement into the substratum is vertically downward, as for other lucinids.

In life position, the long axis of the shell is horizontal. The anterior mucus tube passes nearly vertically upward, but disposition of the posterior siphon is more variable. It generally extends posteriorly a few millimeters and then turns upward, but usually fails to reach the sediment surface. The species is a deep burrower for its size. Twenty individuals at the Salerno locality show a general trend toward increasing depth of burial with increased size, as has been found for other lucinid species. Medium-sized animals in the 1.1 to 1.4 cm length range generally live 10 to 20 cm below the sediment surface.

Dinocardium robustum vanhyningi Clench and L. C. Smith
(Pl. 19, figs. 1-5)

SHELL DESCRIPTION: The shell is large (sometimes attaining a length of 10 cm) and ovate, with a flat posterior dorsal area. Shell height exceeds shell length (to an increasing degree during ontogeny). The valves are thin, and the exterior is traversed by moderately strong, radial ribs that interdigitate ventrally along the commissure.

L/H 0.95, H/W 1.29, AL/L 0.45, T.I. 0.21, O.I. 13

LOCALITIES: This species was collected in great abundance from a bar of clean, fine sand (sed. 19) about 10 m offshore from the mean high water strand line at Marco Island, Florida; individuals are exposed here at spring low tide. It is also a common inhabitant of the sand bottom seaward of the bar.

HABITAT: *D. robustum vanhyningi* is an inhabitant of clean shifting sands, commonly living offshore from sandy beaches and washing ashore during storms.

LIFE HABITS: This large cockle is a rapid and active burrower (B.R.I. 5). The proximal portion of the large, L-shaped foot emerges opposite the hinge, and the pointed distal portion extends anteriorly. A partly emergent foot is shown in Plate 19, figure 3. In burrowing, an individual erects itself with a single, quick burrowing sequence. Once erect, the animal probes with the posterior dorsal area virtually horizontal. Rocking movements are very rapid. Unlike most species, this one rocks forward and back not once, but about 3 times, at the end of a single burrowing sequence. The first rocking cycle carries the animal through an angle of rotation of about 15°, but the second is of lesser magnitude, and the third is barely perceptible. The animal commonly rises slightly just before rocking begins, and a powerful stream of water is emitted just anterior to the foot. The animal moves almost vertically downward into the sediment in the course of its burrowing period.

The life orientation, like the erect probing orientation, is with the posterior dorsal area horizontal. When the siphon tenacles touch the sediment surface, this species, like other cardiids, commonly delays briefly before completing its burrowing period. When activity is resumed, the life position is attained by two or three final burrowing sequences. The siphons then lie with their margins projecting just above the sediment surface (Pl. 19, fig. 4).

Despite its size, this species is capable of jumping. The bent foot emerges in the normal manner but then straightens out rapidly with the anterior portion pressed against the substratum. The animal springs posteriorly a distance of several centimeters. Animals exposed at low tide in the midday sun commonly experience discomfort from heat and dessication and emerge from burial using a mechanism much like that used for jumping. An animal generally does not leap backward, however, but somersaults forward out of the sediment with a less violent pedal movement (Pl. 19, fig. 5).

Observations on 65 individuals at the Marco Island locality revealed that 60 were oriented with the sagittal plane more than 45° from the strand line. For the huge majority, this angle was 80° to 90°. Of these 60 animals, 39 faced shoreward and 21 seaward.

Trachycardium egmontianum (Shuttleworth)

(Pl. 21, figs. 3-5)

SHELL DESCRIPTION: The shell is moderately small (seldom exceeding 5 cm in height) and ovate, with a flattened posterior margin. It is slightly opisthogyre; shell height exceeds shell length, the height/length ratio increasing during ontogeny. The valves are thick and covered with strong radial ribs that bear short, strong, fluted spines; the ribs interfinger along the commissure line.

L/H 0.85, H/W 1.38, AL/L 0.54, T.I. 0.51, O.I. 45

LOCALITIES: This species was collected in large numbers from clean medium to fine carbonate sand just above mean low tide at Bear Cut, Florida, in moderately dense *Thalassia* (sed. 25); it was encountered in less abundance on grass flats in Biscayne Bay south of Cape Florida (sed. 22). Several animals were also found on exposed flats of clean sand at Marco Island, Florida.

HABITAT: *T. egmontianum* is restricted to coarse sediments and commonly inhabits grassy bottoms in moderately exposed intertidal and shallow subtidal environments.

LIFE HABITS: This species is a slow to moderately rapid burrower (B.R.I. 0.5). Burrowing and jumping movements are similar to those of other cardiids, but this species is less active than most. The L-shaped foot is figured in Plate 21, figure 5. The animal erects itself with a single burrowing sequence and uses strong, jerky movements, preceded by a powerful ventral expulsion of water, to penetrate the substratum. The erect probing orientation is with the posterior dorsal area horizontal. Commonly the muscular foot is forced into the substratum by several quick adductor contractions. Movement is directly downward, and the life orientation is the same as the erect probing orientation, with the posterior dorsal area horizontal. The short siphons are disposed much like those of *Dinocardium robustum vanhyningi* (Pl. 19, fig. 4).

Trachycardium muricatum (Linné)

(Pl. 21, figs. 1, 2)

SHELL DESCRIPTION: The shell is moderately small (seldom larger than 4 cm in height or length). It is similar in form to *T. egmontianum*, but more equant and rounded in lateral view and less inflated; the valves are also thinner, the ribs finer, and the spines smaller (often being worn from median ribs). The spines are simple, not fluted.

L/H 0.99, H/W 1.47, AL/L 0.50, T.I. 0.30, O.I. 23

LOCALITIES: This species was found in moderate abundance on *Thalassia*-covered sandy shoals just below the level of mean low tide between Cape Florida and Soldier Key, Florida (sed. 21, 22).

HABITAT: *T. muricatum* occurs in coarse, grassy substrata, often along the margins of bays, near inlets. It appears to prefer slightly quieter conditions than *T. egmontianum*, but the two species commonly coexist on grass-covered bottoms.

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 1). Its behavior is quite similar to that of the other cardiids, but in contrast to the two previously described cardiid species, each burrowing sequence terminates with a single rocking cycle. Rocking is sharper and quicker than in *T. egmontianum*, and rotates the animals through a larger angle (about 25°). Penetration is directly downward. *T. muricatum* lacks the flattened posterior dorsal area of many cardiid species, but the erect probing orientation and life orientation are typical, with the posterior shell margin horizontal.

Laevicardium mortoni (Conrad)
(Pl. 19, figs. 9-11)

SHELL DESCRIPTION: The shell is small (maximum length less than 2.5 cm). It is ovate, equant, and inflated. The valves are thin and smooth.

L/H 1.02, H/W 1.43, AL/L 0.42, T.I. 0.21

LOCALITIES: This species was collected in large numbers from Quisset Harbor, Cape Cod, Massachusetts, from slightly muddy sand (sed. 3) just below mean low tide to depths of about 2 m, in sparse eel grass. It was encountered in less abundance in other ponds and harbors bordering Cape Cod.

HABITAT: *L. mortoni* is generally restricted to muddy, grass-covered bottoms in protected bay and lagoonal settings.

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 1). The L-shaped foot, shown in Plate 19, figure 11, is similar to that of other cardiids, but is unusually long, and the species can jump distances up to several times its shell length. Burrowing movements are rapid, and they rotate the shell through an angle of about 30°. Penetration is directly downward. In the life orientation, as in the erect probing orientation, the posterior shell margin is horizontal. The shell lies just beneath the sediment surface, where the short siphons form a keyhole-shaped opening.

Laevicardium laevigatum (Linné)
(Pl. 19, figs. 6-8)

SHELL DESCRIPTION: The shell is moderately small, seldom exceeding 5 cm in height. It is similar in form to *L. mortoni*, but higher than long and the valves are even thinner and smoother than those of *L. mortoni.* The interior ventral margins bear fine denticulation.

L/H 0.86, H/W 1.58, AL/L 0.36, T.I. 0.15

LOCALITIES: This species was collected from the nets of a shrimp boat, dredging in 3 to 4 m of water in sandy areas of Biscayne Bay, Florida, just southwest of Key Biscayne. It was formerly abundant in grassy areas of Bear Cut bordering Key Biscayne (sed. 25).

HABITAT: *L. laevigatum* was apparently most abundant in sandy bay areas lacking grass. It is also found in deeper water offshore according to Robert C. Work (1967, personal commun.). In general, the species seems to inhabit more protected environments than most ribbed cockles but still prefers coarse sediment.

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 1). Its L-shaped foot is unusually long and slender. Like other cardiids, this species usually erects itself easily with a single burrowing sequence, and rises up slightly before completing the final rocking portion of each contraction sequence. Rocking movements are jerky, and the angle of rotation is small. The burrowing period is somewhat irregular, often being interrupted by delays. Penetration is directly downward. In the erect probing orientation and life orientation, the posterior dorsal area is horizontal. The siphons are very short.

The species has a remarkable ability to jump, and is even more active than the ribbed cockles studied. The long, slender foot may kick 6 or 7 times in rapid succession to hurtle the animal across the bottom of an aquarium. While jumping propels most ribbed cockles posteriorly, it commonly carries this "egg shell cockle" upward and forward (Pl. 19, fig. 8). Once launched with a strong kick, this species can actually swim. Swimming is accomplished by kicking against the water with the foot and simultaneously clapping the thin valves together to expel water ventrally. One individual was observed to achieve such a velocity in this manner that it propelled itself over a barrier 20 cm high with several rapid swimming movements.

Papyridea soleniformis (Bruguière)
(Pl. 20, figs. 1-6)

SHELL DESCRIPTION: The shell is moderately small (length generally less than 4 cm) and its shape is unusual among cardiids. The shell is elliptical in lateral view and moderately elongate; it is also compressed, with a small pedal gape and large siphonal gape. The valves are very thin and bear very weak ribs with tiny fluted spines (worn from the umbonal and mid-ventral regions); the ribs interdigitate ventrally.

L/H 1.27, H/W 1.70, AL/L 0.43, T.I. 0.19, O.I. 4

LOCALITIES: Single individuals were collected at each of 3 localities: shallow, grass-covered sandy shoals south of Cape Florida, Biscayne Bay, Florida (sed. 22); grassy sand south of Cayo Santiago, Puerto Rico, in about 10 m of water; and gravelly sand in front of Media Luna Reef (near La Parguera), Puerto Rico.

HABITAT: *P. soleniformis* apparently prefers coarse, grass-covered substrata in shallow subtidal settings. It is seldom present in large numbers.

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 0.9). It is unusual among the cardiids in both form and habit. The foot (Pl. 20, fig. 3) is atypical in being much less muscular than that of most cockles; no representative of this species was seen to jump. Two or three burrowing sequences are normally required to erect the shell. The erect probing orientation is with the posterior dorsal area tilted forward at an angle of about 30° from horizontal. Rocking movements are sharp and quick and rotate the shell forward through about 25°. Probing is much more time-consuming than in most cardiids, but the burrowing period is quite regular. Relatively little water is expelled prior to rocking, in contrast to most other cardiids.

The life position is illustrated in Plate 20, figures 4, 5. This species has longer siphons and lives buried at a greater depth than other cardiids studied. Disposition of the siphons is also unusual; the siphons diverge outward from the shell. Plate 20, figure 6 illustrates the positions of the siphon tips at the sediment surface. The exhalent siphon is vertically disposed and projects 2 to 3 mm above the sediment; the inhalent siphon bends horizontally so that its distal end lies along the sediment surface.

Americardia media (Linné)
(Pl. 20, figs. 7, 8)

SHELL DESCRIPTION: The shell is moderately small (length seldom exceeding 4 cm) and triangular in lateral view, with a broad, shoulder-like ridge passing from the umbo to the posterior ventral margin. The posterior dorsal region is flat, as in the Arcidae. The shell is slightly higher than long, and the valves are of variable thickness but generally thick. The ornamentation consists of very strong ribs roughened by very fine, closely spaced concentric ridges; the ribs interdigitate along the ventral margin.

L/W 0.93, H/W 1.22, AL/L 0.47, T.I. 0.65, O.I. 22

LOCALITIES: A single individual was dredged from clean, gravelly sand seaward of Medina Luna Reef, La Parguera, Puerto Rico, in about 30 m of water. It was formerly common in intertidal and shallow subtidal sand (sed. 25) at Bear Cut, Key Biscayne, Florida (Robert C. Work, 1967, personal commun.) but was not found alive there in this study.

HABITAT: *A. media* is a sand dweller in moderately protected intertidal and shallow subtidal settings.

LIFE HABITS: Extensive observations on the single Puerto Rican specimen showed the animal to be an unusually sluggish burrower for a cardiid (B.R.I. 0.4). During this study, it was never observed to jump. The erect probing orientation is with the posterior dorsal area horizontal. Rocking movement is smooth, and the angle of rotation is about 30°. Movement is normally directly downward, but if penetration is difficult, the animal may move forward in the process of burrowing. Burrowing activity is commonly interrupted for extended periods of time before complete burial is achieved.

The siphons are extremely short, and the animal is a very shallow burrower. The life position, with the posterior shell margin horizontal and just beneath the sediment surface, requires forward rotation of the shell only a few degrees from the burrowing orientation.

Mercenaria mercenaria (Linné)
(Pl. 21, figs. 6, 7)

SHELL DESCRIPTION: The shell is very large (maximum length 12 to 13 cm) and elliptical in lateral view, with a somewhat pointed posterior. It is strongly prosogyre, enlongate posteriorly, and moderately inflated. The valves are thick and slightly rugose. The ornamentation consists of sharp, fine concentric ridges present only anteriorly and reduced by abrasion in adults, but covering entire valves of first-year spat. The interior ventral valve margins are denticulate.

L/H 1.25, H/W 1.52, AL/L 0.25, T.I. 0.60

LOCALITIES: I have collected this abundant and commercially important species in many areas along Connecticut and Massachusetts shorelines.

HABITAT: *M. mercenaria* is tolerant of an unusually wide range of environmental conditions. It is common in intertidal and shallow subtidal environments. It is found in clean sand and muddy sand, but most commonly in sediments containing a moderate amount of pebble or coarse shell debris, which is required for larval settlement (Carricker, 1961). It prefers bare, rather than grass-covered bottoms.

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 0.8). The foot emerges opposite the hinge and flows slowly into the substratum during a prolonged probing period. Five or 6 burrowing sequences are normally required to erect the heavy shell. The erect probing orientation is with the dorsal area just posterior to the hinge horizontal. The angle of rotation is about 25°. Direction of movement into the sediment is slightly forward (about 25°) from vertical.

Life position varies with substratum type. Pratt and Campbell (1956) have shown that animals in clean sand live more deeply buried (average depth about 2 cm) than those living in muddy sediments (average depth about 1 cm in 30 percent mud). The same authors have shown that individuals living in clean sand sometimes strain water through the overlying sediment layer; sand-dwellers also eject pseudofeces less often and grow more rapidly than mud-dwellers. It has been my observation that animals in compact sand normally live with the long axis of the shell oriented approximately 45° from vertical, whereas those in muddy substrata tend to live with the long axis nearly vertical. In intertidal sand, small animals commonly live more deeply buried than large animals, apparently for protection against disinterrment, to which they are more vulnerable.

Antigona listeri (Gray)
(Pl. 21, figs. 12, 13)

SHELL DESCRIPTION: The shell is large (sometimes attaining a length of 8 to 10 cm). It is elliptical in lateral view, but with a flattened, elongate posterior. The shell is inflated. The valves are thin and bear fine radial ribs intersecting coarse, sharp concentric ridges that are consequently serrate. The interior ventral margins are finely denticulate.

L/H 1.18, H/W 1.36, AL/L 0.31, T.I. 0.29, O.I. 18

LOCALITIES: Numerous empty shells in life position were observed in grass patches in coarse sediment in the area between Bear Cut and Soldier Key, Biscayne Bay, Florida (sed. 21, 22, 25). Mr. Leslie Penzias kindly provided a live individual for study from the Bear Cut locality.

HABITAT: This species is widespread in intertidal and shallow subtidal settings, in large numbers; it is generally restricted to coarse substrata and grassy areas.

LIFE HABITS: The single live individual that was obtained was permitted to burrow several times. The species is a slow burrower (B.R.I. 0.3). The foot emerges opposite the hinge, and the animal has little difficulty erecting itself. In the erect probing orientation, the hinge axis is tilted forward about 30° from horizontal. During the probing part of each burrowing sequence, the siphons are partially extended; their apertures close to seal the mantle cavity just before the pedal muscles contract. The angle of rotation is about 25°. The animal moves forward somewhat in entering the substratum. This forward movement is slight at first, but increases as the animal penetrates more deeply. The animal may turn slightly to the left or the right when entering the substratum.

The life position is with the flattened posterior shell margin tilted backward very slightly from horizontal. Depth of burial is to some extent dependent upon interference by *Thalassia* roots in nature. In the laboratory, when permitted to burrow in its native sediment with the grass removed, the 5.8-cm-long animal that was studied occupied a life position with the posterior shell margin 4.5 cm beneath the sediment surface.

Chione cancellata (Linné)
(Pl. 22, figs. 3-5)

SHELL DESCRIPTION: The shell is moderately small (maximum length 3 to 4 cm); its outline in lateral view is similar to that of *M. mercenaria,* but the height is relatively greater. The shell is inflated and the valves are very thick. The ornamentation is very coarse and cancellate, similar to that of *A. listeri.* The interior ventral margins are denticulate.

L/H 1.20, H/W 1.40, AL/L 0.22, T.I. 0.91, O.I. 47

LOCALITIES: This is one of the most abundant bivalve species of southern Florida and was observed at many localities. Large study collections were made along the southwest side of Rickenbacker Causeway, Biscayne Bay (near Virginia Key) and at Bear Cut, Florida (sed. 14, 15, 25).

HABITAT: *C. cancellata* is generally restricted to clean or slightly muddy sand, which may be bare or carpeted with submarine grass. It inhabits intertidal and shallow subtidal settings.

LIFE HABITS: This species is a slow burrower (B.R.I. 0.3). Erection of the shell is commonly a gradual process, accomplished during partial penetration of the substratum. Normally, the probing orientation is with the hinge axis approximately horizontal, and the angle of rotation is about 20°. Quite commonly, however, penetration of the substratum is so difficult that an animal moves anteriorly along the substratum surface for some distance before achieving burial. In such cases, the erect probing orientation may shift so that the long axis of the shell lies nearly horizontal. Horizontal movements commonly produce sinuous trails like those of *Glycymeris* (compare Pl. 22, fig. 5 and Pl. 7, fig. 3).

The siphons are extremely short and the life position is with the posterior tip of the shell at or near the sediment surface. When exposed in nature, this region of the shell commonly bears a tuft of green algae. As with *Astarte, Venericardia, Glycymeris,* and other shallow burrowers, the life position is somewhat variable. In *C. cancellata,* the siphonal region of the shell is always uppermost, and the long axis of the shell tends to be approximately vertical. The plane of commissure is usually more or less vertical, but may be tilted to either side at angles of up to 45°.

Chione granulata (Gmelin)
(Pl. 22, figs. 1, 2)

SHELL DESCRIPTION: The shell is small (seldom longer than 3 cm) and is similar to the larger *M. mercenaria* in lateral view but slightly less elongate and less pointed posteriorly. The shell is inflated and the valves are thick. The ornamentation consists of weak, beaded, radial ribs. The internal ventral margins are denticulate.

L/H 1.17, H/W 1.42, AL/L 0.28, T.I. 0.69, O.I. 8

LOCALITIES: This species was collected for study in large numbers from very gravelly and slightly muddy coarse carbonate sand (sed. 33) of a tidal flat at the mouth of Salinas El Papayo, La Parguera, Puerto Rico; it was also observed at other nearby localities.

HABITAT: *C. granulata* is an inhabitant of coarse substrata in intertidal and shallow subtidal areas with little or no grass cover.

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 1). It is more active than *C. cancellata;* it probes more often with its foot when placed on an impenetrable substratum and does not cease burrowing activity for as long a period of time if interrupted. The animal generally erects the shell with 2 to 5 burrowing sequences and, unlike *C. cancellata,* nearly always enters the substratum with the plane of commissure nearly vertical. The erect probing orientation is with the posterior dorsal area approximately horizontal. Rocking movement is quick and smooth, and the angle of rotation is about 20°.

The life position is reached by forward rotation of the buried animal from the erect probing orientation to a position in which the long axis of the shell is approximately vertical. The siphons are slightly longer than in *C. cancellata.*

Chione paphia (Linné)
(Pl. 22, figs. 6-8)

SHELL DESCRIPTION: The shell is moderately small, occasionally reaching 4 cm in length. The outline in lateral view very similar to that of *Chione cancellata,* and the shell is inflated. The valves are very thick and are folded externally into very broad, strong concentric ridges with extremely smooth surfaces; the ridges constrict abruptly in posterior region to become sharp, thin flanges. The interior ventral margins are finely denticulate.

L/H 1.20, H/W 1.41, AL/L 0.29, T.I. 1.04, O.I. 22

LOCALITY: This species was dredged from clean gravelly carbonate sand on the seaward side of Media Luna Reef, La Parguera, Puerto Rico, at a depth of about 30 m.

HABITAT: It is an inhabitant of coarse-grained substrata in barren subtidal areas.

LIFE HABITS: This species is a slow burrower (B.R.I. 0.4). The erect probing orientation is with the flat posterior dorsal area horizontal. Forward rocking movement is very smooth and rotates the animal through about 40°. During burrowing, the plane of commissure remains vertical.

The life position is reached by rotation of the shell's long axis forward to lie about 30° from the vertical. The siphons are very short (Pl. 22, fig. 8).

Anomalocardia cuneimeris (Conrad)
(Pl. 21, figs. 8-9)

SHELL DESCRIPTION: The shell is small (maximum length 2 cm) and elongate. The anterior is similar to that of other venerids in lateral view; the posterior is extended and rostrate. The shell is inflated, with the maximum width near anterior end. The valves are moderately thin, with weak, rounded concentric ridges on the exterior; the interior ventral margins are denticulate.

L/H 1.54, H/W 1.38, AL/L 0.29, T.I. 0.39, O.I. 7

LOCALITIES: This species was collected from fine sand (sed. 28) with a sparse *Diplanthera* growth less than 1 m below mean low tide at Matheson Hammock Wading Beach, Biscayne Bay, Florida. It was also found in fine sand (sed. 28) amid sparse *Diplanthera* in a small, largely enclosed pond at the northwest end of Marco Island, Florida. It is present in great profusion at both localities.

HABITAT: *A. cuneimeris* is a common nearshore species, often found in low-salinity environments. The favored substratum type is fine sand carpeted with *Diplanthera* and it is more common in silicate than in carbonate sediments. Durbin Tabb (1967, personal commun.) reports that large numbers of the species occur in subtidal muddy sediments in the shallow estuarine bays north of Florida Bay.

LIFE HABITS: This species is a slow burrower (B.R.I. 0.3). The slender foot emerges opposite the hinge. Erection of the shell is usually accomplished by a single burrowing sequence. The angle of rotation in burrowing is about 30°. In the erect probing orientation, the hinge axis may be at an angle of 45° or nearly horizontal. A more horizontal attitude is normally adopted when penetration is difficult, in which case, the animal may crawl 10 cm or more along the sediment surface. The burrowing period is often interrupted by delays, even when the animal penetrates the substratum easily. The siphons are very short, and the life position is with the margin of the rostrate shell posterior very close to the sediment surface. In nature, this species' life position was observed to be with the long axis vertical, but in the laboratory, most animals failed to rotate forward to this position during the time they were studied.

Anomalocardia brasiliana (Gmelin)
(Pl. 21, figs. 10, 11)

SHELL DESCRIPTION: The shell is about twice the size of *A. cuneimeris* (maximum length approximately 3.5 cm); it is similar in shape to *A.*

cuneimeris, but less elongate, slightly more inflated, and with thicker valves. The ornamentation consists of weak, rounded concentric ridges. The interior ventral margins are denticulate.

L/H 1.31, H/W 1.30, AL/L 0.30, T.I. 0.69, O.I. 8

LOCALITIES: This species was found in great abundance in an isolated marine pond in a mangrove jungle west of La Parguera, Puerto Rico, in peaty mud at depths of less than 1 m. It was also collected in large numbers from a tidal flat at the mouth of Salinas El Papayo, La Parguera, Puerto Rico, in coarse, gravelly sand (sed. 33).

HABITAT: *A. brasiliana* occupies a variety of substrata in stressful nearshore environments.

LIFE HABITS: This species is a slow burrower (B.R.I. 0.3). The erect probing orientation is with the flat dorsal posterior margin horizontal. Pedal contraction rocks the animal forward through an angle of about 30° in each burrowing sequence. The angle of penetration is somewhat variable. Burrowing animals frequently plough forward through the sediment because of difficulty in penetrating downward. Delays in the burrowing period are common. Once buried, an animal rocks forward to its normal life position with the long axis vertical. The siphons are very short, and the posterior shell margin lies just beneath the sediment surface.

Macrocallista nimbosa (Solander)
(Pl. 23, figs. 1-3; Pl. 24, figs. 1-6)

SHELL DESCRIPTION: The shell is very large (commonly reaching a length of 12 to 13 cm); the form is similar to *Mercenaria* but compressed and very elongate. The valves are thin and very smooth exteriorly.

L/H 1.90, H/W 1.77, AL/L 0.27, T.I. 0.29

LOCALITIES: Several individuals were collected from Tampa Bay, Florida, just north of Terra Ceia Island; living just below mean low tide in slightly gravelly fine sand scoured by weak waves (sed. 23). It was previously abundant on moderately exposed sand flats at Mullet Key near the mouth of Tampa Bay. A single individual was found on an exposed sand flat at Marco Island, Florida.

HABITAT: *M. nimbosa* occupies clean or nearly clean sand in intertidal and shallow subtidal settings. It is most commonly found in shifting substrata of exposed tidal flats, but not along sandy beaches pounded by strong surf.

LIFE HABITS: This species is a rapid burrower (B.R.I. 3). The elongate shell is easily erected with one or two burrowing sequences. The posterior dorsal area is horizontal in the erect probing orientation. There is very little rocking relative to other venerids. The animal does not move vertically downward, but glides forward as it penetrates the sediment. The direction of penetration is about 35° from the vertical. A time-lapse sequence of photographs (Pl. 24, figs. 1-6) shows successive stages of burrowing from initial probing and erection of the shell to burial. As with other elongate venerids (for example, *Mercenaria*) the life position varies ontogenetically in a manner which is unusual for other bivalve families (Pl. 23, fig. 3). Small animals normally live at greater depths and with their long axes at higher angles than large animals. The adaptive significance of this slight change in habit appears to be related to the higher susceptibility of small animals to disinterrment by current scouring. They burrow more deeply until increased size makes them less vulnerable to being dislodged near the surface. The high angle of the small shell's long axis lowers the center of gravity still farther, the maximum depth of the posterior shell margin being fixed by the siphon length.

Dosinia elegans (Conrad)
(Pl. 25, figs. 4-6)

SHELL DESCRIPTION: The shell is large (sometimes attaining a diameter of 7 to 8 cm). It is circular in lateral view, but markedly prosogyre and very compressed. The valves are moderately thin, and the exterior is smooth, but covered with very fine concentric grooves.

L/H 1.12, H/W 2.22, AL/L 0.26, T.I. 0.36, O.I. 1

LOCALITIES: This species was collected on intertidal flats. It was found along the south shore of Norris Cut, Biscayne Bay, Florida, living in fine carbonate sand (sed. 27) and near Salerno, Florida, living in clean, medium to coarse sand (sed. 40).

HABITAT: *D. elegans* is an inhabitant of moderately exposed sand flats, where its presence is betrayed at low tide by a keyhole-shaped opening left by withdrawal of its siphons. It is not an inhabitant of wave-ridden sandy beaches, but is usually found in areas scoured by tidal currents. Juveniles occur in the muddy subtidal sediments of Biscayne Bay. Norton (1947) has described the habitat preferences of the very similar *D. discus;* his observations support mine (made in southern Florida for this species). It prefers sand flats protected from strong wave action but washed by moderately strong tidal currents. The ecologic preferences of *D. elegans* and *D. discus* are, according to my observations, virtually identical.

LIFE HABITS: *D. elegans* is a rapid burrower (B.R.I. 2). Two or 3 burrowing sequences are required to erect the disc-like shell. The erect probing orientation is with the ligament axis tilted forward slightly from the horizontal. A strong ventral expulsion of water precedes rocking movement. The rocking movement is very rapid, and the blade-like ventral shell margin slices into the sediment with great effectiveness. The angle of rotation is about 25°, and the animal penetrates vertically downward.

The life position of both *D. elegans* and *D. discus* is somewhat problematical in light of Ansell's observations on the very similar British species of the genus. Ansell (1961) states that the life position of the latter is with the ligament more or less horizontal. My observations on the two Western Atlantic species showed them to be invariably oriented with the long axis vertical, both in nature and in the laboratory (Pl. 25, fig. 6). Mrs. Ellen Crovo and Miss Corinne Edwards, who have collected numerous representatives of these two species, report that this is their normal life position (1967, personal commun.). Both species are deep burrowers. Norton (1947) reports depths of burial of 12 to 18 cm for *D. discus* near Beaufort, North Carolina, but does not specify to what part of the shell he measured. My measurements of depths of burial of *D. discus* and *D. elegans* at the Salerno locality ranged from 2.5 to 8 cm. The two *D. elegans* animals at the Norris Cut locality were buried at depths of 9 to 10 cm. If Norton's measurements were to the lowermost portions of shells, they are in accord with those reported here.

Cyclinella tenuis (Récluz)

(Pl. 25, figs. 1-3)

SHELL DESCRIPTION: The shell is usually small (but may attain a diameter of 5 cm). It is similar in lateral view to that of *Dosinia elegans*, but is less circular and less prosogyre. The anterior is slightly reduced. The shell is compressed, but less so than *D. elegans*. The valves are very thin and the exterior is smooth.

L/H 1.08, H/W 1.78, AL/L 0.23, T.I. 0.18

LOCALITIES: This species was collected from muddy, fine carbonate sand at depths of about 3 m just north of Southwest Point, Key Biscayne, Florida (sed. 20) and from slightly sandy carbonate silt (sed. 35) in Boquerón Bay, Puerto Rico, in about 8 m of water. It occurred in considerable abundance at both localities.

HABITAT: *C. tenuis* is an inhabitant of muddy subtidal sediments in shallow bay and lagoonal environments.

LIFE HABITS: The species is a slow burrower (B.R.I. 0.2). The foot is long and pointed, bearing a superficial resemblance to the partially extended foot of a lucinid, but emerging closer to the anterior end of the shell. Two or more burrowing sequences are commonly required to erect the shell. Sometimes the animal enters the substratum with its plane of commissure at a slight angle from vertical. The erect probing orientation is with the hinge axis tilted a few degrees forward of horizontal. Rocking movements are very slow but carry the shell through an unusually large angle of rotation (about 45°). In life position, the long axis of the shell gives the external appearance of being slightly overturned (ventral region turned posteriorly) because of the expansion of the posterior shell region and the reduction of the anterior region (Pl. 25, fig. 3). The depth of burial, as for most bivalves, increases with increased size. Animals 1 to 2 cm in length are generally buried at depths of 1.5 to 2 cm and animals 2.5 to 3.5 cm, at depths of 4 to 5 cm. The siphons, when retracted, leave a small keyhole-shaped opening at the sediment surface.

Tivela mactroides (Born)
(Pl. 24, figs. 7-10)

SHELL DESCRIPTION: The shell is moderately small (may reach 5 cm in length); it is strongly triangular and nearly symmetrical in lateral view. It is moderately inflated, the valves are thick, and the exterior is smooth.

L/H 1.14, H/W 1.50, AL/L 0.43, T.I. 0.52

LOCALITIES: This species was collected in large numbers in the lower part of the surf zone at Mani Beach, north of Mayaguéz, Puerto Rico, from fine sand (sed. 31).

HABITAT: *T. mactroides* is common along sandy beaches all around Puerto Rico; it is most abundant just below the swash zone.

LIFE HABITS: This species is an extremely rapid burrower (B.R.I. 8). The foot probes very rapidly to penetrate the substratum in initiating burrowing. The animal erects itself with a single burrowing sequence. The erect probing orientation is with the posterior dorsal area approximately horizontal. The animal rocks forward only 10° or 15° during each burrowing sequence, but the pedal muscle contractions are quick, and the resulting movements are jerky. Penetration is aided by a very strong jet of water expelled anterior to the foot. Once erect, the animal moves almost directly downward into the substratum. When the siphons touch the substratum, the animal may slow its burrowing sequences somewhat. Delays at this point are especially noticeable among smaller animals, which accounts for the slightly smaller burrowing speed indices of animals in the lower size range of the species.

The shallow life position is with the long axis of the shell approximately vertical (Pl. 24, fig. 10). It is assumed by forward rotation from the burrowing orientation once the terminal depth is reached.

Mesodesma arctatum (Conrad)
(Pl. 26, figs. 7-9)

SHELL DESCRIPTION: The shell is small (seldom exceeding 3.5 cm in length); it is triangular and elongate in lateral view with a greatly expanded anterior and a truncate posterior. There is a very slight siphonal gape, and the shell is compressed. The valves are moderately thick, and the exterior is moderately smooth.

L/H 1.54, H/W 1.91, AL/L 0.66, T.I. 0.50

LOCALITY: Large numbers of individuals were collected from the beach in front of the Coast Guard station at Plum Island, Massachusetts, from a population living in the lower intertidal zone and just below the low tide mark in clean, slightly gravelly, coarse to very coarse sand (sed. 10); here they are exposed to strong surf.

HABITAT: The Plum Island locality is typical, according to Davis (1963), who studied the general ecology of the species. *M. arctatum* may also occur at greater depths, but is generally restricted to well-sorted sand with a mean diameter of 0.5 to 1.0 mm.

LIFE HABITS: This species is a rapid burrower (B.R.I. 3). The pointed foot emerges from the elongate antero-ventral region of the shell and probes quickly to gain a foothold. Erection of the shell is normally accomplished by a single burrowing sequence. The erect probing orientation is with the anterior dorsal region vertical. Rapid burrowing sequences pull the animal directly downward. Very little rocking movement occurs.

The life orientation is the same as the burrowing orientation, and depth of burial is equal to one-half or three-quarters of the shell length (Pl. 26, fig. 9). Individuals living intertidally were observed to occupy life positions at about twice this depth of burial when the tide was out. Apparently, they dig more deeply into the sediment with the falling tide to seek protection from heat and dessication. Animals that are exhumed by wave scour usually reburrow rapidly, given a brief period of calm water.

Spisula solidissima (Dillwyn)
(Pl. 26, figs. 4-6)

SHELL DESCRIPTION: The shell is very large (may attain a length of 16 to 17 cm); it is triangular and elongate in lateral view, with the posterior length exceeding the anterior length. There is a distinct siphonal gape and a very slight pedal gape. The shell is compressed, and the valves are thin. The exterior is slightly rugose but generally smooth.

L/H 1.46, H/W 1.73, AL/L 0.42, T.I. 0.26

LOCALITIES: This species was encountered at many localities, all of which were tidal channels or sandy beaches, at Cape Cod, Massachusetts. It was collected for study in large numbers at Menemsha Bight, Martha's Vineyard, Massachusetts, where it lives along the shoreline at depths of 1 to 3 m in clean, gravelly, very coarse sand (sed. 45).

HABITAT: *S. solidissima* is an inhabitant of medium- and coarse-grained, shifting sands. It is usually found along sandy beaches or in tidal channels, seldom living above the level of mean low tide. Keyhole-shaped siphonal apertures at the sediment surface betray its presence.

LIFE HABITS: This species is a rapid burrower (B.R.I. 4). The strong, triangular foot emerges opposite the ligament (Pl. 26, fig. 6). It can be extended a distance about equal to the length of the shell. An individual usually erects itself with a single burrowing sequence, sometimes so forcefully that the shell tips over onto the valve that had been uppermost. The erect probing orientation is with the posterior dorsal area horizontal, or tilted slightly forward. Contraction of the pedal muscles is very rapid, so that burrowing movements are quick and jerky. Relatively little rocking movement takes place, especially among large animals. A large animal usually interrupts its burrowing period briefly when its siphons touch the sediment surface.

In the life position, the posterior dorsal area is tilted forward about 20° from horizontal. The siphonal region of the shell lies near the sediment surface (about 2 cm below it, for large animals).

When lying on the sediment surface, an individual can kick or jump a short distance with its powerful foot. Small animals have also been observed to crawl short distances at the sediment surface. Belding (1909) has described some aspects of the ecology of this species; his observations are in accord with those presented here.

Rangia cuneata Gray
(Pl. 27, figs. 1, 2)

SHELL DESCRIPTION: The shell is moderately large (sometimes reaches 7 cm in length), prosogyre, moderately elongate, and resembles typical venerids in lateral view; the posterior is elongate and triangular. The shell is strongly inflated, with slightly separated umbones. The valves are thick and the exterior is rugose.

L/H 1.24, H/W 1.27, AL/L 0.29, T.I. 0.61

LOCALITY: This species was collected in large numbers from Upper Cedar Point, Potomac River, Maryland; living in organic-rich, very muddy, very fine sand in about 1 m of water (sed. 46).

HABITAT: *R. cuneata* was recently introduced to the Chesapeake region from the Gulf of Mexico (Pfitzenmyer and Drobeck, 1964). It is a predominantly estuarine species that inhabits a variety of substrata in low salinity (< 15 parts per thousand) habitats. Some aspects of its ecology have been described by Fairbanks (1962).

LIFE HABITS: This species is a slow burrower (B.R.I. 0.4). Three or four burrowing sequences are commonly required to erect the shell. The erect probing orientation is with the posterior dorsal area horizontal, and rocking movements are slow. The animal moves forward very little in the course of burrowing; penetration is largely downward. The burrowing period is commonly marked by delays.

In life position, the long axis of the shell is vertical, with the posterior margin 1 cm or so beneath the sediment surface and the short, thin siphons extending directly upward.

Mactra fragilis Gmelin
(Pl. 27, figs. 3-6)

SHELL DESCRIPTION: The shell is moderately large (maximum length 5 to 6 cm) and oval but elongate in lateral view; it is compressed. The valves are very thin and the exterior is smooth. There is a large siphonal and a small pedal gape. The siphonal region (coated with thickened periostracum in life) is demarcated by two narrow ridges extending from the umbo to the posterior margin.

L/H 1.54, H/W 1.04, AL/L 0.44, T.I. 0.18

LOCALITIES: Numerous individuals were collected from grass-covered sandy shoals south of Cape Florida (sed. 22) and from a similar setting along the seaward side of Soldier Key, Florida (sed. 21). They were found just below the spring low tide level at both localities. A single animal was found in grass flat just below mean low tide on the western shore of Rickenbacker Causeway, just north of Miami Seaquarium (sed. 14).

HABITAT: *M. fragilis* inhabits intertidal and shallow subtidal settings. It is apparently restricted to grassy bottoms and sandy substrata.

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 1). The slender foot requires two or three burrowing sequences to erect the shell. The erect probing orientation is with the ligament axis horizontal, and the angle of rotation is about 40° at first, decreasing slightly as the animal becomes more deeply buried. Burrowing sequences also require more time as the animal penetrates the sediment. Downward movement is nearly vertical, with only a slight forward component. The life position varies ontogenetically, in the same way as for the mactrid *Tresus nutalli* (Pohlo, 1964). As shown for *M. fragilis* in Plate 27, figure 6, the long axes of small animals typically lie about 15° from vertical, whereas those of large individuals tend to lie about 35° from vertical. There is, correspondingly, a very slight ontogenetic change in shape that brings the siphonal gape of the shell into a position closer to the hinge. The siphons of an adult animal emerge from the shell at an angle of about 35° from the shell's long axis. Representatives of this species have been observed to jump for distances up to 3 times their own length, using the slender foot in the same manner as *Spisula.*

Mulinia lateralis (Say)
(Pl. 26, figs. 1-3)

SHELL DESCRIPTION: The shell is very small (less than 1.5 cm in length) and triangular in lateral view, but with a rounded ventral margin. The siphonal region is demarcated by a narrow ridge passing from the beak to the posterior ventral margin. The shell is inflated, the valves are thin, and the exterior is smooth.

L/H 1.26, H/W 1.49, AL/L 0.45, T.I. 0.26

LOCALITY: This species was collected for study from the lower portions of the tidal flat south of Sandy Point, New Haven Harbor, Connecticut. Here it occurs in moderate numbers in silty, very fine sand (sed. 44).

HABITAT: *M. lateralis* is a lagoonal species that tolerates a wide range of salinities and substratum types. Dead shell accumulations show that it has abounded in the past in the muddy central portions of Long Island Sound and Buzzards Bay (northeastern United States). Moore (1961) summarizes its occurrence in Mississippi, where it is found in shallow water on both sides of Mississippi Sound in sand and muddy sand. It is tolerant of extremely hypersaline conditions, as evidenced by its occurrence in Laguna Madre, Texas (Parker, 1960). It is not generally found in clean, shifting sands.

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 0.8). The erect probing orientation is somewhat variable, but the posterior dorsal area is usually more or less horizontal. The angle of rotation is about 40°. Animals occasionally have a difficult time penetrating the substratum and move forward along the surface before achieving burial.

The life position is with the long axis of the shell approximately vertical. The siphons are very short (Pl. 26, fig. 3).

Donax denticulatus Linné
(Pl. 28, figs. 1-6)

SHELL DESCRIPTION: The shell is small (maximum length less than 3 cm); it is triangular and elongate in lateral view, with a greatly extended anterior and a truncate posterior. The siphonal region is defined by a flattened sector of the shell margin bounded by two posterior ridges emanating from the umbo. The shell is moderately inflated at the maximum width (near the posterior), but tapers anteriorly. The valves are very thick and bear very weak radial ribs that become denticles on the interior ventral margin.

L/H 1.47, H/W 1.52, AL/L 0.59, T.I. 0.90, O.I. 2

LOCALITIES: This species was found in great profusion in clean medium sand (sed. 36) in the wash zone at Mani Beach, north of Puerto Rico.

HABITAT: *D. denticulatus* is common in exposed sandy beach habitats all around Puerto Rico, where individuals may be seen being washed out of the sediment by incoming waves and reburrowing rapidly to avoid wave transport and predation. Wade (1967), who has made a detailed ecologic study of the species, reports that it is generally restricted to the wash zones of exposed sandy beaches where the mean grain size of the sediment is 0.150 to 0.375 mm.

LIFE HABITS: This species is a very rapid burrower (B.R.I. 17). The huge foot emerges from the pointed antero-ventral end of the shell (Pl. 28, figs. 4 to 6). The foot probes very rapidly with a series of quick jabbing movements to initiate burrowing. A single burrowing sequence erects the shell, and a succession of 10 to 18 additional burrowing sequences buries the animal. At 28° C, these sequences were completed at an average rate of about 2 per second. The animal rocks very little, simply wedging into the sediment by virtue of its shape. Unlike most bivalves, members of this genus frequently respond to disturbances by attempting to burrow, rather than withdrawing into their shell. The erect probing orientation and the life position (Pl. 28, fig. 3) are with the anterior dorsal shell margin approximately vertical. Animals migrate with the changing tide by placing themselves at the mercy of the advancing surf or the backwash of a wave, but use the siphons and foot as a braking mechanism (Wade, 1967).

Donax variabilis Say
(Pl. 28, figs. 7-9)

SHELL DESCRIPTION: The shell is similar in general shape to *D. denticulatus*, but smaller (maximum length 2 cm), more elongate, and lacking features defining the siphonal region. The valves are also thinner and bear weaker radial ribbing; the exterior is nearly smooth.

L/H 1.78, H/W 1.51, AL/L 0.67, T.I. 0.63

LOCALITIES: This species was collected for study from clean fine sand (sed. 19) along the exposed intertidal beach at Marco Island, Florida. It was observed previously at Mustang Island, Texas.

HABITAT: Like *D. denticulatus*, *D. variabilis* is an inhabitant of the wash zones of exposed sandy beaches.

LIFE HABITS: This species is a rapid burrower (B.R.I. 7). Its burrowing behavior and life position (Pl. 28, fig. 9) are similar to those of *D. denticulatus*. Like the latter species, it undertakes tidal migrations to maintain its position in the wash zone. Turner and Belding (1957) and Loesch (1957) have proposed that individuals respond to the acoustic shock of waves in emerging from the sand to be carried up and down the beach with the tide, but confirmation of this idea is lacking.

Iphigenia brasiliensis (Lamarck)
(Pl. 29, figs. 1-4)

SHELL DESCRIPTION: The shell is moderately large (sometimes attaining a length of 6 cm). It is triangular and elongate in lateral view with an extended anterior but a less truncate posterior than that of *Donax* spp. The ventral margin is more rounded than that of *Donax*, and the anterior and posterior margins are slightly more pointed. The valves are moderately thick, and the exterior is smooth.

L/H 1.51, H/W 1.57, AL/L 0.46, T.I. 0.46

LOCALITIES: This species was collected in moderate numbers along the bay side of Virginia Key, Florida, just inside Norris Cut from a moderately exposed intertidal sand flat (sed. 17); here it is absent in areas of muddy sand. Many shells were observed along the sandy north shore of St. Lucie Inlet, but no live animals were collected.

HABITAT: *I. brasiliensis* is an inhabitant of clean, shifting sands in intertidal and shallow subtidal settings. It is not found in areas scoured by strong surf.

LIFE HABITS: This species is a rapid burrower (B.R.I. 4). It requires two or three burrowing sequences to erect the shell, and burrows with its siphons partly protruded. The initial erect probing orientation is with the anterior dorsal margin vertical, but the shell rotates during penetration of the sediment so that the posterior dorsal margin is horizontal by the time the animal disappears beneath the sediment. The angle of rotation is very small. The animal moves forward only slightly as it enters the sediment. Its life position is with the posterior dorsal region horizontal (Pl. 29, fig. 3). The depth of burial is somewhat variable, but for an adult animal (5 to 6 cm long), it is about 2 to 4 cm. The siphons diverge slightly as they pass to the sediment surface. They are longer than the siphons of *Donax*, but are thick and inflexible compared to those of deposit-feeding tellinids (Pl. 29, fig. 4). *Iphigenia* is a suspension feeder.

Tagelus plebeius (Solander)
(Pl. 30, figs. 1-5)

SHELL DESCRIPTION: The shell is large (sometimes reaching 9 to 10 cm in length); it is quadrate and extremely elongate in lateral view and moderately inflated. There are large pedal and siphonal gapes, and the ligament is short, permitting rocking of the valves about a central dorso-ventral axis. The valves are thin to very thin, and the exterior is slightly rugose but lacks ornamentation.

L/H 2.81, H/W 1.64, AL/L 0.55, T.I. 0.21

LOCALITIES: This species was collected in large numbers along the western shore of Bass River, Massachusetts, just inland from the mouth. It was found to be living intertidally in slightly silty fine to very fine sand in a moderately exposed situation (sed. 12). It was also found in abundance in a small, isolated pond opening into Squeteague Harbor, Massachusetts, where it lives in medium to coarse sand (sed. 2).

HABITAT: *T. plebeius* is a predominantly intertidal species that prefers moderately sheltered conditions and muddy sand substrata. It is common along the margins of bays and estuaries.

LIFE HABITS: This so-called "false razor clam" is a slow burrower (B.R.I. 0.4) and is in many ways unlike true solenid razor clams in mode of life. The animal erects its shell with difficulty. It enters the substratum with very little rocking motion and with its long axis at an angle of about 15° to 30° from the vertical.

The animal forms a permanent burrow that, like the angle of entry, usually lies about 15° to 30° from the vertical. The burrow is Y-shaped, the upper branches of the Y being formed by the animal's siphons, which diverge at an angle of 30° to 60°. The two siphon holes are visible at low tide. When the tide is in, the animal occupies the upper portion of the burrow for feeding. The main shaft of the burrow passes downward to a considerable depth. At the Bass River locality, the total burrow depth was found to average about 25 cm for an animal 7 cm long and 40 to 45 cm for an animal 8 to 9 cm long. At low tide, when disturbed, the animal descends to the lower part of its burrow. Most burrows measured were deep enough to permit their inhabitants to move downward a distance equal to about two or three times the length of the shell. The species is similar to *Ensis* in being able to move up and down within its burrow, but it occupies a more permanent burrow in relatively stable substrata and in this regard is more like *Mya* than *Ensis*. The siphons are stiff and rigid compared to those of deposit-feeding tellinids, and *Tagelus* is a suspension feeder. The two shell halves rock relative to one another about the ligament as a fulcrum (Pl. 30, figs. 3, 4), permitting extrusion of the foot (Pl. 30, fig. 5).

Tagelus divisus (Spengler)
(Pl. 29, figs. 7, 8)

SHELL DESCRIPTION: The shell is small (seldom exceeding 3.5 cm in length). The shape is similar to that of *T. plebeius* but with the anterior and posterior rounded and bent ventrally, so that the shell is curved slightly (in the opposite direction from *Ensis directus*). The shell is slightly more compressed than that of *T. plebeius*. The valves are very thin and smooth; each is supported by a central internal rib emanating ventrally from the umbo.

L/H 2.81, H/W 1.82, AL/L 0.46, T.I. 0.18

LOCALITIES: This species is found in great abundance along the southwest side of Rickenbacker Causeway, Biscayne Bay, Florida, just north of Miami Seaquarium, where it lives intertidally in slightly silty fine to very fine sand amid fine grass (sed. 14). It was also collected in large numbers from the bay side of Virginia Key, Florida, just inside

Norris Cut, where it lives intertidally in muddy fine sand (sed. 16). It is not found here in patches of clean sand occupied by *Iphigenia.* A few individuals were found in about 2 cm of water at Quisset Harbor, Massachusetts in muddy sand (sed. 4).

HABITAT: *T. divisus* is predominantly intertidal and generally restricted to muddy sand substrata. It is not limited to grassy bottoms. Aspects of its biology have been discussed by Fraser (1967).

LIFE HABITS: This species is a rapid burrower (B.R.I. 2) and is fairly active. The foot may emerge through the pedal gape in the shell or more posteriorly, in which case, it rotates to pass through the pedal gape when the animal erects itself. Erection is usually accomplished with a single burrowing sequence. The animal moves into the sediment vertically, or with the long shell axis as much as 30° from vertical. Like *T. plebeius,* it forms a Y-shaped burrow, although the siphon tubes are less divergent. X-radiographs show that the burrow tends to curve toward its lower end and sometimes actually bends into a J-shape. The dorsal margin of the shell invariably occupies the convex side of the curve. Burrow depth varies but seldom exceeds 20 cm. The siphon tips normally lie flush with the sediment surface in life, but may project 1 mm or so above it. The species is unquestionably a suspension feeder (as also suggested by Fraser, 1967). The foot is quite active and like *Ensis,* the animal can jump by kicking.

Asaphis deflorata (Linné)
(Pl. 29, figs. 5, 6)

SHELL DESCRIPTION: The shell is large (may attain a length of nearly 8 cm); it is quadrate and elongate in lateral view. The valves are moderately thin, and the ornamentation consists of very weak ribs deflected by moderately strong rugosity.

L/H 1.51, H/W 1.36, PL/L 0.40, T.I. 0.34, O.I. 4

LOCALITIES: This species was collected in moderate abundance high in the intertidal zone at Northwest Point, Key Biscayne, Florida, in medium carbonate sand which filled small pockets in eroded limestone (sed. 26). Numerous dead shells in life position were found intertidally in sand among mangrove roots at Norris Cut, Virginia Key, Florida.

HABITAT: *A. deflorata* is apparently largely intertidal and commonly inhabits restricted sand pockets. Casual observations in Bermuda revealed that this species also burrows deeply into broad sand flats.

LIFE HABITS: This species is a slow burrower (B.R.I. 0.2). It erects itself gradually in the process of entering the sediment. In the erect probing orientation, the hinge axis is roughly horizontal. Rocking movement is slow and rotates the shell through only about 10°; it is preceded by a powerful ventral expulsion of water that erupts at the sediment surface even after the animal has achieved burial. The animal moves forward very little during downward movement. Observations on the species' behavior in the laboratory support the field observation that the animal is accustomed to living in restricted pockets of sediment. Four specimens averaging about 6 cm in length wedged themselves into a square sediment container that was only 9 cm on a side. Few other bivalve species would tolerate this degree of crowding. The normal life position appears to be with the antero-posterior axis tilted backward at an angle of about 20° from the vertical. For animals 6 cm long, the separate siphons normally lie 3 to 5 cm apart at the sediment surface. Life position and depth of burial in nature are in part controlled by boundary effects. Some animals were found to be living in such shallow pockets of sand that their shells were partly exposed and were oriented with the antero-posterior axis nearly horizontal. When allowed to burrow in greater thicknesses of sediment in the laboratory, animals tended to bury themselves quite deeply (at depths slightly greater than their shell lengths). The siphons tips lie approximately flush with the sediment surface. Sometimes the exhalent siphon does not extend quite to the sediment surface, and the exhalent current issues from the sediment as a concentrated stream of water.

Semele proficua (Pulteney)
(Pl. 30, figs. 6-9)

SHELL DESCRIPTION: The shell is moderately small (maximum diameter approximately 4 cm) and circular in lateral view. The beaks are centrally located and slightly prosogyre. The shell is very compressed (discoid). The valves are thin and bear very fine concentric ridges.

L/H 1.09, H/W 2.53, AL/L 0.43, T.I. 0.26

LOCALITY: A single individual was collected from slightly gravelly medium to fine carbonate sand (sed. 38) with a dense growth of *Thalassia*, just below the low tide mark southeast of Guánica, Puerto Rico.

HABITAT: *S. proficua* is an inhabitant of shallow-water grass flats.

LIFE HABITS: This species is a rapid burrower (B.R.I. 4). The animal erects itself readily with one or two burrowing sequences. The erect probing orientation is with the hinge line approximately horizontal; the angle of rotation is about 30°. The ventral margin of the disc-like shell slices into the sediment very effectively with each rocking movement, as in the discoid venerid *Dosinia*. Downward movement of the animal is not exactly vertical, but has a slight forward component.

In its life position, the animal lies on its left side, with the plane of commissure about 15° from the horizontal and the siphonal region uppermost (Pl. 30, fig. 9). The 2.1-cm-long animal that was studied assumed a depth of burial of about 3 cm. After assuming its life position in the X-ray aquarium, the animal changed locations twice, but in its native habitat, amid a dense growth of *Thalassia* roots, the species could not be expected to make extensive lateral movements. The individual studied in the laboratory was never observed to deposit feed. The thick, flared inhalent siphon, with 6 prominent marginal lobes, suggests that the species is a suspension feeder; this siphon normally projects 2 to 3 mm above the sediment surface (Pl. 30, fig. 8).

Cumingia tellinoides Conrad
(Pl. 31, figs. 1-3)

SHELL DESCRIPTION: The shell is small (seldom exceeds 2 cm in length). The shape is somewhat variable, but elongate, with an elliptical anterior and triangular posterior. The posterior tip (siphonal region) is twisted slightly in an irregular fashion. Valves are thin, and the umbones are often worn to a fragile thickness by abrasion. The ornamentation consists of very fine concentric ridges.

L/H 1.41, H/W 1.74, AL/L 0.47, T.I. 0.22

LOCALITY: The species was collected in great numbers from the north shore of Quisset Harbor, Massachusetts, where it lives in slightly muddy medium sand amid sparse eel grass (sed. 3) at depths of about 1 to 4 m.

HABITAT: Grave (1927, p. 208) summarized the distribution of this species as follows: "*Cumingia tellinoides* is found principally in sandy bottoms containing a strong admixture of humus, with sparse or moderate growth of eel grass, and where the tidal currents run swiftly as in narrow channels." This habitat description fits the Quisset Harbor locality perfectly and seems to be accurate for the species in general.

LIFE HABITS: As a slow to very slow burrower (B.R.I. 0.09), this species is quite sluggish compared to most tellinaceans. The erect probing orientation is with the posterior dorsal region horizontal. Rocking movements are moderately pronounced, but are not as rapid as for other tellinaceans. The animal usually moves nearly vertically downward into the sediment, but it may move slightly anteriorly or posteriorly. Large animals (1.6 to 1.7 cm long) burrow to a depth of 3 to 4 cm in their native sediment. The life position is with the long axis of the shell approximately vertical. Disposition of the siphons is variable (Pl. 31, fig. 1). In addition, the siphons are shifted from time to time, leaving hollow tubes in the sediment. The animal itself moves very little, once in place. The species is a siphonate deposit feeder, however, and emits large volumes of pseudofeces.

Tellina tampaensis Conrad
(Pl. 31, figs. 4-7)

SHELL DESCRIPTION: The shell is small (maximum size less than 2 cm) and moderately elongate in lateral view; it is triangular, but the anterior ventral region is expanded and rounded. The shell is very compressed, and the posterior is bent to the right. The valves are thin, and the exterior is smooth.

L/H 1.31, H/W 2.16, AL/L 0.51, T.I. 0.21

LOCALITIES: This species was collected in large numbers from two very similar habitats, where it lives in fine quartz sand with sparse growths of *Diplanthera* just below mean low tide: at Matheson Hammock Wading Beach, Biscayne Bay, Florida (sed. 18) and in a small, restricted pond at the northwest end of Marco Island, Florida (sed. 28).

HABITAT: The two widely separate occurrences described above indicate a preference for fine quartz sand, fine grass, and shallow subtidal conditions. The species appears also to prefer moderately sheltered habitats.

LIFE HABITS: This species is a rapid burrower (B.R.I. 2). The foot emerges perpendicular to the hinge axis and probes very quickly. Small animals require only a single burrowing sequence for shell erection; larger animals require more. The rocking movement is very rapid but rotates the shell through a rather small angle (about 15°). The erect probing orientation is with the hinge horizontal. The animal moves forward slightly as it enters the substratum, in a direction roughly parallel to the anterior dorsal margin of the shell. Like all other tellinids studied in this project that have curved commissure planes, *T. tampaensis* lies on its left side (concave-up), and attains this position whether burrowing begins with the left valve or right valve uppermost. The pattern of burrowing for each of the initial orientations has been described for similar species by Holme (1961) and is shown in Figure 47. The life

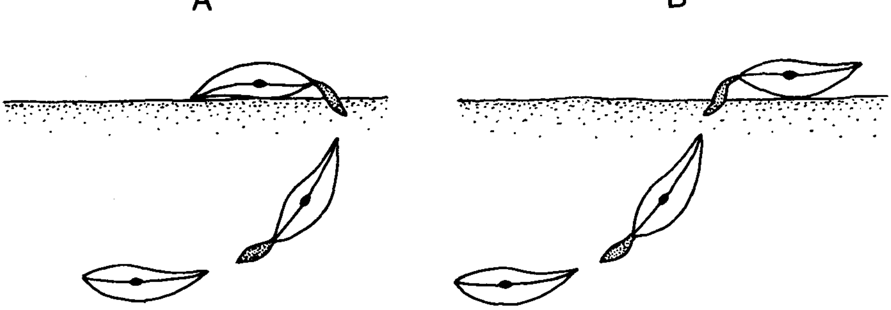


Figure 47. Burrowing behavior of a typical tellinid. A = animal placed on right valve; B = animal placed on left valve (*after* Holme, 1961).

position of *T. tampaensis* is with the longest dimension of the bent shell at an angle of about 40° from the horizontal and the siphonal region uppermost (Pl. 31, fig. 7). The animal moves laterally in the course of its deposit feeding activities, periodically relocating its siphons, as shown in the X-radiograph. The inhalent siphon passes nearly vertically upward to the sediment surface. The exhalent siphon passes downward at a low angle to discharge into the sediment.

Tellina similis Sowerby
(Pl. 32, figs. 1-7)

SHELL DESCRIPTION: The shell is small (maximum size approximately 2.5 cm) and very elongate. The anterior is expanded and elliptical in lateral view; the posterior is moderately truncate and bent to the right. The valves are very thin, and the exterior is generally smooth but traversed by extremely fine asymmetrical ridges (with steep dorsal slopes) passing anteriorly from the dorsal margin and turning posteriorly to intersect the ventral margin at an acute angle; the ornamentation terminates posteriorly along a line defining the siphonal region of the shell.

L/H 1.62, H/W 2.21, AL/L 0.55, T.I. 0.20

LOCALITIES: This species was collected in large numbers from slightly muddy and gravelly medium carbonate sand (sed. 37) in about 0.5 m of water behind Cayo Caracoles, La Parguera, Puerto Rico. It was absent from areas of the bottom covered by eel grass. Two or three animals were dredged from muddy sand (sed. 20) in about 3 m of water near the margin of Biscayne Bay, Florida (just north of Southwest Point).

HABITAT: *T. similis* prefers barren muddy sand substrata in shallow subtidal areas.

LIFE HABITS: This species is a rapid burrower (B.R.I. 2). The animal erects itself readily with one or two burrowing sequences and burrows with quick movements and relatively little rocking motion. The hinge line is approximately horizontal in the erect probing orientation.

The animal assumes a deep life position, lying on its right side at an angle of 15° to 25° from the horizontal. The inhalent siphon passes to the sediment surface at an angle of about 10° from the vertical, and the exhalent siphon extends posteriorly approximately parallel to the shell's long axis, to discharge into the sediment (Pl. 32, fig. 7).

I have observed members of this species while they were actively deposit feeding. About 1 cm of the inhalent siphon extends above the sediment surface and twists in a circular motion to pass along the substratum surface during part of each rotation and to suck in loose debris (Pl. 32, fig. 6).

Tellina agilis Stimpson
(Pl. 32, figs. 11-14)

SHELL DESCRIPTION: The shell is very small (maximum size slightly more than 1 cm) and very elongate. The anterior is expanded and elliptical in lateral view; the posterior is truncate and triangular. The shell is very compressed, and the posterior is bent to the right. The valves are very thin and fragile, and the exterior is smooth.

L/H 1.69, H/W 2.07, AL/L 0.61, T.I. 0.17

LOCALITIES: This species was collected intertidally from fine sand (sed. 1) at Barnstable Harbor, Massachusetts, and from coarse sand (sed. 7) along the eastern shore of Bass River, Massachusetts, just inland from the mouth. It was also found subtidally in less than 1 m of water in a small pond adjoining Squeteague Harbor, Massachusetts, where it occurs in limited numbers in medium to coarse sand (sed. 2).

HABITAT: *T. agilis* is generally restricted to barren sand substrata in intertidal and very shallow subtidal environments.

LIFE HABITS: This species is a rapid burrower (B.R.I. 3). The active foot emerges opposite the hinge axis and probes very rapidly. The shell is usually erected by a single burrowing sequence and with a series of very rapid jerking movements that involve only a small angle of rotation. The erect probing orientation is with the hinge axis (and posterior dorsal region) horizontal. As for *T. tampaensis,* the direction of movement is roughly parallel to the anterior dorsal shell margin.

The life position for an adult animal is at a depth of about 3 cm. Shell orientation and siphon disposition are shown in Plate 32, figure 14. Animals shift locations frequently, and feed at the sediment surface with the vermiform inhalent siphon. This species can jump posteriorly for short distances by curling its foot under the shell and straightening it very rapidly.

Tellina alternata Say
(Pl. 33, figs. 1-4)

SHELL DESCRIPTION: The shell is moderately large (may reach a length of 6 to 7 cm) and very elongate. The anterior is expanded and elliptical in lateral view; the posterior is bluntly pointed. The shell is extremely compressed. The posterior is bent to the right, and the shell margin is deflected slightly in the siphonal region, producing a shallow groove on the left valve and a ridge on the right valve. The valves are thin; the smooth exterior bears fine, widely spaced concentric grooves.

L/H 1.66, H/W 3.01, AL/L 0.54, T.I. 0.29

LOCALITIES: This species was collected in two very similar settings: from muddy fine carbonate sand (sed. 20) in about 3 m of water in Biscayne Bay, Florida, just north of Southwest Point, and from slightly sandy carbonate silt (sed. 35) in about 8 m of water at Boquerón Bay, Puerto Rico.

HABITAT: *T. alternata* is largely restricted to muddy, subtidal substrata in protected bay and lagoonal environments.

LIFE HABITS: This species, like most tellinids, is a rapid burrower (B.R.I. 4). It erects itself with a single burrowing sequence, and its burrowing movements are similar to those of *T. tampaensis* and *T. agilis*.

The life orientation differs from the latter two species in that the long axis of the shell lies at a lower angle (about 10° to 15° from horizontal), as shown in Plate 33, figure 4. The inhalent siphon passes nearly vertically upward, and the exhalent siphon discharges into the sediment a centimeter or so from the posterior tip of the shell. Animals in thin aquaria observed by X-radiography migrated laterally as a matter of habit and were presumed to deposit feed but were never seen to do so.

Tellina listeri Röding
(Pl. 33, figs. 8-11)

SHELL DESCRIPTION: The shell is large (sometimes reaching a length of 9 to 10 cm), elliptical, and very elongate. The posterior is bent to the right and bluntly pointed. The margin in the siphonal region is deflected to form a distinct convex fold in the right valve and a corresponding sulcus in the left valve. The shell is very compressed. The valves are moderately thick and covered with very narrow, weak concentric ridges.

L/H 1.89, H/W 2.12, AL/L 0.48, T.I. 0.43, O.I. 4

LOCALITY: A single individual was collected in Hawk Channel, southwest of Rodriguez Key, Florida in about 6 m of water, from clean, slightly gravelly coarse carbonate sand (sed. 30). Several animals were also found on the north side of Trunk Island, Harrington Sound, Bermuda.

HABITAT: *T. listeri* is an inhabitant of coarse, clean subtidal sands in areas of moderately strong currents.

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 0.8). The foot emerges at right angles to the hinge axis, and the shell is erected with a single burrowing sequence or two. The erect probing orientation is with the posterior dorsal shell margin tilted forward about 15° from the horizontal. The animal pulls itself into the sediment in a direction approximately parallel to the shell's long axis, with very little rocking motion.

The life position is with the shell's long axis nearly horizontal and the left valve undermost (Pl. 33, fig. 11). The inhalent siphon passes to the sediment surface in an arcuate pattern. The exhalent siphon is directed downward at a steep angle to discharge into the sediment. Once buried, the animal undertakes periodic lateral movements. The species is assumed to be a deposit feeder, but the single individual studied was not observed to deposit feed.

Tellina radiata Linné
(Pl. 34, figs. 1-3)

SHELL DESCRIPTION: The shell is large (may attain a length of 10 cm), elliptical, and very elongate. The anterior is expanded, and the posterior is bent to the right. The ventral margin is indented slightly just anterior to the siphonal region, producing a very slight sulcus in each valve. The shell is very compressed. The valves are moderately thin, and the exterior is very smooth.

L/H 2.13, H/W 2.13, AL/L 0.52, T.I. 0.32

LOCALITY: A single individual was dredged from slightly gravelly, medium to coarse, carbonate sand (sed. 39) in 6 to 10 m of water at Sandy Point, St. Croix, Virgin Islands. The bottom here is swept by moderately strong currents and there are sparse local growths of marine grass. Numerous empty shells were also dredged at this site and shells of live animals collected here are present in the mollusk collection of the Institute of Marine Biology of the University of Puerto Rico.

HABITAT: The Sandy Point habitat is apparently typical for the species. In South Florida, the animal is also normally encountered in coarse, clean sands in subtidal areas swept by tidal currents (Robert C. Work, 1967, personal commun.).

LIFE HABITS: The single animal studied was a juvenile (1.2 cm) and its B.R.I. of 1 can only be used to represent the species in an approximate way, but the animal did provide an opportunity to observe the burrowing habits of the species. In general, the animal's behavior is similar to that of *T. listeri.* The animal erects its shell to a moderately high angle (long axis more than 45° from horizontal) and pulls itself into the sediment in a direction parallel to the long axis, with very little rocking motion.

The life position is with the animal's long axis nearly horizontal. The depth of burial, although not measured, is similar to that of *T. listeri* in being shallow for the animal's size in comparison to other tellinid species.

Tellina martinicensis Orbigny
(Pl. 32, figs. 8-10)

SHELL DESCRIPTION: The shell is very small (maximum length less than 1.5 cm) unusually equant in lateral view for a tellinid. The anterior ventral region is round and expanded; the posterior is bluntly triangular and bent to the right; the siphonal region is demarcated by a faint ridge. The shell is compressed. The valves are moderately thin and the exterior bears extremely fine concentric ridges.

L/H 1.16, H/W 1.73, AL/L 0.48, T.I. 0.39

LOCALITIES: This species was collected in large numbers from subtidal areas of Biscayne Bay, Florida, in 3 to 5 m of water; for example, it was taken from muddy, fine carbonate sand (sed. 20) just north of Southwest Point.

HABITAT: *T. martinicensis* occurs in shallow subtidal settings in quiet water, where it inhabits muddy sands.

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 0.6), but is unusually sluggish for a tellinid. The foot emerges opposite the hinge axis. Commonly, more than one burrowing sequence is required to erect the shell. The posterior dorsal shell margin is approximately horizontal in the erect probing orientation but may be tilted backward slightly if penetration of the sediment is difficult. Rocking movement is slow and the angle of rotation is about 20°. In life position, an individual normally lies buried at a depth of 1 to 2 cm with its long axis horizontal and its left valve undermost. The siphons extend outward and upward to the surface in an arcuate pattern. Unlike most other tellinid species, *T. martinicensis* migrates very little once the life position is attained. Its sluggish burrowing actively corresponds to this relatively sedentary existence.

Arcopagia fausta (Pulteney)
(Pl. 33, figs. 5-7)

SHELL DESCRIPTION: The shell is large (may attain a length of 9 to 10 cm); it is elliptical and equant in lateral view. The posterior is bluntly terminated and bent to the right with a small inflection of the commissure where the siphons emerge. The shell is very compressed. The valves are moderately thin, and the exterior is slightly rugose.

L/H 1.18, H/W 2.23, AL/L 0.51, T.I. 0.35

LOCALITIES: This species was collected at several locations along grass-covered margins of Biscayne Bay, Florida. It is especially abundant on the southwest side of Soldier Key amid *Thalassia* in slightly muddy and gravelly, fine to medium carbonate sand (sed. 22) and along Rickenbacker Causeway, just north of Miami Seaquarium in sediment of similar grain size (sed. 14) but covered by finer grass. Numerous articulated shells were collected in similar environments along the southwest coast of Puerto Rico.

HABITAT: *A. fausta* is generally restricted to grass-covered sandy substrata, usually just below mean low tide.

LIFE HABITS: This species is a rapid burrower (B.R.I. 5). Regardless of which valve is initially undermost at the sediment surface, the animal enters the substratum with the surface of commissure in a nearly vertical position. In the erect probing orientation, the posterior dorsal shell margin lies approximately horizontal, and the angle of rotation is about 20°. The disc-like shell slices very efficiently into the sediment. The animal then turns to the right when it approaches the final depth of burial, to assume a life position with the left valve undermost. Depth of burial varies, depending on substratum type and interference from grass roots. An individual of moderate size (4 to 6 cm) commonly lies at a depth of 10 to 15 cm. The shell lies in a nearly horizontal position, with the dorsal and posterior regions slightly elevated. The inhalent siphon passes vertically to the sediment surface. The exhalent siphon passes downward at an angle of about 45°, to discharge into the sediment. The normal exhalent current and the current used for pseudofeces ejection from the inhalent siphon are used to excavate the tunnels for siphon extension in the compact native sediment. Although not observed in the act of deposit feeding during this study, *Arcopagia* is presumed to be at least a part-time deposit feeder.

Macoma tenta (Say)
(Pl. 34, figs. 4-10)

SHELL DESCRIPTION: The shell is small (maximum length approximately 2 cm) and very elongate. The anterior is expanded and elliptical, and the posterior is bluntly pointed. The shell is compressed. The entire commissure surface is broadly curved, with the posterior bent to the right. The valves are extremely thin and fragile, and the exterior is smooth.

L/H 1.70, H/W 1.92, AL/L 0.60, T.I. 0.11

LOCALITIES: This species was collected in large numbers from bare areas of the bottom of Quisset Harbor, where it lives at depths of 4 to 8 m in organic-rich, very sandy mud (sed. 6). It was also found in considerable abundance at Mayaguëz Harbor, Puerto Rico, where it lives in carbonate silt (sed. 32).

HABITAT: *M. tenta* is an inhabitant of organic-rich, muddy bottoms, in shallow, restricted subtidal settings.

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 0.6) but not as rapid as most tellinids. The animal erects its fragile shell very easily, with a single burrowing sequence. The long axis of the shell is tilted slightly to the left as the animal enters the substratum. The posterior dorsal shell margin is oriented about 45° from the horizontal. The elongate shell rocks very little (about 10° to 15°) with each burrowing sequence, and movements are slow, rather than jerky, as in many tellinids. The animal's forward movement is in a direction nearly parallel to the long axis of the shell, as in *T. interrupta* and *T. radiata.*

Regardless of their size, animals tend to occupy positions at the base of the upper soupy layer of mud, about 1 to 2 cm below the surface (Pl. 34, fig. 7). The convex left valve is undermost and the long axis of the shell, more or less horizontal. The exhalent siphon discharges into the sediment a few millimeters beyond the posterior margin of the shell.

For deposit feeding, an animal extends 2 to 3 cm of its inhalent siphon along the surface of the sediment. The siphon does not feed by twisting in circles, as do most tellinid species. Instead, it makes a series of radial feeding traverses by extension and withdrawal, while the tip sucks in surface sediment (Pl. 34, figs. 8-10). The result is a radiating pattern of grooves in the surface of the sediment. Some animals actually excavate a pit through prolonged feeding at one site. X-radiographs of buried animals showed that they shift locations frequently. When lying free on the substratum, individuals have the capacity to leap distances of 2 cm or more, but they are not nearly as active as *T. agilis.*

Macoma balthica (Linné)
(Pl. 35, figs. 1-9)

SHELL DESCRIPTION: The shell is moderately small (sometimes attaining a length of 3 to 4 cm) and elliptical in lateral view. The anterior is round and the posterior is slightly pointed. The beaks are located slightly anteriorly. The commissure is planar, in contrast to most tellinids. The valves are very thin, and often eroded in the umbonal and mid-ventral regions; the exterior is rugose.

L/H 1.28, H/W 2.02, AL/L 0.45, T.I. 0.17

LOCALITIES: This species was collected in large numbers for study from a small pond continuous with Squeteague Harbor, Massachusetts, where it lives in organic-rich, medium to coarse sand, less than 1 m below the low tide mark (sed. 2). It was found in less abundance at other localities along the Connecticut and Massachusetts shoreline.

HABITAT: *M. balthica* is a common intertidal and shallow subtidal species that lives in muddy sands in relatively quiet water.

LIFE HABITS: This species is a moderately rapid burrower (B.R.I. 0.7). The foot emerges opposite the hinge axis (Pl. 35, fig. 3). Commonly, 3 or more burrowing sequences are required to erect the shell. The erect probing orientation and angle of rotation are shown in Plate 35, figures 4 and 5. The animal moves vertically downward into the sediment (Pl. 35, figs. 6-8) by a series of slicing movements of the blade-like ventral shell margin.

It rotates slightly forward from the erect probing orientation to achieve the final life position (Pl. 35, figs. 8, 9). The inhalent siphon passes vertically to the sediment surface, but the exhalent siphon assumes a characteristic sinuous disposition, to emerge at the surface at least 1 cm from the inhalent siphon. Depth of burial varies considerably, but large animals (2.5 cm long) were found to live at depths of 15 to 20 cm. Only rarely were adult animals found living in upper 5 cm of sediment in nature.

Brafield and Newell (1961) suggest that *M. balthica* living intertidally is primarily a suspension feeder when immersed in water, and a deposit feeder at low tide. They have observed movements of individuals through sediment at low tide and formation of J-shaped furrows at the sediment surface as the inhalent siphon sucks in sediment. Brafield and Newell suggest that the orientation of furrows is correlated with position of the sun and that movements are oriented by photoresponse. While submerged in aquaria, animals in my experiments were never observed to make lateral movements after burial, and, in support of Brafield and Newell's conclusions, were never seen to deposit feed; however, extensive observations on intertidal populations in nature were not undertaken in the present study.

Strigilla carnaria (Linné)
(Pl. 36, figs. 5-8; Pl. 37, fig. 2)

SHELL DESCRIPTION: The shell is small (maximum length approximately 2 cm) and circular in lateral view, with a flattened posterior dorsal margin; the posterior is slightly elongate. The shell is very compressed (discoid), the valves are moderately thin, and the exterior is scored by very fine divaricate ridges (like those of *Divaricella*) that terminate abruptly posteriorly at the margin of the siphonal region.

L/H 1.13, H/W 2.03, AL/L 0.38, T.I. 0.32

LOCALITY: This species was collected in abundance from just below the breaker zone (slightly seaward of the largest populations of *Tivela mactroides*) at Mani Beach, north of Mayaguéz, Puerto Rico, where it lives in medium sand (sed. 31).

HABITAT: Dead shell accumulations on beaches similar to the Mani Beach in other areas of Puerto Rico indicate that the sandy shore habitat is typical for *S. carnaria.*

LIFE HABITS: This species is an extremely rapid burrower (B.R.I. 20). The foot probes very actively, as in *Donax*, with a rapid series of short thrusting movements. The shell is erected with a single burrowing sequence. The erect probing orientation is with the hinge axis approximately horizontal, the angle of rotation is about 30°, and the animal slices directly downward into the sediment. Complete burial normally requires only about 4 burrowing sequences.

The animal moves almost vertically downward to its deep life position, in which the commissure plane of the shell lies about 45° from horizontal with the siphonal region uppermost. The inhalent siphon passes vertically upward and the exhalent siphon vertically downward, discharging into the sand (Pl. 36, figs. 7, 8). X-ray studies of animals in thin aquaria have shown that buried individuals may occasionally shift position or location. Whether such movements are associated with deposit feeding is uncertain; I have not observed deposit feeding in this species.

Strigilla mirabilis (Philippi)
(Pl. 36, figs. 1-4; Pl. 37, fig. 1)

SHELL DESCRIPTION: The shell is similar to that of *S. carnaria,* but much smaller (maximum length less than 1 cm), moderately inflated rather than discoid, and with slightly thicker valves for its size.

L/H 1.08, H/W 1.57, AL/L 0.41, T.I. 0.40

LOCALITIES: This species was collected in great abundance with *Strigilla pisiformis* and *S. carnaria* just below the surf zone at Mani Beach north of Mayaguëz, Puerto Rico, in medium sand (sed. 31).

HABITAT: The Mani occurrence is typical for *S. mirabilis,* whose habitat seems to be similar, if not identical, to those of the two congeneric species mentioned above.

LIFE HABITS: This species is an extremely rapid burrower (B.R.I. 14). Burrowing orientation and movements are very similar to *S. carnaria,* but rocking movement in this smaller species is slightly more pronounced (the angle of rotation being about 40°).

In life position, the animal is less deeply buried than *S. carnaria,* in correspondence to its smaller size. The orientation is somewhat variable, but the long axis of the shell is usually approximately vertical, and the siphonal region invariably uppermost (Pl. 36, figs. 3, 4). Unlike the condition in *S. carnaria,* both siphons are directed upward and their disposition is variable. Although the X-radiographs obtained for the species are somewhat equivocal, it appears that the exhalent siphon, as well as the inhalent siphon, reaches the sediment surface. After achieving their life position, animals make periodic shifts of location. I have not observed deposit feeding activity in this species.

Ensis directus (Conrad)
(Pl. 38, figs. 1-7)

SHELL DESCRIPTION: The shell is very large (occasionally exceeding 20 cm in length), quadrate in lateral view, curved, and extremely elongate; it is terminated by large pedal and siphonal gapes, and the posterior is expanded greatly, to constitute nearly the entire shell. The shell is compressed. The adductors are elongate parallel to long axis of shell, the valves are thin, and the exterior is smooth.

L/H 5.41, H/W 1.96, AL/L 0.06, T.I. 0.23

LOCALITIES: Large numbers of individuals were collected for study from intertidal flats near Huckins Island, Barnstable Harbor, Massachusetts. Here most animals live in fine sand (sed. 1) along margins of tidal channels. A few live in coarser sands that form megaripples in the centers of tidal channels. This species has also been observed at various other localities along the New England coast.

HABITAT: *E. directus* is largely restricted to low intertidal and shallow subtidal settings. It is nearly always found living in cohesive fine sand, which may have a very small admixture of mud, but it is not common in medium or coarse sand. It is most abundant in areas swept by moderately strong currents, such as tidal channel margins and exposed tidal flats.

LIFE HABITS: Like other solenids, this species is a very rapid burrower (B.R.I. 6). The physiology of burrowing in the Solenidae has been considered in detail by Fraenkel (1927). Drew (1907) has made observations on the habits of *Ensis directus.* This species erects its shell from a position in which the dorsal surface lies undermost. Even when placed on its side or its ventral surface, the foot, which emerges through the gape at the end of the tubular shell, twists as it probes to turn the shell to this ventral-up position (Pl. 38, figs. 6, 7). Small animals erect their shell with a single burrowing sequence, but large animals commonly require more than one. Fraenkel (1927), shows the similar species *Solen ensis* entering the substratum in such a way that the shell is erected gradually as the animal penetrates downward; the shell continues to rotate in a ventral direction until life position, with the long axis about 25° from the vertical and the ventral margin undermost, is attained. In fact, the animal does not rotate once it has penetrated the sediment. Initial erection of the shell brings it into a position with the long axis nearly vertical. The animal enters the sediment at a high angle. As it penetrates the sediment, the shell moves in an arcuate pattern, the radius of curvature of the burrow being approximately equal to that of the shell. The initial burrowing effort may only achieve burial of the shell (Pl. 38, fig. 3). Subsequently, however, the animal digs farther into the sediment, forming a burrow with a constant radius of curvature that, if extended far enough, will open to the surface. A very narrow aquarium was used for clarity in the experiment recorded by the X-radiographs of Plate 38. It tended to constrict the initial downward movement of the animal so that the angle of entry is lower than in nature. Nevertheless, the X-radiographs show quite graphically the curved shape of the burrow, which was also observed in nature. Drew (1907) erroneously rejected Verrill's earlier claim that *Ensis directus* does not maintain a permanent burrow. In fact, it is only by the use of this burrow that individuals in feeding position, with their siphon tips level with the sediment surface, are able to disappear rapidly from view when disturbed. Even a moderately small animal (10 cm long) requires about 45 sec at summer temperatures to burrow the length of its shell in solid sediment. Animals commonly descend a short distance into their burrows when exposed at low tide. But, when disturbed by a nearby footstep, they rapidly retreat even farther downward.

This species is capable of two principal types of locomotion at the sediment surface. Both types have been described previously by various authors. The first type is a posterior leaping movement accomplished by the foot, which bends back dorsally beneath the shell and straightens out suddenly. The second type is an anterior swimming movement accomplished as in *Solemya* by retracting the extended, plug-like foot and adducting the valves to expel a jet of water posteriorly.

Corbula caribaea Orbigny
(Pl. 39, figs. 4, 5)

SHELL DESCRIPTION: The shell is very small (maximum length about 1.5 cm). It is elongate with an elliptical anterior and triangular posterior. The siphonal region is demarcated by a sharp ridge emanating from the umbo. The shell is strongly inflated and the right valve overlaps the left valve, most strongly in the posterior region. The valves are thick, and the ornamentation consists of fine concentric ridges.

L/H 1.47, H/W 1.16, AL/L 0.51, T.I. 0.65

LOCALITY: Numerous individuals were dredged in Mayaguéz Harbor and Boquerón Bay, Puerto Rico, from carbonate silt (sed. 32, 34) at depths of about 6 m.

HABITAT: This species prefers muddy substrata and sheltered subtidal conditions.

LIFE HABITS: *C. caribaea* is an exceedingly sluggish burrower; it was not timed, because individuals required several days to bury themselves completely, pausing for long intervals in the process. Individuals commonly crawl short distances along the sediment surface before achieving burial.

The life position is variable, but most animals tend to orient themselves with the long axis of the shell more than 45° from the horizontal. The siphons are very short.

Animals of all sizes studied (up to 1 cm in length) were observed to secrete a byssus, normally consisting of 3 or 4 threads. In thin aquaria used for X-radiography, animals attached byssal threads to the glass walls after burrowing. Two or three individuals crawled up the walls of plastic containers partly filled with sediment, attached byssal threads to the walls, and temporarily suspended themselves above the sediment surface.

Mya arenaria Linné
(Pl. 39, figs. 1-3)

SHELL DESCRIPTION: The shell is large (occasionally exceeding 10 cm in length); its shape is somewhat variable, but always very elongate and elliptical. The posterior is slightly pointed and elongate. The shell is moderately inflated, with a large siphonal and a small pedal gape.

The ligament is compact and enclosed with a chondrophore; the valves rock about a dorso-ventral axis passing through the ligament. The valves are very thin and often deformed, and the exterior is rugose.

L/H 1.65, H/W 1.67, AL/L 0.44, T.I. 0.15

LOCALITIES: This species was observed at many localities along the New England coast. Specimens were collected for study from slightly muddy fine sand (sed. 13) in the salt marsh of Huckins Island, Barnstable Harbor, Massachusetts.

HABITAT: *M. arenaria* prefers muddy sand substrata of intertidal estuarine environments. It is most common in intertidal areas not subjected to strong currents or waves, but also occurs subtidally. Weymouth (1920) states that the species does not occupy "beaches open to the sea" because large animals are incapable of rapid movements and are subject to mass mortality in storms. They can neither clear sand that plugs their siphons nor, if disinterred, reburrow easily. Substratum preferences and the effects of substratum on growth of *M. arenaria* have been discussed by Newcombe (1935), Swan (1952), and Allen (1954). In general, individuals grow more rapidly and secrete thinner shells in sandy substrata than in muddy substrata. Vlés (1909) and Yonge (1923) have provided detailed anatomical studies of the species, and Pfitzenmeyer and Schuster (1960) have compiled a detailed bibliography on its biology.

LIFE HABITS: This species is a slow burrower (B.R.I. 0.2). It is sometimes claimed that large individuals, once disinterred, cannot reburrow. A 10-cm-long animal from the Barnstable Harbor locality reburrowed in its native sediment when left overnight in the laboratory. In the laboratory, the sediment was fluid, whereas in nature, bound by marsh grass roots and dessicated twice daily, it is much stiffer and probably would not permit reburrowing by such a large individual. This and other laboratory observations do, however, show that reburrowing is possible, even for large animals, under proper circumstances. At the start of burrowing, the small foot emerges at an angle of about 30° to the shell's long axis and probes for an extended period of time. Animals commonly require several contraction sequences for shell erection, which takes place gradually. Following erection, the probing orientation is with the shell's long axis tilted about 15° forward from the horizontal. There is no rocking motion, but a strong spurt of water is discharged anterior to the foot before each downward movement. The shell tilts slowly forward during penetration, to enter the sediment with its long axis about 60° from horizontal. The life position is with the long axis of the shell vertical. The siphons extend directly upward to the surface. They fill a permanent tube, through which they can withdraw, although in large animals they cannot be completely retracted into the shell. Depth of burial varies with habitat. At the Barnstable Harbor locality, large animals (8 to 9 cm long) were living at depths of about 20 cm. Depths of burial for smaller animals (5 to 6 cm) ranged from about 10 to 20 cm.

Lyonsia hyalina (Conrad)
(Pl. 39, figs. 6-8)

SHELL DESCRIPTION: The shell is small (maximum length approximately 2 cm) and very elongate. The anterior is elliptical; the posterior is expanded and somewhat rostrate. The shell is moderately inflated, with the maximum width occurring near the anterior. There are small siphonal and pedal gapes, the valves are very thin, and the exterior is traversed by extremely fine radial ribs. Sand grains often adhere to the ventral margin.

LOCALITIES: Several specimens were found in Quisset Harbor, Massachusetts, primarily in the muddy sand environment (sed. 4) in which *Solemya velum* and *Nucula proxima* were found (in sparse eel grass at depths of about 3 m). A single individual representing the subspecies *floridana* was collected from the shoals south of Cape Florida, Biscayne Bay, Florida, living in slightly muddy and gravelly, fine to medium sand (sed. 22) amid dense *Thalassia.*

HABITAT: *L. hyalina* apparently prefers muddy sand substrata and restricted, subtidal conditions.

LIFE HABITS: Burrowing movements of the species are sluggish and involve relatively small rocking movements. Burrowing was not timed, because animals rarely, if ever, achieved more than partial burial without temporary cessation of activity.

Animals of both subspecies assumed life positions with the long axis of the shell at a low angle (about 30°) from horizontal and anchored themselves in place by weak byssal attachment to grains of sediment (Pl. 39, fig. 8). The posterior tip of the shell and the short siphons project slightly above the sediment surface. This life position differs from the vertical position reported by Ansell (1967) for *Lyonsia norvegica.* The latter is also a shallow burrower that uses a weak byssus for stability, however.

Pandora gouldiana (Dall)
(Pl. 39, figs. 9-11)

SHELL DESCRIPTION: The shell is small, seldom exceeding 3.5 cm in length; it is elongate and crescentic in lateral view, with a reduced and rounded anterior. The shell is extremely compressed and inequivalve, the left valve being more convex than the right. The siphonal region is defined by a twist in the commissure line, producing two posterior ridges on the left valve and a single ridge on the right valve. The valves are very thick, and the exterior is rugose, with a faint groove emanating from the umbo diagonally backward to intersect the shell margin midventrally.

L/H 1.40, H/W 1.67, AL/L 0.44, T.I. 0.72

LOCALITIES: This species was collected in moderately large numbers from the south shore of Barnstable Harbor, Massachusetts, near the local yacht club, where it lives in very gravelly coarse sand (sed. 42) about 1 m below mean tide. It was also dredged in small numbers from sandy bottoms at the mouth of New Haven Harbor, Connecticut.

HABITAT: The gravelly substratum at the Barnstable locality is apparently well suited to *P. gouldiana.* Sanders (1956), however, found it to be rare or absent in Long Island Sound at his stations where either gravel or mud content of the sediment exceeded 10 percent. At any rate, the animal requires hard, coarse substrata and appears to prefer areas of the bottom swept by moderately strong currents. It is almost exclusively subtidal in distribution. Allen and Allen (1955) report that the British species *P. inaequivalvis* lives in very sheltered habitats.

LIFE HABITS: This species is a very slow burrower (B.R.I. 0.05), and its burrowing period tends to be irregular. Animals studied in aquaria refused to burrow unless bathed in a moderately strong flow of water. Buried individuals emerged from the sediment when the current flow was cut off, and they crawled about, to a limited extent. In burrowing, the animal erects itself in 2 to 5 burrowing sequences. The erect probing orientation is shown in Plate 39, figure 11. The angle of rotation is about 40° at the start of downward penetration, but rocking movement is hardly discernible after the animal is about half buried. At the Barnstable Harbor locality, numerous individuals were found lying on the sediment surface amid pebbles, cobbles, and shell debris. The siphons (Pl. 39, fig. 11) are very short and the life position is one of shallow burial. Buried animals are apparently easily dislodged by currents. They tend to lie on one side in the sediment. Allen and Allen (1955) found that the preferred life position for *P. inaequivalvis* is with the left (flat) valve up, whether burrowing is begun with the left or right valve undermost. Different results were obtained for *P. gouldiana* in the present study (Fig. 48). Original orientation of the animal on the sediment surface exerted a strong control over final life position. Whether assuming a position with the left valve or the right valve uppermost, animals tend to lie with the plane of commissure at an angle of 25° to 45° from vertical and the long axis tilted backward 5° to 25° from vertical.

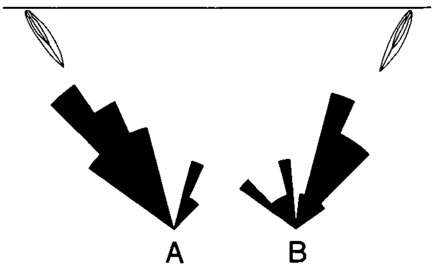


Figure 48. Life orientation of 19 *Pandora gouldiana* individuals placed on their right valves (A) and their left valves (B) and permitted to burrow in their native sediment (no. 42).

References Cited

Abbott, R. T., 1954, American seashells: Princeton, Van Nostrand, 541 p.

Allen, J. A., 1958, On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia): Royal Soc. London Philos. Trans. (B), v. 241, p. 421-484.

Allen, J. F., 1954, The influence of bottom sediments on the distribution of five species of bivalves in the Little Annemessex River, Chesapeake Bay: Nautilus, v. 68, p. 56-65.

Allen, M. F., and Allen, J. A., 1955, On the habits of *Pandora inaequivalvis* (Linné): Malacol. Soc. London Proc., v. 31, p. 145-185.

Ansell, A. D., 1961, The functional morphology of the British species of Veneracea (Eulamellibranchia): Marine Biol. Assoc. United Kingdom Jour., v. 41, p. 489-515.

—— 1962, Observations on burrowing in the Veneridae (Eulamellibranchia): Biol. Bull., v. 123, p. 521-530.

—— 1967, Burrowing in *Lyonsia norvegica* (Gmelin) (Bivalvia: Lyonsiidae): Malacol. Soc. London Proc., v. 37, p. 387-393.

Atkins, D., 1936, On the ciliary mechanisms and interrelationships of lamellibranchs. Part 1: New observations on sorting mechanisms: Microsc. Sci. Quart. Jour., v. 79, p. 181-308.

Baird, R. H., 1958, On the swimming behavior of escallops (*Pecten maximus* L.): Malacol. Soc. London Proc., v. 33, p. 67-71.

Belding, D. L., 1909, The growth and habits of the sea clam (*Mactra solidissima*): Comm. Fish and Game Rept., Commonwealth Mass., Boston, p. 26-41.

Blainville, H. M. D. de, 1825, Manuel de Malacologie et de Conchyliologie: Paris, F. G. Levrault, 664 p.

Boss, K. J., 1965, Symbiotic erycinacean bivalves: Malacologia, v. 3, p. 183-195.

Bourne, N., 1964, Scallops and the offshore fishery of the Maritimes: Canada Fisheries Research Bd. Bull. 145, p. 15-16.

Brafield, A. D., and Newell, G. E., 1961, The behaviour of *Macoma balthica* (L.): Marine Biol. Assoc. United Kingdom Jour., v. 41, p. 81-87.

Bretsky, S. S., 1967, Environmental factors influencing the distribution of *Barbatia domingensis* (Mollusca, Bivalvia) on the Bermuda Platform: Peabody Mus. Postilla, no. 108, 14 p.

Buddenbrock, W. von, 1911, Untersuchungen über die Schwimmbewegungen und die Statocysten der Gattung Pecten: Sitz. Heidelberger Akad. Wiss., Jahrg. 1911, 28, Abh., p. 1-24.

Carricker, M. R., 1961, Interrelation of functional morphology, behavior, and autecology in early stages of the bivalve *Mercenaria mercenaria*: Elisha Mitchell Sci. Soc. Jour., v. 77, p. 168-241.

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

—— 1968, On the biology and palaeontology of some predators of bivalved Mollusca: Palaeogeography, Palaeoclimatology, Palaeoecology: v. 4, p. 29-65.

Cloud, P. E., 1958, Geology of Saipan, Mariana Islands. Pt. 4. Submarine topography and shoal-water ecology: U.S. Geol. Survey Prof. Paper 280, p. 367-451.

Davis, F. M., 1925, Quantitative studies on the fauna of the sea bottom, no. 2. Southern North Sea: Great Britain Fish. Invest., ser. 11, v. 8, p. 1-50.

Davis, J. D., 1963, A study of the arctic wedge clams, *Mesodesma deauratum* (Turtan) and *Mesodesma arctatum* (Conrad) of the northwestern Atlantic: Ph.D. Dissert., New Hampshire Univ., Durham, New Hampshire, 142 p.

Dechaseau, C., 1952, Classe de bivalves, *in* Piveteau, J., *Editor,* Traité de Paleontologie, T. 2: Paris, Masson et Cie, p. 220-364.

Dexter, R. W., 1947, The marine communities of a tidal inlet at Cape Ann, Massachusetts: A study in bio-ecology: Ecology Mon. 17, p. 261-294.

Drew, G. A., 1899, The anatomy, habits, and embryology of *Yoldia limatula* Say: Johns Hopkins Univ. Biol. Mem. 4, p. 1-37.

—— 1900, Locomotion in *Solenomya* and its relatives: Anat. Anzeig., v. 17, p. 257-266.

—— 1906, The habits, anatomy, and embryology of the giant scallop, (*Pecten tenuicostatus,* Mighels): Maine Univ. Studies, no. 6, p. 3-71.

—— 1907, The habits and movements of the razor-shell clam, *Ensis directus,* Con.: Biol. Bull., v. 12, p. 127-138.

Fairbanks, L. D., 1962, Biodemographic studies of the clam *Rangia cuneata* Gray: Tulane Studies Zoology, v. 10, p. 3-47.

Field, I. A., 1922, Biology and economic value of the sea mussel *Mytilus edulis*: U.S. Bur. Fish. Bull., v. 38, p. 127-259.

Fraenkel, G., 1927, Die Grabbewegung der Soleniden: Zeitschr. vergleich. Physiol., v. 6, p. 168-220.

Fraser, T. H., 1967, Contributions to the biology of *Tagelus divisus* (Tellinacea: Pelecypoda) in Biscayne Bay, Florida: Bull. Marine Sci., v. 17, p. 111-132.

Geesteranus, R. A. Maas, 1942, On the formation of banks by *Mytilus edulis* L.: Arch. Néerl. Zool., T. 10, p. 283-326.

Grave, B. H., 1927, The natural history of *Cumingia tellinoides*: Biol. Bull., v. 53, p. 208-219.

Hallam, A., 1968, Morphology, paleoecology and evolution of the genus *Gryphaea* in the British Lias: Royal Soc. London Philos. Trans., v. 254, p. 91-128.

Holme, N. A., 1961, Notes on the mode of life of the Tellinidae (Lamellibranchia): Marine Biol. Assoc. United Kingdom Jour., v. 41, p. 699-703.

Hornell, J., 1909, Report upon the anatomy of *Placuna placenta,* with notes upon its distribution and economic uses: Marine Zoology Okhamandal Rept., v. 1, p. 43-97.

Hunter, W. R., 1949, The structure and behaviour of *Hiatella gallicana* (Lamarck) and *H. arctica* (L.): Royal Soc. Edinburgh Proc., v. 54, p. 271-289.

Huxley, J. S., 1932, Problems of relative growth: London, McVeagh, 276 p.

Kármán, Th. von, and Burgers, J. M., 1963, General aerodynamic theory—perfect fluids, *in* Durand, W. F., *Editor,* Aerodynamic theory: New York, Dover, v. 2, p. 1-367.

Kauffman, E. G., 1967, Coloradoan macroinvertebrate assemblages, central Western Interior, United States, *in* Kauffman, E. G., and Kent, H. C., *Editors,* Symposium on paleoenvironments of the Cretaceous seaway in the western interior, Colorado School Mines, Golden, Colorado, p. 67-143.

Krumbein, W. C., and Pettijohn, F. J., 1938, Manual of sedimentary petrography: New York, Appleton-Century-Crofts, 549 p.

Kuenen, D. J., 1942, On the distribution of mussels on the intertidal sand flats near Den Helder: Arch. Néerl Zool., T. 6, p. 117-160.

Kuenzler, E. J., 1961, Structure and energy flow of a mussel population in a Georgia salt marsh: Limnology and Oceanography, v. 6, p. 191-204.

Lim, C. F., 1966, A comparative study of the ciliary feeding mechanisms of *Anadara* species from different habitats: Biol. Bull., v. 130, p. 106-117.

Lison, L., 1949, Recherches sur la forme et la mechanique de dévelopment de coquilles des lamellibranches: Belgique Inst. Royal Sci. Nat. Mém., Fasc. 34, p. 1-87.

Loesch, H. C., 1957, Studies of the ecology of two species of *Donax* on Mustang Island, Texas: Texas Univ., Inst. Marine Sci. Pubs., v. 4, p. 201-227.

McDougall, K. D., 1943, Sessile marine invertebrates of Beaufort, North Carolina: Ecology Mon., v. 13, p. 321-374.

McLean, R. A., 1951, The Pelecypoda or bivalve mollusks of Porto Rico and the Virgin Islands: New York Acad. Sci., Sci. Survey Porto Rico and the Virgin Islands, v. 17, 183 p.

Menard, H. W., and Boucot, A. J., 1951, Experiments on the movement of shells by water: Am. Jour. Sci., v. 249, 131-151.

Mercer, E. H., 1952, Observations on the molecular structure of byssus fibres: Australian Marine and Freshwater Research Jour., v. 3, p. 199-204.

Moore, D. R., 1961, The marine and brackish water Mollusca of the state of Mississippi: Gulf Research Repts. v. 1, p. 1-58.

Morse, E. S., 1913, Observations on living Solenomya: Biol. Bull., v. 25, p. 261-281.

Moseley, H., 1838, On the geometrical forms of turbinated and discoid shells: Royal Soc. London Philos. Trans., p. 351-370.

Newcombe, C. L., 1935, Growth of *Mya arenaria* L. in the Bay of Fundy region: Canadian Jour. Research, v. 13, p. 97-137.

Nicol, D., 1958, A survey of inequivalve pelecypods: Washington Acad. Sci. Jour., v. 48, p. 56-62.

—— 1964, Lack of shell-attached pelecypods in arctic and antarctic waters: Nautilus, v. 77, p. 92-93.

—— 1965, Ecologic implications of living pelecypods with calcareous spines: Nautilus, v. 78, p. 109-116.

—— 1967, Some characteristics of cold-water marine pelecypods: Jour. Paleontology, v. 41, p. 1330-1340.

Norton, O. A., 1947, Some ecological observations on *Dosinia discus* Reeve at Beaufort, North Carolina: Ecology, v. 28, p. 199-204.

Ockelman, W. K., 1958, The zoology of East Greenland, marine Lamellibranchiata: Medd. om Grønland, Bd. 122, Nr. 4, 256 p.

Owen, G., 1953, The shell in the Lamellibranchia: Microsc. Sci. Quart. Jour., v. 94, p. 57-70.

—— 1959, Observations on the Solenacea with reasons for excluding the family Glaucomyidae: Royal Soc. London Philos. Trans. (B), v. 242, p. 59-96.

—— 1961, A note on the habits and nutrition of *Solemya parkinsoni* (Protobranchia: Bivalvia): Microsc. Sci. Quart Jour., v. 102, p. 15-21.

Parker, R. H., 1960, Ecology and distributional patterns of marine macroinvertebrates, northern Gulf of Mexico, *in* Shepard, F. P., Phleger, F. B., and Andel, T. H. van, *Editors*: Tulsa, Am. Assoc. Petroleum Geologists, p. 302-337.

Perry, L. M., 1940, Marine shells of the southwest coast of Florida: Bull. Am. Paleontology, v. 26, 260 p.

Pettijohn, F. J., 1957, Sedimentary rocks: New York, Harper, 718 p.

Pfitzenmeyer, H. T., and Drobeck, K. G., 1964, The occurrence of the brackish water clam, *Rangia cuneata,* in the Potomac River, Maryland: Chesapeake Sci., v. 5, p. 209-215.

Pfitzenmeyer, H. T., and Shuster, C. N., 1960, A partial bibliography of the soft shell clam, *Mya arenaria* L.: Chesapeake Biol. Lab., Contr. 123, 29 p.

Pohlo, R. H., 1964, Ontogenetic changes in form and mode of life in *Tresus* nuttalli (Bivalvia: Mactridae): Malacologia, v. 1, p. 321-330.

Pratt, D. M., and Campbell, D. A., 1956, Environmental factors affecting growth in *Venus mercenaria*: Limnology and Oceanography, v. 1, p. 2-17.

Pulley, T. E., 1952, An illustrated check list of the marine mollusks of Texas: Texas Jour. Sci., v. 4, p. 167-199.

Quayle, D. B., 1949, Movements in *Venerupis* (*Paphia*) *pullastra* (Montagu): Malacol. Soc. London Proc., v. 28, p. 31-37.

Raup, D. M., 1966, Geometric analysis of shell coiling: General problems: Jour. Paleontology, v. 40, p. 1178-1190.

Rhoads, D. C., 1963, Rates of sediment reworking by *Yoldia limatula* in Buzzards Bay, Massachusetts and Long Island Sound: Jour. Sed. Petrology, v. 33, p. 723-727.

Rudwick, M. J. S., 1964a, The function of zigzag deflections in the commissures of fossil brachiopods: Palaeontology, v. 7, p. 135-171.

——1964b, The inference of function from structure in fossils: British Philos. Sci. Jour., v. 15, p. 27-40.

Sanders, H. L., 1956, Oceanography of Long Island Sound, 1952-1954. X. The biology of marine bottom communities: Yale Univ. Bingham Oceanogr. Collection Bull., v. 15, p. 345-413.

——1960, Benthic studies in Buzzards Bay III. The structure of the soft-bottom community: Limnology and Oceanography, v. 5, p. 138-153.

Schmidt, H., 1937, Zur Morphologenie der Rhynchonellidae: Senckenbergiana, v. 19, p. 22-60.

Seilacher, A., 1954, Ökologie der triassischen Muschel *Lima lineata* (Schloth) und ihrer Epöken: Neues Jahrb. Geologie u. Paläontologie Monatsh., v. 4, p. 163-183.

Stanley, S. M., 1968, Post-Paleozoic adaptive radiation of infaunal bivalve molluscs—a consequence of mantle fusion and siphon formation: Jour. Paleontology, v. 42, p. 214-229.

Stasek, C. R., 1961, The form, growth, and evolution of the Tridacnidae (giant clams): Arch. zool. expér. et général, T. 101, p. 1-40.

——1963, Geometrical form and gnomonic growth in the bivalved Mollusca: Jour. Morphology, v. 112, p. 215-231.

——1965, Feeding and particle-sorting in *Yoldia ensifera* (Bivalvia: Protobranchia), with notes on other nuculanids: Malacologia, v. 2, p. 349-366.

——1966, Views on the comparative anatomy of the bivalved Mollusca: Malacologia, v. 5, p. 67-68.

Stehli, F. G., McAlester, A. L., and Helsley, C. E., 1967, Taxonomic diversity of Recent bivalves and some implications for geology: Geol. Soc. America Bull., v. 78, p. 455-466.

Studnitz, G. von, 1931, Die Morphologie und Anatomie von *Lima inflata*, der Feilenmuschel, nebst biologischen Untersuchungen an *Lima hians* Gmel.: Zool. Jahrb., abt. Anat. Ont. Tiere, 53, p. 199-316.

Swan, E. F., 1952, Growth of the clam *Mya arenaria*, as affected by the substratum: Ecology, v. 33, p. 530-534.

Tebble, N., 1966, British bivalve seashells: London, British Mus. (Nat. History), 212 p.

Thiele, J., 1935, Handbuch der Systematischen Weichtierkunde, Bd. 2: Jena, Germany, G. Fischer, p. 779-1154.

Thompson, D'A. W., 1942, On growth and form: Cambridge, Cambridge Univ. Press, 1116 p.

Thorson, G., 1957, Bottom communities: Geol. Soc. America Mem. 67, p. 461-534.

Trueman, E. R., 1964, Adaptive morphology in paleoecological interpretation, *in* Imbrie, J., and Newell, N., *Editors*, Approaches to paleoecology: New York, John Wiley and Sons, p. 45-74.

——1966, Bivalve mollusks: Fluid dynamics of burrowing: Science, v. 152, p. 523-525.

Trueman, E. R., Brand, A. R., and Davis, P., 1966, The effect of substrata and shell shape on the burrowing of some common bivalves: Malacol. Soc. London Proc., v. 37, p. 97-109.

Turner, H. J., and Belding, D. L., 1957, The tidal migrations of *Donax variabilis* Say: Limnology and Oceanography, v 2, p. 120-124.

Turner, R. D., 1966, A survey and illustrated catalogue of the Teredinidae: Cambridge, Harvard Univ. Mus. Comp. Zoology, 265 p.

Verrill, A. E., 1897, A study of the family Pectinidae, with a revision of the genera and subgenera: Connecticut Acad. Arts and Sci. Trans., v. 10, p. 41-96.

Verwey, J., 1952, On the ecology of distribution of cockle and mussel in the Dutch Waddensea, their role in sedimentation and the source of their food supply: Arch. Néerl. Zool., T. 10, p. 171-239.

Vlés, F., 1909, Monographie Sommaire de la Mye (*Mya arenaria* Linné 1767): Soc. Zool. France Mém., T. 22.

Wade, Barry A., 1967, Studies on the biology of the West Indian beach clam, *Donax denticulatus* Linné. 1. Ecology: Bull. Marine Sci., v. 17, p. 149-174.

Warmke, G. L., and Abbott, R. T., 1953, The gross anatomy and occurrence in Puerto Rico of the pelecypod *Yoldia perprotracta*: Washington Acad. Sci. Jour., v. 43, p. 260-261.

—— 1961, Caribbean seashells: Narberth, Pennsylvania, Livingston Pub. Co., 348 p.

Weymouth, F. W., 1920, The edible clams, mussels and scallops of Californa: California Fish and Game Comm., Fish Bull. no. 4, 74 p.

White, K. M., 1937, *Mytilus*: Liverpool Marine Biol. Comm. Mem. 31, 117 p.

Wiborg, K. F., 1946, Undersøkelser over oskjellet (*Modiola modiolus* L.). I. Alminnelig biologi, vekst og økonomisk betydning: Fiskeridirekt. Skrifter, v. 8, no. 5.

Wilbur, K. M., and Owen, G., 1964, Growth, *in* Wilbur, K. M., and Yonge, C. M., *Editors*, Physiology of Mollusca, Vol. I: New York, Academic Press, p. 211-242.

Yonge, C. M., 1923, Studies on the comparative physiology of digestion. I. The mechanism of feeding, digestion, and assimilation in the Lamellibranch *Mya*: British Exper. Biol. Jour., v. 1, p. 15-63.

—— 1936a, Mode of life, feeding, digestion, and symbiosis with zooxanthellae in the Tridacnidae: Great Barrier Reef Exp. 1928-1929, British Mus. Sci. Rept. 1, p. 283-321.

—— 1936b, The evolution of the swimming habit in the Lamellibranchia: Belgique Mus. Royal d'Hist. Nat., 2 sér., Fasc. 3, p. 77-100.

—— 1939, The protobranchiate Mollusca: A functional interpretation of their structure and evolution: Royal Soc. London Philos. Trans. (B), v. 230, p. 79-147.

—— 1946, On the habits and adaptations of *Aloidis* (*Corbula*) *gibba*: Marine Biol. Assoc. United Kingdom Jour., v. 26, p. 358-376.

—— 1950, Life on sandy shores: Sci. Progress, v. 38, p. 430-444.

—— 1953, The monomyarian condition in the Lamellibranchia: Royal Soc. Edinburgh Trans., v. 62, pt. 2, p. 443-478.

Yonge, C. M., 1958, Observations on *Petricola carditoides* (Conrad): Malacol. Soc. London Proc., v. 33, p. 25-31.

—— 1962, On the primitive significance of the byssus in the Bivalvia and its effects in evolution: Marine Biol. Assoc. United Kingdom Jour., v. 42, p. 113-125.

—— 1963, Rock-boring organisms, *in* Mechanisms of hard tissue destruction: Am. Assoc. Adv. Sci. Pub. no. 75, p. 1-24.

—— 1967, Form, habit and evolution in the Chamidae (Bivalvia) with reference to conditions in the rudists (Hippuritacea): Royal Soc. London Philos. Trans. (B), v. 252, p. 49-105.

MANUSCRIPT RECEIVED BY THE SOCIETY AUGUST 19, 1968
REVISED MANUSCRIPT RECEIVED MARCH 3, 1969

Plates

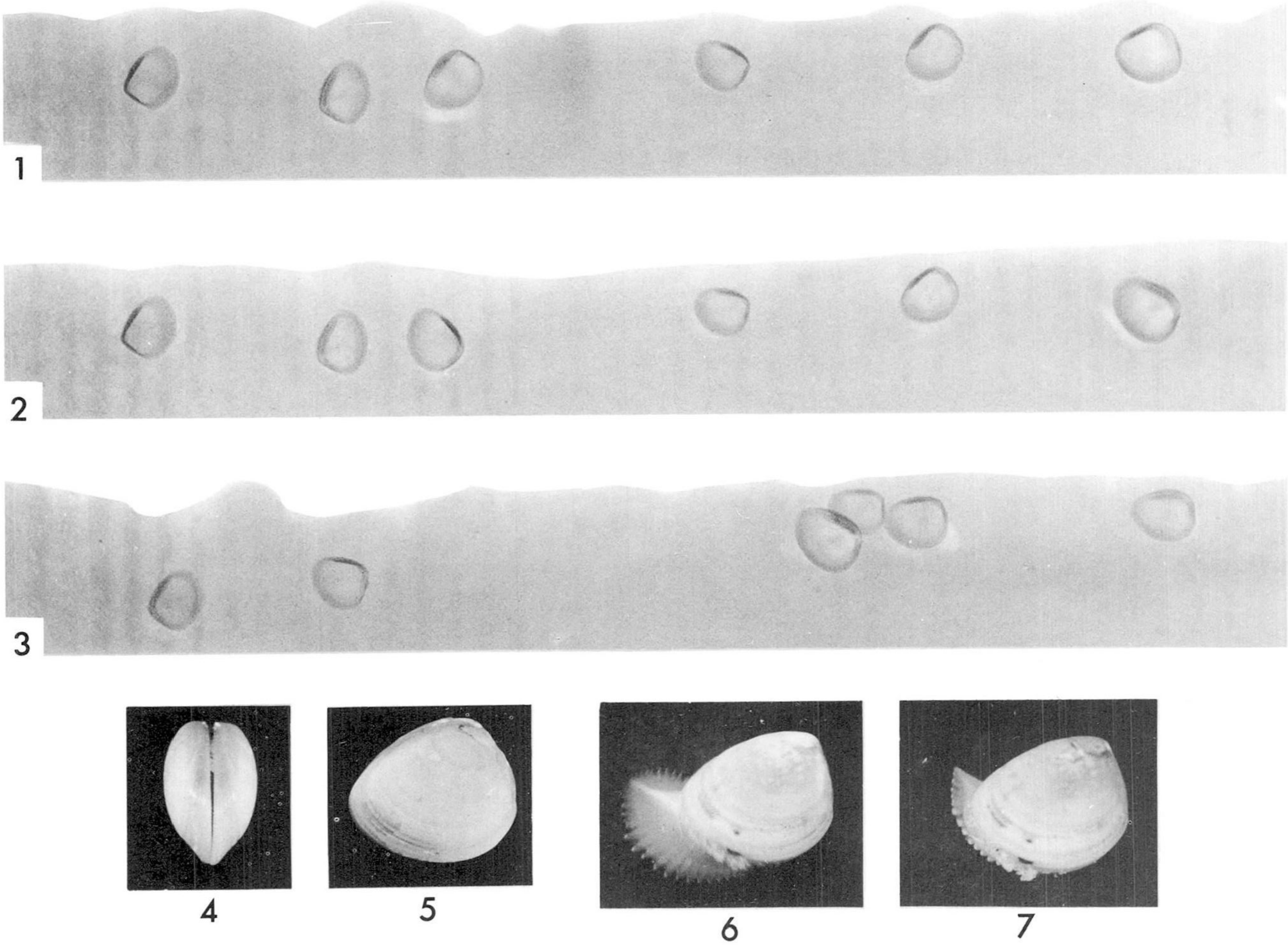
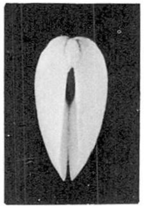
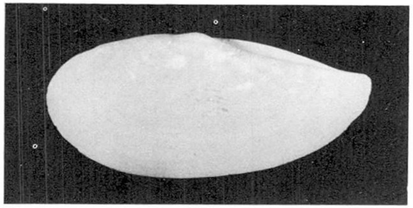


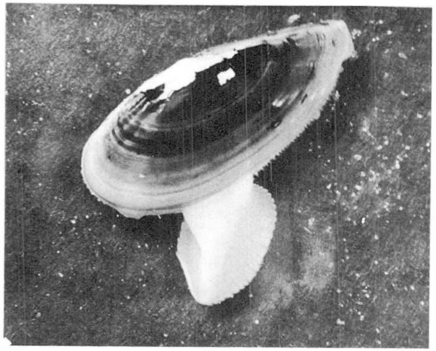
PLATE 1. NUCULA

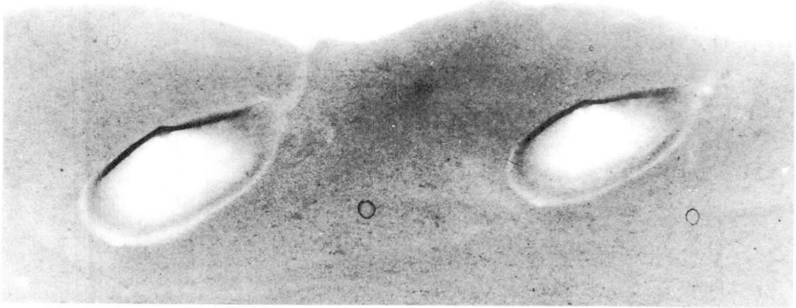
NUCULA

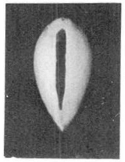
Figures 1-7. *Nucula proxima* (Say) (*see* p. 115). Figures 1-3. X-radiographs of animals in sediment 1, showing movements and variable life orientation; foot sometimes visible. Exposures 15 min, 30 min, and 26 hr from the time when the animals were placed in the aquarium. (X 1). Figures 4, 5. Anterior and left lateral views. (X 2.7). Figures 6, 7. Movements of the foot. (X 2.8). Locality: Quisset Harbor, Massachusetts.

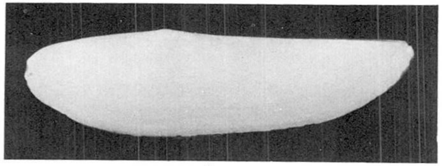

1


2


3


4


5


6

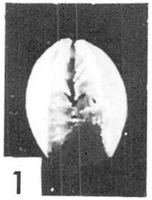

7

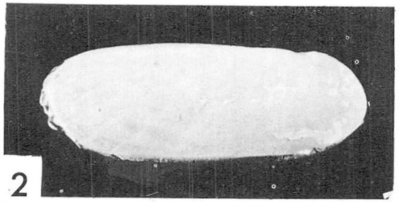
PLATE 2. YOLDIA

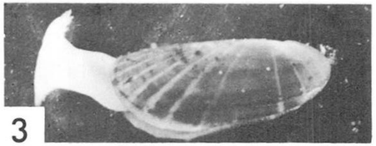
YOLDIA

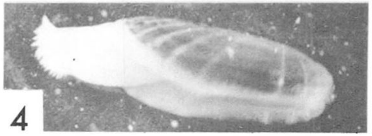
Figures 1-4. *Yoldia limatula* (Say) (*see* p. 117). Figures 1, 2. Anterior and left lateral views. (X 1.7). Figure 3. Live animal with foot extended and flared. (X 4.1). Figure 4. X-radiograph of animals in life position (sed. 1). Animals in native mud live with long shell axis at slightly higher angle. (X 1). Locality: Quisset Harbor, Massachusetts.

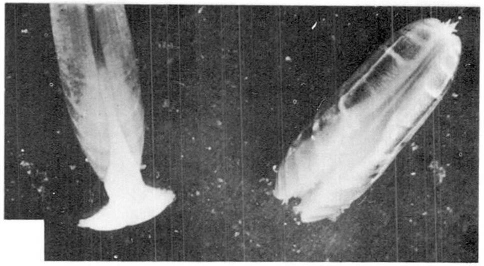
Figures 5-7. *Yoldia perprotracta* Dall (*see* p. 118). Figures 5, 6. Anterior and left lateral views. (X 2). Figure 7. X-radiograph of animals in life position in native sediment (34). (X 1). Locality: Mayaguéz Harbor, Puerto, Rico.


1


2


3


4


5

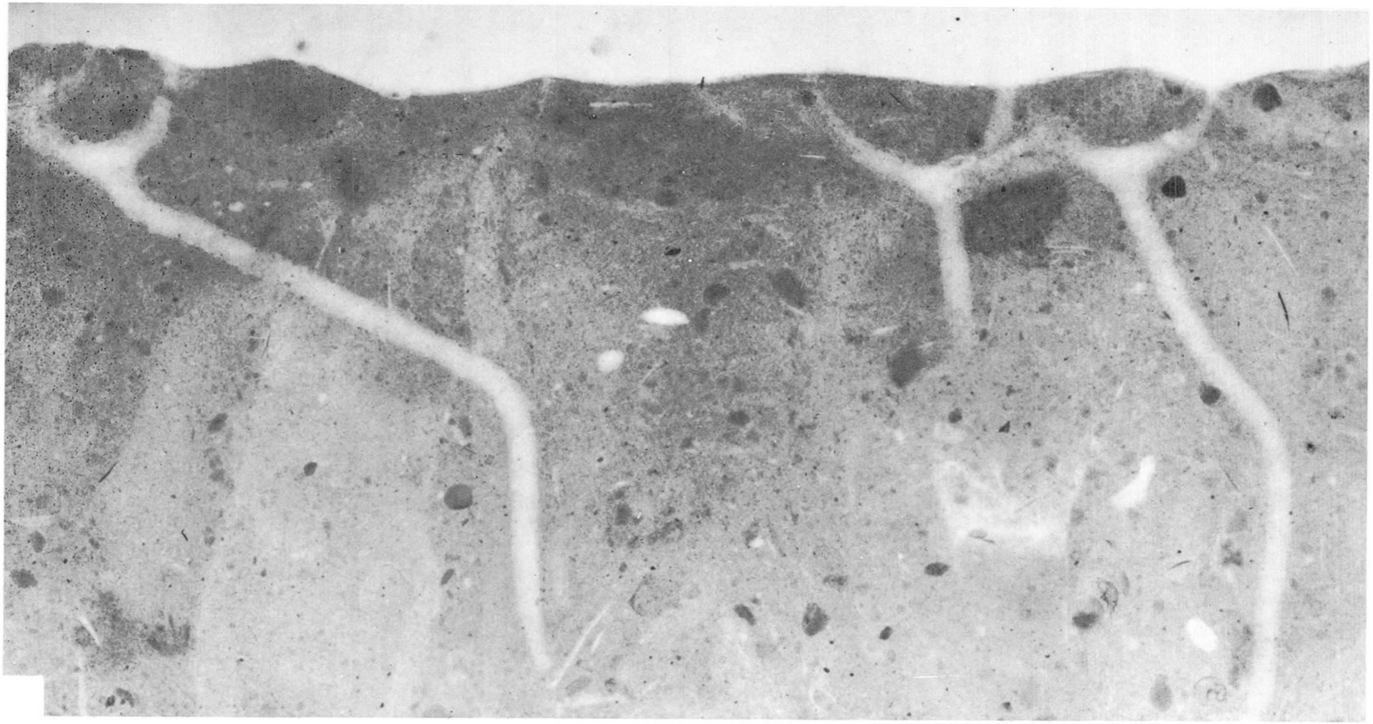
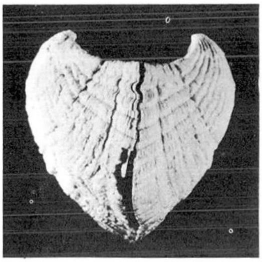
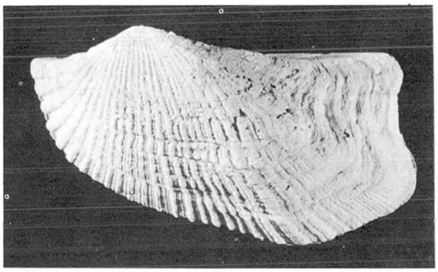


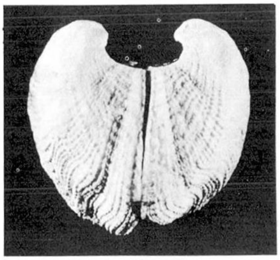
PLATE 3. SOLEMYA

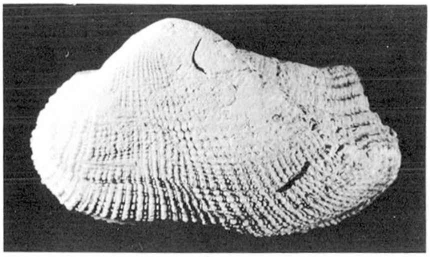
SOLEMYA

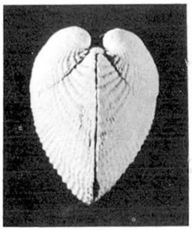
Figures 1-6. *Solemya velum* Say (*see* p. 119). Figures 1, 2. Anterior and left lateral views. (X 2.7). Figures 3-5. Movements of the foot. (X 2). Figure 6. X-radiograph of Y-shaped burrows in native sediment (4). (X 1). Locality: Mayagüez Harbor, Puerto Rico.

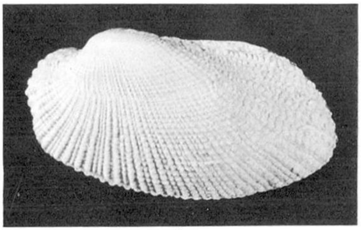

1

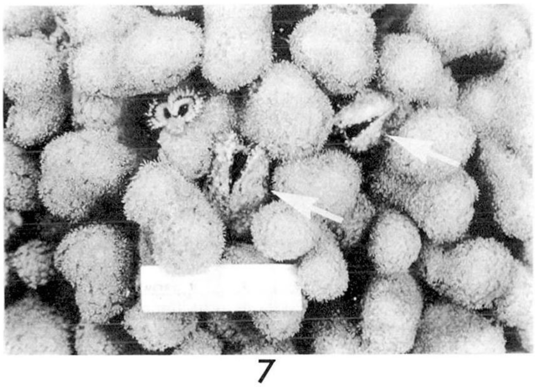

2


3

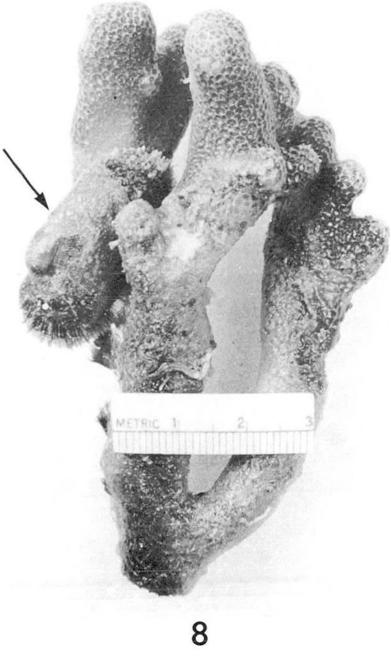

4


5


6



7



8

PLATE 4. ARCA, BARBATIA

ARCA, BARBATIA

Figures 1, 2. *Arca zebra* Swainson (*see* p. 121). Anterior and left lateral views. (X 1.1). Locality: La Parguera, Puerto Rico.

Figures 3, 4. *Arca imbricata* Bruguiere (see p. 121). Anterior and left lateral views. (X 1.3). Locality: Bear Cut, Biscayne Bay, Florida.

Figures 5-8. *Barbatia cancellaria* (Lamarck) (*see* p. 122). Figures 5, 6. Anterior and left lateral views. (X 1.5). Figure 7. Current-bearing posteriors of two animals wedged in among terminal branches of the coral *Porites* (scale 3 cm long). Figure 8. Single animal attached in life position to terminal *Porites* branches (scale 3 cm long). Locality: Magueyes Island, La Parguera, Puerto Rico.

BARBATIA, ARCOPSIS, ANADARA

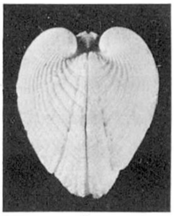
Figures 1, 2. *Barbatia tenera* (C. B. Adams) (*see* p. 122). Anterior and left lateral views. (X 1.1). Locality: La Parguera, Puerto Rico.

Figures 3, 4. *Barbatia domingensis* (Lamarck) (*see* p. 123). Anterior and left lateral views. (X 1.8). Locality: Biscayne Bay, Florida.

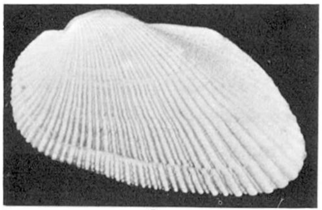
Figures 5, 6. *Arcopsis adamsi* (Dall) (*see* p. 123). Anterior and left lateral views. (X 2.6). Locality: Biscayne Bay, Florida.

Figures 7-10. *Anadara ovalis* (Brugière). (*see* p. 124). Figures 7, 8. Anterior and left lateral views. (X 1.3). Figure 9. Burrowing animal in erect probing orientation (scale 3 cm long). Figure 10. Animal in life position, with shell posterior slightly exposed. (X 0.8). Locality: Biscayne Bay, Florida.

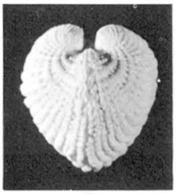
Figures 11, 12. *Anadara notabilis* (Röding) (*see* p. 125). Anterior and left lateral views. (X 0.9). Locality: Bear Cut, Biscayne Bay, Florida.



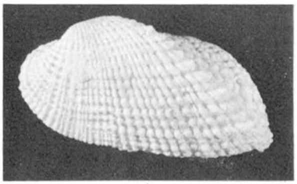
1



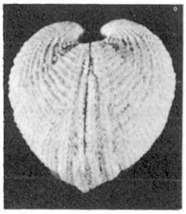
2



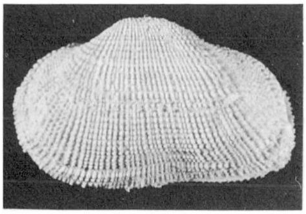
3



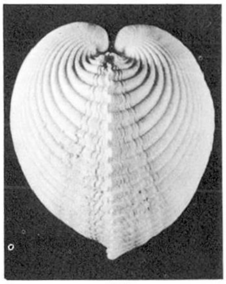
4



5

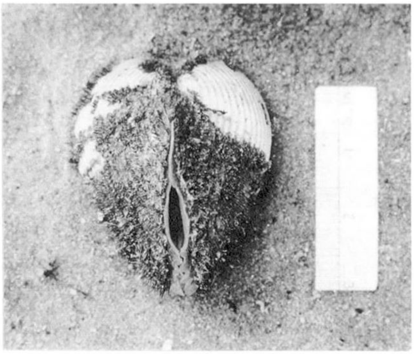


6



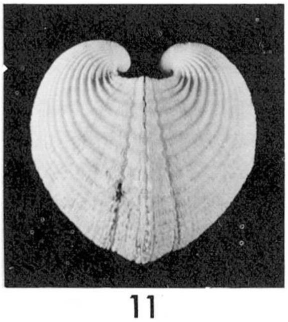
7

8

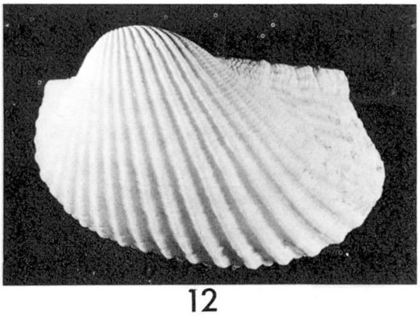


9

10

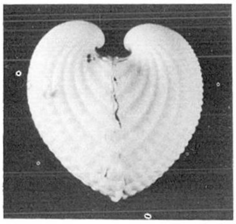


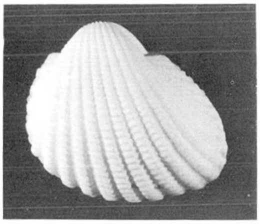
11

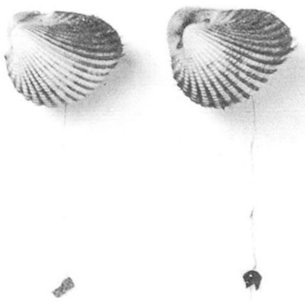


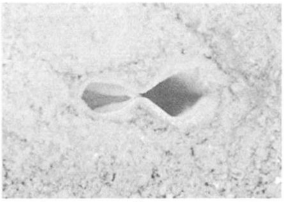
12

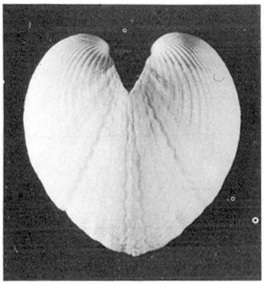
PLATE 5. BARBATIA, ARCOPSIS, ANADARA

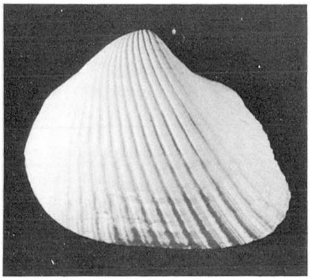

1


2

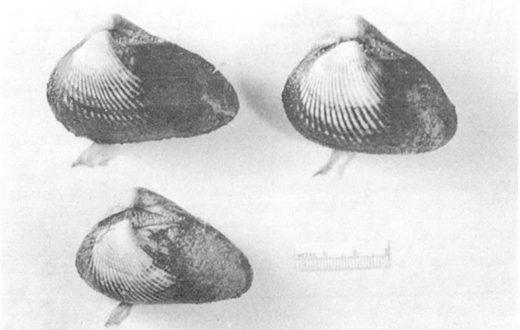

3

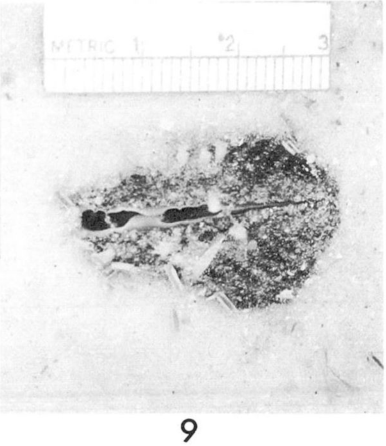

4


5


6

7


8



9

PLATE 6. ANADARA, NOETIA

ANADARA, NOETIA

Figures 1-4. *Anadara chemnitzi* (Philippi) (*see* p. 125). Figures 1, 2. Anterior and left lateral views. (X 1.6). Figure 3. Live animals, showing unusual byssal thread with terminal pad. (X 1.2). Figure 4. Inhalent (right) and exhalent (left) current apertures of animal in life position. (X 3). Locality: Mayagüez Harbor, Puerto Rico.

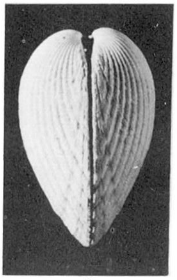
Figures 5-9. *Noetia pondorosa* (Say) (*see* p. 126). Figures 5, 6. Anterior and left lateral views. (X 0.7). Figure 7. Burrowing animal in erect probing orientation (scale 3 cm long). Figure 8. Live animals, showing ribbon-like byssus (scale 3 cm long). Figure 9. Inhalent and exhalent current apertures of animal in life position (scale 3 cm long). Locality: Marco Island, Florida.

GLYCYMERIS, BRACHIDONTES, MYTILUS

Figures 1-4. *Glycymeris pectinata* (Gmelin) (*see* p. 127). Figures 1, 2. Anterior and left lateral views. (X 1.1). Figure 3. Animal crawling forward while burrowing, to produce a sinuous trail. (X 0.8). Figure 4. Inhalent (above) and exhalent (below) current apertures (scale 3 cm long). Locality: south of Cape Florida, Biscayne Bay, Florida.

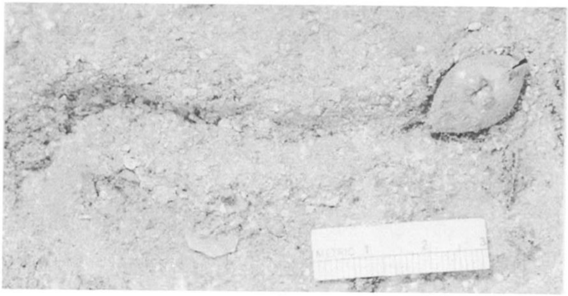
Figures 5, 6. *Brachidontes recurvus* (Rafinesque) (*see* p. 134). Anterior and left lateral views. (X 1). Locality: Reedsville, Virginia.

Figures 7-9. *Mytilus edulis* Linné (*see* p. 129). Figures 7, 8. Anterior and left lateral views. (X 0.8). Figure 9. Animals colonizing intertidal rocky surface (scale 15 cm long). Locality: Woodmont, Connecticut.

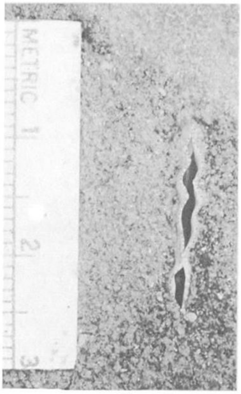


1

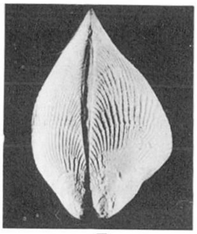
2



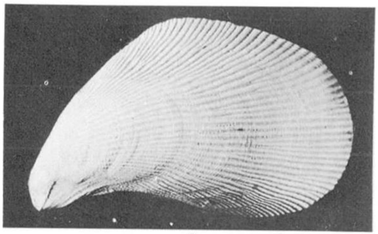
3



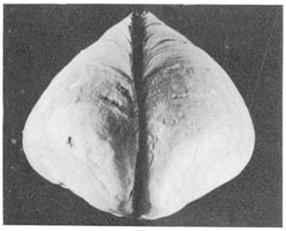
4



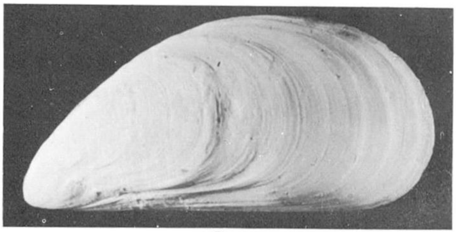
5



6



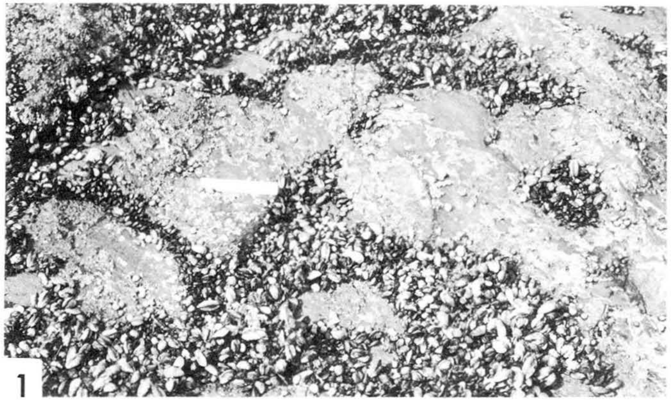
7



8

9

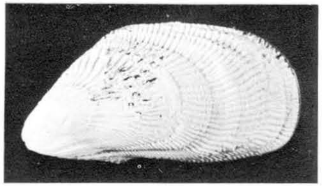
PLATE 7. GLYCYMERIS, BRACHIDONTES, MYTILUS


1


2


3


4


5


6

PLATE 8. MYTILUS, BRACHIDONTES

MYTILUS, BRACHIDONTES

Figures 1-3. *Mytilus edulis* Linné (*see* p. 129). Figure 1. Animals preferentially colonizing crevices, intertidal rocky surface, Woodmont, Connecticut. (X 0.07). Figure 3. Incipient colonization of an intertidal sand flat, Barnstable Harbor, Massachusetts. Figure 4. One of the scattered clumps visible in Figure 3. (X 0.3).

Figures 4-6. *Brachidontes exustus* (Linné) (*see* p. 133). Figures 4, 5. Anterior and left lateral views. (X 2.2). Figure 6. Cluster of animals on rocky surface. (X 0.7). Locality: Magueyes Island, La Parguera, Puerto Rico.

BRACHIDONTES, MODIOLUS

Figures 1-3. *Brachidontes citrinus* (Röding) (*see* p. 134). Figures 1, 2. Anterior and left lateral views. (X 1.6). Figure 3. Live animal attached to coarse substratum particles. (X 1.6). Locality: Guánica, Puerto Rico.

Figures 4-6. *Modiolus modiolus* (Linné) (*see* p. 130). Figures 4, 5. Anterior and left lateral views. (X 0.5). Figure 6. Animal in life orientation attached to substratum gravel. Sharp boundary between bare shell and coralline algae (and other epibionts) on shell posterior marks position of sediment-water interface in life. (X 0.4). Locality: Nahant, Massachusetts.

Figures 7-9. *Modiolus demissus* (Dillwyn) (*see* p. 132). Figures 7, 8. Anterior and left lateral views. (X 1). Figure 9. Animal exposed in life position, mostly buried in marsh peat. (X 0.8). Locality: Woodmont, Connecticut.

Figures 10, 11. *Modiolus americanus* Leach (*see* p. 133). Anterior and left lateral views. (X 0.9). Locality: south of Cape Florida, Biscayne Bay, Florida.

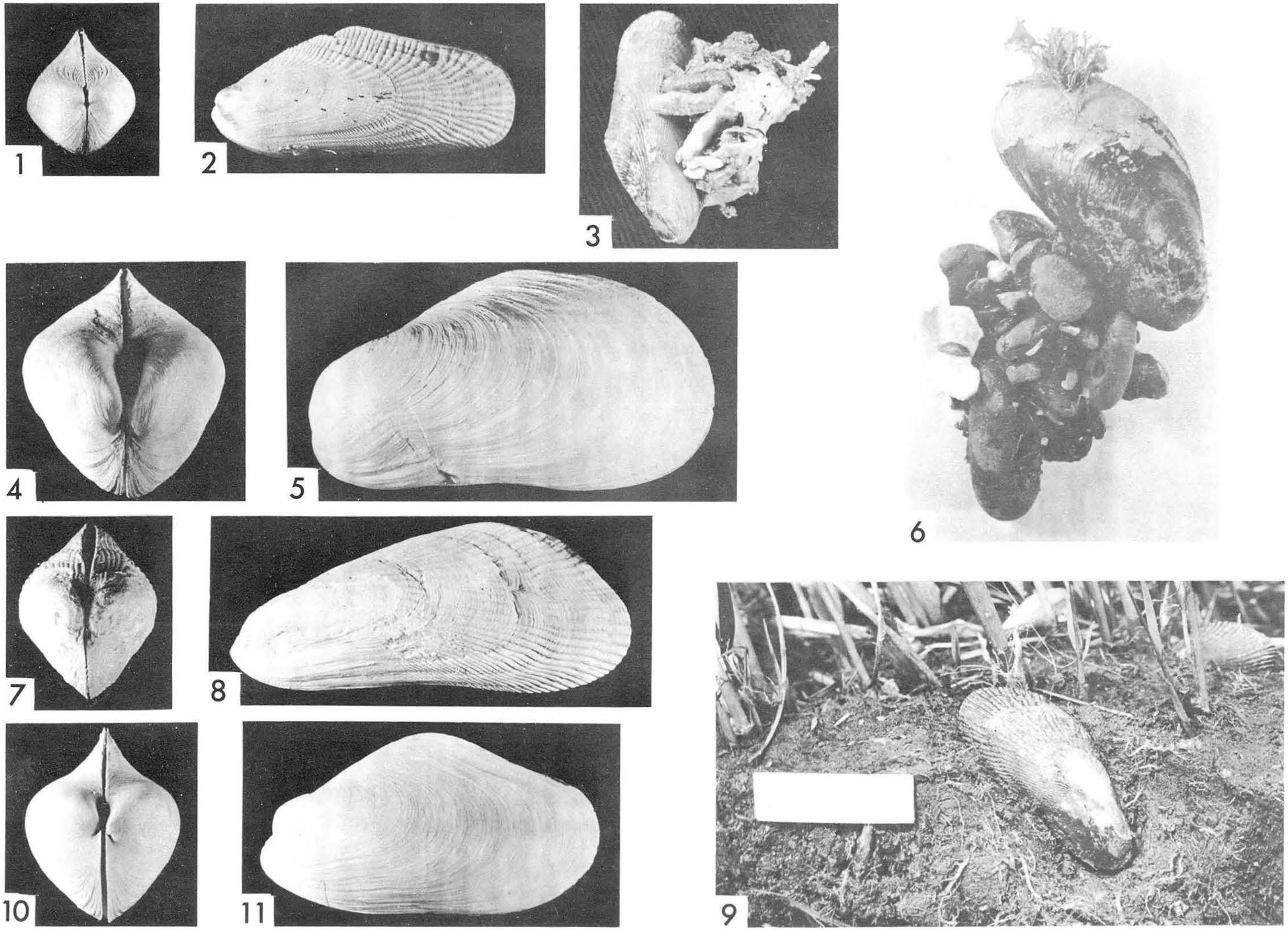
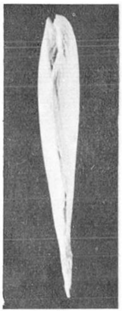
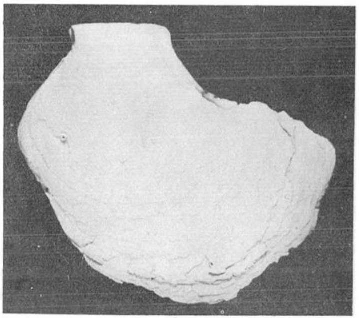


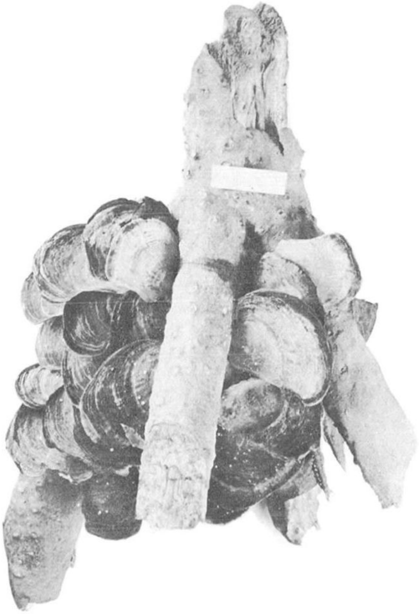
PLATE 9. BRACHIDONTES, MODIOLUS



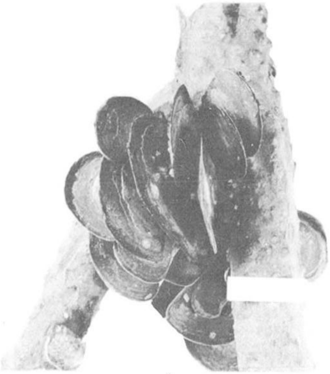
1



2

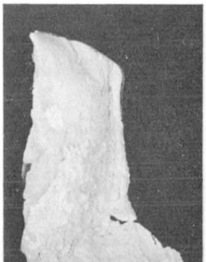


3

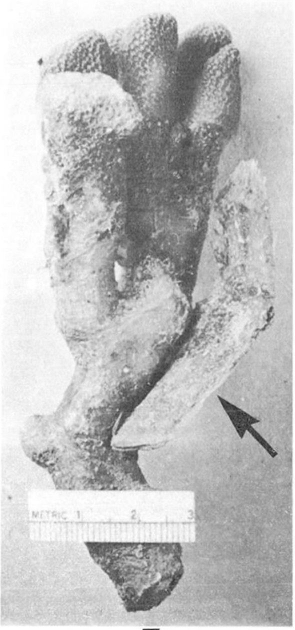


4

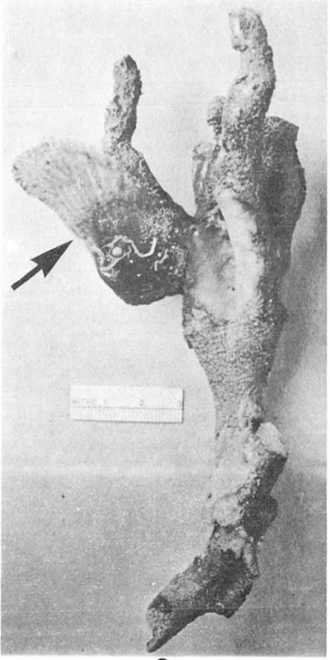
5



6



7



8

PLATE 10. ISOGNOMON

ISOGNOMON

Figures 1-4. *Isognomon alata* (Gmelin) (*see* p. 135). Figures 1, 2. Ventral and left lateral views. (X 0.7). Figures 3, 4. Animals attached in life to mangrove prop roots. (X 0.35). Locality: La Parguera, Puerto Rico.

Figures 5-8. *Isognomon radiata* (Anton) (*see* p. 135). Figures 5, 6. Ventral and left lateral views. (X 0.7). Figures 7, 8. Animals attached in life to *Porites* coral branches (broken from colony for photograph) (scale 3 cm long). Locality: La Parguera, Puerto Rico.

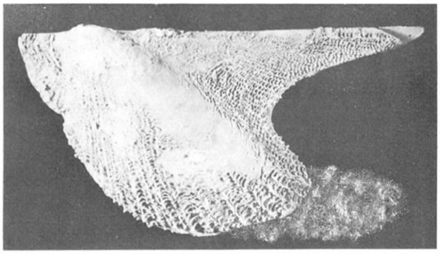
PTERIA, PINCTADA, PINNA

Figures 1-4. *Pteria colymbus* (Röding) (*see* p. 136). Figures 1, 2. Ventral and left lateral views. (X 1). Figure 3. Live animals in typical attachment orientation on alcyonarian branch. (X 0.7). Figure 4. Exhalent current of live animal shown by introduction of powdered charcoal. (X 0.6). Locality: La Parguera, Puerto Rico.

Figures 5-7. *Pinctada radiata* (Leach) (*see* p. 136). Figures 5, 6. Ventral and left lateral views. (X 0.7). Figure 7. Exhalent current of live animal shown by introduction of powdered charcoal. (X 0.7). Locality: La Parguera, Puerto Rico (7); Bimini, Bahamas-YPM 6889 (5, 6).

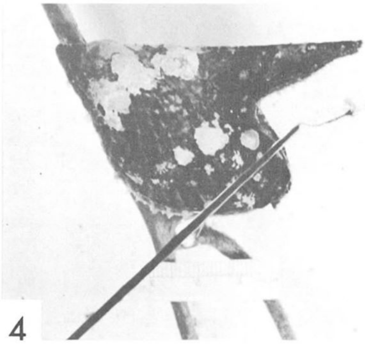
Figures 8, 9. *Pinna carnea* Gmelin (*see* p. 137). Ventral and left lateral views. (X 0.4). Locality: Bermuda-YPM 6946.

1

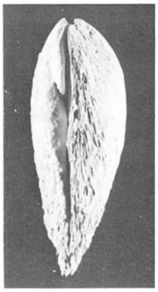


2

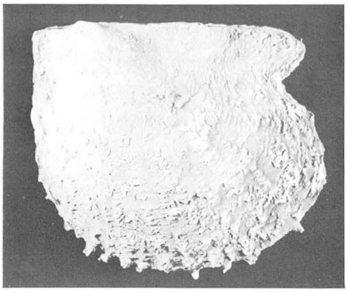
3



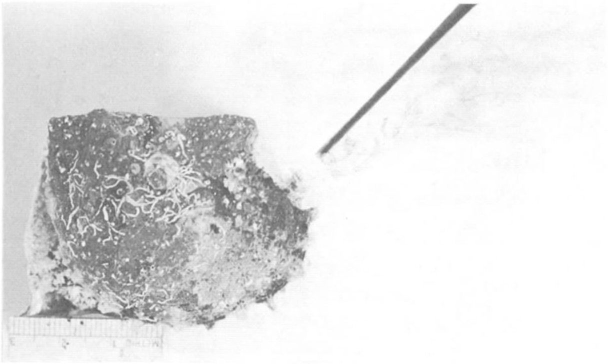
4



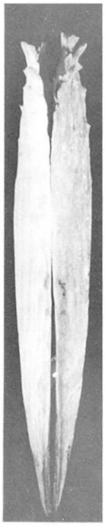
5



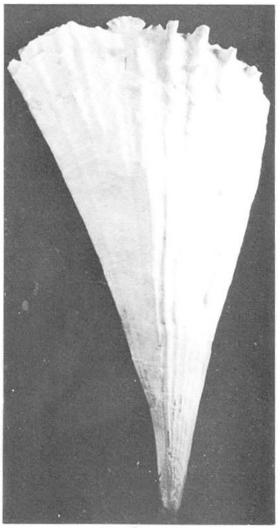
6



7

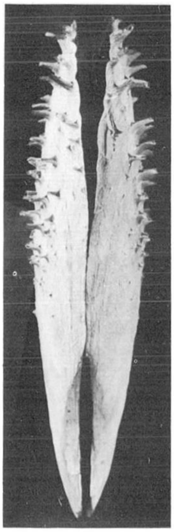


8

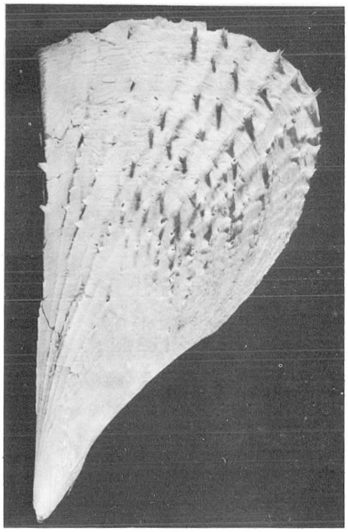


9

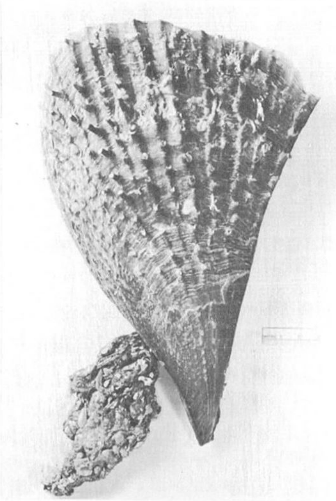
PLATE 11. PTERIA, PINCTADA, PINNA



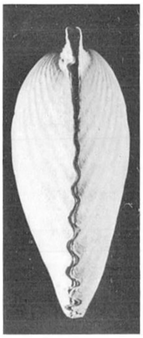
1



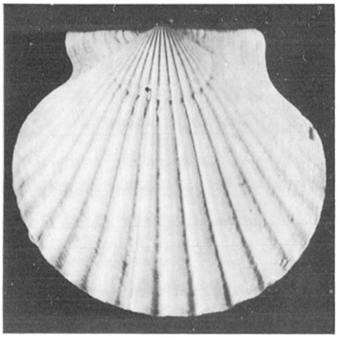
2



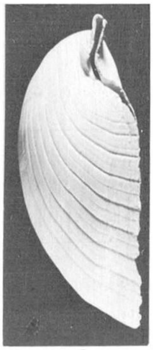
3



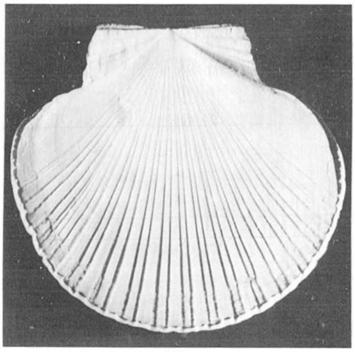
4



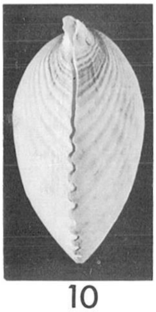
5



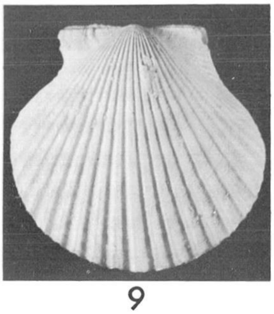
6



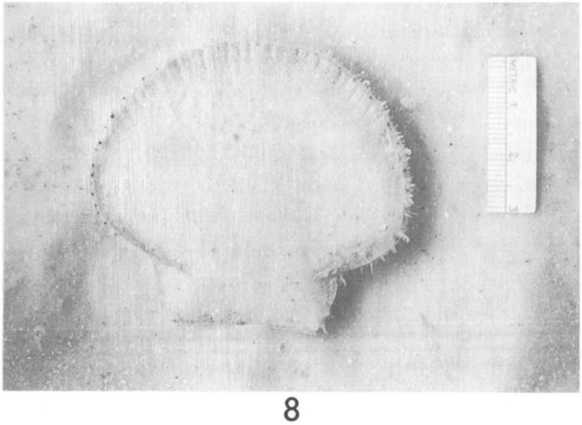
7



10



9



8

PLATE 12. ATRINA, AEQUIPECTEN, PECTEN

ATRINA, AEQUIPECTEN, PECTEN

Figures 1-3. *Atrina rigida* (Solander) (*see* p. 138). Figures 1, 2. Ventral and left lateral views. (X 0.3). Figure 3. Live animal with byssus and attached gravel. (X 0.25). Locality: Rickenbacker Causeway, Biscayne Bay, Florida.

Figures 4, 5. *Aequipecten irradians irradians* (Lamarck) (*see* p. 138). Ventral and left lateral views. (X 0.6). Locality: Squeteague Harbor, Massachusetts.

Figures 6-8. *Pecten ziczac* (Linné) (*see* p. 140). Figures 6, 7. Ventral and left lateral views. (X 0.6). Figure 8. Live animal burying itself by water expulsion. (X 0.7). Locality: Biscayne Bay, Florida.

Figures 9, 10. *Aequipecten gibbus nucleus* (Born) (*see* p. 139). Left lateral and ventral views. (X 1). Locality: Biscayne Bay, Florida.

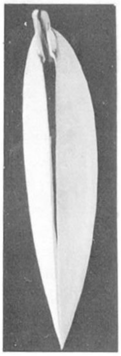
PLACOPECTEN, CHLAMYS, LIMA

Figures 1, 2. *Placopecten magellanicus* (Gmelin) (*see* p. 141). Ventral and left lateral views. (X 0.4). Locality: 20 mi south of Block Island, Rhode Island (MCZ 225821).

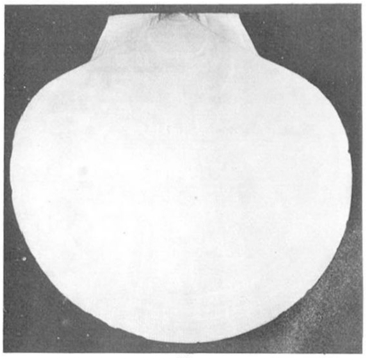
Figures 3, 4. *Chlamys sentis* (Reeve) (*see* p. 142). Ventral and left lateral views. (X 1). Locality: Biscayne Bay, Florida.

Figures 5-8. *Lima scabra* (Born) (*see* p. 142). Figures 5, 6. Ventral and left lateral views. (X 1). Figure 7. Live animal with tentacles extended. (X 0.6). Figure 8. Flared byssal aperture for loose attachment. (X 1.2). Locality: La Parguera, Puerto Rico.

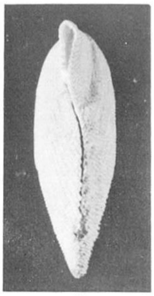
Figures 9-14. *Lima lima* (Linné) (*see* p. 143). Figures 9, 10. Ventral and left lateral views. (X 1.3). Figures 11-14. Animal climbing aquarium wall with byssal threads. (X 1.2). Locality: Norris Cut, Biscayne Bay, Florida.



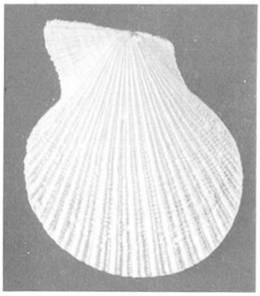
1



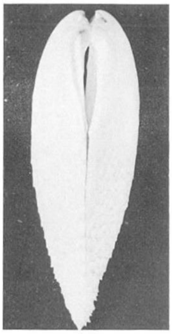
2



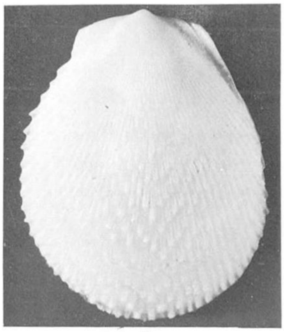
3



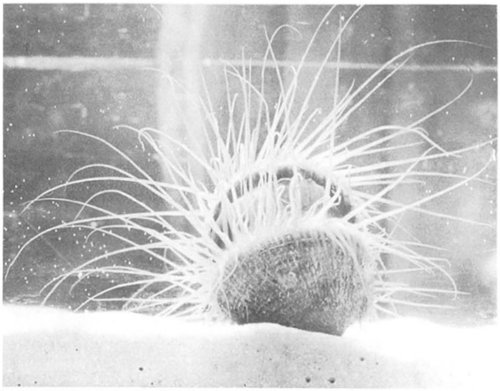
4



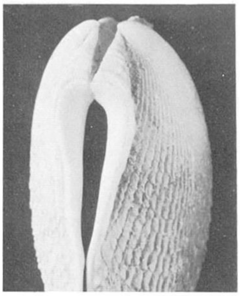
5



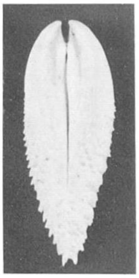
6



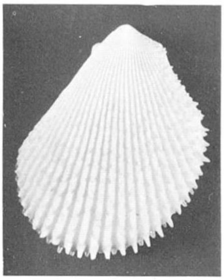
7



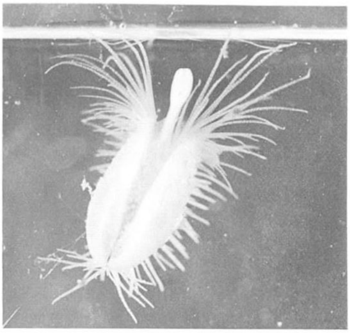
8



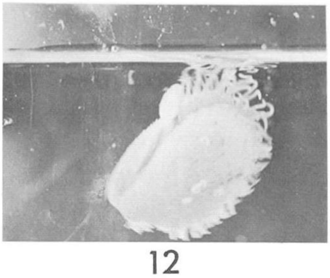
9



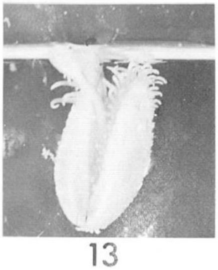
10



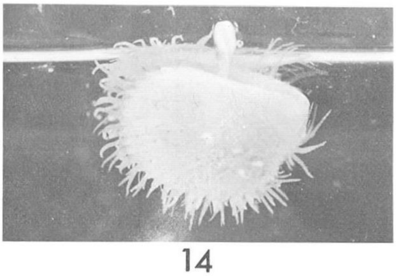
11



12

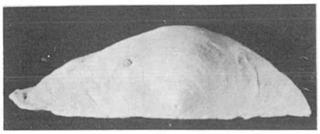


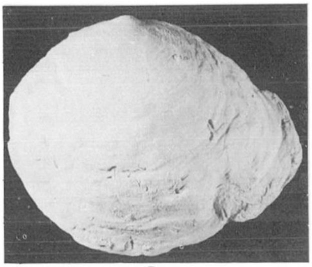
13

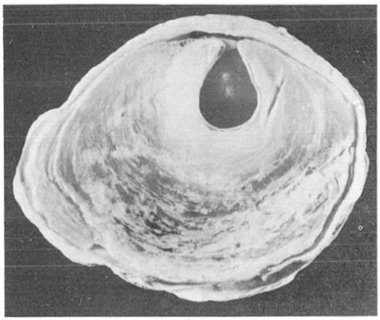


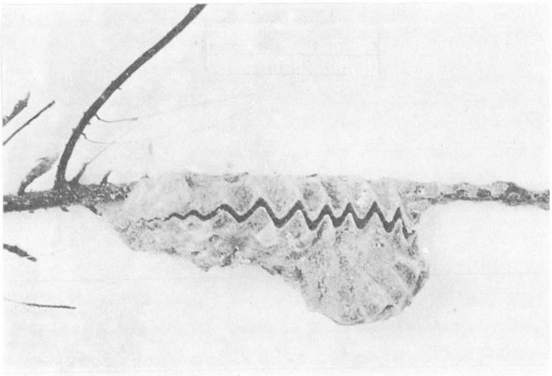
14

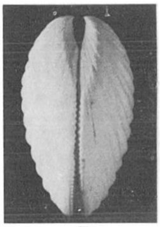
PLATE 13. PLACOPECTEN, CHLAMYS, LIMA

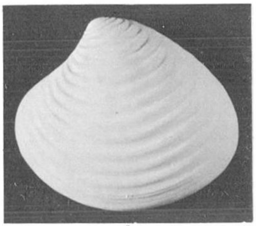

1

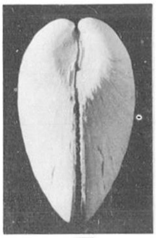

2


3


4

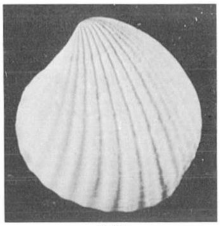

5

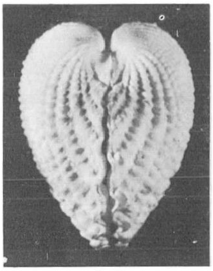

6

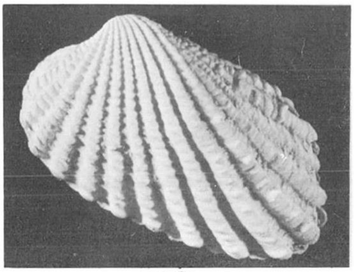

7


8


9


10


11


12

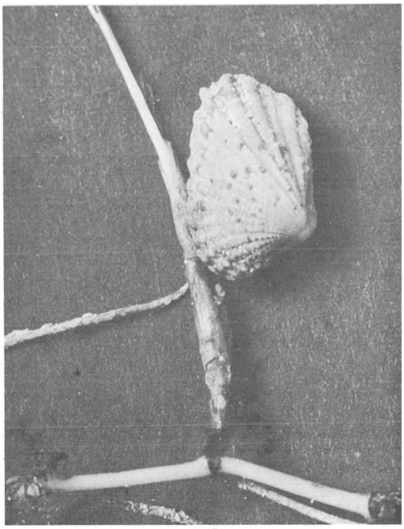

13

PLATE 14. ANOMIA, OSTREA, ASTARTE, VENERICARDIA, CARDITA

ANOMIA, OSTREA, ASTARTE, VENERICARDIA, CARDITA

Figures 1-3. *Anomia simplex* Orbigny (*see* p. 144). Figures 1, 2. Dorsal and left lateral views. (X 0.9). Figure 3. Right lateral view. (X 1). Locality: Barnstable Harbor, Massachusetts.

Figure 4. *Ostrea frons* (Linné). Animal attached to dead alcyonarian branch. (X 0.8). Locality: Boquerón Bay, Puerto Rico.

Figures 5, 6. *Astarte undata* Gould (*see* p. 144). Anterior and left lateral views. (X 1.1). Locality: near Quicks Hole, Buzzards Bay, Massachusetts.

Figures 7, 8. *Astarte castanea* (Say) (*see* p. 145). Anterior and left lateral views. (X 1.2). Locality: near Quicks Hole, Buzzards Bay, Massachusetts.

Figure 9, 10. *Venericardia borealis* (Conrad) (*see* p. 146). Anterior and left lateral views. (X 1). Locality: west of Penikese Island, Buzzards Bay, Massachusetts.

Figures 11-13. *Cardita floridana* Conrad (*see* p. 147). Figures 11, 12. Anterior and left lateral views. (X 2). Figure 13. Live animal attached to buried portion of *Diplanthera* stem. (X 2.1). Localities: Matheson Hammock, Biscayne Bay, Florida (11, 12), Rickenbacker Causeway, Biscayne Bay, Florida (13).

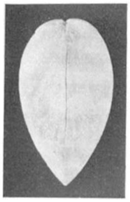
DIPLODONTA, DIVARICELLA, ANODONTIA, PHACOIDES

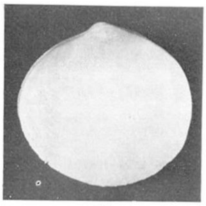
Figures 1-5. *Diplodonta notata* Dall and Simpson (*see* p. 148). Figures 1, 2. Anterior and left lateral views. (X 2.1). Figure 3. Live animal with foot partially extended. (X 2.4). Figures 4, 5. X-radiographs of animals in native sediment (32). Animals lie with anterior dorsal margin undermost and horizontal; anterior mucus tube follows arcuate path to sediment surface. Arrows indicate inhalent currents. (X 1). Locality: Mayaguéz Harbor, Puerto Rico.

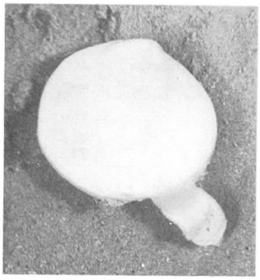
Figures 6, 7. *Divaricella quadrisulcata* (Orbigny) (*see* p. 153). Anterior and left lateral views. (X 2.35). Locality: near Salerno, Florida.

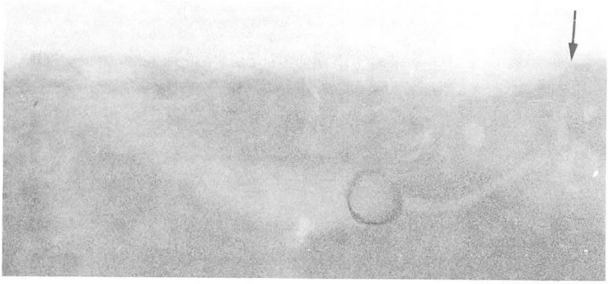
Figures 8, 9. *Anodontia alba* Link (*see* p. 151). Anterior and left lateral views. (X 1). Locality: Rickenbacker Causeway, Biscayne Bay, Florida.

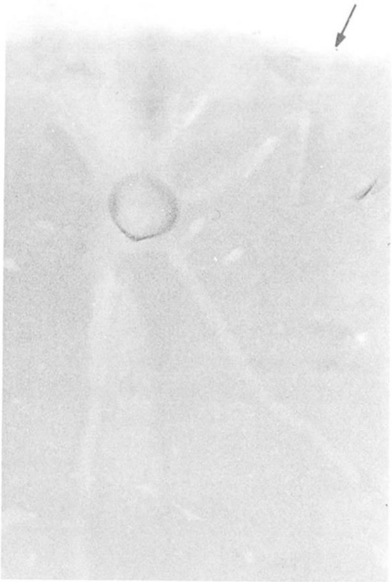
Figures 10-12. *Phacoides muricatus* (Spengler) (*see* p. 150). Figures 10, 11. Anterior and left lateral views. (X 3.4). Figure 12. Live animal with foot partially extended. (X 2.3). Locality: Mayaguéz Harbor, Puerto Rico.

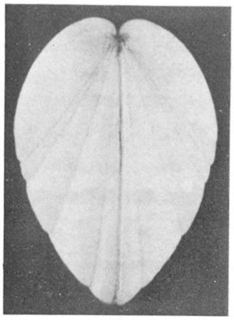

1

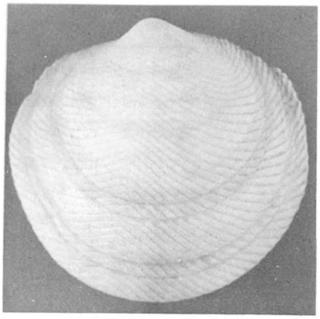

2

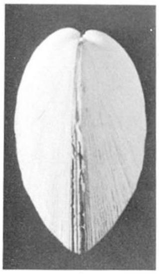

3


4

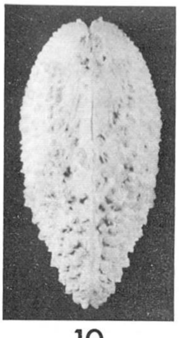

5

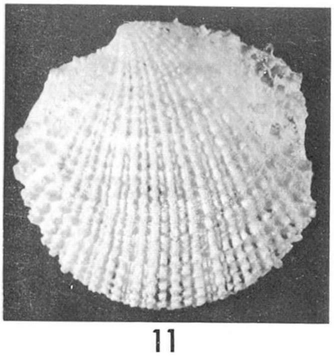

6


7


8


9


10


11

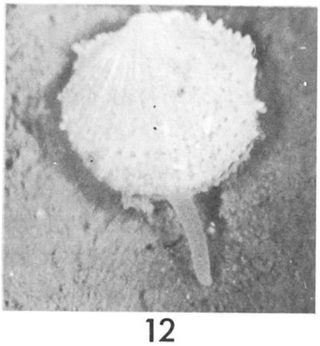

12

PLATE 15. DIPLODONTA, DIVARICELLA, ANODONTIA, PHACOIDES

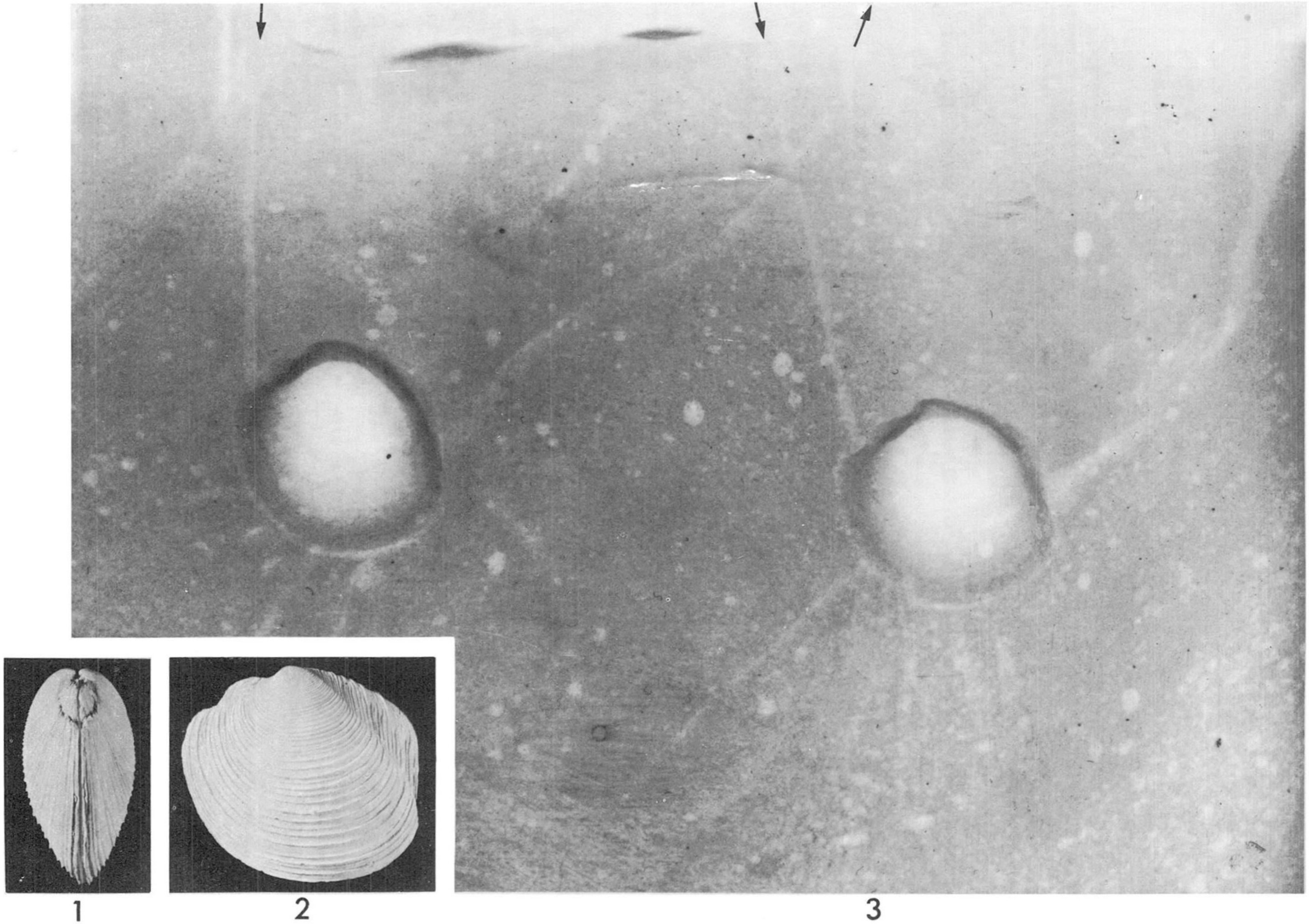
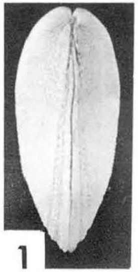


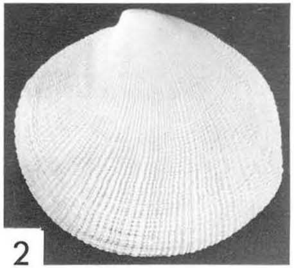
PLATE 16. PHACOIDES

PHACOIDES

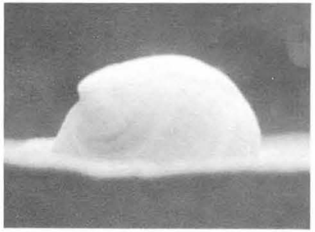
Figures 1-3. *Phacoides pectinatus* (Gmelin) (*see* p. 149). Figures 1, 2. Anterior and left lateral views. (X 0.8). Figure 3. X-radiograph of live animals in life position; depths of burial shallower than in nature. Arrows indicate inhalent and exhalent current appertures. (X 1). Locality: Rickenbacker Causeway, Biscayne Bay, Florida.



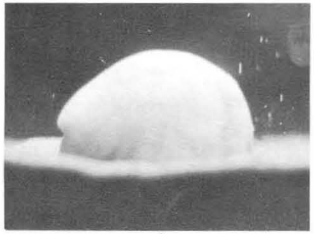
1



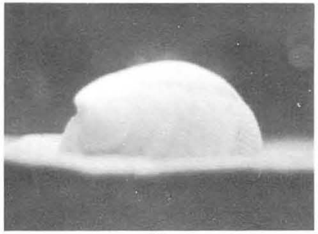
2



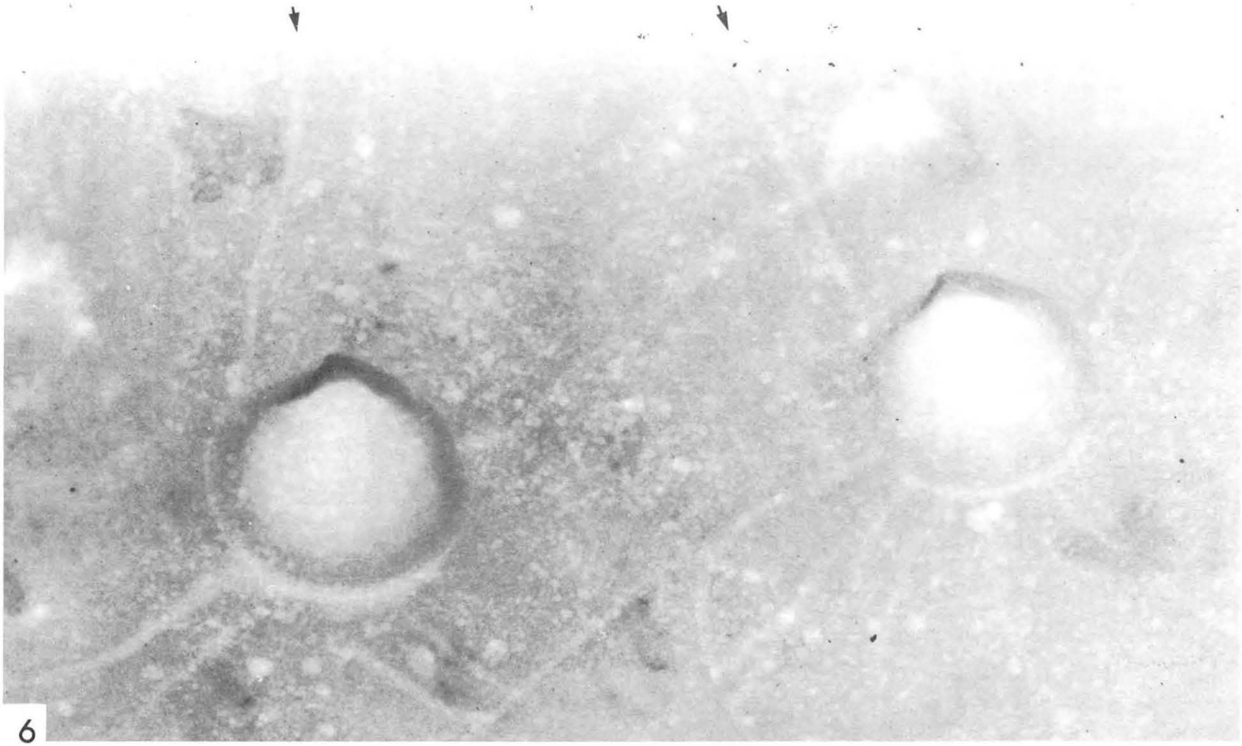
3



4



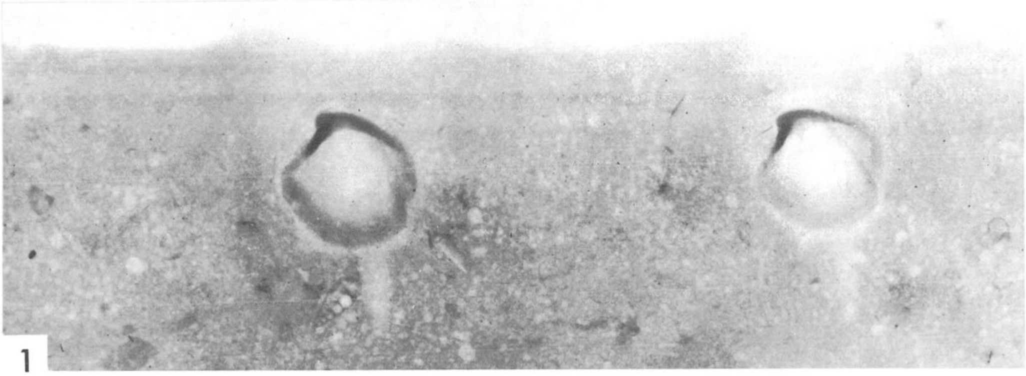
5



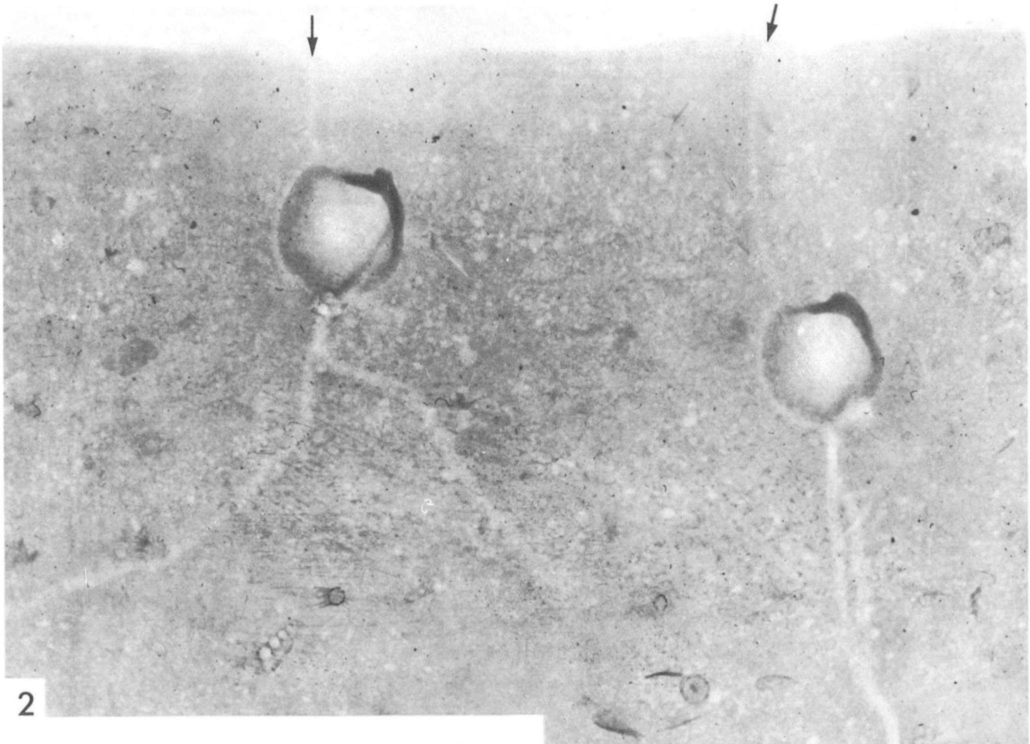
6

CODAKIA

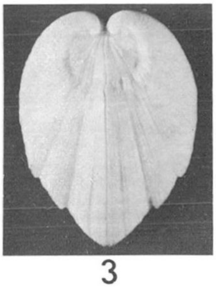
Figures 1-6. *Codakia orbicularis* (Linné) (*see* p. 148). Figures 1, 2. Anterior and left lateral views. (X 1). Figure 3. Erect probing orientation of burrowing animal. (X 0.7). Figure 4. Position following forward rocking movement. (X 0.7). Figure 5. Deeper erect probing orientation following backward rocking movement. (X 0.7). Figure 6. X-radiograph of animals in life position in native sediment (14). Arrows indicate inhalent currents at mucus tube apertures. Pedal probing marks visible below animals. (X 1). Locality: Rickenbacker Causeway, Biscayne Bay, Florida.



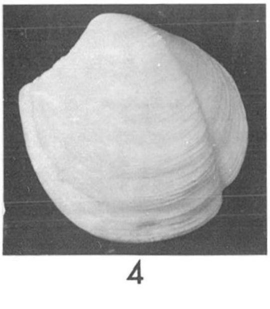
1



2



3



4

PLATE 18. LUCINA

LUCINA

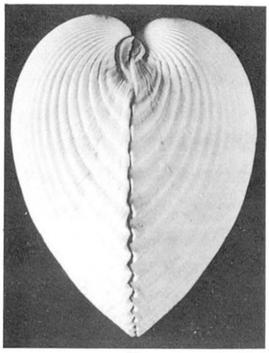
Figures 1-4. *Lucina pensylvanica* (Linné) (*see* p. 152). Figure 1. X-radiograph of animals burrowing vertically downward in native sediment (21). (X 1). Figure 2. X-radiograph of animals of Figure 1 in life position; depths of burial shallower than in nature. Disturbance of aquarium caused animals to retract and re-extend downward-directed posterior siphon before X-ray exposure. Arrows indicate inhalent currents at mucus tube apertures. (X 1). Figures 3, 4. Anterior and left lateral views. (X 1). Locality: Soldier Key, Biscayne Bay, Florida.

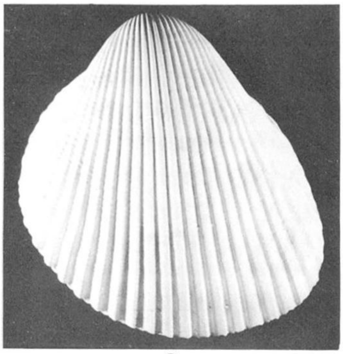
DINOCARDIUM, LAEVICARDIUM

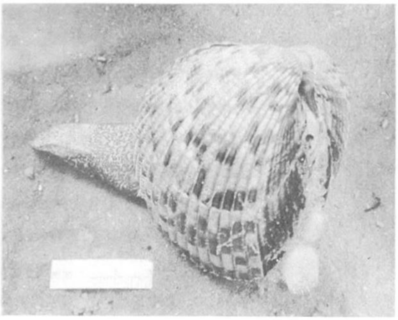
Figures 1-5. *Dinocardium robustum vanhyningi* Clench and L. C. Smith (*see* p. 153). Figures 1, 2. Anterior and left lateral views. (X 0.4). Figure 3. Live animal with siphons and foot partly extended. (X 0.45). Figure 4. Inhalent (left) and exhalent (right) siphon apertures of animal in life position. (X 0.7). Figure 5. Dessicated animal in laboratory emerging from burial with L-shaped foot, which somersaults animal forward. (X 0.3). Locality: Marco Island beach, Florida.

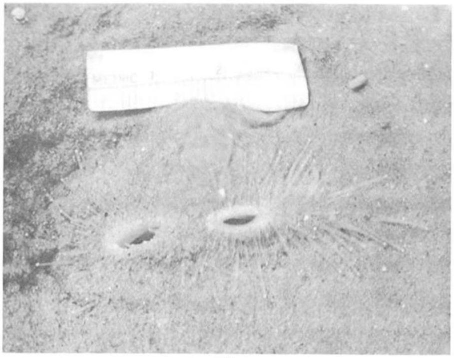
Figures 6-8. *Laevicardium laevigatum* (Linné) (*see* p. 156). Figures 6, 7. Anterior and left lateral views. (X 1). Figure 8. Forward jumping movement. (X 0.8). Locality: Biscayne Bay, Florida.

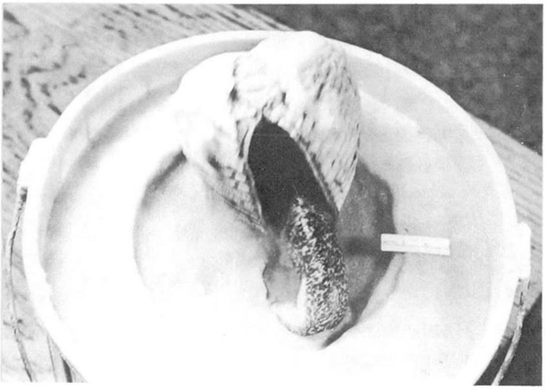
Figures 9-11. *Laevicardium mortoni* (Conrad) (*see* p. 156). Figures 9, 10. Anterior and left lateral views. (X 1.5). Figure 11. Live animals with feet partly extended. (X 1.2). Locality: Quisset Harbor, Massachusetts.

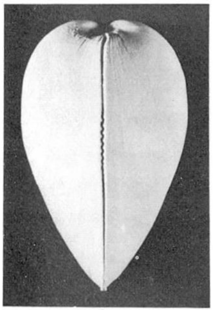

1

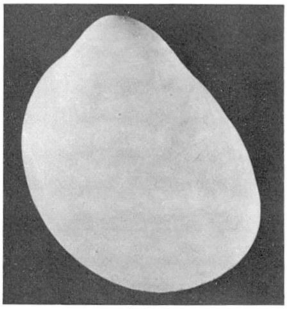

2

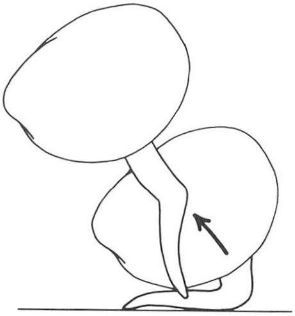

3

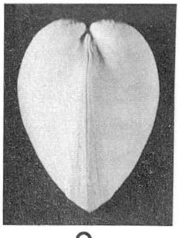

4

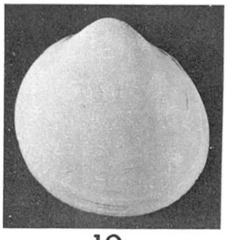

5


6


7


8


9


10

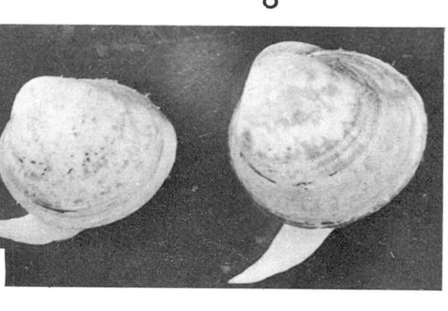
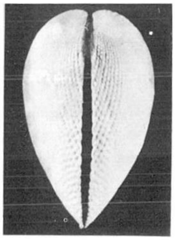
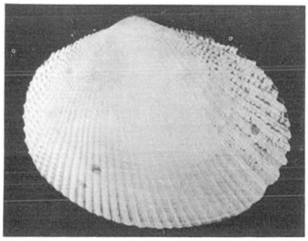
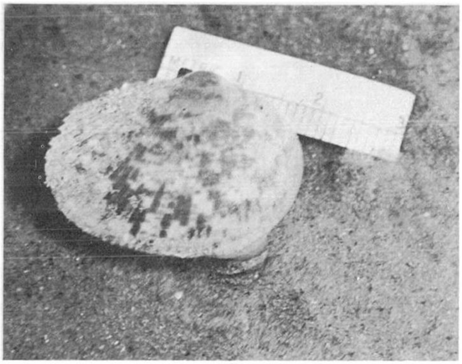

11

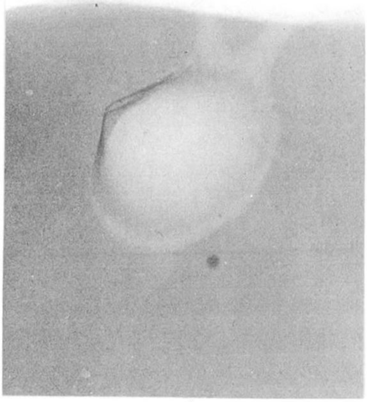
PLATE 19. DINOCARDIUM, LAEVICARDIUM

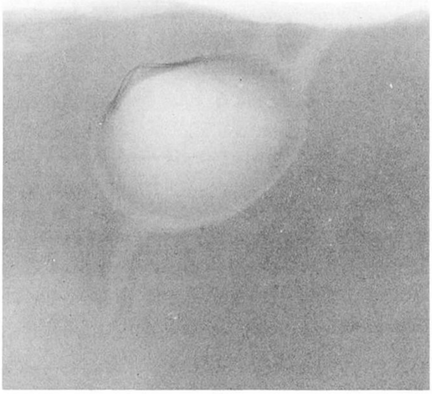

1

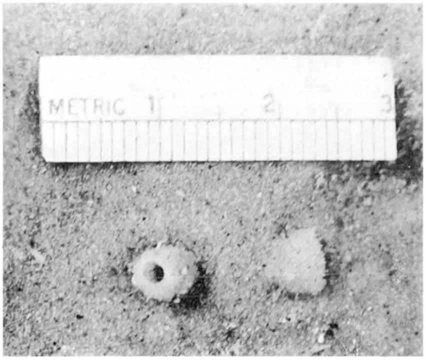

2



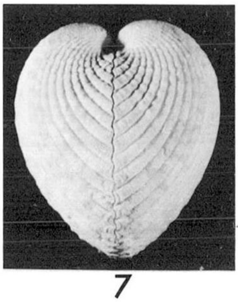
3


4


5



6


7

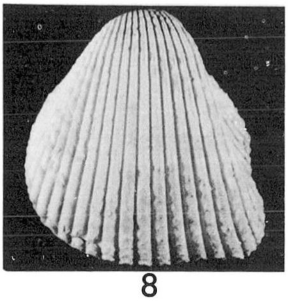

8

PLATE 20. PAPYRIDEA, AMERICARDIA

PAPYRIDEA, AMERICARDIA

Figures 1-6. *Papyridea soleniformis* (Bruguière) (*see* p. 157). Figures 1, 2. Anterior and left lateral views. (X 1.4). Figure 3. Reclining animal probing with foot. (X 1.1). Figures 4, 5. X-radiograph of animals in life position in sediment 1. (X 1). Figure 6. Siphons of animal in life position. Inhalent siphon (right) bends at sediment surface to lie nearly horizontal. Localities: Cayo Santiago, Puerto Rico (1, 2, 4); off Media Luna Reef, La Parguera, Puerto Rico (3, 5, 6).

Figures 7, 8. *Americardia media* (Linné). Anterior and left lateral views. (X 1.4). Locality: off Media Luna Reef, La Parguera, Puerto Rico.

TRACHYCARDIUM, MERCENARIA, ANOMALOCARDIA, ANTIGONA

Figures 1, 2. *Trachycardium muricatum* (Linné) (*see* p. 155). Anterior and left lateral views. (X 1.2). Locality: south of Cape Florida, Biscayne Bay, Florida.

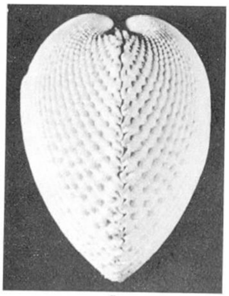
Figures 3-5. *Trachycardium egmontianum* (Shuttleworth) (*see* p. 155). Figures 3, 4. Anterior and left lateral views. (X 1.1). Figure 5. L-shaped foot. (X 0.8). Locality: Bear Cut, Biscayne Bay, Florida.

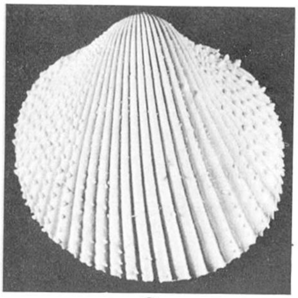
Figures 6, 7. *Mercenaria mercenaria* (Linné) (*see* p. 159). Anterior and left lateral views. (X 0.4). Locality: Barnstable Harbor, Massachusetts.

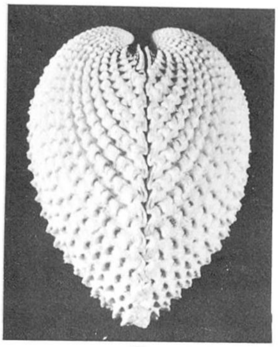
Figures 8, 9. *Anomalocardia cuneimeris* (Conrad) (*see* p. 163). Anterior and left lateral views. (X 1.9). Locality: Marco Island, Florida.

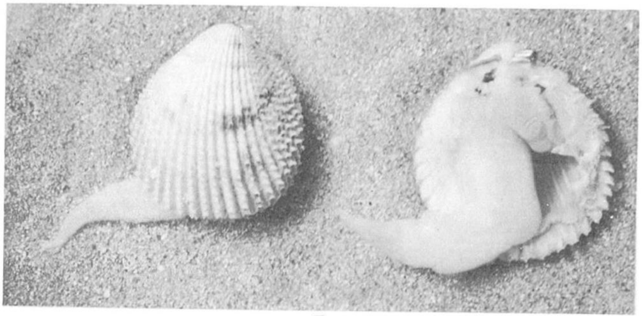
Figures 10, 11. *Anomalocardia brasiliana* (Gmelin) (*see* p. 163). Left lateral and anterior views. (X 1.2). Locality: La Parguera, Puerto Rico.

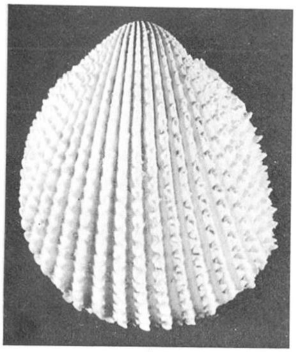
Figures 12, 13. *Antigona listeri* (Gray) (*see* p. 160). Left lateral and anterior views. (X 0.8). Locality: Bear Cut, Biscayne Bay, Florida.

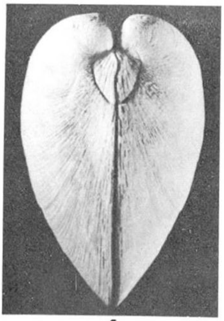

1

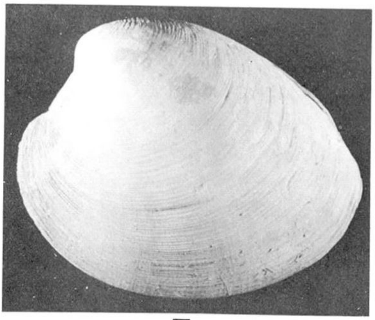

2

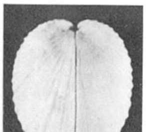

3

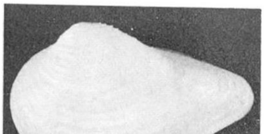

5

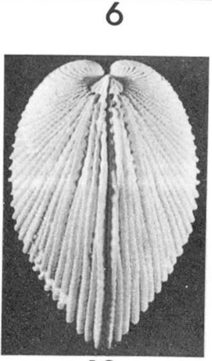

4


6

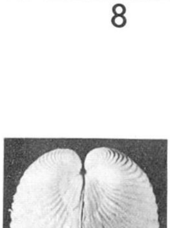

7


8


9


13


12


11

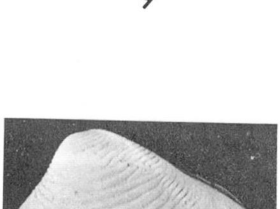
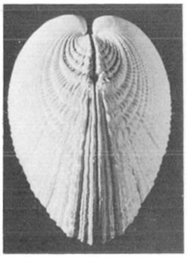
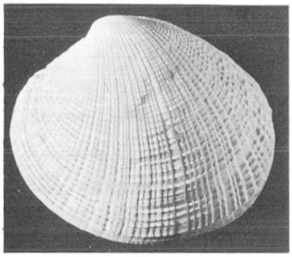

10

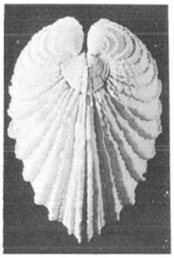
PLATE 21.
TRACHYCARDIUM, MERCENARIA, ANOMALOCARDIA, ANTIGONA



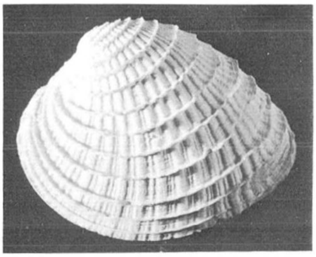
1



2

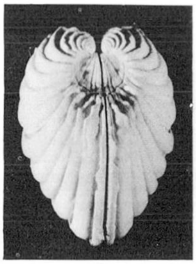


3

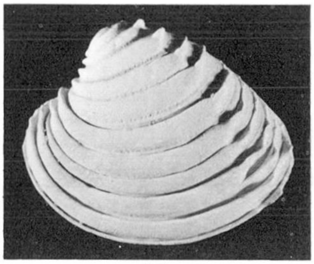


4

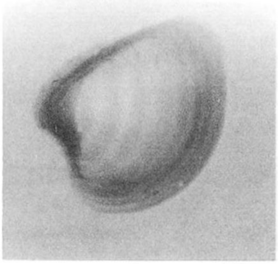
5



6



7



8

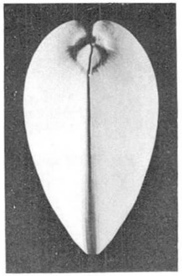
PLATE 22. CHIONE

CHIONE

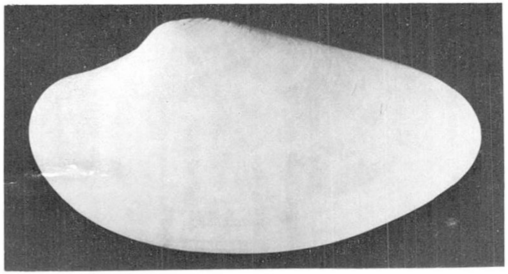
Figures 1, 2. *Chione granulata* (Gmelin) (*see* p. 161). Anterior and left lateral views. (X 1.2). Locality: Salinas El Papaya, La Parguera, Puerto Rico.

Figures 3-5. *Chione cancellata* (Linné) (*see* p. 161). Figures 3, 4. Anterior and left lateral views. (X 1.2). Figure 5. Animals in the laboratory, crawling forward to produce sinuous trails in the act of burrowing. (Scale 3 cm long). Locality: Bear Cut, Biscayne Bay, Florida.

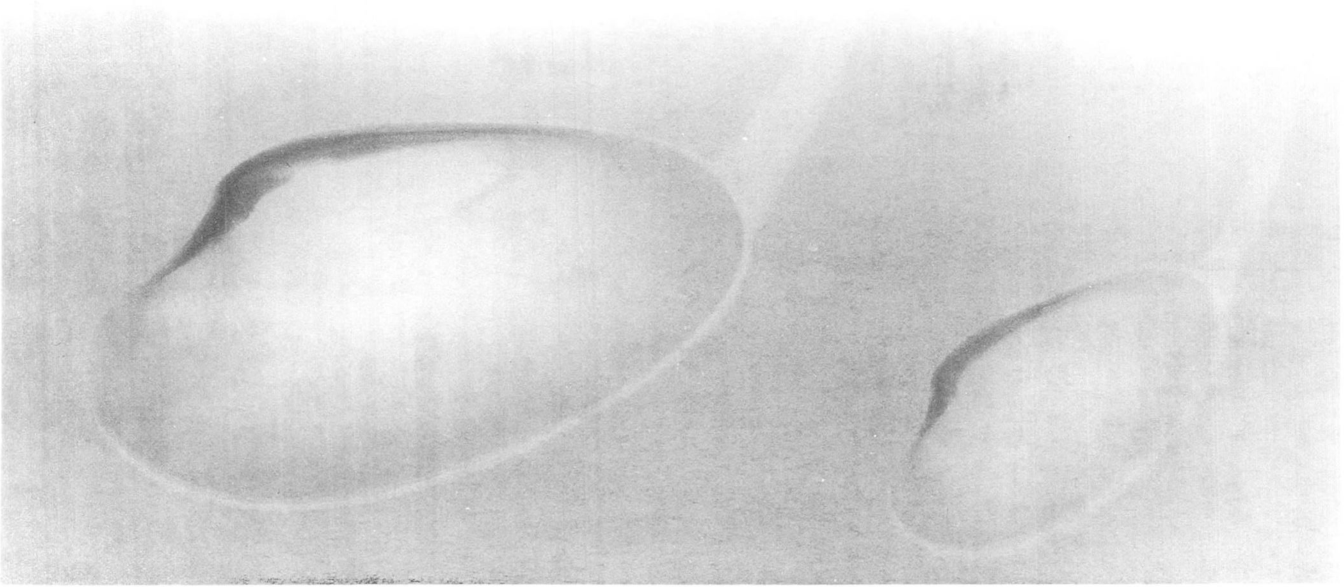
Figures 6-8. *Chione paphia* (Linné) (*see* p. 162). Figures 6, 7. Anterior and left lateral views. (X 1). Figure 8. X-radiograph of animal in life position in sediment 1. (X 1). Localities: Key West, Florida—MCZ 162177 (6, 7); off Media Luna Reef, La Parguera, Puerto Rico (8).



1



2



3

PLATE 23. MACROCALLISTA

MACROCALLISTA

Figures 1-3. *Macrocallista nimbosa* (Solander) (*see* p. 164). Figures 1, 2. Anterior and left lateral views. (X 0.5). Figure 3. X-radiograph of large and small animal in life position in sediment no. 19. (X 1). Locality: Tampa Bay, Florida.

MACROCALLISTA, TIVELA

Figures 1-6. *Macrocallista nimbosa* (Solander) (*see* p. 164). Burrowing, from shell erection to shell burial. (X 0.45). Locality: Tampa Bay, Florida.

Figures 7-10. *Tivela mactroides* (Born) (*see* p. 167). Figures 7, 8. Anterior and left lateral views. (X 0.8). Figure 9. Live animal with siphons and foot partly extended. (X 0.9). Figure 10. X-radiograph of animal in life position in native sediment (31). (X 1). Locality: Mani Beach, Puerto Rico.


1

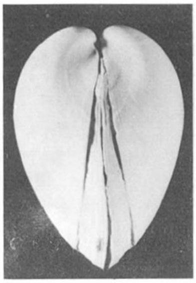

2

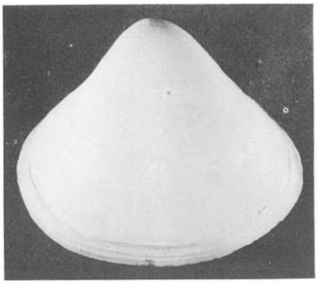

3

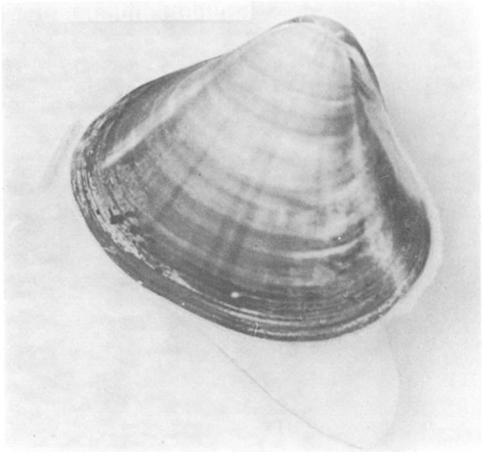

4


5


6

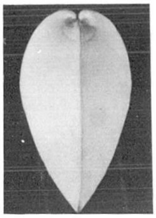

7

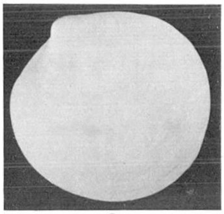

8

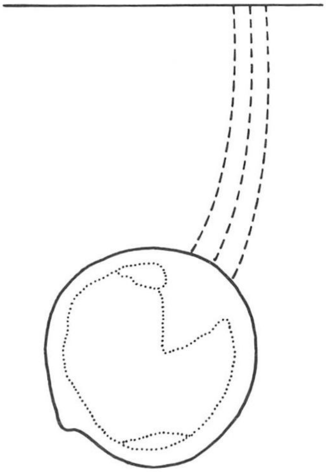

9

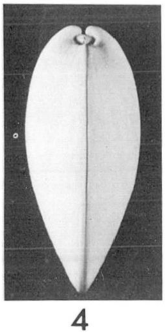

10

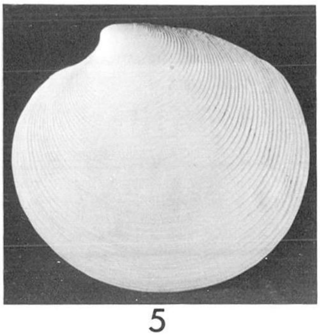
PLATE 24. MACROCALLISTA, TIVELA


1


2


3


4


5

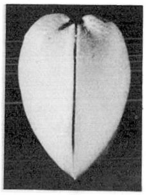

6

PLATE 25. CYCLINELLA, DOSINIA

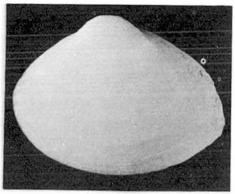
CYCLINELLA, DOSINIA

Figures 1-3. *Cyclinella tenuis* (Récluz) (*see* p. 166). Figures 1, 2. Anterior and left lateral views. (X 0.8). Figure 3. Drawing of life position and siphon orientation. (X 1). Locality: Biscayne Bay, Florida.

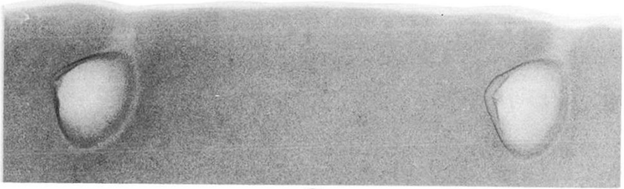
Figures 4-6. *Dosinia elegans* (Conrad) (*see* p. 165). Figures 4, 5. Anterior and left lateral views. (X 0.8). Figure 6. X-radiograph of animal in life position in native sediment (27). (X 1). Locality: Sarasota, Florida.



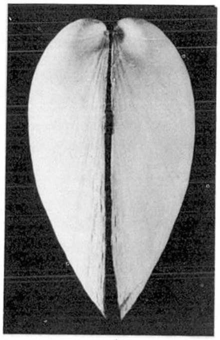
1



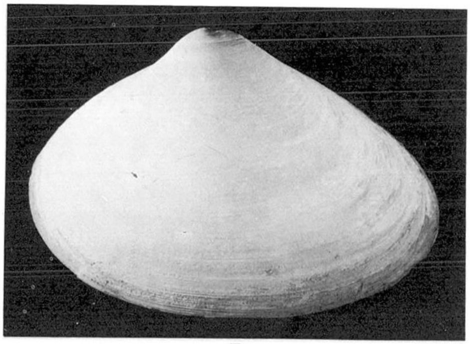
2



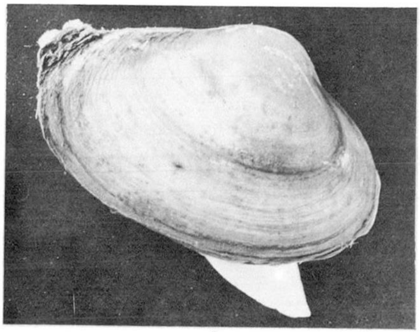
3



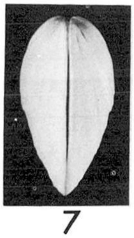
4



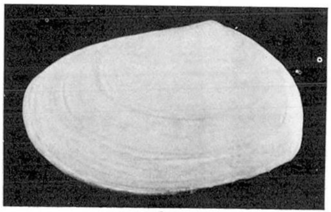
5



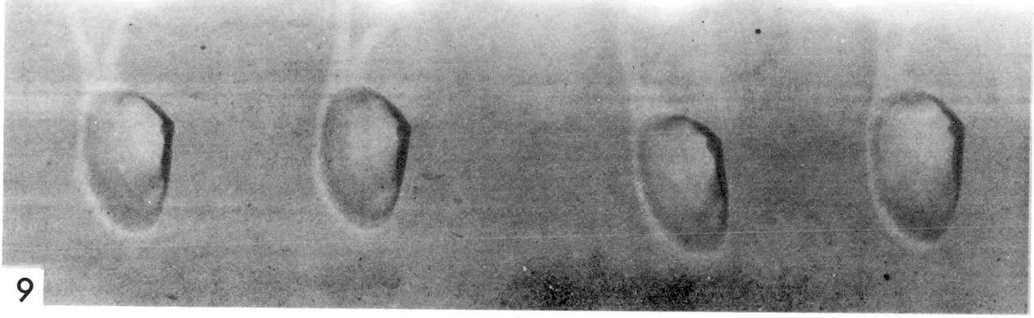
6



7



8



9

PLATE 26. MULINIA, SPISULA, MESODESMA

MULINIA, SPISULA, MESODESMA

Figures 1-3. *Mulinia lateralis* (Say) (*see* p. 170). Figures 1, 2. Anterior and left lateral views. (X 1.9). Figure 3. X-radiograph of animals in life position in sediment 1. (X 1). Locality: New Haven Harbor, Connecticut.

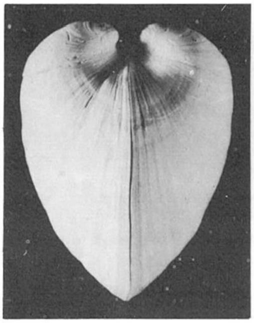
Figures 4-6. *Spisula solidissima* (Dillwyn) (*see* p. 168). Figures 4, 5. Anterior and left lateral views. (X 0.4). Figure 6. Live animal with foot partly extended. (X 0.5). Locality: Menemsha Bight, Martha's Vineyard, Massachusetts.

Figures 7-9. *Mesodesma arctatum* (Conrad) (*see* p. 167). Figures 7-8. Anterior and left lateral views. (X 1.4). Figure 9. X-radiograph of animals in life position in sediment no. 1. (X 1). Locality: Plum Island, Massachusetts.

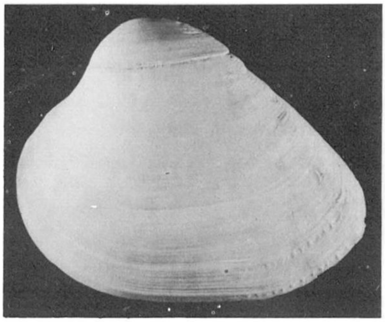
RANGIA, MACTRA

Figures 1, 2. *Rangia cuneata* Gray (*see* p. 169). Anterior and left lateral views. (X 0.7). Locality: Upper Cedar Point, Maryland.

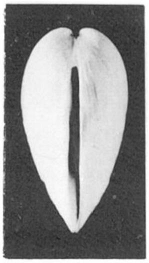
Figures 3-6. *Mactra fragilis* Gmelin (*see* p. 170). Figures 3, 4. Anterior and left lateral views. (X 1). Figure 5. Live animal with siphons partly extended. (X 1.1). Figure 6. X-radiograph of animals in life position in sediment no. 19. (X 1). Locality: south of Cape Florida, Biscayne Bay, Florida.



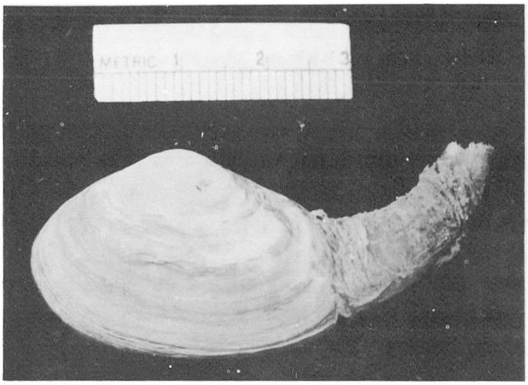
1



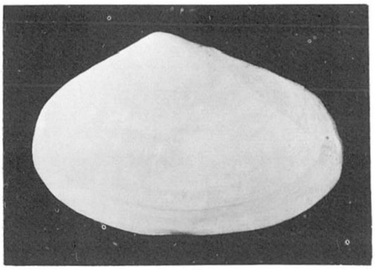
2



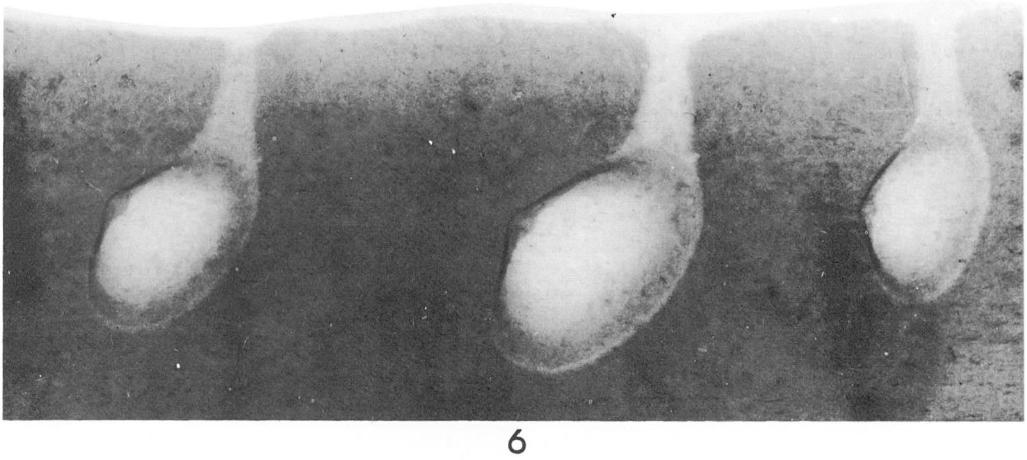
3



5



4



6

PLATE 27. RANGIA, MACTRA

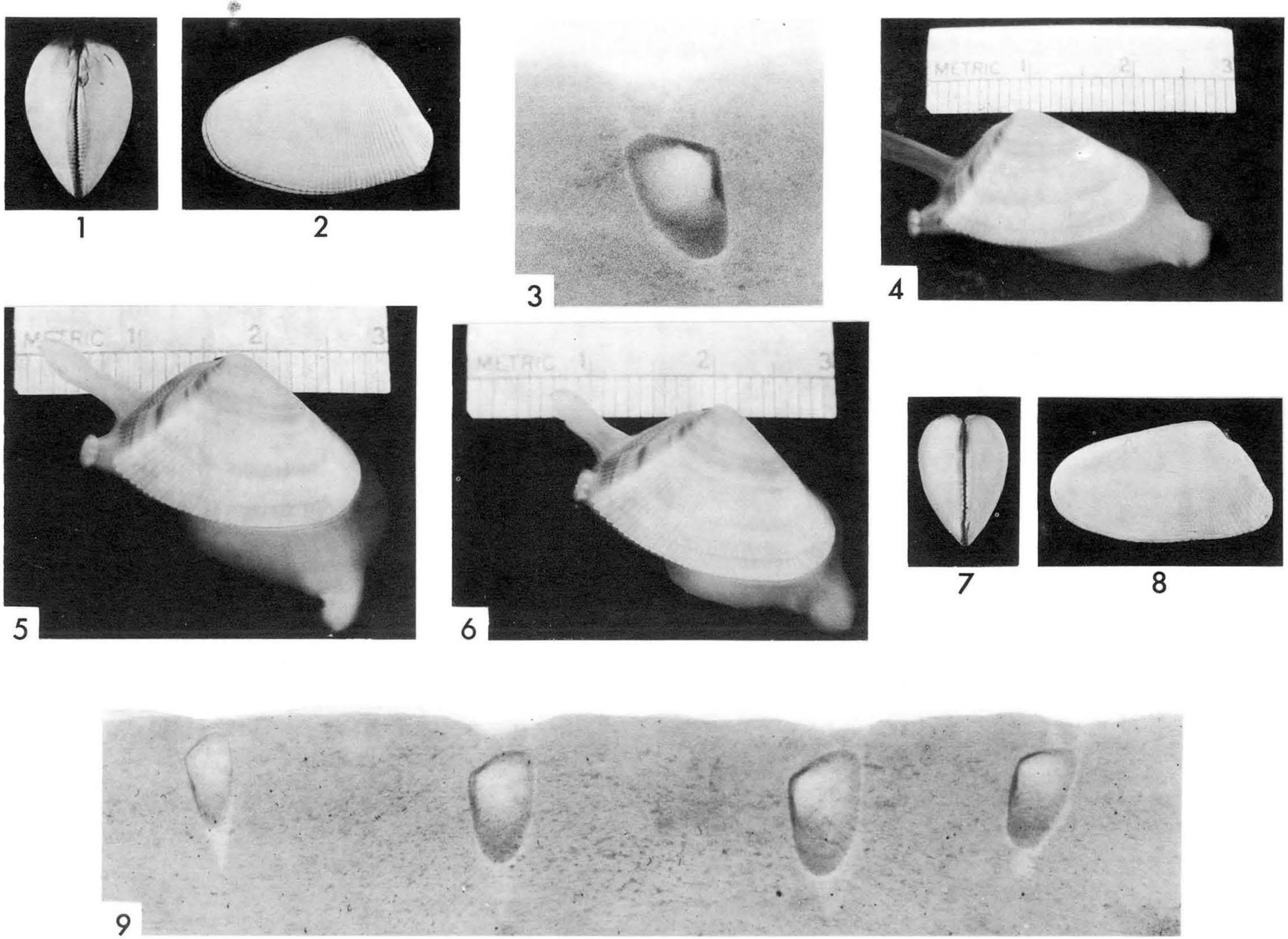


PLATE 28. DONAX

DONAX

Figures 1-6. *Donax denticulatus* Linné (*see* p. 171). Figures 1, 2. Anterior and left lateral views. (X 1.5). Figure 3. X-radiograph of animal in life position in native sediment (36). (X 1). Figures 4-6. Live animals with siphons and foot partly extended (scale 3 cm long). Locality: Mani Beach, Puerto Rico.

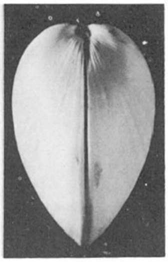
Figures 7-9. *Donax variabilis* Say (*sec* p. 172). Figures 7, 8. Anterior and left lateral views. (X 1.8). Figure 9. X-radiograph of animals in life position in native sediment (19). (X 1). Locality: Marco Island beach, Florida.

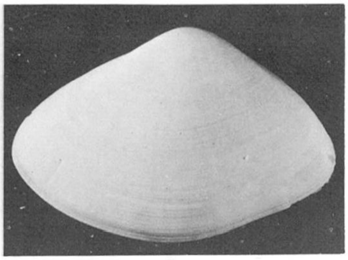
IPHIGENIA, ASAPHIS, TAGELUS

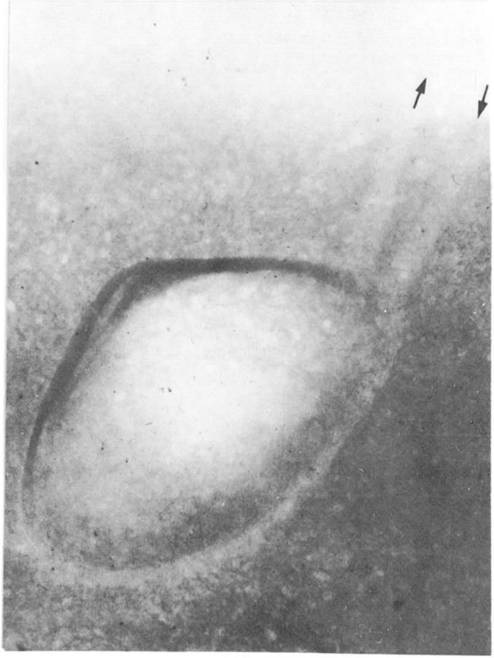
Figures 1-4. *Iphigenia brasiliensis* (Lamarck) (*see* p. 172). Figures 1, 2. Anterior and left lateral views. (X 1). Figure 3. X-radiograph of animal in life position in native sediment (17). (X 1). Figure 4. Thick siphons emerging at sediment surface (scale 3 cm long). Locality: Norris Cut, Biscayne Bay, Florida.

Figures 5, 6. *Asaphis deflorata* (Linné) (*see* p. 175). Anterior and left lateral views. (X 0.9). Locality: Bear Cut, Biscayne Bay, Florida.

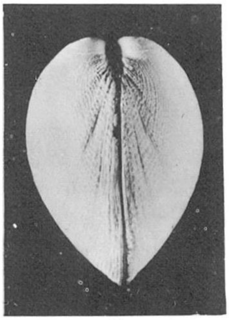
Figures 7, 8. *Tagelus divisus* (Spengler) (*see* p. 174). Anterior and left lateral views. (X 1.7). Locality: Norris Cut, Biscayne Bay, Florida.

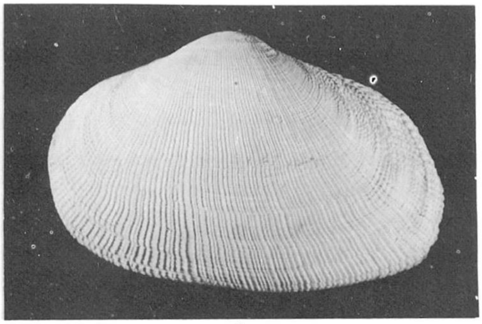

1

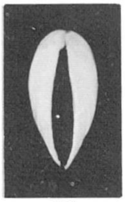

2


3

4


5


6


7

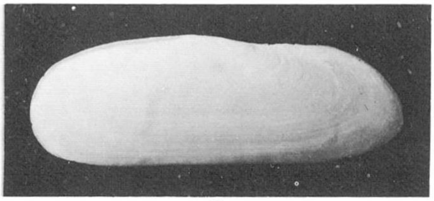
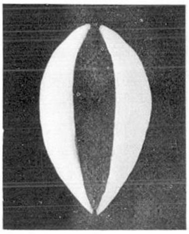
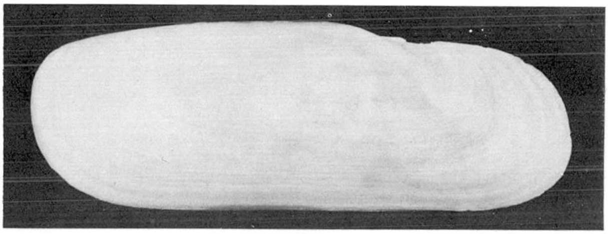

8

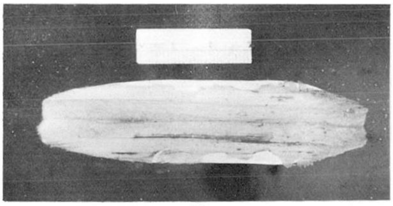
PLATE 29. IPHIGENIA, ASAPHIS, TAGELUS



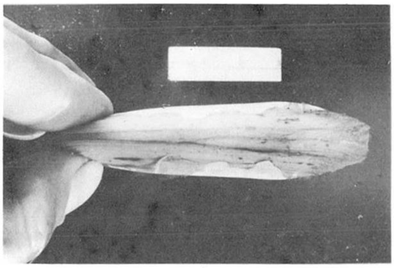
1



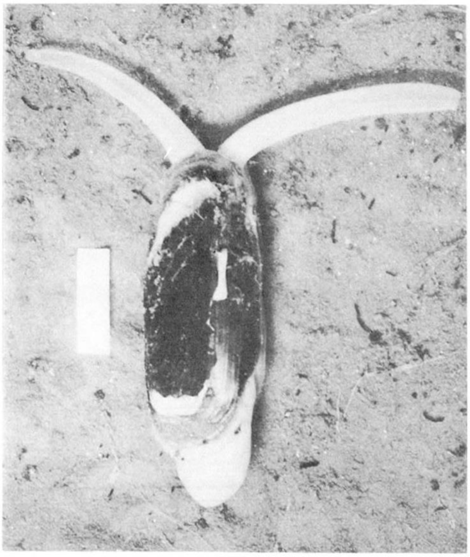
2



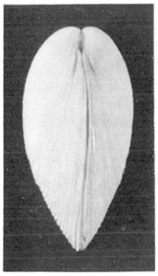
3



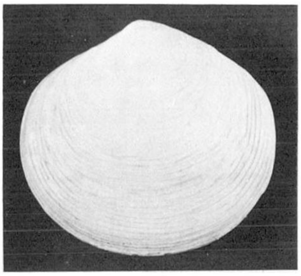
4



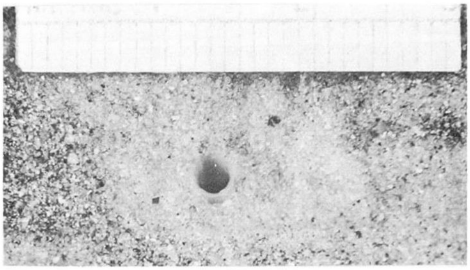
5



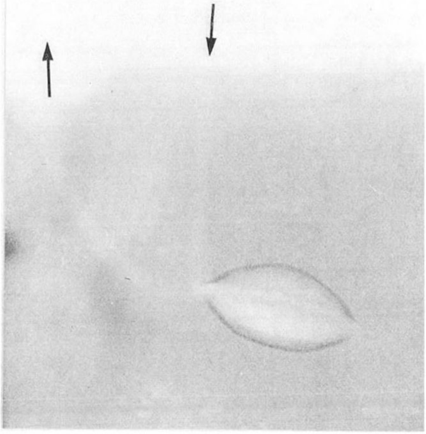
6



7



8



9

PLATE 30. TAGELUS, SEMELE

TAGELUS, SEMELE

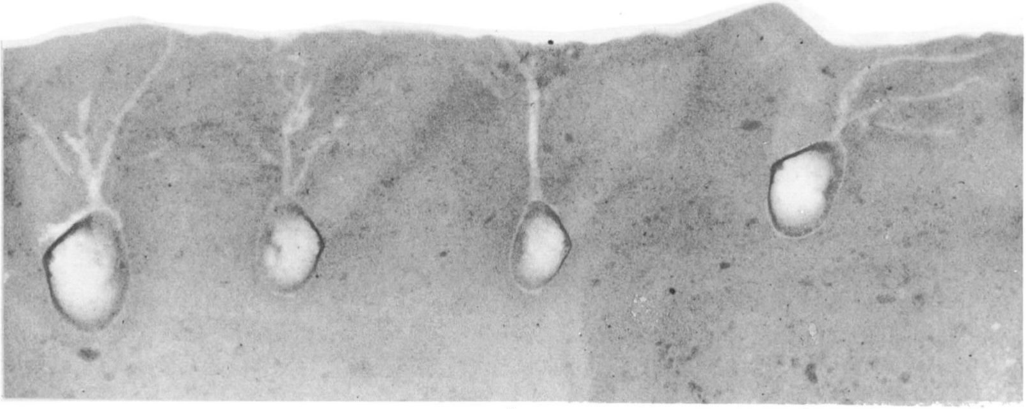
Figures 1-5. *Tagelus plebeius* (Solander) (*see* p. 173). Figures 1, 2. Anterior and left lateral views. (X 0.8). Figures 3, 4. Rocking movement of valves about a dorso-ventral axis. (X 0.5). Figure 5. Live animal with foot and siphons partly extended. (X 0.5). Locality: Bass River Mouth, Cape Cod, Massachusetts.

Figures 6-9. *Semele proficua* (Pulteney) (*see* p. 176). Figures 6, 7. Anterior and left lateral views. (X 1.2). Figure 8. Inhalent siphon aperture. (X 2). Figure 9. X-radiograph of animal in life position; arrows indicate water currents. (X 1). Locality: Guánica, Puerto Rico.

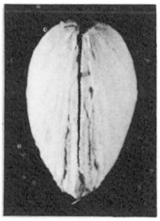
CUMINGIA, TELLINA

Figures 1-3. *Cumingia tellinoides* Conrad (*see* p. 177). Figure 1. X-radiograph of animals in life position in sediment no. 1; movement of siphons indicated by numerous channels in the sediment. (X 1). Figures 2, 3. Anterior and left lateral views. (X 2.1). Locality: Quisset Harbor, Massachusetts.

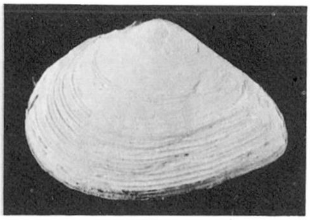
Figures 4-7. *Tellina tampaensis* Conrad (*see* p. 178). Figures 4-6. Anterior, left lateral, and ventral views. (X 1.9). Figure 7. X-radiograph of burrowing animal in life position in native sediment (28); successive feeding positions marked by channels formed by inhalent and exhalent siphons. Arrows show water currents. (X 1). Locality: Marco Island, Florida.



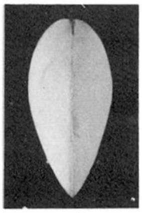
1



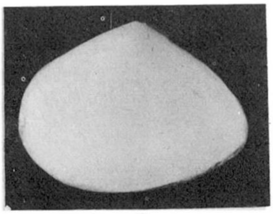
2



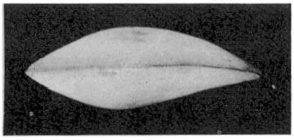
3



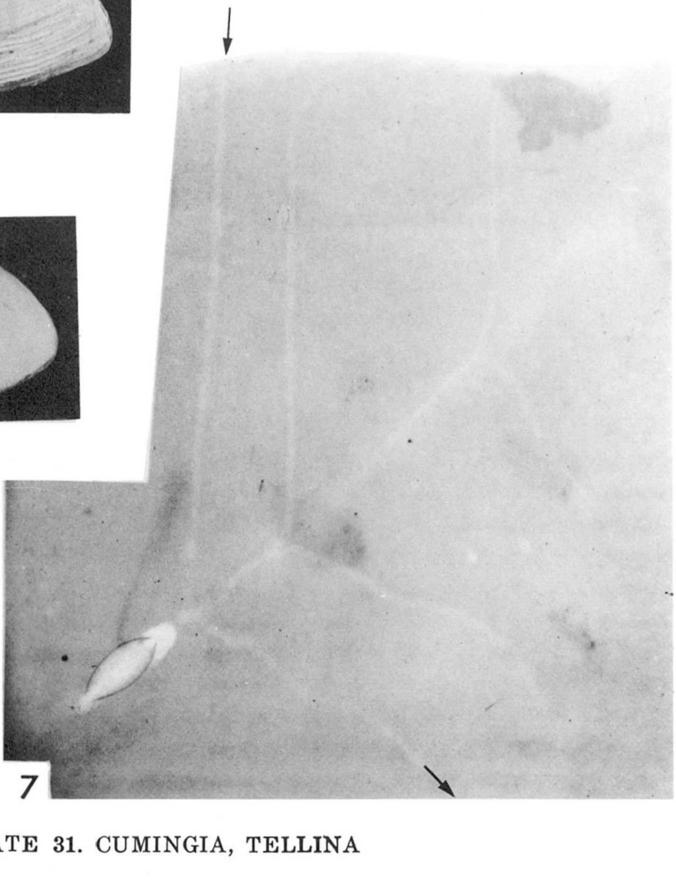
4



5

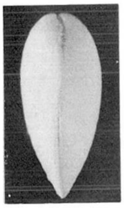


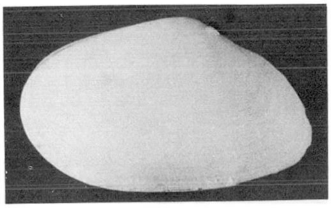
6

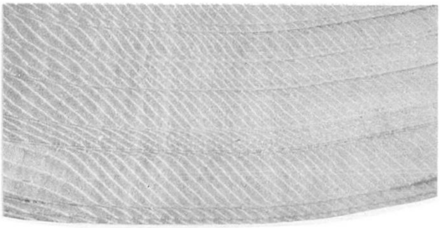


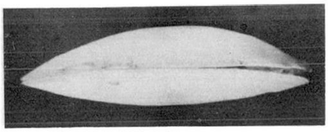
7

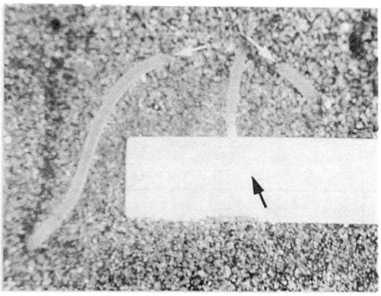
PLATE 31. CUMINGIA, TELLINA

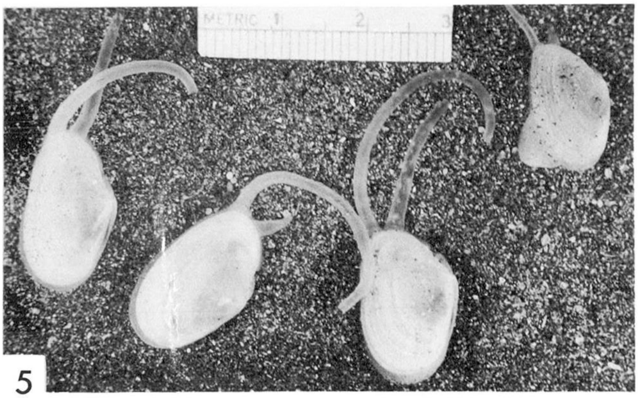

1


2

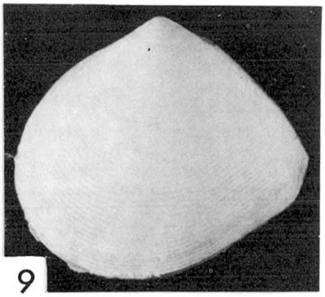

4

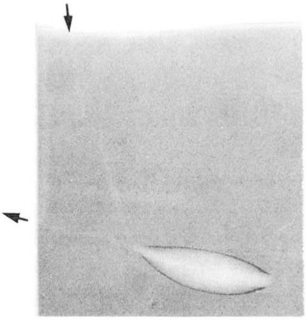

3

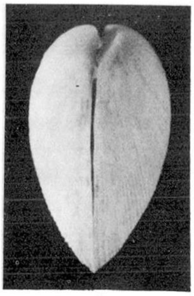

6

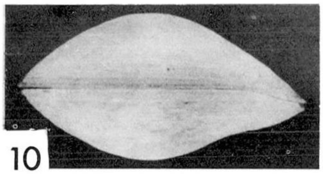


5

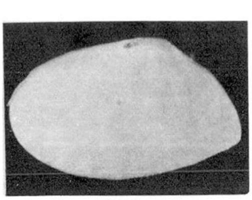

9

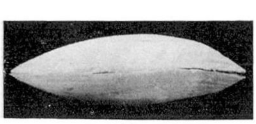

7


8


10


11


12


13

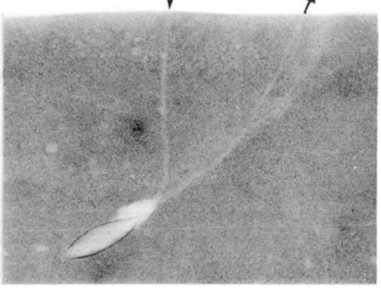

14

PLATE 32. TELLINA

TELLINA

Figures 1-7. *Tellina similis* Sowerby (*see* p. 179). Figures 1-3. Anterior, left lateral, and ventral views. (X 2). Figure 4. Ornamentation (mid-ventral region of left valve); lighting from right. (X 7). Figure 5. Live animals showing partly extended siphons and foot (scale 3 cm long). Figure 6. Siphons of buried animals in the act of deposit feeding (scale 3 cm long). Figure 7. X-radiograph of animal in life position in sediment no. 19. Arrows indicate water currents. (X 1). Locality: behind Cayo Caracoles, La Parguera, Puerto Rico.

Figures 8-10. *Tellina martinicensis* Orbigny (*see* p. 182). Anterior, left lateral, and ventral views. (X 3). Locality: Biscayne Bay, Florida.

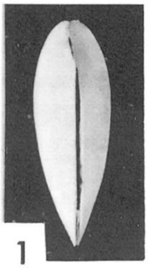
Figures 11-14. *Tellina agilis* Stimpson (*see* p. 180). Figures 11-13. Anterior, left lateral, and ventral views. (X 2.6). Figure 14. X-radiograph of animal in life position in sediment no. 1. Arrows indicate water currents. (X 1). Locality: Bass River, Cape Cod, Massachusetts.

TELLINA, ARCOPAGIA

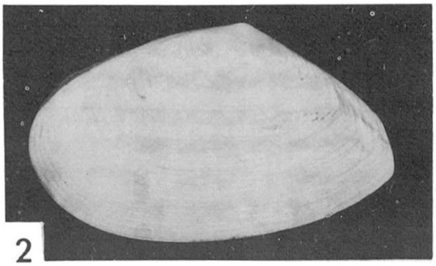
Figures 1-4. *Tellina alternata* Say (*see* p. 180). Figures 1-3. Anterior, left lateral, and ventral views. (X 1.7). Figure 4. X-radiograph of animal in life position in sediment no. 1. Arrows indicate inhalent and exhalent currents. (X 1). Locality: Boquerón Bay, Puerto Rico.

Figures 5-7. *Arcopagia fausta* (Pulteney) (*see* p. 183). Anterior, left lateral, and ventral views. (X 0.6). Locality: Rickenbacker Causeway, Biscayne Bay, Florida.

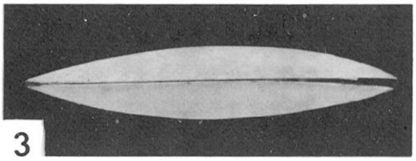
Figures 8-11. *Tellina listeri* Röding (*see* p. 181). Figures 8-10. Anterior, left lateral, and ventral views. (X 0.9). Figure 11. X-radiograph of animal in life position in sediment no. 19. Arrows indicate water currents. (X 1). Locality: southwest of Rodriguez Key, Florida.



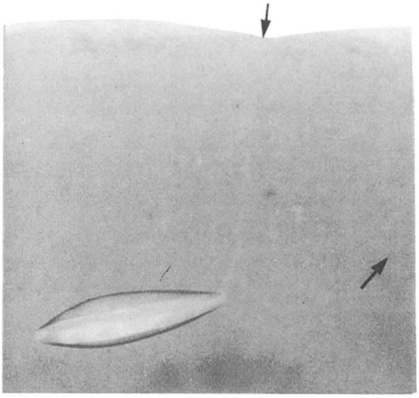
1



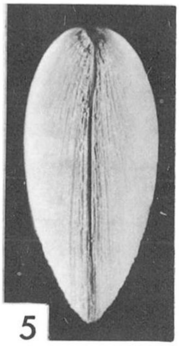
2



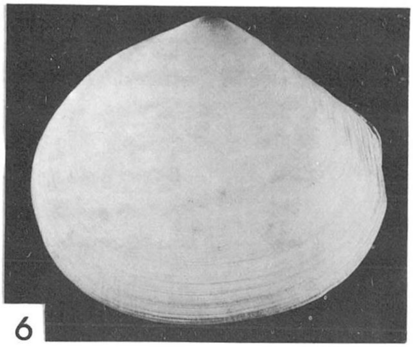
3



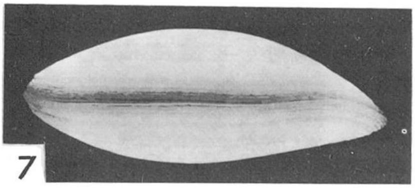
4



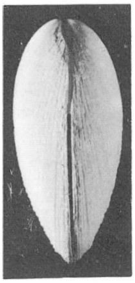
5



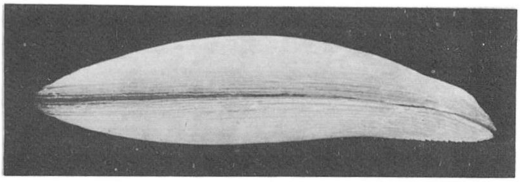
6



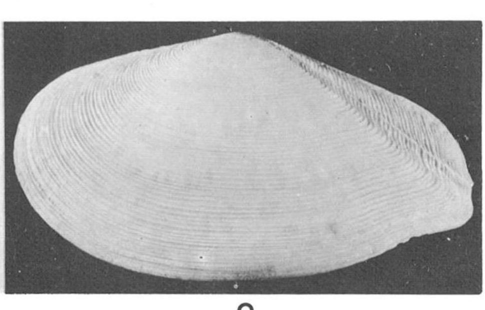
7



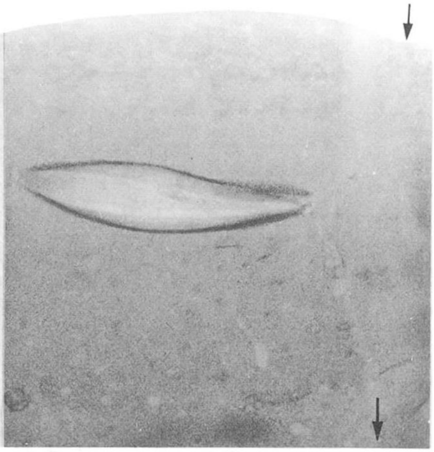
8



10

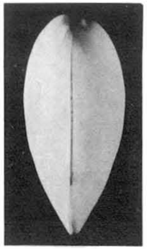


9

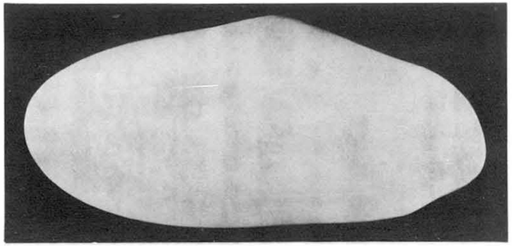


11

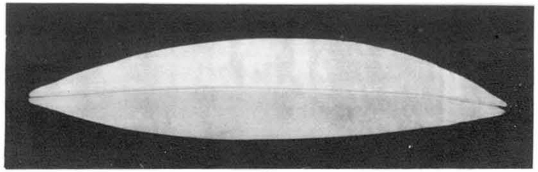
PLATE 33. TELLINA, ARCOPAGIA



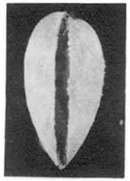
1



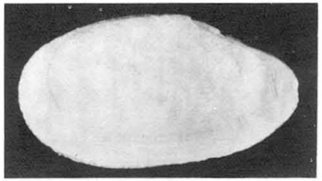
2



3

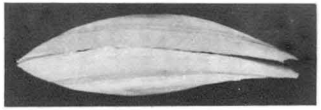


4



5

7



6

8

9

10

PLATE 34. TELLINA, MACOMA

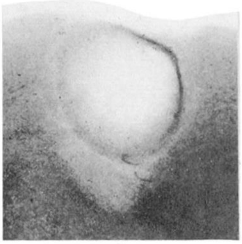
TELLINA, MACOMA

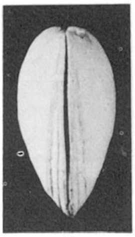
Figures 1-3. *Tellina radiata* Linné (*see* p. 182). Anterior, left lateral, and ventral views. (X 0.9). Locality: Key West, Florida.

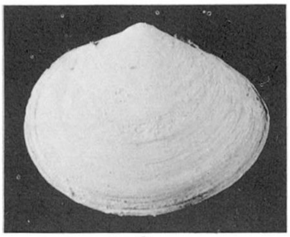
Figures 4-10. *Macoma tenta* (Say) (*see* p. 184). Figures 4-6. Anterior, left lateral, and ventral views. (X 2.3). Figure 7. X-radiograph of animals in life position in native sediment (6). (X 1). Figures 8-10. Feeding activity of the inhalent siphon at the sediment surface. (X 1.1). Locality: Quisset Harbor, Massachusetts.

MACOMA

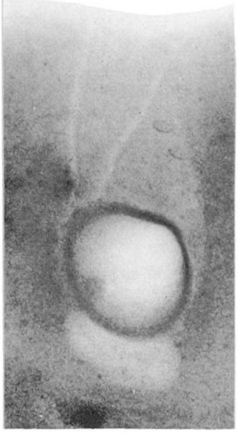
Figures 1-9. *Macoma balthica* (Linné) (*see* p. 185). Figures 1-2. Anterior and left lateral views. (X 1.6). Figure 3. Live animal with siphons and foot partly extended. (X 1.4). Figures 4-5. Orientation following forward rocking movement, and erect probing orientation. (X 1). Figures 6-8. X-radiographs of successive positions in burrowing (foot plainly visible in 7). (X 1). Figure 9. X-radiograph of animals in life position in sediment no. 1; depth of burial less in fine sand here than in coarser native sand. Arrows indicate water currents. (X 1). Locality: ponded portion of Squeteague Harbor, Massachusetts.

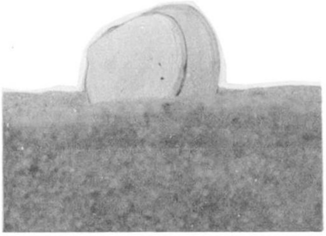

6

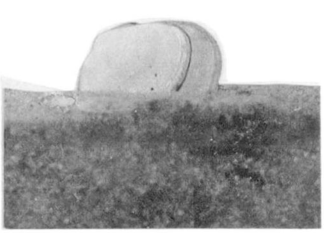

1

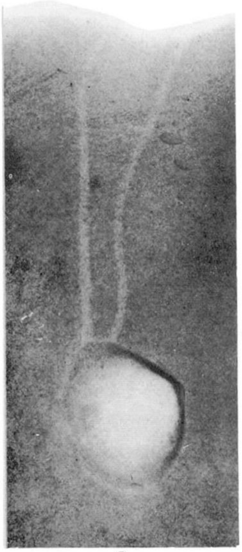

2


3


7


4


5


8

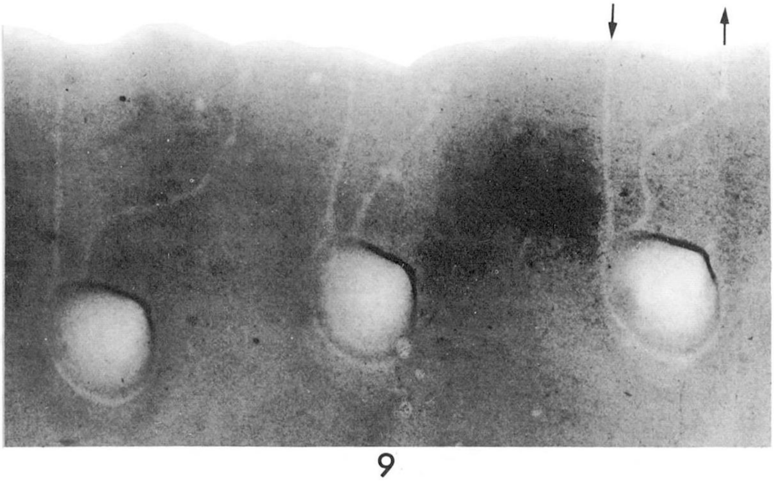
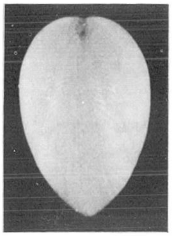
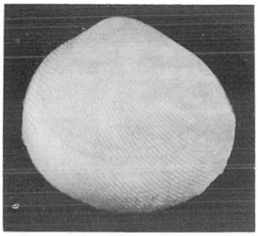
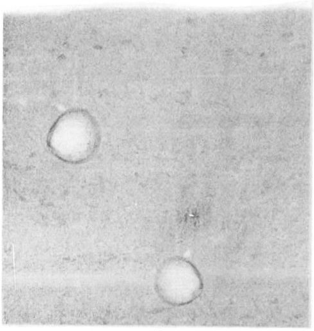

9

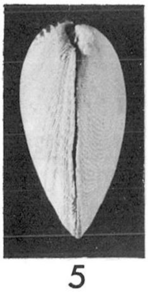
PLATE 35. MACOMA

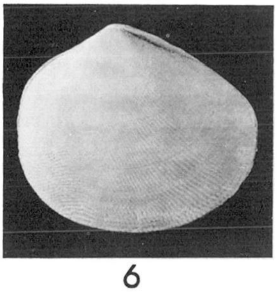

1

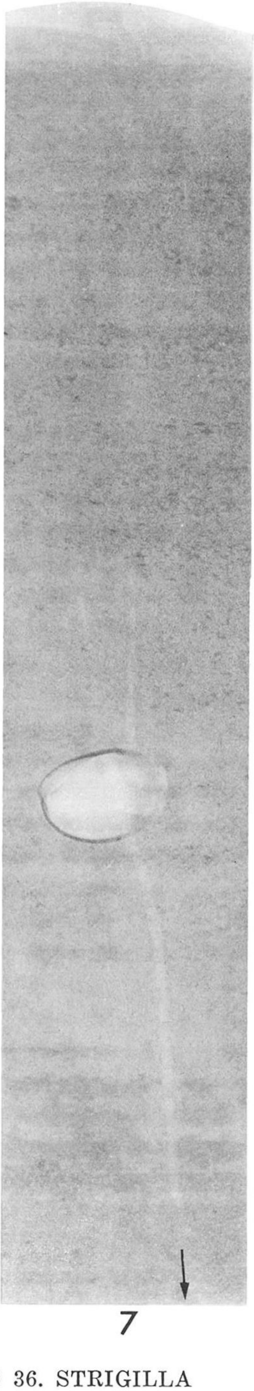

2


3


4


5


6


7

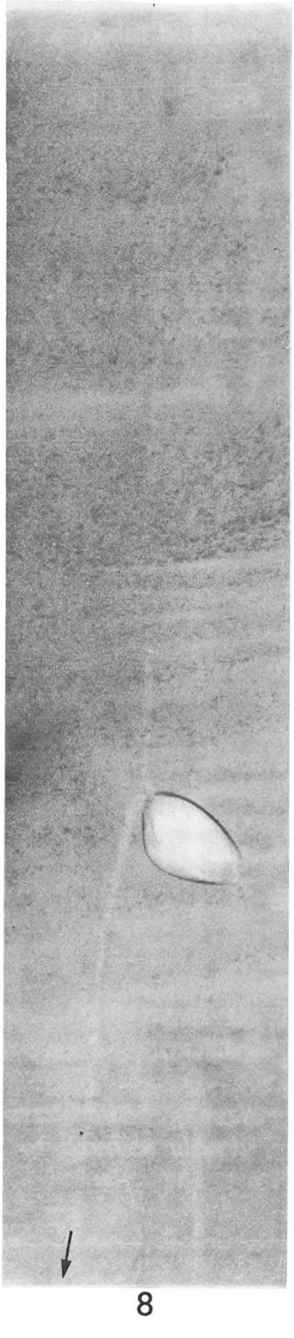

8

PLATE 36. STRIGILLA

STRIGILLA

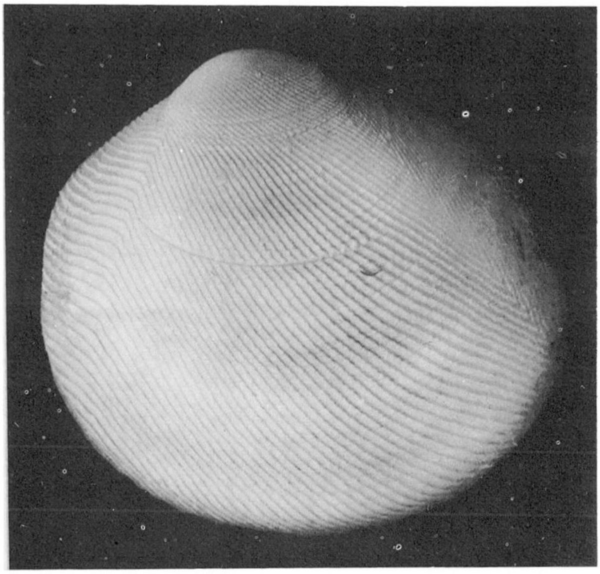
Figures 1-4. *Strigilla mirabilis* (Philippi) (*see* p. 187). Figures 1, 2. Anterior and left lateral views. (X 3.5). Figures 3, 4. X-radiographs of animals in native sediment (31). (X 1). Locality: Mani Beach, Puerto Rico.

Figures 5-8. *Strigilla carnaria* (Linné) (*see* p. 186). Figures 5, 6. Anterior and left lateral views. (X 1.7). Figures 7, 8. X-radiographs of animals in native sediment (31); arrows indicate water currents. (X 1). Locality: Mani Beach, Puerto Rico.

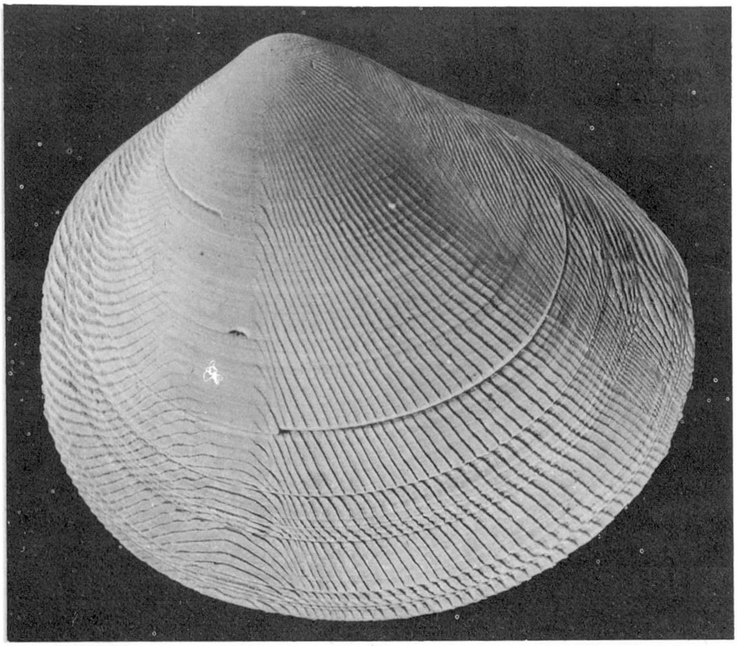
STRIGILLA

Figure 1. *Strigilla mirabilis* (Philippi) (*see* p. 187). Left valve. (X 8.1). Locality: Mani Beach, Puerto Rico.

Figure 2. *Strigilla carnaria* (Linné) (*see* p. 186). Left valve. (X 4.6). Locality: Mani Beach, Puerto Rico.



1



2

PLATE 37. STRIGILLA

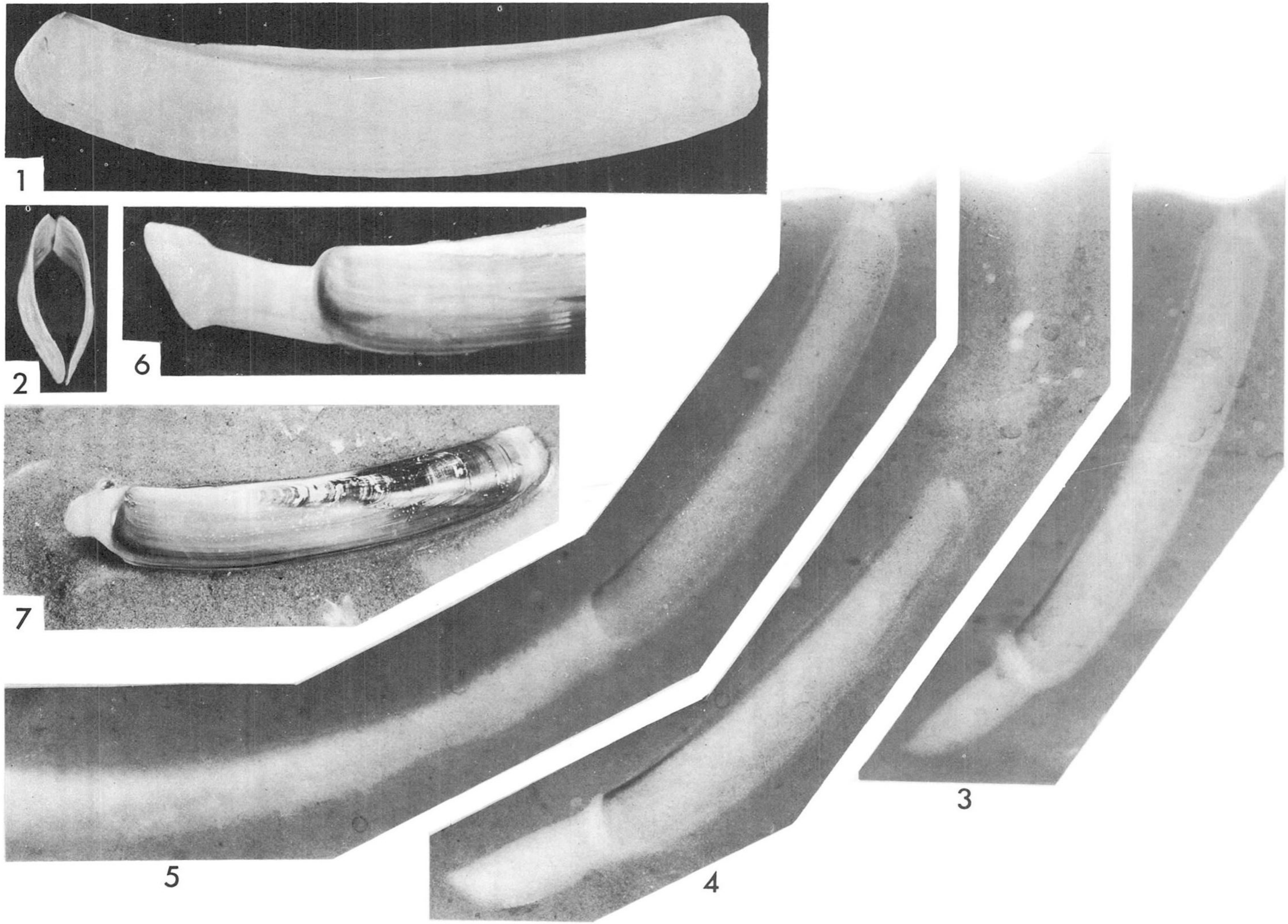


PLATE 38. ENSIS

ENSIS

Figures 1-7. *Ensis directus* (Conrad) (*see* p. 187). Figures 1, 2. Anterior and left lateral views. (X 0.8). Figures 3, 4. X-radiographs showing stages of burrowing native sediment (1). (X 1). Figure 5. X-radiograph showing animal in life position after formation of burrow. Constricting effect of aquarium walls has caused animal to burrow more shallowly than in nature. (X 1). Figure 6. Anterior of live animal with foot partly extended. (X 1.7). Figure 7. Rapid probing of the foot to obtain anchorage for shell erection. (X 0.6). Locality: Barnstable Harbor, Massachusetts.

MYA, CORBULA, LYONSIA, PANDORA

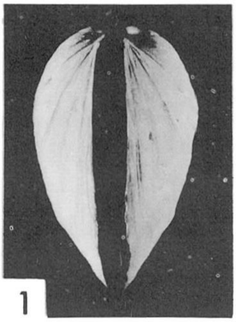
Figures 1-3. *Mya arenaria* Linné (*see* p. 189). Figures 1, 2. Anterior and left lateral views. (X 0.7). Figure 3. Live animal with partly extended siphons (scale 3 cm long). Locality: Barnstable Harbor, Massachusetts.

Figures 4, 5. *Corbula caribaea* Orbigny (*see* p. 189). Anterior and left lateral views. (X 3). Locality: Mayaguëz Harbor.

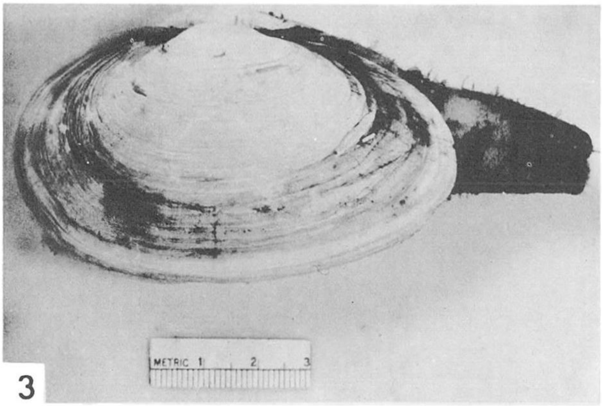
Figures 6, 7. *Lyonsia hyalina* (Conrad) (*see* p. 191). Anterior and left lateral views. (X 2.4). Locality: Quisset Harbor, Massachusetts.

Figure 8. *Lyonsia hyalina floridana* (Conrad) (*see* p. 191). Live animal byssally attached to grains of sediment. (X 1.5). Locality: south of Cape Florida, Biscayne Bay, Florida.

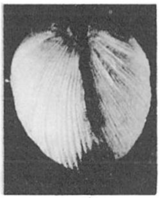
Figures 9-11. *Pandora gouldiana* (Dall) (*see* p. 191). Figures 9, 10. Anterior and left lateral views. (X 1.3). Figure 11. Burrowing animal in erect probing orientation (scale 3 cm long). Locality: Barnstable Harbor, Massachusetts.


1

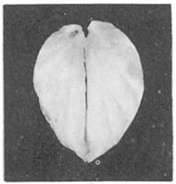

2

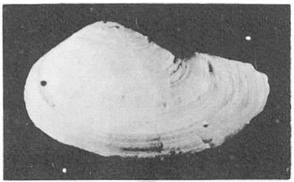


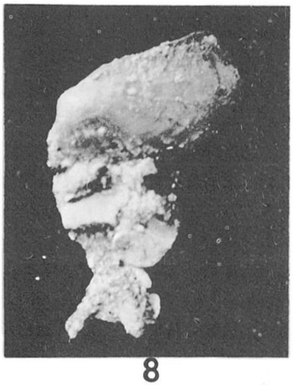
3


4

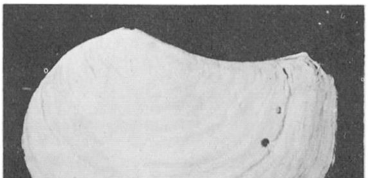

5


6


7

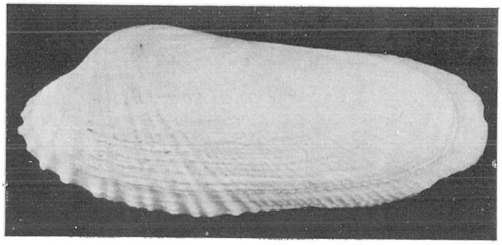

8


9

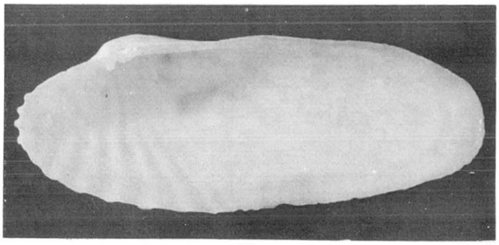

10

11

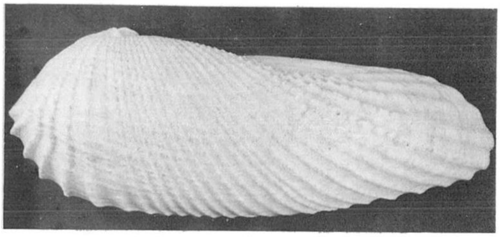
PLATE 39. MYA, CORBULA, LYONSIA, PANDORA



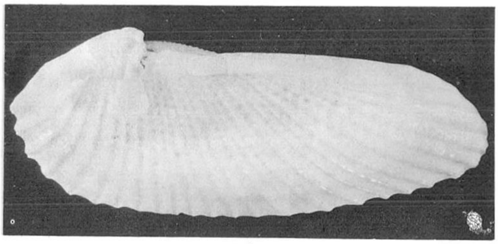
1



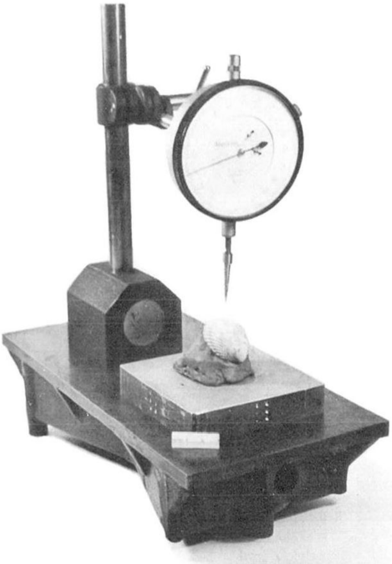
2



3



4



5

PLATE 40. PETRICOLA, PHOLAS, AND INDICATOR GAUGE

PETRICOLA, PHOLAS, AND INDICATOR GAUGE

Figures 1, 2. *Petricola pholadiformis* Lamarck. Left valve exterior and right valve interior (X 2.1). Locality: Black Beach, Squeteague Harbor, Massachusetts.

Figures 3, 4. *Pholas.* Left valve exterior and right valve interior. (X 0.4). Locality: unknown.

Figure 5. Indicator gauge used for measuring shell surface relief. (X 0.2).