Chapter 6

Growth Patterns within the Molluscan Shell

An Overview

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1. Introduction

Growth patterns on the external surface of the molluscan shell (Fig. 1) have long been the subject of both biological and paleontological research (Isely, 1913, 1931; Mossop, 1921, 1922; Orton, 1923, 1926; Gutsell, 1931; Weymouth et al., 1931; Weymouth and Thompson, 1931; Moore, 1934, 1958; Newcombe, 1935, 1936; Davenport, 1938; Tang, 1941; Matteson, 1948; Shuster, 1951; Fairbridge, 1953; Savilov, 1953; Haskin, 1954; Mason, 1957; Lubinsky, 1958; Sastry, 1961; Craig and Hallam, 1963; Merrill et al., 1965; Clark, 1968, 1969a,b, 1974, 1975; Olsen, 1968; Andrews, 1972; Seed, 1973, 1976; Thiesen, 1973; for an earlier compendium, see Weymouth, 1923) (also see Chapters 8, 11, and 12 of this volume for dis-

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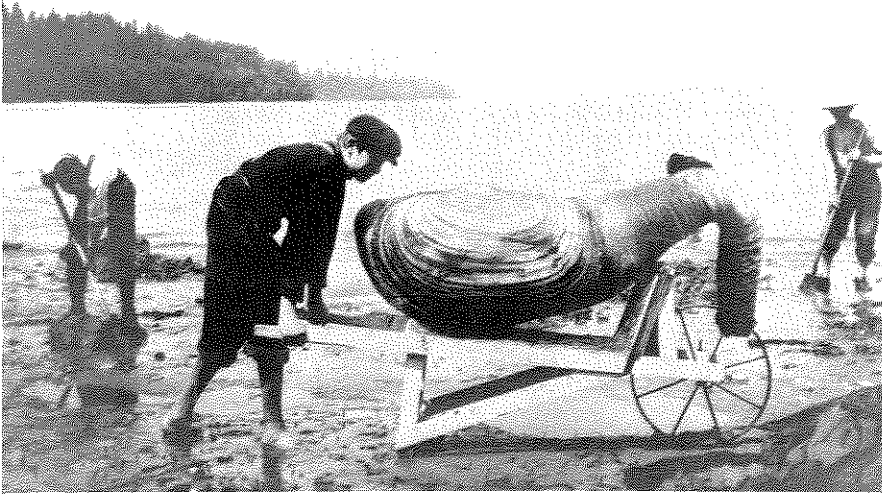
Figure 1. The geoduck, *Panope generosa* (Gould). Distinct growth patterns are visible on the external surface of the shell. Note wheelbarrow for scale. Origin of photograph unknown.

cussions of external growth patterns). Excellent discussions on the interpretation of such growth patterns, as well as the effects of various environmental variables on shell growth and surface morphology, are presented by Hedgepeth (1957), Moore (1958), Hallam (1965), and Clark (1974). Despite these extensive studies, the usefulness of external shell growth patterns in ecological and paleoecological studies has been limited.* The principal difficulty encountered in interpreting shell surface growth features arises from an inability to distinguish spawning and disturbance lines from annual patterns (Lutz, 1976a). Problems associated with distinguishing these growth features have been reduced over the past two decades by the discovery of periodic patterns of growth within the shells, i.e., internal growth patterns, of numerous Recent and fossil molluscs (Barker, 1964, 1970; Berry and Barker, 1968, 1975; House and Farrow, 1968; Pannella and MacClintock, 1968; Rhoads and Pannella, 1970; Farrow, 1971, 1972; Evans, 1972; Cunliffe, 1974; Pannella, 1975; Lutz, 1976a; Lutz and Rhoads, 1977; Gordon and Carriker, 1978; Jones et al., 1978). In addition to facilitating interpretation of the temporal significance and causes for observed surface morphological features, such internal growth patterns have proven useful in: (1) geophysical studies for defining Phanerozoic changes in the rate of the earth's rotation (Berry and Barker,

* Limitations discussed do not apply to external growth patterns of all species. Many bivalves (e.g., certain pectinids) have periodic external shell patterns that are potentially extremely useful in both ecological and paleoecological studies (see Chapter 11).

1968, 1975; Pannella and MacClintock, 1968; Pannella et al., 1968; Pannella, 1972, 1975; Dolman, 1975; Rosenberg and Runcorn, 1975; Weinstein and Keeney, 1975; Whyte, 1977); (2) ecological and paleoecological studies for assessing the effects of various biological and environmental stresses (Pannella and MacClintock, 1968; Rhoads and Pannella, 1970; Farrow, 1972; Kennish and Olsson, 1975; Kennish, 1977a–c, 1978) (also see Chapter 7); and (3) archeological studies for reconstructing settlement patterns of prehistoric hunter–gatherers (Coutts, 1970, 1975; Coutts and Higham, 1971; Koike, 1973, 1975; Ham and Irvine, 1975; Clark, 1977, 1979).

Although internal shell growth patterns may potentially be found within all classes of molluscs, the Bivalvia have been by far the most universally studied. This apparent research bias is largely a reflection of the relative ease with which a complete record of bivalve growth can be obtained. Such an ontogenetic record is revealed by sectioning or fracturing the shell along a plane passing from the oldest part of the shell, the umbo, to the growing margin along the axis of maximum growth (Pannella and MacClintock, 1968; Rhoads and Pannella, 1970) (see Chapter 1 for illustration of maximum axis of growth and Appendix 1.A.1 for details of preparation procedures). Complete ontogenetic records are difficult, if not impossible, to obtain from tightly coiled or otherwise torqued shells (e.g., gastropods) using current methods (see Chapter 10 for discussion).

The primary purpose of this chapter is to provide a comprehensive review of the types of internal growth patterns thus far described within molluscan (primarily bivalve) shells. We will also speculate on the origins of these growth patterns. Realized, as well as potential, ecological and paleoecological applications are discussed at some length.* In the following discussion, internal growth patterns have been assigned to one of two categories: (1) microgrowth increments and their sequential changes or (2) shell structural changes. Growth patterns within the former category are associated with alternating regions containing variable concentrations of organic material, while those patterns within the latter category are associated with changes in shell microstructure (e.g., nacreous, prismatic, crossed lamellar; see Appendix 2.B) within a given shell layer or shifts in the relative position of shell layer boundaries on the depositional surface.† When viewed in acetate-peel or thin-section preparations (see Ap-

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* For an in-depth discussion of the manner in which many of these internal patterns can be utilized in studies of population dynamics, see Chapter 7.

† While microgrowth increments may be considered "structural" features, we have avoided the use of the term "structure" when referring to such increments in order to avoid confusion. In this chapter, we use the term structure in reference to shell structural types (i.e., shell microstructures) outlined in Appendix 2.B or in reference to the arrangement of shell layers. The term structure is employed in a slightly different manner in Chapter 2.

pendix 1.A.1,2), microgrowth increment patterns often appear superimposed on shell structural changes.

It should gradually become evident to the reader of this chapter that most, if not all, growth patterns within the molluscan shell are a reflection of complex interactions between environmental variables and the organism's physiology. A change in the external environment will often induce physiological (particularly respiratory) changes that result in altered concentrations of metabolic end products within the extrapallial fluid. Such fluid chemistry changes can, in turn, have profound effects on the composition and structure of the shell. In the following discussion, we will consider in detail the types of internal growth patterns, resulting from such shell compositional and structural changes, that various workers have described.

2. Microgrowth Increments

Microgrowth increments within the molluscan shell were first described in detail by Barker (1964) in his thin-section observations of four genera of bivalves (*Mactra, Mercenaria, Anadara,* and *Chione*). Since
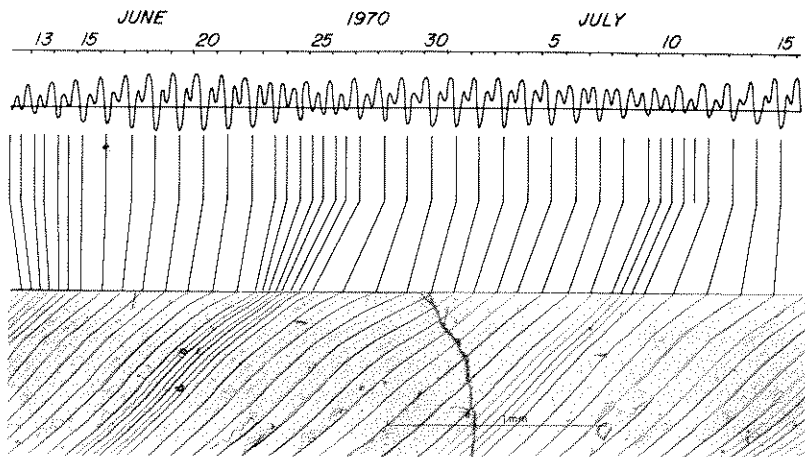
Figure 2. Microgrowth increments in the outer shell layer of the intertidal cockle *Clinocardium nuttalli* collected at Charleston, Oregon, compared with tidal predictions for the same period for Empire, Oregon. The horizontal line drawn through the tidal curves marks the intertidal position at which the specimen was collected. The optical micrograph is of an acetate peel of a polished and etched, radially sectioned shell valve. Diurnal, semidiurnal, and fortnightly patterns are apparent. Slightly modified from figures that appeared in Evans (1972) and Clark (1974). Reprinted with permission. Copyright © 1972 by the American Association for the Advancement of Science.

Barker's original study, similar "microscopic periodicity structures" have been found in numerous other molluscs, and the micro- and ultrastructures of such increments have been described in detail (for a review, see Clark, 1974). It is now generally accepted that many, if not all, microgrowth increments within the molluscan shell are a reflection of variations in the relative proportions of organic material (conchiolin) and calcium carbonate (aragonite or calcite). Alternation of calcium-carbonate-rich regions and organic-rich regions or lines has been well documented for numerous Recent and fossil species through optical- and electron-microscope studies of thin sections, acetate peels, and polished and etched surfaces of the shell (see Appendix 1.A.1–3 for preparation techniques). These growth lineations were originally interpreted as reflections of solar time (House and Farrow, 1968; Pannella and MacClintock, 1968; Pannella et al., 1968; Farrow, 1971). More recent studies, however, have revealed a complex relationship between incremental shell growth and lunar and solar cycles (Clark, 1974, 1975; Pannella, 1975, 1976; Thompson, 1975; Whyte, 1975). Although a one-to-one correspondence has not been established, the formation of microgrowth increments in bivalves is highly correlated with shell valve movements (Thompson, 1975; Gordon and Carriker, 1978).* Because the valves of many species are usually closed during low tide and open during high tide, a high positive correlation also exists between the number of increments and the number of tides to which an organism has been subjected (Evans, 1972, 1975) (Fig. 2). While valve-movement rhythmicity is usually most pronounced in intertidal specimens, subtidal specimens of at least one species [*Mercenaria mercenaria* (L.)] exhibit biological rhythms in relative synchrony with the tidal cycle (Thompson, 1975).† There has been general agreement among growth-line workers that when the valves are open and the organism is actively pumping, shell material is deposited that is rich in calcium carbonate relative to the adjacent shell material (which contains higher concentrations of organic material). Until recently, however, hypotheses attempting to explain the origin of layers relatively rich in organic content have been based on the assumption that calcium carbonate and organic material were *deposited* at variable rates during daily or tidal cycles (Pannella and MacClintock, 1968; Evans, 1972, 1975; Pannella, 1975, 1976), although a few references were made to the possibility that shell disso-

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* Difficulty in establishing a one-to-one correspondence between the formation of increments and valve movements arises as a result of the lack of clearly defined microgrowth increments, when viewed in shell section, near the shell margin. The absence of growth lines in this region has been reported by several workers (Thompson, 1975; Gordon and Carriker, 1978) and may be related to the lack of polymerization of the organic matrix of the shell near the growing margin (Gordon and Carriker, 1978).

† Gordon and Carriker (1978), in their laboratory study of *Mercenaria mercenaria*, did not find circadian locomotor (valve-movement) rhythms reported by Thompson (1975).

lution might play a role in the formation of organic-rich layers (Rhoads and Pannella, 1970; Wilbur, 1972; Rhoads, 1974; Thompson, 1975). In 1977, Lutz and Rhoads (1977) published a hypothesis of growth-line formation that proposed that organic concentrations in various regions of the shell were simply residues left behind as a result of dissolution of shell material during periods of anaerobiosis. Independent quantitative evidence in partial support of this hypothesis has recently been presented by Gordon and Carriker (1978). In the following section, we summarize the mechanism of growth-line formation as outlined by Lutz and Rhoads (1977).

2.1. Formation of Microgrowth Increments

Prior to describing the physiologically controlled mechanism of growth line formation, it is necessary that we provide a brief background based on recent studies of molluscan anaerobiosis and shell organic–inorganic relationships. In the following sections, we consider the implications of these studies in detail.

2.1.1. Anaerobic Respiration in Molluscs

The ability of molluscs to respire anaerobically has been well documented. Excellent reviews of this subject have been presented by von Brand (1944), Hochachka and Mustafa (1972), and de Zwann and Wijsman (1976). The biochemical pathways operating during anaerobiosis, at least in bivalves, appear different from those described in vertebrates. In contrast to vertebrate pathways, in which quantities of lactic acid are produced during anaerobic metabolism, the major end products of molluscan anaerobic respiration are succinic acid and alanine (Stokes and Awapara, 1968; de Zwann and Zandee, 1972; de Zwann and van Marrewijk, 1973). Early studies (Collip, 1920, 1921) suggested that calcium carbonate from the shell served to buffer the acidic products of anaerobic metabolism, and visible corrosion of the growth surfaces of *Mercenaria mercenaria* was observed after prolonged periods of shell closure (Dugal, 1939). This hypothesis has been confirmed through studies of chemical changes in the composition of the extrapallial fluid (Crenshaw and Neff, 1969; Gordon and Carriker, 1978) (also see Figs. 3 and 4) and measurement of ^{45}Ca deposition and solution (Crenshaw and Neff, 1969); at least a portion of the succinic acid produced during anaerobic metabolism is neutralized by dissolution of $CaCO_3$ from the shell. Furthermore, measurements of the oxygen tension and succinate levels in the extrapallial fluid have demonstrated that *M. mercenaria* becomes anaerobic when the valves are closed (Figs. 3 and 4). As alluded to by Wilbur (1972), periodic valve
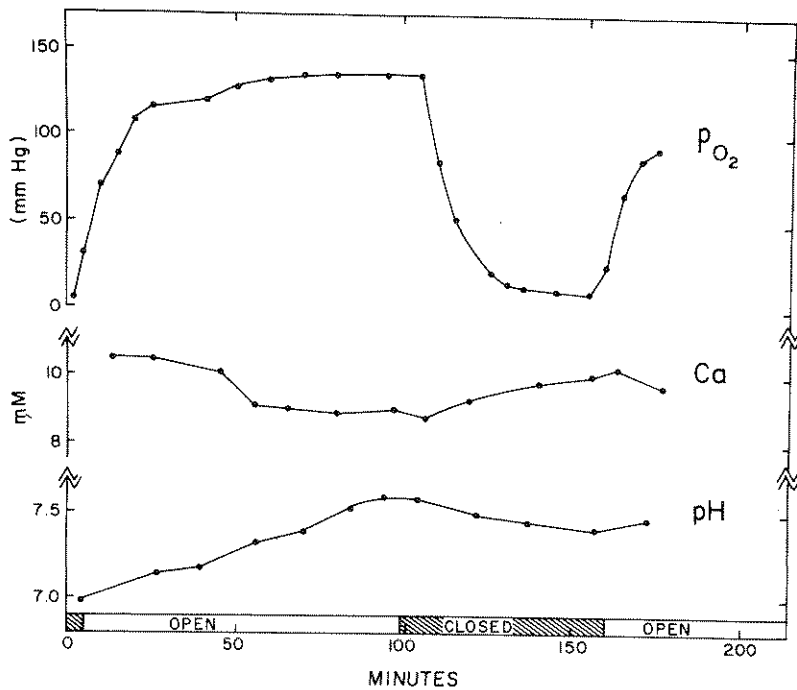
Figure 3. Oxygen tension (P_{O_2}), calcium (Ca) concentration, and pH of the extrapallial fluid of one *Mercenaria mercenaria* specimen with respect to the opening and closing of the shell valves. Valve position is indicated by the bar at the bottom of the graph. Reprinted with permission from Crenshaw and Neff (1969).

closure should therefore result in an alternation of shell deposition and decalcification. Any theory on growth-line formation must account for decalcification at the interface between the mantle and shell and its effect on preservation of the complete record of growth found within the shells of numerous species (Berry and Barker, 1968; Pannella and MacClintock, 1968; Rhoads and Pannella, 1970; Farrow, 1971, 1972; Kennish and Olsson, 1975; Kennish, 1978).

2.1.2. Organic–Inorganic Relationships

Recent shell structure research has contributed greatly to our understanding of micro- and ultrastructural relationships between organic material and inorganic crystals of calcium carbonate within the shells of bivalves, gastropods, and cephalopods (Watabe and Wilbur, 1960, 1961; Oberling, 1964; Hudson, 1967, 1968; Wise and Hay, 1968a,b; Kennedy *et al.*, 1969; Mutvei, 1969, 1970, 1972; Taylor, J. D., *et al.*, 1969; Grégoire, 1972; Crenshaw and Ristedt, 1975) (also see Appendix 2.B). While struc-
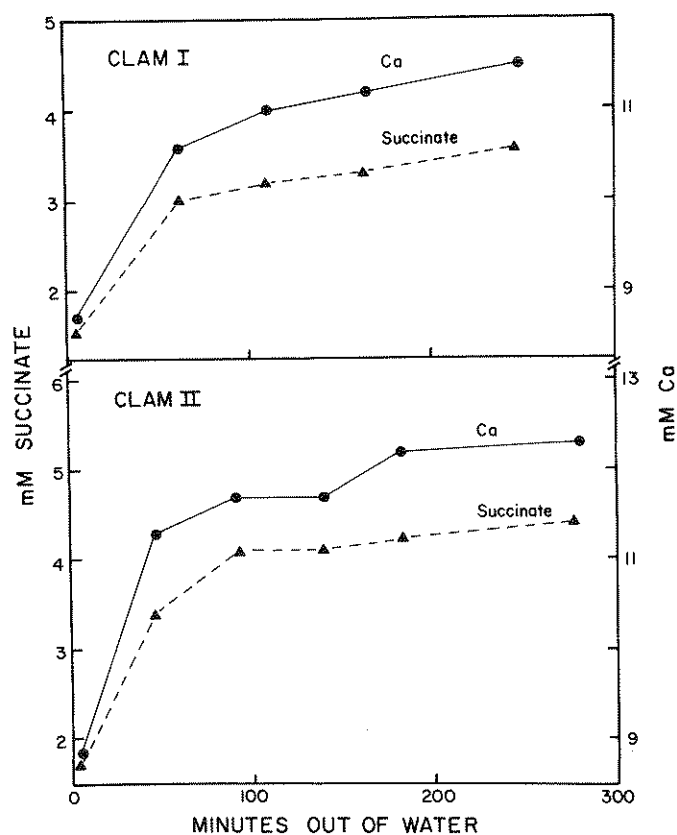
Figure 4. Concentration of calcium and succinate in the extrapallial fluids of two clams (*Mercenaria mercenaria*) with respect to time out of water. Reprinted with permission from Crenshaw and Neff (1969).

tures such as interlamellar, intercrystalline, and interprismatic organic matrices are universally recognized, the structural organization of intracrystalline and intraprismatic organic material has been the subject of some controversy (Watabe, 1963, 1965; Towe and Hamilton, 1968a,b; Travis, 1968; Travis and Gonsalves, 1969; Mutvei, 1970; Towe, 1972; Towe and Thompson, 1972). Sometimes this organic material assumes the form of coherent matrices or "envelopes" located within prisms or aragonitic nacreous tablets. However, some workers (Towe and Hamilton, 1968a,b; Towe, 1972; Towe and Thompson, 1972) have suggested that such organic matter, when present, may represent impurities in the carbonate in the form of trapped proteins or polypeptides. It was originally suggested that such intracrystalline organic matter was water-soluble

(Crenshaw, 1972), but subsequent studies have refuted this hypothesis and indicate that the water-soluble fraction appears to be adsorbed on crystal surfaces (Erben, 1974; M. A. Crenshaw, personal communication).

2.1.3. Lutz–Rhoads Hypothesis

With the foregoing discussion serving as a background, we offer the following as an explanation of growth-line formation in the molluscan shell. During aerobic metabolism, molluscs deposit calcium carbonate in the form of aragonite or calcite, together with organic material, resulting in shell construction. Aerobic metabolism is usually associated with periods of active pumping during high tide in well-oxygenated waters. As the concentration of dissolved oxygen falls, such as in the internal microenvironment created by the organism during periods of shell closure, anaerobic respiratory pathways are employed, and the level of succinic acid (or other acidic end products) within the extrapallial fluid rises. The acid produced is gradually neutralized by the dissolution of shell calcium carbonate, leading to increased levels of Ca^{2+} and succinate (or other end products) within the extrapallial and mantle fluids (Fig. 4) (also see Crenshaw and Neff, 1969). As a result of this decalcification, the ratio of relatively acid-insoluble organic material to calcium carbonate increases at the interface between the mantle and shell* One need not invoke the complication of an increased concentration of organic material in a given volume, although a collapse of unsupported matrix structures or a movement of the mantle as a compensatory response to the increased distance between mantle and shell could result in increased concentrations of freed organic material in specific regions of the extrapallial fluid. With the opening of the valves and the resumption of aerobic metabolism (see Fig. 3), the deposition of calcium carbonate and organic material within an area containing an insoluble residue of organic material should result in a localized increase in the ratio of organic material to calcium carbonate within the specific shell region. The end product of this process, from a strictly structural viewpoint, is one growth increment.†

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* It is also conceivable that the ratio of organic material to calcium carbonate at the mantle–shell interface could increase as a result of cessation of calcium carbonate deposition, with continued deposition of organic material. This hypothesis does not require shell dissolution and might be invoked to explain growth-line formation, as well as to explain some of the ultrastructural observations described elsewhere in this chapter. Evidence in support of this hypothesis, however, is unavailable at present.

† The presence of intraprismatic and intracrystalline coherent organic matrices would generally be more compatible with this hypothesis than would reincorporation into the shell of organic inclusions freed during decalcification, although the latter interpretation is certainly tenable.

2.1.4. Supporting Evidence

As mentioned earlier, evidence in partial support of the hypothesis discussed above has recently been provided by Gordon and Carriker (1978) based on measurements of extrapallial fluid pH,* rates of shell dissolution during valve closure [from the data of Crenshaw and Neff (1969)], thickness of subdaily growth lines, and duration of valve closure of *Mercenaria mercenaria*. In their study, Gordon and Carriker measured thicknesses of organic-rich "subdaily growth striations" ranging from 0.45 to 0.9 μm. Crenshaw and Neff (1969) calculated that at measured rates of calcium carbonate dissolution, an organism with a shell weight of 100 g would lose about 2 mg of shell per hour. Shell weights of *M. mercenaria* specimens used by Gordon and Carriker (1978) ranged from 40 to 80 g, with internal shell surface areas of 44–64 cm^2. Assuming the dissolution rate to be uniform over the entire internal surface, Gordon and Carriker calculated the thickness of shell that would be removed for every hour the shell is closed:

(shell loss per hour/unit weight) $\times$ (total weight/surface area)
$$\times \; (1/\text{density}) \; = \; \text{thickness lost per hour}$$

For example, one specimen with valves weighing 64 g and an internal surface area of 56 cm^2 would lose 7.8×10^{-2} μm/hr (using a density of 2.93 g/cm^3 for aragonite). Experimental organisms in the study of Gordon and Carriker (1978) kept their valves closed for 2.5–12 hr. At the calculated rate of shell dissolution, the thickness of shell removed would be 0.2–0.94 μm. These values are sufficiently close to the measured widths (0.45–0.9 μm) of subdaily lines to suggest a causative relationship between the dissolution and subdaily line thickness.

As a result of the measurements and calculations discussed above, Gordon and Carriker (1978) conclude that:

> To account for subdaily striations, then, it is only necessary to envision continuous and simultaneous secretion of organic matrix and calcium carbonate during the aerobic shell-building part of the animal's growth cycle. In the anaerobic period, increasing acid in the extrapallial fluid dissolves a portion of newly deposited shell. Some of the associated matrix may also dissolve, but at least part of it is sufficiently insoluble to resist attack by metabolic acids and remains behind as a residue to be covered by a new layer of calcified material during the next cycle of aerobic deposition. Because the matrix at this point is hardened by polymerization of the protein, it maintains its structural integrity during and after decalcification. As a result, the width of residual matrix provides a record of the length of time that the shell was exposed to metabolic acids.

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* Since calibration buffers of suitable ionic strength were not used in their study, Gordon and Carriker (1978) actually measured electrode potential rather than hydrogen ion concentration.
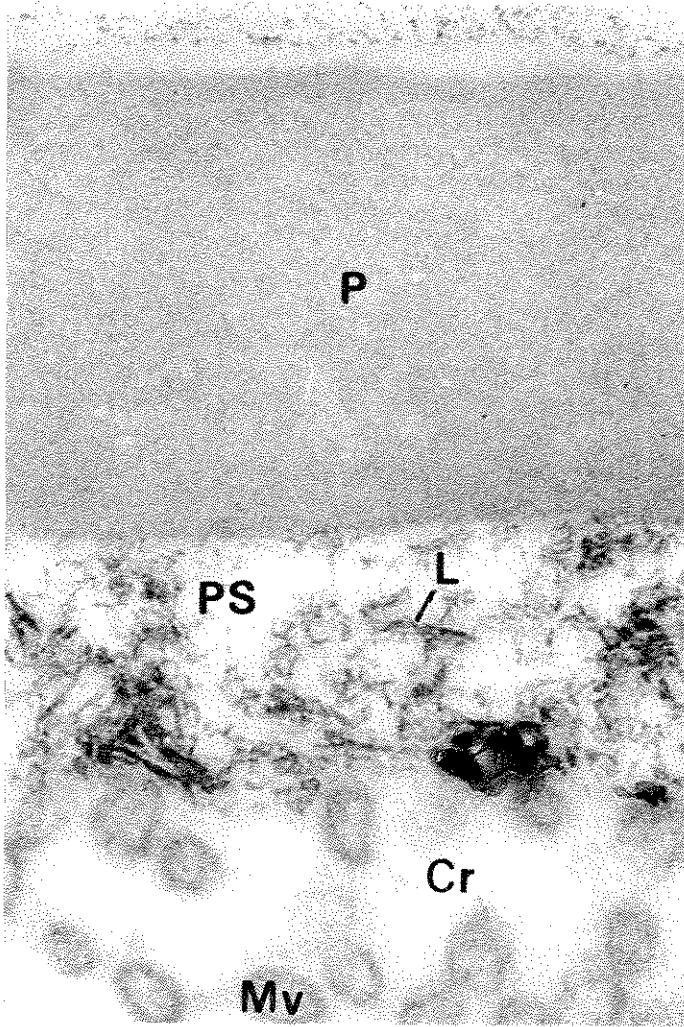
Figure 5. Electron micrograph of a vertical section of the pallial region of *Pinctada radiata*. The live specimen was relaxed in a solution of magnesium sulfate prior to fixation in glutaraldehyde and osmium tetroxide. Calcium carbonate crystals (Cr) and fragments of "electron-dense lamellae" (L) are seen scattered throughout the pallial space (PS). (P) Periostracum; (Mv) microvilli of mantle cells. Unstained section ×110,000. Reprinted with permission from Nakahara and Bevelander (1971).

Thus, results and conclusions from the study of Gordon and Carriker (1978) lend considerable support to the hypothesis of growth-line formation outlined above.

Further evidence suggesting the importance of respiratory changes in producing microgrowth increments is provided by a reinterpretation of the works of Bevelander and Nakahara (Bevelander and Nakahara, 1969; Nakahara and Bevelander, 1971). In their electron-microscope study of the formation and growth of the prismatic layer of *Pinctada radiata* (Leach), Nakahara and Bevelander (1971) envisioned fragments of "electron-dense lamellae" at the internal boundary of future prisms (Figs. 5 and 6) as migrating through the extrapallial fluid and ultimately forming envelopes within which crystal nucleation and growth occur. If the micrographs they presented (Figs. 5 and 6) are reinterpreted and the process of prism formation they described is envisioned as occurring in reverse, we can observe quite vividly the process of gradual shell destruction. As calcium carbonate slowly dissolves, relatively insoluble organic envelopes, matrices, or inclusions remain at the mantle–shell interface, presenting the appearance of an electron-dense lamella (Figs. 5 and 6). That this organic residue is subsequently incorporated into the shell, as proposed by our hypothesis, is strongly suggested by the presence of "intraprismatic organic strands" approximately paralleling the inner growth surface of the prisms (Fig. 6c). While details of the treatment of the studied pearl oysters prior to anesthetization were not presented by Nakahara and Bevelander (1971), one can reasonably assume that laboratory conditions and/or exposure to air prior to or during the placement of the organisms in magnesium sulfate could have induced valve closure and subsequent anaerobiosis.

Results of an earlier study conducted by Bevelander and Nakahara (1969) on the formation and growth of nacre have been interpreted as

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Figure 6. Electron micrographs of the pallial region of *Pinctada radiata*. The live specimens were relaxed in a solution of magnesium sulfate prior to fixation in glutaraldehyde and osmium tetroxide. All sections have been stained with uranyl acetate and lead citrate. (A) Vertical section of a mantle cell (bottom of micrograph), pallial space (Ps), lamella (L), and portion of a prism (Pr). This region was located proximal to the outer fold of the mantle. (Mv) Microvilli. ×27,000. (B) Vertical section in a region of pallial space showing a portion of a prism (Pr) containing scattered calcium carbonate crystals (Cr), interprismatic wall (IW), lamella (L), and tips of microvilli (Mv). Decalcified section ×76,000. (C) Vertical section of mantle cells (bottom of micrograph), pallial space (Ps), lamella (L), and portion of three prisms (Pr). Microvilli of mantle cells extend into the pallial space. The prisms are separated from one another by substantial interprismatic walls (IW); "intraprismatic organic strands" (IS) and "remnants of envelopes and ground substance" (Nakahara and Bevelander, 1971) are seen between the walls. Decalcified section ×6700. All micrographs reprinted with permission from Nakahara and Bevelander (1971).
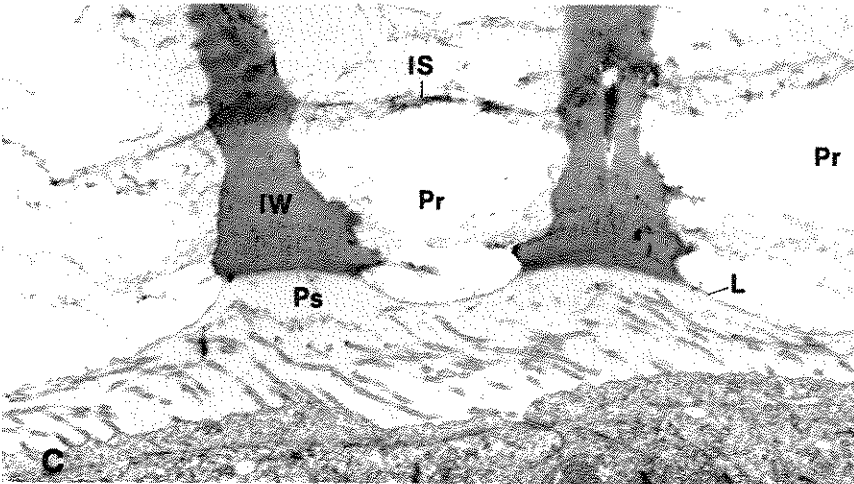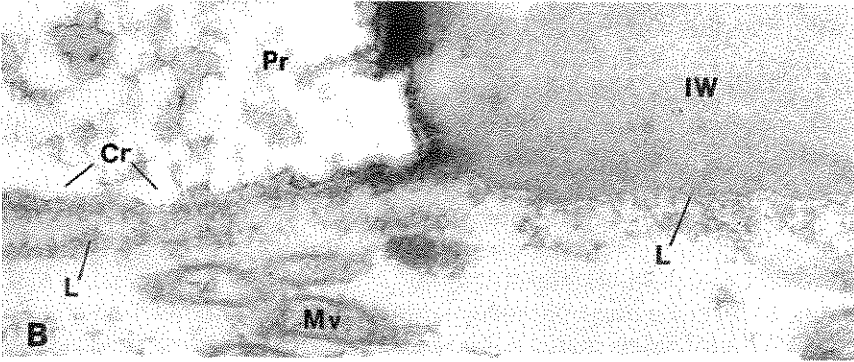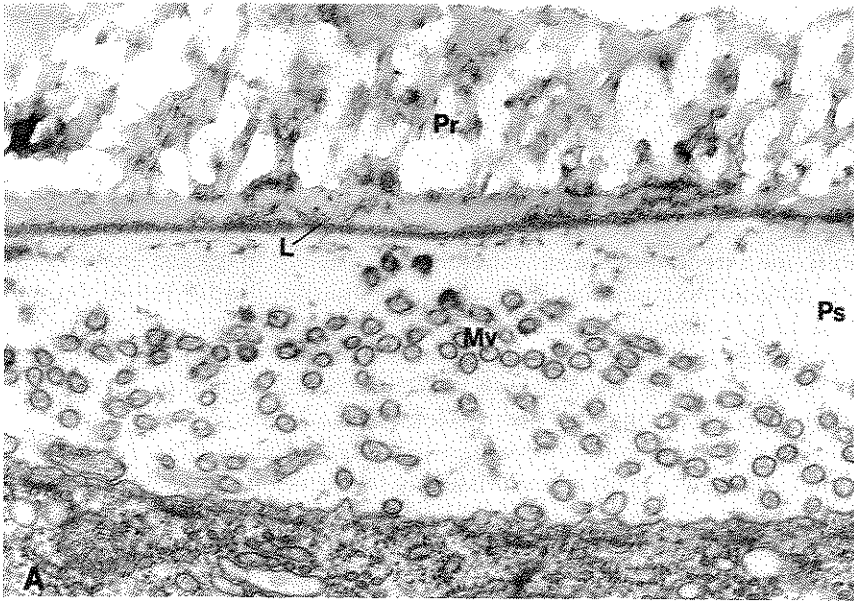
illustrative of shell dissolution (Erben, 1972, 1974; J. D. Taylor, personal communication). That their organic "compartments" (Fig. 7) at the mantle–shell interface may indeed be reflections of shell dissolution is suggested by an examination of the treatment of their studied bivalves prior to fixation. For a period of 1 hr before fixation, the molluscs were placed in a refrigerator at 5°C. As implied earlier (also see Crenshaw and Neff, 1969), such treatment is almost certainly sufficient to induce anaerobiosis, with release of succinic acid into the extrapallial fluid. Neutralization of this acid by calcium carbonate from the shell would be expected to result in selective shell destruction in a manner virtually identical to that seen in Figure 7. While microgrowth increments have seldom, if ever, been reported in nacre, they do occur. Nonreflected growth lines* within the middle nacreous layer† of the Atlantic ribbed mussel, *Geukensia* (= *Modiolus*) *demissa* (Fig. 8) show clustering patterns similar to those reported in a number of species (Pannella and MacClintock, 1968; Evans, 1972, 1975; Clark, 1974; Pannella, 1975, 1976). Mechanisms of growth-line formation within nacreous structures may or may not be precisely analogous to the process within the prismatic layer of *Pinctada*. If intracrystalline organic matrices are present, the process may be almost identical to that occurring in *Pinctada* prisms. In light of the current controversy over the presence or absence of such organic structures (for a discussion, see Towe, 1972), we suggest an alternative mechanism of growth-line formation in nacre.

It has been proposed that nacreous crystal nucleation occurs on the surface of an organic substratum and that during growth these crystals are enclosed within tight-fitting organic envelopes (Erben, 1972, 1974; Mutvei, 1972; Erben and Watabe, 1974). As a result of the lateral fusion of the crystals to form a mature nacreous lamina, adjacent lateral and distal portions of the envelopes merge to become intercrystalline and interlamellar organic matrices, respectively. If crystal nucleation and growth occasionally occur within organic compartments remaining after decalcification, and subsequent growth proceeds as described above, lateral fusion of adjacent crystals should result in a marked increase in the thickness of interlamellar and intercrystalline organic matrices. Such an increased con-

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* See Pannella and MacClintock (1968) for a detailed description of nonreflected growth lines within the bivalve shell.

† L. F. Gainey, Jr., and M. J. Greenberg (personal communication) have indicated that this middle layer is equivalent to the "inner nacreous layer" described by Blackwell *et al.* (1977). Also see Lutz and Rhoads (1978) for a critique of the study by Blackwell *et al.* (1977), as well as a detailed description of the shell structure of *Geukensia demissa* (Dillwyn).
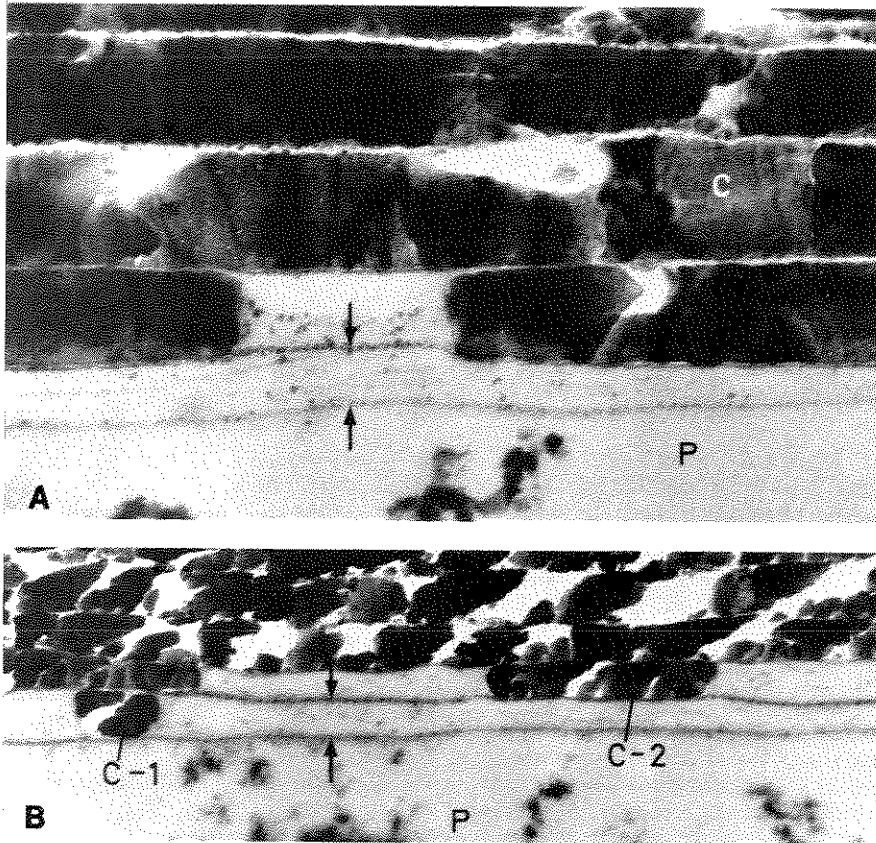
Figure 7. (A,B) Electron micrographs showing portions of the pallial space (P) and formed shell (C) of *Mytilus exustus*. The live specimens were placed in a refrigerator at 5°C for 1 hr prior to fixation in glutaraldehyde and osmium tetroxide. Such prefixation treatment may have induced anaerobiosis, with release of succinic acid into the extrapallial fluid. "Compartments" are delimited by organic lamellae (arrows). (C-1, C-2) Incomplete (partially dissolved?) aragonitic tablets in adjacent nacreous laminae. (A) ×46,000; (B) ×20,000. Both micrographs reprinted with permission from Bevelander and Nakahara (1969).

centration of conchiolin relative to calcium carbonate could explain growth patterns observed on acetate peels of polished and etched sections of *G. demissa* nacre. Evaluation of the above alternation of shell dissolution and deposition in the perspective of the current controversy associated with the *template* and *compartment* hypotheses (Bevelander and Nakahara, 1969; Nakahara and Bevelander, 1971; Mutvei, 1972; Towe, 1972; Erben and Watabe, 1974) suggests that while compartments may
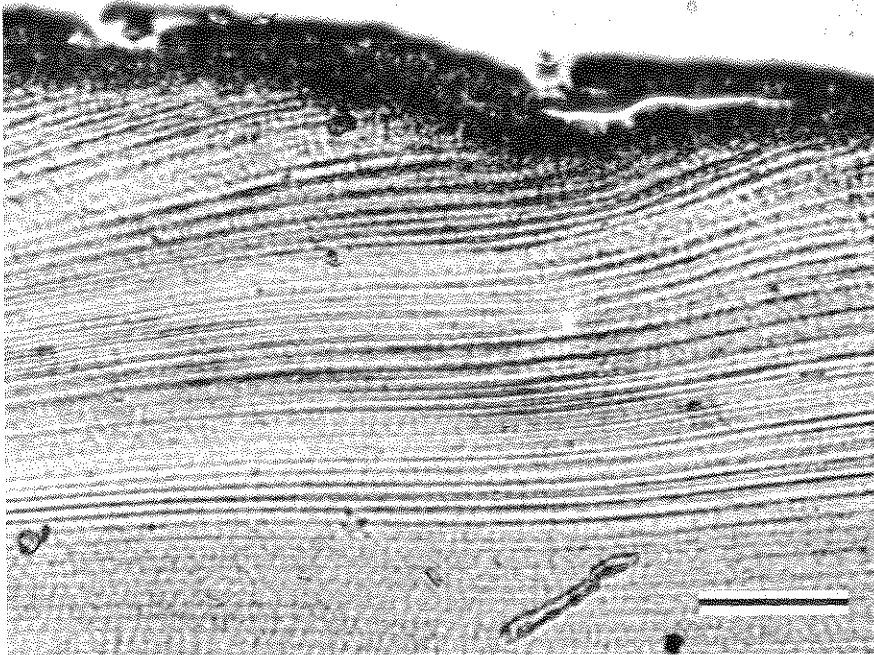
Figure 8. Optical micrograph of an acetate peel of a polished and etched longitudinal shell section showing nonreflected growth lines within the middle nacreous layer of *Geukensia demissa.* Note the pronounced clustering of microgrowth increments. Scale bar: 100 μm. Reprinted with permission from Lutz and Rhoads (1977). Copyright © 1977 by the American Association for the Advancement of Science.

exist from a strictly structural viewpoint, they are not primary features, but rather are "residual" in nature, and should be considered of only incidental importance in the formation of nacre. A similar point of view concerning the presence (or lack) of preformed matrix layers or compartments has been expressed by Gordon and Carriker (1978).

2.2. Summary of Documented Microgrowth Increment Patterns

The following discussion is intended to provide a current literature review* of microgrowth increment patterns described to date within the molluscan shell. Detailed descriptions and micrographs of the various types of patterns may be found in Chapter 7. For the purposes of this review, we have assigned documented microgrowth increment patterns to one of the following five temporal categories: (1) semidiurnal and diur-

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* For earlier compendia, see Rhoads and Pannella (1970) and Clark (1974).

nal; (2) fortnightly; (3) monthly; (4) annual; (5) semiperiodic or random events.*

2.2.1. Semidiurnal and Diurnal

As mentioned above, Barker (1964) has been credited with the discovery of microgrowth increments (and their sequential patterns) within the molluscan shell. As a result of his examination of several species of bivalves, Barker (1964) suggested that these small-scale internal growth features might reflect semidiurnal or diurnal periodicities, or both. Since 1964, considerable research has been conducted to test the validity of this hypothesis.

The first convincing evidence that diurnal periodicities were indeed recorded within the molluscan shell was provided by Pannella and MacClintock (1968). In their study of *Mercenaria mercenaria*, these workers counted from 360 to 370 lines and from 720 to 725 lines for growth periods of 368 and 723 days, respectively. These results strongly suggested that such microscopic growth increments were formed with a solar periodicity. "Solar" daily increments were also described by Pannella and MacClintock (1968) in *Tridacna squamosa*. More recently, other workers have examined and analyzed growth patterns in *M. mercenaria* and *T. squamosa* in greater detail, increasing our understanding of factors responsible for the formation of diurnal (and semidiurnal) increments in these and other species of molluscs (MacClintock and Pannella, 1969; Rhoads and Pannella, 1970; Thompson and Barnwell, 1970; Evans, 1972, 1975; Pannella, 1972, 1975,† 1976; Cunliffe and Kennish, 1974; Kennish and Olsson, 1975; Thompson, 1975; Kennish, 1976, 1977b, 1978; Gordon and Carriker, 1978). It is now generally accepted that such microgrowth increments are largely reflections of complex interactions between lunar and solar cycles (Clark, 1974, 1975; Pannella, 1975, 1976; Thompson, 1975; Whyte, 1975). At about the same time that Pannella and MacClintock (1968) reported the results of their study of growth patterns in *M. mercenaria*, House and Farrow (1968) independently suggested that similar microscopic features within the shell of *Cerastoderma* (= *Cardium*) *edule* were formed daily. Since these early studies, periodic microgrowth increments have been found in many other Recent and fossil species of

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* A few workers (Pannella and MacClintock, 1968; Kennish and Olsson, 1975) (also see Chapter 7) offer a description of bidaily patterns in *Mercenaria mercenaria*. Such patterns have not been described in detail in other species and will not be discussed in this section. Similarly, growth patterns reflecting a semiannual cycle (for a discussion of this type of periodicity, see Clark, 1974) have not been well documented and are not considered in this discussion.

† Pannella (1975) also described daily increments within the shell of the closely related venerid, *Mercenaria campechiensis*.

molluscs. Pannella *et al.* (1968) reported the presence of well-preserved "daily" growth increments in 12 species of molluscs from several geological periods (Middle Devonian to Upper Miocene). Barker (1970) prepared thin sections of the shells of over 98 species of bivalves and described numerous subannual structures within these shells that he felt might be related to daily or tidal cycles within the environment. Other detailed studies providing evidence for the presence of diurnal and/or semidiurnal periodicity structures within molluscan shells include those of Rhoads and Pannella (1970), Farrow (1971, 1972), Evans (1972, 1975) (also see Fig. 2), Pannella (1975), Whyte (1975), and Lutz and Rhoads (1977).

2.2.2. Fortnightly

Microgrowth patterns recurring at approximately fortnightly intervals have been described in a large number of molluscs, particularly those inhabiting intertidal and shallow subtidal environments (Barker, 1964; Berry and Barker, 1968; Pannella and MacClintock, 1968; Pannella *et al.*, 1968; House and Farrow, 1968; Rhoads and Pannella, 1970; Evans, 1972, 1975; Clark, 1974; Kennish and Olsson, 1975; Kennish, 1976, 1977b; Pannella, 1975, 1976) (also see Chapter 7). Barker (1964), in his detailed examination of "microtextural variation" in the bivalve shell, described "3rd-order layers" composed of microgrowth increments cyclically varying in thickness and hypothesized that such "layers" might recur at intervals of approximately 15 days. Later, Pannella and MacClintock (1968), and more recently Pannella (1975), published detailed micrographs of acetate peels of sectioned *Mercenaria mercenaria* and *Tridacna squamosa* showing fortnightly "clusters" of microgrowth increments within the outer shell layers of these two Recent bivalves.* These workers described similar "fortnightly cycles of deposition" within the shells of numerous fossil specimens† and presented micrographs of "fortnightly" patterns within *Mercenaria campechiensis ochlockoneenis* (Upper Miocene), *Crassatella mississippiensis* (Upper Eocene), *Limopsis striatopunctatus* (Upper Cretaceous), and *Conocardium* sp. (Upper Pennsylvanian). Similar clustering (fortnightly?) patterns of microgrowth increments have been observed within the middle nacreous layer of the Recent mytilid *Geukensia demissa* (Fig. 8) (also see Lutz and Rhoads, 1977). Evans (1972,

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* Kennish and Olsson (1975) and Kennish (1976, 1977b) provide additional discussions of fortnightly patterns of microgrowth increments in *Mercenaria mercenaria* (also see Chapter 7).

† The "fortnightly" periodicity of patterns in these fossil specimens was inferred from their structural similarity to those patterns that Pannella and MacClintock (1968) observed within the shells of *Mercenaria mercenaria*.

1975) presented a micrograph (see Fig. 2) of an acetate peel of *Clinocardium nuttalli* that illustrates a fortnightly pattern of microgrowth increments within the outer shell layer of this cockle. Pannella (1976) published a similar micrograph of *Limopsis striatopunctatus* (Upper Cretaceous) showing an inferred "fortnightly" pattern of growth. Dolman (1975), in his Fourier analysis of microgrowth periodicities in *Cerastoderma* (= *Cardium*) *edule*, recognized weakly developed fortnightly growth cycles in this species. Pannella (1975) photographically illustrated fine structures* within the shell of an unidentified Middle Devonian cephalopod and suggested that observed clusters of these structures might reflect a fortnightly periodicity. Earlier brief reviews of fortnightly patterns within the molluscan shell are presented by Rhoads and Pannella (1970) and Clark (1974).

2.2.3. Monthly

Numerous workers have provided evidence for the presence of monthly microgrowth patterns within the shells of various species of molluscs (House and Farrow, 1968; Pannella and MacClintock, 1968; Pannella *et al.*, 1968; Rhoads and Pannella, 1970; Farrow, 1972; Kennish and Olsson, 1975; Kennish, 1976, 1977b) (also see Chapter 7). House and Farrow (1968), in their analysis of microgrowth increments within the shell of *Cerastoderma edule*, observed "a regular bunching" of growth increments that occurred with a frequency of 29 days. Farrow (1972), in a later study of this same bivalve, showed that this monthly periodicity could be related to prolonged exposure due to very low high tides at every other neap tide for part of the year. Pannella and MacClintock (1968) reported a similar (synodic) monthly periodicity in *Mercenaria mercenaria* characterized by groupings of fortnightly "clusters" in pairs, with one fortnightly cluster more pronounced than the other. This internal pattern is also expressed, at least on some parts of the outer surface of this species, by concentric undulations with a wavelength periodicity of 29 days (also see Kennish and Olsson, 1975; Kennish, 1976, 1977b; Chapter 7). Pannella *et al.* (1968) reported the presence of "synodic-month patterns" in numerous fossil molluscs ranging in geological age from the Middle Devonian to Upper Miocene. The "monthly" periodicity of patterns within the shells of these fossil specimens was inferred from the structural similarity of patterns to those patterns that Pannella and MacClintock (1968) observed within the shells of *Mercenaria mercenaria*. Rhoads and Pannella (1970) photographically illustrated "monthly clustering" patterns of microgrowth increments formed during the autumn months in *Nucula prox-*

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* Such fine structures were shell surface topographic features and need not correspond with microgrowth increments within the shell.

ima from 6 m of water in Long Island Sound. More recently, Kahn and Pompea (1978) have suggested that septal formation within the cephalopod *Nautilus pompilius* may take place at monthly intervals* and reported the presence of similar "monthly" structures within the shells of numerous fossil cephalopods (Upper Ordovician to Upper Miocene). Possible factors responsible for the formation of monthly growth patterns in molluscs are discussed by Pannella and MacClintock (1968), Clark (1974), and Pannella (1976).

2.2.4. Annual

Annual patterns of microgrowth increments have been observed within the shells of the majority† of specimens that have been examined and analyzed in detail. Such patterns are generally a result of seasonal variations in growth that, in turn, usually result in the formation of relatively thick microgrowth increments during certain seasons (e.g., northern hemisphere, high latitude, summer) and relatively thin increments during others (e.g., northern hemisphere, high latitude, winter). These annual patterns constitute the "1st-order layers" described by Barker (1964) in his detailed examination of *Mercenaria mercenaria, Spisula (= Mactra) solidissima, Chione cancellata,* and *Anadara ovalis.* Pannella and MacClintock (1968), and later Rhoads and Pannella (1970), Kennish and Olsson (1975), and Kennish (1976, 1977b) (also see Chapter 7), presented detailed micrographs illustrating these patterns within *M. mercenaria.* Similar annual patterns were described in detail by House and Farrow (1968) and Farrow (1971, 1972) in their examination of microgrowth increments in *Cerastoderma edule.* Spawning patterns, while sometimes occurring with an annual periodicity in certain species of bivalves, are considered in this chapter to be more accurately described as semiperiodic events and will therefore be considered in the next section. Further discussions of annual growth patterns within the molluscan shell may be found in Rhoads and Pannella (1970) and Clark (1974), and in Chapter 7.

2.2.5. Semiperiodic or Random Events

Many patterns are encountered within the shells of molluscs that do not occur with definite cyclic periodicities. "Subdaily" growth incre-

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* Similarly, Martin *et al.* (1977), in their study of *Nautilus macromphalus,* interpreted observed periodic weight fluctuations, occurring at intervals of approximately 30 days, to indicate the formation of new septa.

† Annual patterns have generally not been recognized in deep-water molluscan species; in such species, major growth patterns have been interpreted to mark spawning events (Rhoads and Pannella, 1970).

ments described by numerous workers may be examples of such aperiodic features (Pannella and MacClintock, 1968; Kennish and Olsson, 1975; Kennish, 1976, 1977b; Gordon and Carriker, 1978) (also see Chapter 7). Distinct microgrowth patterns also result from damage to the shell margin (see Chapter 7 for detailed illustrations and discussions of these patterns). Notching of the shell with a small file, for instance, causes formation of a distinct disturbance line and microgrowth pattern (see Pannella and MacClintock, 1968; Kennish and Olsson, 1975; Kennish, 1976, 1977b) (also see Chapter 7). Shell damage caused by predator attacks may result in similar growth patterns. Storm events are often recorded in the shell and can sometimes be recognized by the presence of associated silt particles that are trapped between the mantle and the shell during the storm and are then subsequently incorporated into the shell (Barker, 1974; House and Farrow, 1968; Rhoads and Pannella, 1970; Kennish and Olsson, 1975) (also see Chapter 7). Certain pollution events, such as the discharge of heated effluent waters from nuclear or fossil fuel power plants, may also result in the formation of microgrowth patterns within the shell (Kennish and Olsson, 1975) (also see Chapter 7). Rhoads and Pannella (1970) demonstrated that the transplantation of organisms to different environments will often result in marked differences in the pattern of microgrowth increments before and after transplantation. Spawning events, which may be considered semiperiodic, have been found to be reflected in microgrowth patterns within almost all molluscan shells that have been examined in detail. Even bivalves (e.g., *Malletia*) from depths as great as 4970 m have patterns that have been interpreted to mark spawning events (Fig. 9) (also see Rhoads and Pannella, 1970). Pannella and MacClintock (1968), and later Rhoads and Pannella (1970), Kennish and Olsson (1975), and Kennish (1976, 1977b, 1978) (also see Chapter 7), presented detailed descriptions and illustrations of the appearance of spawning patterns in a few species of shallow-water bivalves. For a further detailed discussion of the types of semiperiodic and random events that can be recorded within the molluscan shell, see Chapter 7.

2.3. Ecological and Paleoecological Applications

Ecology has been defined as the study of relationships between organisms and their environment. In functioning ecosystems, it is possible to make direct observations of these relationships and their temporal changes. Organism–environment relationships cannot always be directly measured, however, but may require an indirect or deductive approach; for instance, one may wish to assess the effect of a storm, pollution event, change in salinity, temperature, or other factor on a population after the
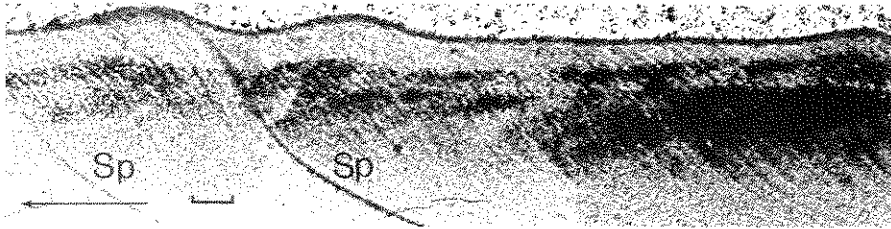
Figure 9. Optical micrograph of a thin section of the outer shell layer of *Malletia* sp. from 4970 m on the lower continental rise. Two major breaks in shell deposition have been interpreted by Rhoads and Pannella (1970) to mark spawning events (Sp). Arrow indicates direction of growth. Scale bar: 100 μm. Thin section YPM-IP 28157. Reprinted with permission from Rhoads and Pannella (1970).

event has taken place. In the absence of data about predisturbance rates of growth, death, and reproduction, one is totally dependent on indirect techniques. This kind of after-the-fact problem is common in paleoecology and promises to be an increasingly important approach in ecological studies. In this section, we will consider the various ways in which detailed analyses of molluscan microgrowth patterns have been applied to ecological and paleoecological studies, and we will speculate on their future applications.

Microgrowth increments have proven especially useful in recognizing how seasonally variable environmental factors affect molluscan growth. For instance, through analysis of patterns of "daily" microgrowth increments, Farrow (1971) found that a substantial portion of a population of the shallow subtidal cockle *Cerastoderma edule* from the Thames estuary in England stopped growing during winter because of subzero temperatures. Similarly, Tevesz (1972) observed that *Gemma gemma* Totten grew very little in the winter; growth increments were very closely spaced, and the inner shell layer had a brownish hue. During the summer, *G. gemma* grew rapidly; microgrowth increments were widely spaced, and the inner shell layer was clear and translucent in appearance. Through an examination of microgrowth increments in numerous acetate peels, Evans and LeMessurier (1972) were able to demonstrate striking winter growth rate differences between two sympatric species of bivalves. They found winter growth of the rock-boring clam *Penitella penita* to be approximately 75% of the summer growth rate, while the growth rate of the cockle *Clinocardium nuttalli* which inhabited a neighboring mud flat, decreased during the winter, relative to the summer, by a factor of as much as 19. For further examples and discussions of the usefulness of microgrowth increments for reconstructing seasonal variations in molluscan growth, see House and Farrow (1968), Pannella and MacClintock (1968), and Rhoads and Pannella (1970).

Microgrowth increment patterns can also supply detailed information on the age of individual specimens at the time of death, as well as the season of their death. In those species for which the periodicities of microgrowth patterns have been established, the age at death is readily obtained by simply counting the total number of patterns. The periodicity with which the counted patterns occur (e.g., daily, fortnightly, annual) will determine the precision of the age estimate. The season of death is determined by relating the position of the last increment at the margin of the shell to the seasonal growth pattern (Fig. 10). For example, a margin preceded by a complete summer depositional record represents death early in the fall. A margin that follows a long period of winter growth represents late winter or early spring death. Often, however, when the shell margin is preceded by a few days of growth slowdown, comparison of several specimens may be necessary to determine whether growth-rate changes reflect a moribund condition prior to death or are related to seasonal changes (Rhoads and Pannella, 1970). By counting the number of microgrowth increments (or patterns of increments), it is also often possible to relate the season of death to absolute age at death. Furthermore, the identification of the season of death and age at time of death in a mollusc assemblage may be used to distinguish a mass mortality from a death assemblage produced by natural mortality. As emphasized by
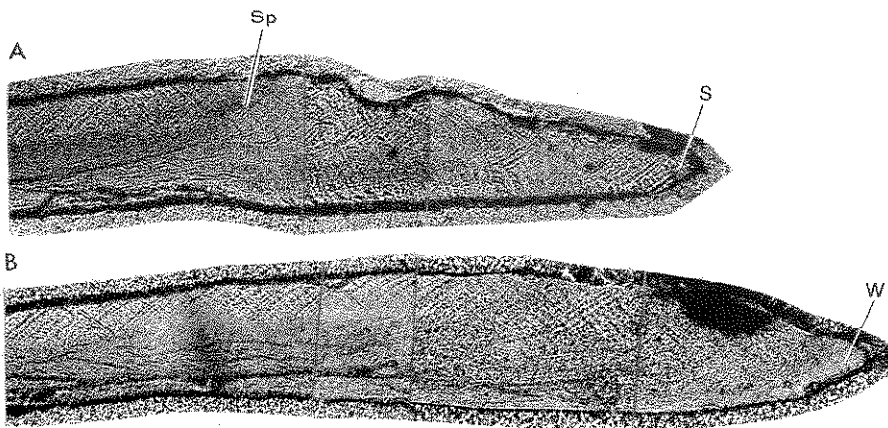
Figure 10. Summer and winter death recorded in microgrowth increment patterns of *Gemma gemma* Totten. (A,B) Optical micrographs of acetate peels of polished and etched shell sections. (A) Summer death (S). The shell edge is preceded by relatively large increments characteristic of summer growth. In the earlier part of the shell, the thin increments are probably related to spawning (Sp). Acetate peel YPM-IP 28158. (B) Winter death (W). The shell edge is preceded by thin increments marking a period of slow growth. Thicker bandings in the early part the shell mark the preceding summer's growth. Acetate peel YPM-IP 28163. Reprinted with permission from Rhoads and Pannella (1970).

Rhoads and Pannella (1970), this information may be used to determine seasons of peak environmental stress. This technique can be especially useful when applied to drilled shells. By determining the season of death of drilled members of a population, one may identify the season of peak predator activity (Rhoads and Pannella, 1970).

Microgrowth increment patterns can also frequently be utilized to determine the age at sexual maturity and season of reproduction by relating the position of spawning breaks to absolute age and the seasonal pattern of growth. An illustration of how growth patterns have been used for such purposes is provided by Rhoads and Pannella (1970) in their analysis of microgrowth patterns in the shell of Gemma gemma.

Variations in environmental parameters including food supply, substratum type, salinity, dissolved oxygen, turbidity, temperature, and population density can influence the growth of bivalves. Hallam (1965) reviews these various environmental parameters as causes of stunting and dwarfing of living and fossil marine benthic invertebrates. Several studies conducted over the past few years have used microgrowth increments to define the effects on bivalve growth of various environmental perturbations, such as those outlined by Hallam (1965). Rhoads and Pannella (1970), for example, through careful examination of microgrowth patterns on both acetate peels and thin sections, have shown that Mercenaria mercenaria grows faster in sandy sediments than in mud when other variables are eliminated. Also, these workers analyzed microgrowth increment patterns within Astarte castanea Say and M. mercenaria to demonstrate that growth rate (and shell structural) changes occur when specimens of these species are transplanted from a natural subtidal environment to a laboratory holding tank without substratum (Fig. 11). Farrow (1971) used microgrowth increments within the shell of Cerastoderma edule to illustrate that high-density populations of this species had a much shorter growing season than low-density populations. An inverse relationship between individual cockle size and cockle population density was also noted. In a subsequent study, Farrow (1972) used microgrowth increments within the outer shell layer of C. edule to demonstrate that individual specimens living in the high intertidal zone were stunted relative to low intertidal specimens. The higher-shore cockles were situated near the high-water mark and, consequently, were aerially exposed for several days during neap tides. Following neap tide deceleration, there was a resumption of vigorous growth. Many of the high-intertidal cockles were some two thirds the size of specimens in the lower intertidal zone, where growth was more continuous.

Microgrowth patterns can also provide evidence about the biology of deep-water molluscs. Preliminary data of Rhoads and Pannella (1970) indicate that such patterns can shed light on problems related to deep-
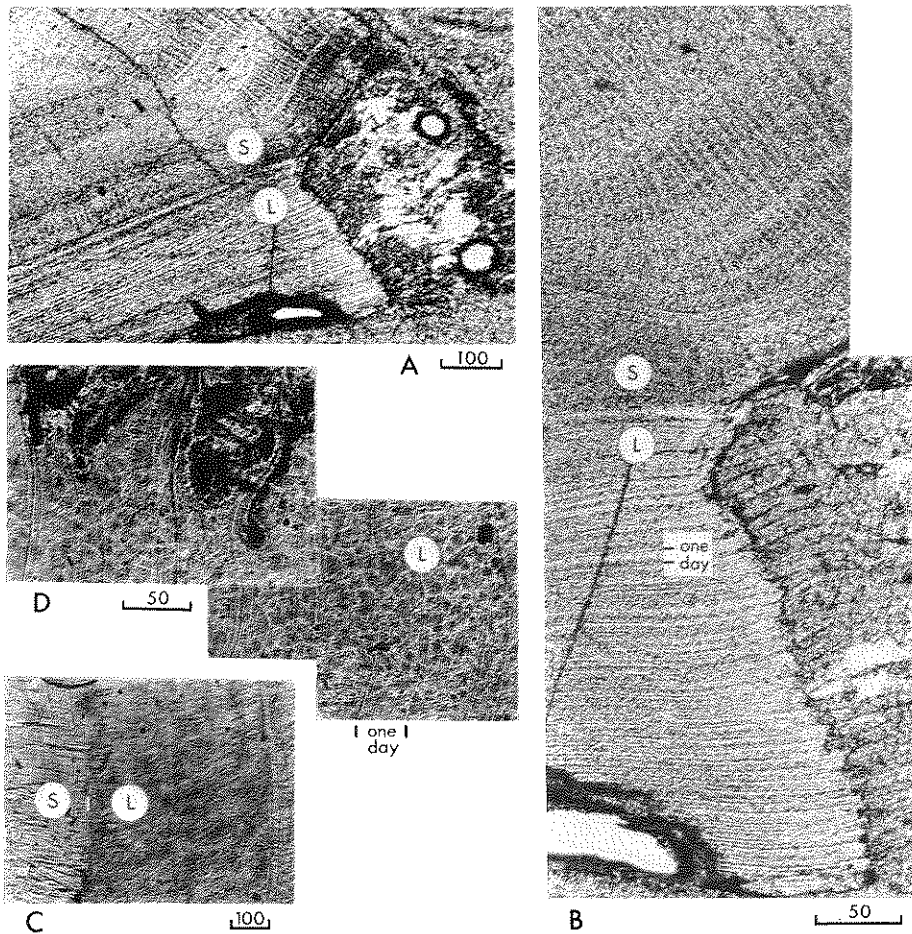
Figure 11. (A–D) Optical micrographs of acetate peels prepared from polished and etched shell sections. (A) Acetate peel of an *Astarte castanea* Say specimen transplanted from a subtidal environment (S) to a laboratory holding tank without substratum (L). Periostracal extensions and changes in shell structure and growth rate mark the transplant event. (B) Enlargement of (A). A daily growth increment is shown. Acetate peel YPM-IP 28159. (C,D) Acetate peels of a *Mercenaria mercenaria* (Linnaeus) specimen transplanted from a subtidal environment (S) to a laboratory holding tank without substratum (L). (C) Changes in shell structure and growth rate mark the transplant event; (D) enlargement of periostracal extensions showing a large daily growth increment. Acetate peel YPM-IP 28161. Scale bars in micrometers. Reprinted with permission from Rhoads and Pannella (1970).

water periodicity in growth and reproduction, as well as yield information on temporal variations in the deep-water environment. Furthermore, study of the relationship of microgrowth patterns to bathymetry has yielded information on the effect of water depth on calcification (Rhoads and Pannella, 1970). Preliminary results suggest that microgrowth patterns within the shells of fossil molluscs may be of use in paleobathymetric studies for defining relative depth gradients in Phanerozoic marine environments. As discussed by Rhoads and Pannella (1970), a bathymetric change from shallow to deep water is accompanied by decreased surface wave motion at the bottom, decreased light penetration, and decreased variation in temperature, salinity, and food supply. Depth variation in the fluctuation of the physical–chemical environment should be reflected in features of microgrowth patterns.* Microgrowth increments of deepwater species are relatively regular in thickness and have poorly defined boundaries that are delimited by color variation. Shallow-water bivalves, especially those living in the boreal intertidal zone, show sharply delimited microgrowth increment boundaries, and these increments show differences in thickness related to tidal and seasonal periodicities. Data available at present (i.e., Rhoads and Pannella, 1970) are limited to species from extremes in bathymetric range. Further work on the relationship of microgrowth patterns to water depth is required for species from intermediate water depths, especially on either side of the seasonal thermocline.

Clark (1974), in his review of growth lines in marine invertebrate skeletons, summarizes a few potential ecological uses of microgrowth increment patterns that have not been discussed above. For example, he points out that the presence of disturbance lines, or variation in the spacing of periodic lines, can be used as an index of environmental variability, and high variability argues for relatively shallow water. Similarly, the presence of annual patterns of microgrowth increments suggests a climate with well-defined seasons, and the presence of increments occurring with a tidal periodicity implies a habitat in or near the intertidal zone. Clark (1974) summarizes his review by stating that "virtually any approach which can be used to demonstrate that growth lines form today as reflections of the environment can be turned about to make interpretations of past environments from fossil lines . . . ." Along these same lines, Pannella and MacClintock (1968) have suggested that seasonal and climatic variations of microgrowth patterns can be useful in the study of latitudinal distributions of fossil assemblages. Similarly, Hall (1975) found that the number of microgrowth increments in "biochecks and bands of fast

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* Pannella (1976) has more recently extended and refined these ideas, providing evidence that microgrowth patterns within the shells of fossil molluscs can be used to reconstruct tidal curves of paleoseas.

growth" within the shells of *Tivela stultorum* and *Callista chione* varied with age, latitude, and water depth, and has suggested that counts of microgrowth increments in similar shell regions of fossil specimens might be of use in reconstructing both paleolatitudes and paleoclimate.

In all the examples discussed in the preceding paragraphs, observed changes in microgrowth increment patterns result from natural environmental perturbations. With the increased potential environmental impact of many of man's activities (e.g., dredge-spoil dumping, oil spills, thermal discharges, disposal of chemical and radioactive wastes), the number of environmental perturbations of anthropogenic origin has been steadily increasing, and these anthropogenic changes in the environment can also be recorded in skeletal growth. One of the best examples of how such pollution events can be manifested within the molluscan shell comes from a recent study conducted by Kennish and Olsson (1975). These workers analyzed in detail microgrowth increments within the shell of *Mercenaria mercenaria* to define the effects of thermal discharges from a nuclear power plant on the growth of this species. They found that clams from within a mile radius of the mouth of the discharge canal of the nuclear plant had a much higher number of shell-growth interruptions, thinner shells, and slower summer growth rates than did clams farther from the plant. By counting growth increments back from the shell margin, they were able to determine that many of the growth breaks* were associated with rapidly changing water temperatures that resulted from abrupt shutdowns and startups of the power plant.† Kennish and Olsson (1975) also suggested that the thermal effluent may be adversely affecting physiological functions other than growth. At the station nearest the effluent, no spawning breaks were observed within the shells, while such breaks were seen in specimens from all control sites.

In summary, the fact that microgrowth increment patterns reflect environmental changes has many applications to ecological and paleoecological problems. As we have attempted to emphasize, comparison of growth patterns among specimens collected from different biotopes may be used to identify clinal gradients in growth. Recognition of growth gradients (both spatial and temporal) in Recent and fossil assemblages may greatly assist both the ecologist and the paleoecologist in recognizing environmentally related stress gradients. When these and the other appli-

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* Such breaks were associated with relatively unique patterns of microgrowth increments within the shell. See Chapter 7, Plate IIe–g, for photographic illustrations of this type of break (and associated microgrowth increment patterns) in *Mercenaria mercenaria*.

† The growth rate of *M. mercenaria* generally increases with increasing temperatures and peaks between 20 and 24°C; Haskin (communicated to Kennish and Olsson, 1975) found decreased growth of *M. mercenaria* above 26°C. The thermal effluent raised water temperature in areas around the nuclear plant 3–5°C above ambient.

cations discussed above are combined, the molluscan shell might well be interpreted as a long-term continuous environmental recorder.

3. Shell Structural Changes

At this point, it is imperative that the reader recognize that we are no longer discussing microgrowth increment patterns. A distinction was made, in the introduction to this chapter, between patterns of microgrowth increments and patterns associated with shell structural changes. We thus emphasize once again that shell structural changes, which are considered in the following discussion, are associated either with changes in shell microstructure (see Appendix 2.B for a guide to shell microstructures) within a given layer or shifts in the relative position of shell layer boundaries on the depositional surface.* As stated earlier, we use the general term "structure" in reference to shell structural types (i.e., shell microstructures) or in reference to the arrangement of shell layers.

In Chapter 2, Carter emphasizes that the type of structure deposited within the molluscan shell is strongly biologically (genetically) controlled and more or less independent of environmental influences. It is also pointed out in Chapter 2 that notable exceptions to this generalization exist—in particular, structural changes associated with changes in (1) employed respiratory pathways and (2) shell mineralogy. In the following discussion we will consider these exceptions in detail and summarize a few other apparent exceptions that may or may not be related to metabolic changes. Before discussing the growth patterns themselves and their applications, we will outline hypothesized mechanisms responsible for the formation of certain structural changes within the shell.

3.1. Formation of Structural Changes

For over 50 years workers have recognized that structural changes observed within the shells of certain bivalves may reflect changes in environmental conditions (Weymouth, 1923; Dodd, 1964; Davies and Sayre, 1970; Kennish and Olsson, 1975; Lutz and Rhoads, 1977). Only recently, however, have mechanisms responsible for some of these changes been considered in detail. In 1970, Davies and Sayre (1970) suggested that various conditions of environmental stress could lead to shell dissolution and, furthermore, that such dissolution events were recorded in the ultrastructure of the shell. More recently, Lutz and Rhoads (1977) have hy-

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* We include here the addition of a shell layer (e.g., addition of a calcitic layer to cooler-water representatives of a largely aragonitic species).

pothesized that extensive reworking of original shell microstructure occurs as a result of environmentally controlled alternating periods of shell deposition and dissolution associated with utilization of aerobic and anaerobic pathways, respectively. Evidence that such shell-destructive mechanisms may be operating in bivalves during periods of environmental stress has been provided by Lutz (1976b, 1977) and Lutz and Rhoads (1977, 1978) through a detailed analysis of seasonal and geographical variation in the shell structure of a Recent mytilid (*Geukensia demissa*). In the following paragraphs we will summarize the results obtained by these workers to provide an example of the manner in which environmentally induced metabolic changes might drastically alter the original structure of a bivalve shell. Preparation procedures for analysis of described structural changes may be found in Appendix 1.A.1–3.

The structure of the inner shell layer of *G. demissa* varies not only with season, but also with latitude. If specimens from relatively cold-water (high-latitude) environments, such as the Gulf of Maine, are examined, the seasonal sequence of events occurring on the growth surface of the inner shell layer is summarized as follows: During the warm summer months (June through September), very regular hexagonal nacreous tablets are arranged in steplike patterns characteristic of bivalve nacre (Fig. 12A). As water temperatures decline, the nacreous tablets become smaller and less regular,* showing visible signs of corrosion in the form of marked pitting and hollow crystals (Erben, 1972; Wada, 1972), as well as increased proportions of fine-grained structures (Fig. 12B–D). An increased stacking of nacreous tablets (i.e., increased proportions of columnar nacre) is also apparent in various areas of the inner layer growth surface (Fig. 13). During the colder months of the year (January to March, with water temperatures below 3°C), shell corrosion becomes visible to the naked eye, the entire inner shell surface often presenting a chalky white appearance. Ultrastructurally, this surface appears uniformly fine-grained (Fig. 12E). Similar macroscopically visible corrosion has been reported in *Mercenaria mercenaria* after long periods of valve closure resulting from extended periods of anaerobiosis (Dugal, 1939). The ability of *G. demissa* to respire anaerobically for extended periods of time has been described (Kuenzler, 1961; Lent, 1967, 1968, 1969), as has the relative increased efficiency, in this species, of some of the citric acid cycle enzymes in an anaerobic direction (Hammen and Lum, 1966). The observed shell corrosion may well be a reflection of buffering of acidic end products from anaerobic metabolism during the colder months, when oxygen transport into the cells should theoretically be reduced relative to that occurring at higher

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* A similar irregularity of nacreous crystals as a result of dissolution during reduced winter temperatures (as low as 8°C) was found by Wada (1972) in his examination of growth surfaces of *Pinctada martensii* and *Pinna attenuata*.
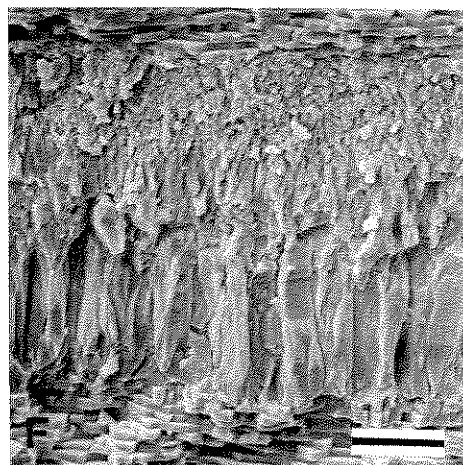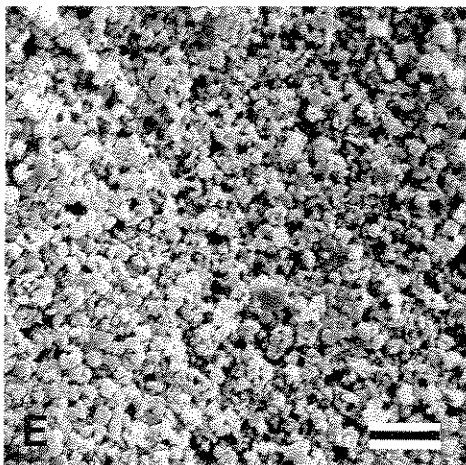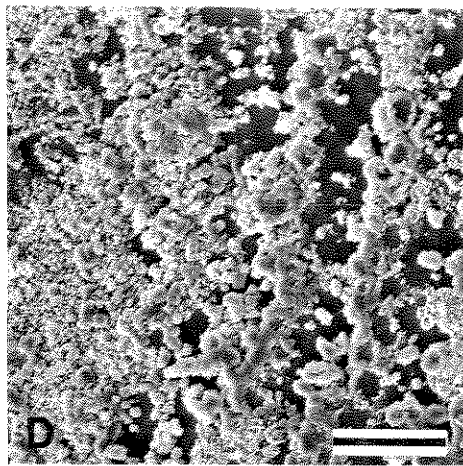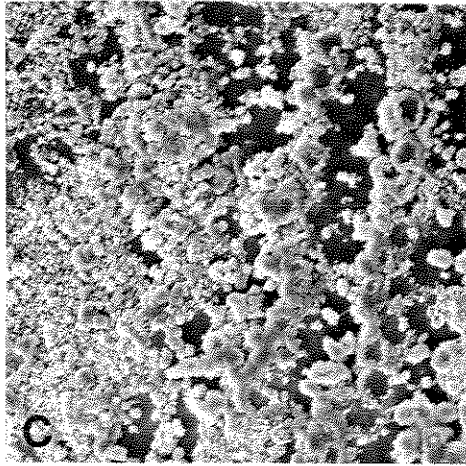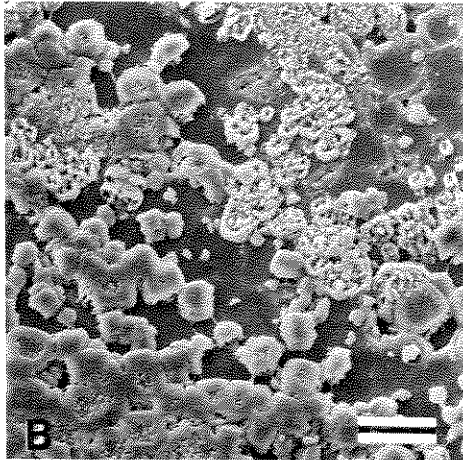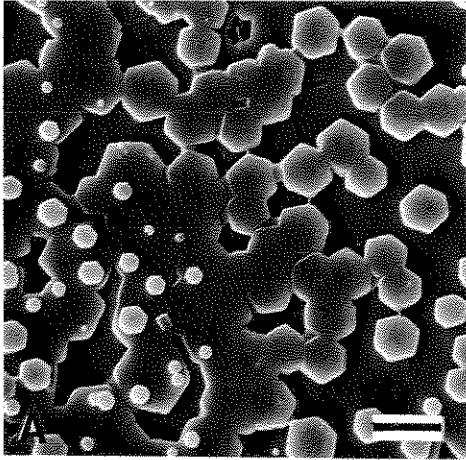
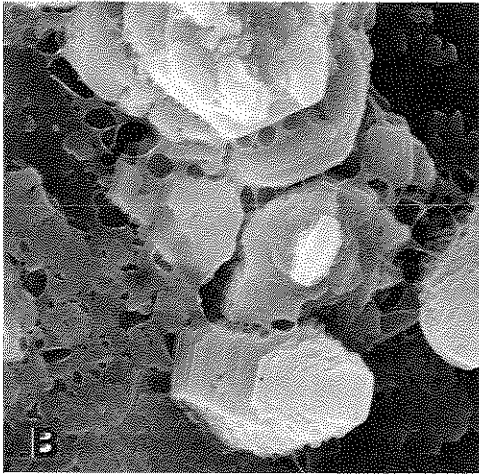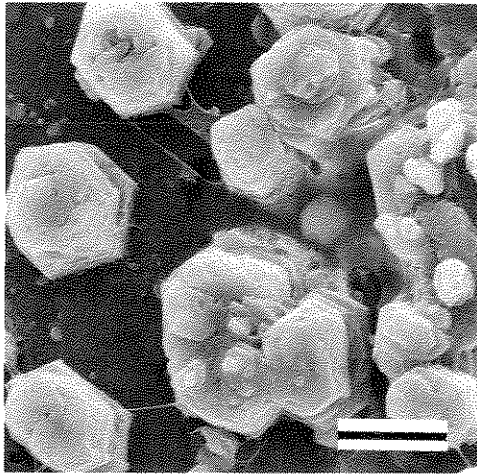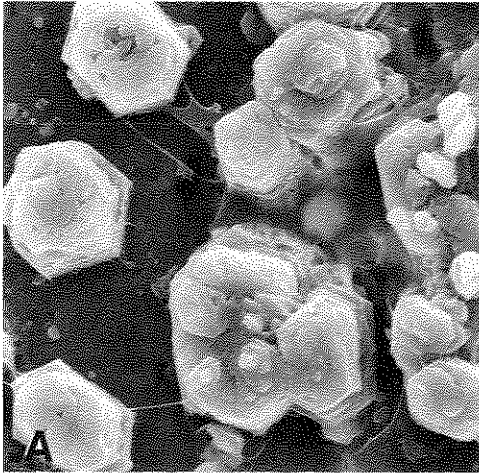temperatures (Lange *et al.*, 1972). Wilbur (1972) has suggested that during periods of "adverse environmental conditions," shell decalcification may predominate over growth. The gradation in fractured, as well as polished and etched, vertical shell sections of *G. demissa* nacreous laminae into fine-grained structures (suggestive of massive corrosion) instead of regular prisms (Fig. 12F) tends to support this view. As water temperatures increase during the spring, the sequence of events described above is reversed. Examination of growth surfaces during transition periods (spring and fall) between normal nacreous deposition (summer) and drastic corrosion (winter) reveals differential dissolution of calcium carbonate and organic material, with corroded aragonitic tablets above and below exposed sheets of inter-lamellar organic matrices (Fig. 13). Despite such shell dissolution, successive monthly samples often indicate a net gain of shell material during these "transition" periods. We therefore suggest that the observed growth surfaces are a reflection of alternating periods (not necessarily rhythmic) of shell deposition and destruction. Here, alternating periods of aerobic and anaerobic metabolism, respectively, which have already been demonstrated to occur in at least one species [*M. mercenaria* (Crenshaw and Neff, 1969; Gordon and Carriker, 1978)], could easily provide the driving forces.

In the preceding paragraph we have described changes occurring primarily on the growth surface itself. When the shell is viewed in section, using fracture, acetate-peel, or thin-section techniques (see Appendix 1.A. 1,2), one is able to observe how these changes are recorded within the shell. Figures 12F and 15B depict, respectively, a fractured section and an acetate peel of a polished and etched longitudinal section of the inner layer of a *G. demissa* shell valve from the Gulf of Maine (Damariscotta River, Lincoln County, Maine). In these sections one observes a gradation (progressing toward the inner shell layer growth surface) of nacreous laminae into fine-grained "homogeneous" structure that gradually becomes

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Figure 12. Scanning electron micrographs of *Geukensia demissa* (Dillwyn). (A–E) Inner shell layer growth surface as seen during various months of the year. (A) Regular hexagonal nacreous tablets arranged in steplike patterns characteristic of bivalve nacre (August sample). Scale bar: 10 μm. (B) Small, irregular nacreous tablets showing visible signs of corrosion in the form of marked pitting and increased proportions of fine-grained structures (November sample). Scale bar: 5 μm. (C,D) Extremely irregular nacreous tablets with considerable amounts of fine-grained structures (December sample). The stereo pair was taken with a 6° angular displacement between exposures. Scale bar: 10 μm. (E) Fine-grained structures reflective of extensive shell dissolution during the colder months of the year (February sample). Scale bar: 10 μm. (F) Vertical fracture through the inner shell layer. Nacreous tablets grade into fine-grained structures at the top of the micrograph, and the prisms grade into nacre at the bottom. The most recently deposited crystals are at the bottom of the micrograph. Scale bar: 10 μm. Micrographs A, B, E, and F reprinted with permission from Lutz and Rhoads (1977). Copyright © 1977 by the American Association for the Advancement of Science.
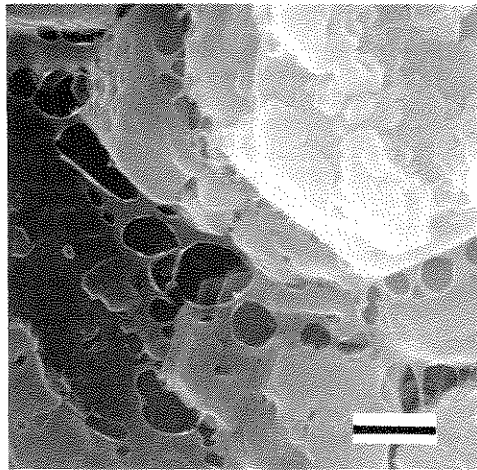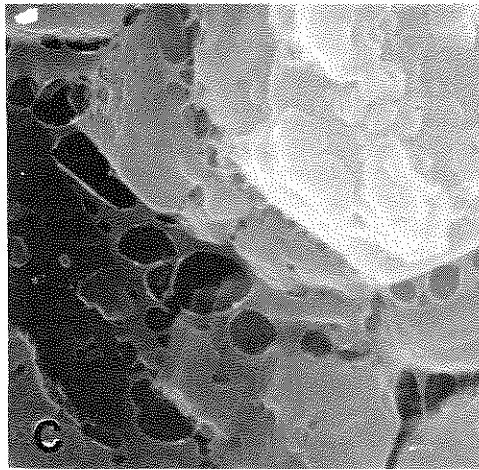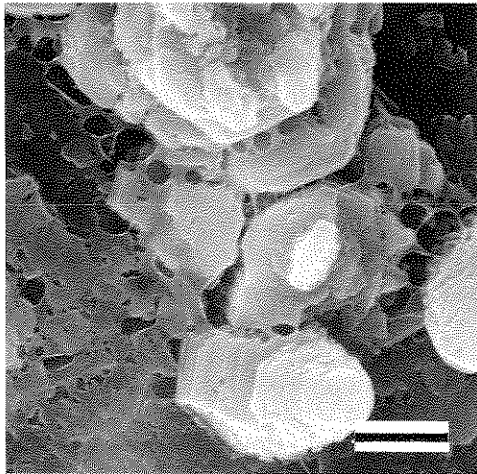
increasingly coarse-grained and subsequently grades into simple aragon-
itic prisms. In turn, these simple prisms, which are strikingly similar in
appearance to myostracal prisms, grade into nacreous tablets. It is also
interesting to note that at the bottom of Figure 12F, the first few nacreous
tablets appear to be stacked upon one another, while subsequently de-
posited tablets assume a more steplike [Treppen (see Schmidt, 1923; Wise,
1970a,b)] pattern. These repetitive changes result in a series of distinct
sublayers within the inner shell layer of mature specimens.

We have described above the sequence of seasonally related changes
occurring on the growth surface and within the shell of G. *demissa* spec-
imens from relatively cold-water (high-latitude) environments. Seasonal
changes occurring on the inner shell layer surface of specimens from
warmer-water environments (e.g., south of Cape Cod on the east coast of
North America) are somewhat more complex. In these populations, one
still sees alternating sublayers associated with cold-water shell deposition
and dissolution, but one also encounters irregular prismatic sublayers that
are associated with extremely warm summer temperatures (Lutz and
Rhoads, 1978). These irregular prismatic sublayers may be associated with
the increased utilization of anaerobic pathways during the hot summer
months when oxygen solubility is markedly reduced. However, in all the
specimens examined to date from south of Cape Cod (Lutz, 1976b, 1977;
Lutz and Rhoads, 1978), we have never observed homogeneous structures
in "warm-water" sublayers. This may well indicate decreased shell-de-
structive processes at relatively high (relative to extremely low) temper-
atures. When viewed in longitudinal section, such complex seasonal var-
iation often results in an alternation of three distinct types of sublayers
within the inner layer: (1) irregular prismatic ("warm-water" sublayer);
(2) homogeneous + irregular prismatic ("cold-water" sublayer); and (3)
nacre. These three types of sublayers are generally present in the majority
of specimens sampled from relatively temperate environments (e.g., Cape
Cod to Cape Hatteras) (Figs. 14 and 15C). In subtropical environments
(e.g., south of Cape Hatteras), homogeneous structures are absent, result-
ing in an alternation of only irregular prisms and nacre (Fig. 15D).

Structural patterns described in the preceding discussion are sum-
marized in Fig. 15. The micrographs in this figure depict acetate peels of
the inner shell layer of G. *demissa* specimens from four geographically

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Figure 13. Scanning electron micrographs of the inner shell layer growth surface of Geu-
kensia demissa (Dillwyn) showing natural shell dissolution. Stereo pairs were taken with
a 6° angular displacement between exposures. Note the marked pitting and stacked ap-
pearance of nacreous tablets. The differential solubility of calcium carbonate and organic
matrices is apparent. Scale bars: (A) 5 μm; (B) 2 μm; (C) 1 μm. Reprinted with permission
from Lutz and Rhoads (1977). Copyright © 1977 by the American Association for the Ad-
vancement of Science.

Figure 14. Optical micrograph of an acetate peel prepared from a polished and etched anteroposterior longitudinal section of a *Geukensia demissa* shell from Wachapreague, Virginia. The micrograph is taken in the region of the umbo. Three types of sublayers are apparent: (1) nacre (n); (2) irregular prismatic (p); (3) irregular prismatic (p) + homogeneous (h). Note the decreased percentage of nacre in the most recently formed regions (bottom of micrograph) of the shell. Scale bar: 100 μm.
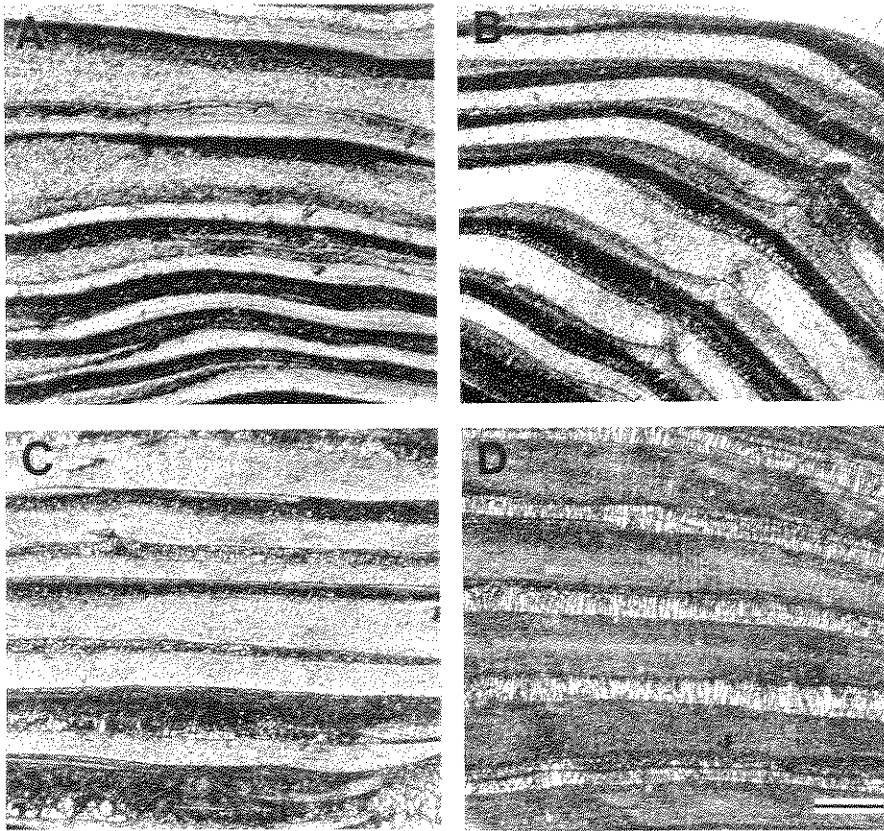
Figure 15. Optical micrographs of acetate peels prepared from polished and etched anteroposterior sections of the inner shell layer of *Geukensia demissa* specimens from four latitudinally separated populations. All micrographs were taken in the region of the umbo. The direction of growth is toward the left. (A) Specimen sampled from St. Peter's Bay, Prince Edward Island. (B) Specimen sampled from the Damariscotta River, Lincoln County, Maine. (C) Specimen sampled from Wachapreague, Virginia. (D) Specimen sampled from Cape Kennedy, Florida. Scale bar (applicable to all four micrographs): 100 μm.

separated populations from Prince Edward Island to Florida. Marked differences in the percentages of various structural types are obvious.

The mechanism described above for the formation of structural changes has important implications. For example, in paleotemperature studies based on oxygen isotope analyses, it is important to realize that truncated seasonal paleotemperature curves may reflect a net loss of shell material during certain times of the year (see Chapter 5). Similarly, shell dissolution may account for certain apparent ontogenetic discontinuities in elemental (or chemical) distribution patterns within the shells of individual specimens (see Chapter 4). We hope that the implications of shell

dissolution and redeposition discussed above will eventually result in the realization that the shell is far more than a simple accretionary deposit.

3.2. Documented Growth Patterns and Their Ecological, Paleoecological, and Phylogenetic Applications

In the previous section, we proposed a hypothesis for the mechanisms responsible for the formation of *certain* structural changes within the molluscan shell. At this point, it is important for the reader to realize that not all the patterns that will be discussed here necessarily reflect periodic or aperiodic respiratory changes. Alternate hypotheses for the formation of structural growth patterns are discussed by Carter in Chapter 2.* The reader should also realize that relatively few studies have been conducted in which patterns of structural change within molluscan shells have been adequately documented and analyzed. Thus, while it may appear that we have summarized the results of only a few relatively specific studies, we have, in fact, presented a comprehensive review of the status of current knowledge.

Environmentally controlled variation in the mineralogy of the molluscan shell is discussed in Chapter 2 and will therefore not be considered in detail here. Worth mentioning, however, is some early work that is relevant to subsequent studies of shell structural variation. In 1954, Lowenstam (1954) showed that the relative amounts of aragonite and calcite composing the shells of certain molluscs can reflect environmental conditions at the time of shell formation. Since aragonite and calcite are present in distinct structural units in molluscan shells (Bøggild, 1930), the variation in shell mineralogy found by Lowenstam (1954) suggested to Dodd (1963, 1964) that variation in the structure of the shell should also occur. As a result, Dodd conducted two detailed studies of the effect of temperature on the shell mineralogy and structure of the Recent mytilid

* As mentioned in Chapter 2, sublayers of simple aragonitic prisms possibly result from temporary mantle attachment (Taylor, J. D., et al., 1969). While this might be viewed as an alternate hypothesis of structural growth pattern formation, it may not be independent of the mechanisms outlined in this chapter. It is conceivable, for example, that mantle attachment itself may be a direct consequence of anaerobiosis. Personal observations on *Arctica islandica* specimens that have been kept for extended periods of time under anoxic conditions have suggested that the entire surface inside the mantle inside the pallial line may be attached to the shell during anaerobiosis. If this is indeed the case, the entire surface of the mantle might be acting, during such periods, as a "muscle" that attaches the shell to the soft tissues. If so, the genetic term "myostracal prisms," which has been used by J. D. Taylor et al. (1969, 1973), may well appropriately characterize simple prisms occurring within sublayers in the inner shell layer of this (see Fig. 19) and other species of molluscs. Before the term "myostracal prisms" can be employed, however, it must be demonstrated that the entire mantle surface can be appropriately termed a "muscle"; until evidence for this is provided, it is probably best to refer to such simple aragonitic prisms as "myostracal-like" prisms.

Mytilus californianus. Significant results obtained by Dodd (1963, 1964) for this species were as follows: (1) the percentage of aragonite in the shell varies with temperature; (2) the extent and development of the inner calcitic prismatic layer are strongly dependent on growth temperature; (3) wedges of nacreous structure that often project into the inner prismatic layer form annually, making age determination of the shell possible; (4) growth rates determined from these wedges are directly proportional to mean temperature of the growth locality; and (5) quantitative paleotemperature determination based on shell-structure variation in this species is possible. Moreover, Dodd suggested that the shell structure of other species of molluscs, particularly those having shells composed of a combination of calcite and aragonite, could potentially be used for determining paleotemperatures.

Since the pioneering work of Dodd (1963, 1964), several workers have examined the effects of temperature (or latitude) on the shell structure of various species of bivalves. Blackwell *et al.* (1977) considered the possibility that the structure of the "middle" aragonitic prismatic layer of *Geukensia demissa* varied with latitude, but concluded that the observed variation reflected subspecific differences and not a climatic gradient coinciding with the geographical range of this species. More recently, however, Lutz (1976b, 1977) and Lutz and Rhoads (1977, 1978) have shown that the structure of the inner shell layer of this species varies with both season and latitude. The extent of this variation can be seen in Fig. 15. It should be apparent from a close examination of the micrographs in this figure that there is a relatively sharp decrease in the percentage of homogeneous structure with decreasing latitude (or increasing mean temperature). In light of this, it may eventually be possible to develop a quantitative approach [similar to that developed by Dodd (1964) for *M. californianus*] for the analysis of growth patterns within the shells of *G. demissa* and other closely related Recent and fossil species. Such an approach may prove useful in ecological studies for defining the effect of thermal stress gradients (e.g., power-plant waste-heat gradients) on bivalve shell growth and in paleoecological studies for defining both spatial and temporal paleotemperature patterns. Furthermore, analysis of structures adjacent to the inner shell layer surface of *G. demissa* from death assemblages* should prove useful in ecological, paleoecological, and ar-

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* In analyzing the shells of specimens from death assemblages, one needs to distinguish postmortem shell dissolution from shell dissolution that occurred while the organism was alive and respiring anaerobically. In the case of *G. demissa,* this is readily done by comparing growth surfaces of shell layers on either side of the pallial line. During anaerobiosis, shell structural changes in this species are apparent only within that portion of the shell inside the pallial line; evidence of dissolution of nacre on both sides of the pallial line (i.e., in both the middle nacreous layer and the inner layer of the shell) would indicate postmortem diagenesis.
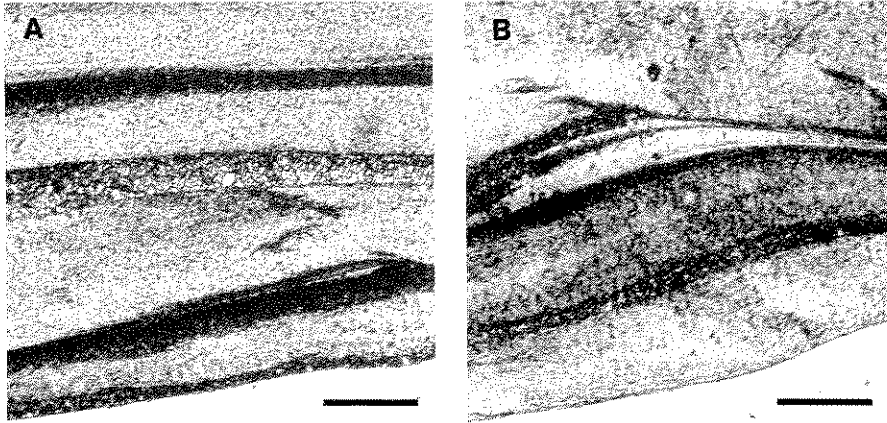
Figure 16. Optical micrographs of acetate peels of polished and etched anteroposterior longitudinal sections of *Geukensia demissa* shells sampled at different times of the year. Examination of structures adjacent to the inner shell layer surface should prove useful for defining the season of death of individual specimens. (A) Specimen sampled on August 4, 1976, at Wachapreague, Virginia. Note irregular prismatic structure at the growth surface (bottom of micrograph. Scale bar: 50 μm. (B) Specimen sampled during mid-October at Crisfield, Maryland. Note nacre at the growth surface (bottom of micrograph). Scale bar: 50 μm.

cheological studies for defining the season of death of individual specimens (Fig. 16).

Other studies in which structural changes have been observed to be associated with thermal stress include those of Kennish and Olsson (1975), Kennish (1976, 1977a,b, 1978) (also see Chapter 7), and Farrow (1972). In their studies of the effects of thermal discharges on the microstructural growth and mortality of *M. mercenaria*, Kennish and Olsson (1975) and Kennish (1976, 1977a,b, 1978) found that "crossed lamellar structure"* replaced prismatic structure in the outer shell layer of this species throughout the duration of high-temperature stress periods. Farrow (1972) reported a somewhat similar phenomenon in *Cerastoderma edule*, in which a greater prominence of "crossed lamellar structure" in the outer shell layer was observed to be associated with winter reduction in growth rate. Farrow further observed that the lamellae became "markedly deflected" if an actual "stoppage" of growth took place.

Bryan (1969) described drastic changes within the shell of the gastropod *Nucella lapillus* that occurred subsequent to addition of oil-spill removers ("detergents") to the organisms' natural environment (following

* For an interpretation of regions containing "crossed lamellar structure" in the outer shell layer of *Mercenaria mercenaria* and *Cerastoderma edule*, see Chapter 2.

a large spill of Kuwait crude oil). When N. lapillus shells were sectioned longitudinally or transversely, it was found that "the shell edges had often been temporarily sealed by continuing the inner nacreous layer of the shell to the outer surface. Later growth of the shell was laid down on this nacreous layer partition and this produced a growth mark and a line of weakness in the shell" (Bryan, 1969, pp. 1074–1075).

Many of the studies in which shell structural changes have been documented have been primarily concerned with the usefulness of observed growth patterns for determining the age of examined specimens. Weymouth (1923) commented on the presence of "translucent regions" within the inner shell layer of Tivela stultorum and provided evidence that such regions were formed with an annual periodicity (during winter) and, hence, could be of value in estimating the age of individual specimens. More recently, Rhoads and Pannella (1970) have demonstrated the annual nature of pigmented growth bands within the inner "homogeneous" layer of the hard-shelled clam, M. mercenaria. Similar annually formed pigmented bands have been found by Jones et al. (1978) within the inner shell layer of Spisula solidissima and were used by these workers to determine the age and growth rate of this species in both inshore and offshore populations (for a more detailed discussion of growth patterns in S. solidissima, see Chapter 2). Lutz (1976a) has presented evidence that structural patterns within the inner nacreous layer of Mytilus edulis reflect annual cycles of growth and has suggested that careful examination of these patterns can provide a relatively accurate estimate of the age of individual mussels (Fig. 17). The ultrastructure of the patterns described by Lutz (1976a) is shown in Figure 18. Relatively thick aragonite crystalline laminae abruptly decrease in size to form a zone of fine laminae that gradually increase in thickness toward the inner shell surface. It is interesting to note that the zone of fine laminae was observed to form only during the spring of each year when water temperatures were rising (Fig. 18C). If, as suggested by Lutz (1976a), the thickness of nacreous laminae is temperature-dependent, one would expect to observe within the shell a *gradual* decrease in the thickness of nacreous tablets, rather than the abrupt decrease seen in Fig. 18A and C. We suggest that the observed structural patterns within M. edulis may reflect anaerobiosis-related shell dissolution during the late winter and early spring (perhaps related to gametogenesis). If shell-destructive processes are indeed operating during this period, nacreous laminae may actually be destroyed, and one would expect to encounter only relatively thick, previously deposited nacreous laminae at the inner shell surface (e.g., Fig. 18B). With increased utilization of aerobic pathways during the late spring, net shell growth takes place, albeit perhaps irregularly at first, resulting in the formation of thin, irregular nacreous laminae that gradually increase in thickness (Fig. 18C
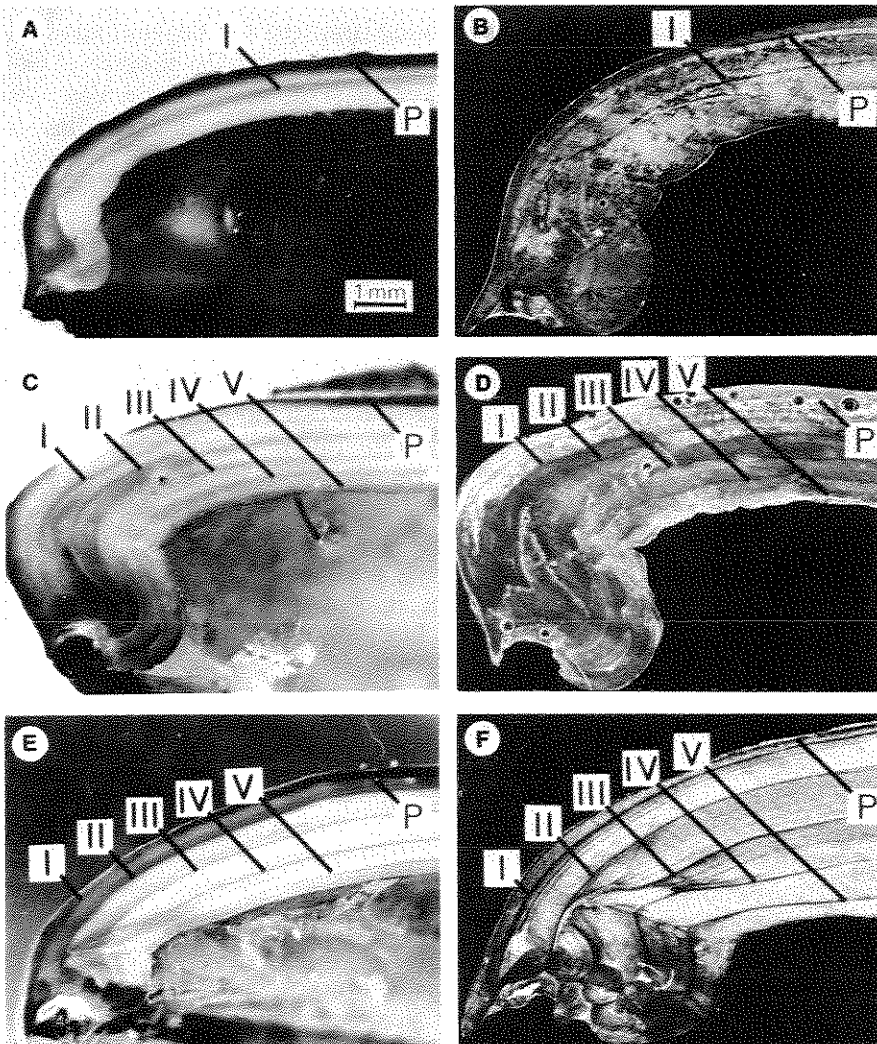
Figure 17. Finely polished and etched anteroposterior longitudinal shell sections (left) of *Mytilus edulis* L. with corresponding acetate peels (right). Roman numerals designate annual growth patterns. The scale for all shell sections appears in (A). All specimens were sampled from the Damariscotta River, Lincoln County, Maine. (A) 1½-year-old specimen from a constantly submerged (rafted) population (larval settlement, May, 1971; sampling date, January 4, 1973). (B) Acetate peel of umbonal region of (A). (C) Specimen sampled from a constantly submerged population on the underside of a floating platform that was launched in July, 1967 (sampling date, August 4, 1972). (D) Acetate peel of umbonal region of (C). (E) Specimen sampled from an intertidal population during the month of November. (F) Acetate peel of umbonal region of (E). Reprinted with permission from Lutz (1976a).

and D) as anaerobic pathways are employed less and less. Patterns morphologically very similar to those described above in *M. edulis* have been found by Hudson (1968; personal communication)* within the inner shell layer of the Jurassic mytilid *Praemytilus strathairdensis*. Hudson (1968) speculates on the annual origin of these "sublayer junctions." If such patterns are indeed analogous to those encountered within *M. edulis*, they should be of considerable assistance in reconstructing growth rates of *P. strathairdensis* in various paleoenvironments. Finally, Wada (1961, 1972) has commented on the presence of somewhat similar structural changes in various bivalves (particularly *Pinctada*). He comments on seasonal variations in the size of aragonite crystals, as well as the effects of extrapallial fluid pH, viscosity, and impurities on nacre tablet size, shape, and texture.

In the remainder of this chapter, we would like to discuss briefly several of the phylogenetic and paleoecological implications of our ideas on the relationships between bivalve metabolism and shell structure. For purposes of illustration, we will discuss many of the implications in light of the patterns within the shell of *G. demissa* described above.

It has been proposed that the stacked "mode of deposition" of nacre is a primitive trait among molluscan species that has been lost by degrees in bivalves during their evolution of a "new (bivalve) shell form" (Wise, 1970a,b). More recently, J. D. Taylor (1973; personal communication) has suggested that the "vertical component" of nacre is more closely related to geometry of the shell rather than the antiquity of the lineage, arguing that bivalves with low expansion rates (high convexity) have better-developed stacked nacre than forms with high rates of expansion. A similar point of view has been expressed by Carter (see Chapter 2), who suggests that the major variations in nacre tablet-stacking mode reflect adaptive secretory strategies for controlling shell-accretion rate (also see Wise, 1970b). One may alternatively view the various configurations of nacre within the bivalve shell as reflecting changing metabolic pathways (Lutz and Rhoads, 1977). Assuming that atmospheric oxygen levels increased from the late Precambrian to present levels in the Ordovician (Berkner and Marshall, 1965; Cloud and Nelson, 1966; Brinkman, 1969; Rhoads and Morse, 1971; Crimes, 1974), we suggest that aerobic respiration pro-

* In his paper, Hudson (1968, p. 173), in referring to "sublayer junctions" within the inner nacreous layer of *Praemytilus strathairdensis*, states that aragonite laminae "tend to grade into those above [i.e., older], and have a sharp junction with those below." Plate 33, Fig. 2, of his paper, however, shows just the reverse, with crystalline laminae grading into those below (i.e., younger) and having a sharp junction with those above. In personal communications (see Lutz, 1976a), Dr. Hudson has indicated that the text statement is in error and that the structural patterns within the inner shell layer of *P. strathairdensis* are very similar to those found within the shells of *M. edulis*.
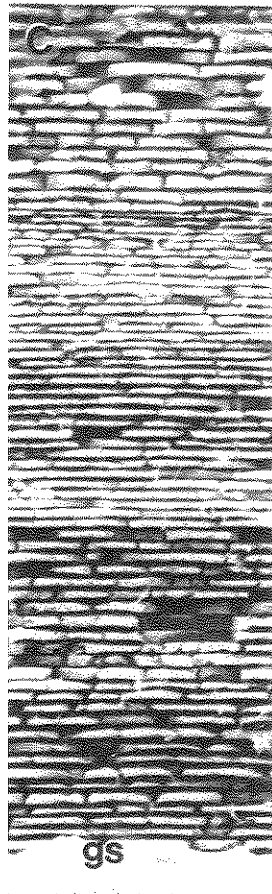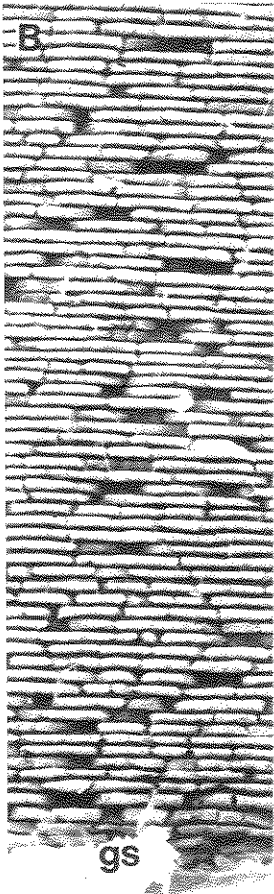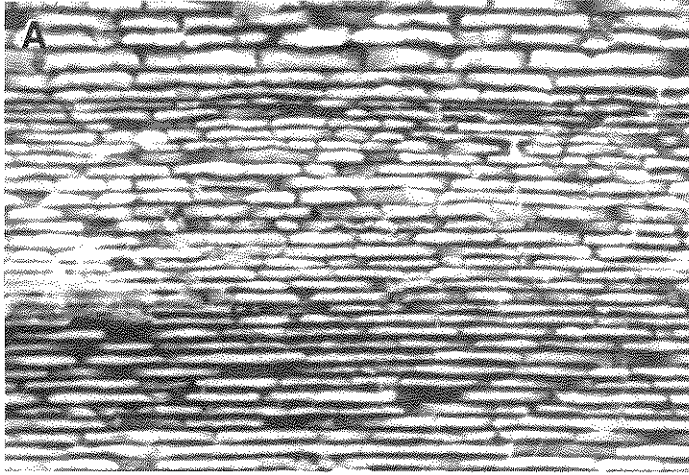
gressively increased over this same period of geological time and resulted in an increased shell deposition/shell dissolution ratio and, hence, increased proportions of sheet nacre (see Appendix 2.B)* in certain bivalves. Moreover, in *G. demissa*, during "transition" periods described in the previous section, increased stacking of crystals† actually results in structural changes, during which nacre subtly grades into simple aragonitic prisms, or the reverse (see Figs. 12F and 13). Physiological and/or other mechanisms responsible for the increased stacking of nacreous tablets (i.e., increased proportions of columnar nacre) and for this gradation of nacre into simple prisms warrant additional research.‡ Similar bands of simple aragonitic prisms are found alternating with complex crossed lamellar and homogeneous structures within the inner shell layer of *Arctica islandica* (Fig. 19), an organism known to respire anaerobically during

* Schmidt (1923) used the terms *Backsteinbau, Treppen,* and *Vertikalschichtung* for, respectively, brick-wall, stepped, and columnar (or lenticular) patterns of nacre (also see Lutz and Rhoads, 1977). Schmidt's terms were defined by him (and are used by most workers) in only two dimensions. In the microstructure guide presented in Appendix 2.B, the various stacking modes of nacre are classified according to a three-dimensional scheme. "Sheet" nacre includes *Backsteinbau* and *Treppen* in various vertical two-dimensional views. "Row stack" nacre appears as *Backsteinbau* or *Treppen* in some vertical two-dimensional views, and as *Vertikalschichtung* in others. Finally, "columnar" nacre appears as *Vertikalschichtung* in all vertical two-dimensional views.

† A similar stacking of nacreous tablets may be seen in micrographs presented by Wise (1970b) of the surfaces of *Pinna carnea* and *Nucula annulata* [= *Nucula proxima* (Hampson, 1971)].

‡ Similar structural changes (i.e., sublayers of simple aragonitic prisms) within the shells of numerous molluscs, such as the Pennsylvanian gastropod *Shansiella carbonara* (Batten, 1972), the Jurassic bivalves *Lithiotis problematica, Cochlearites loppianus,* and *Lithiopedalion* sp. from the "Lithiotis" facies (Loriga and Neri, 1976; Benini and Loriga, 1977; Benini, personal communication), the Recent bivalves *Modiolus modiolus, Cyclinella saccata,* and *Pholadomya candida* (Taylor, J. D., et al., 1969, 1973), and numerous species within the superfamily Chamacea (Kennedy et al., 1970), may result from periods of anaerobiosis.

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Figure 18. Scanning electron micrographs of polished and etched anteroposterior longitudinal sections of the inner nacreous shell layer of *Mytilus edulis* L. All specimens were sampled from the Damariscotta River, Lincoln County, Maine. (A) Annually formed ultrastructural crystalline pattern. The most recently formed aragonite crystalline laminae are at the bottom of the micrograph. ×2800. (B) Aragonite crystalline laminae adjacent to the inner shell surface (gs) of a specimen sampled May 16, 1974. ×1400. (C) Aragonite crystalline laminae adjacent to the inner shell surface (gs) of a specimen sampled June 18, 1974. ×1400. (D) Aragonite crystalline laminae adjacent to the inner shell surface (gs) of a specimen sampled July 2, 1974. Although the actual junction between thick and thin laminae is above the upper border of the micrograph, a gradual increase in the thickness of crystal laminae with decreasing distance from the inner shell growth surface (gs) is apparent. ×1400. Reprinted with permission from Lutz (1976a).
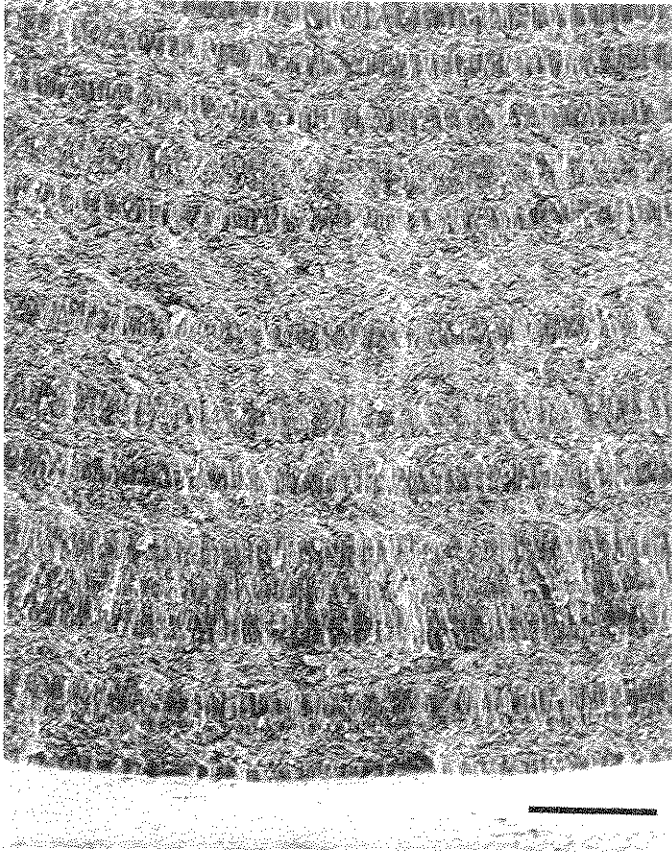
Figure 19. Scanning electron micrograph of a vertical fracture through the inner shell layer of *Arctica islandica* near the umbo. Bands of simple aragonitic prisms are seen alternating with complex crossed lamellar structures. Scale bar: 40 μm.

extended aperiodic burrowing activities (Taylor, A. C., 1976).* This suggests that such aragonitic prisms may represent a shell microstructure that reflects low-oxygen environments. Such a view is compatible with the phylogenetic tree presented by J. D. Taylor *et al.* (1973), in which the relationships among bivalve superfamilies, their possible histories, and

* Thompson and Jones (1977) have recently suggested that these bands of simple aragonitic prisms may occur with an annual periodicity. These workers have arrived at age estimates, based on counts of such "annual" bands, as high as 150 years for certain specimens. If these simple prismatic sublayers are related to the aperiodic burrowing activity of this species, such age estimates may be unrealistically high.

their shell structures have been summarized. The earliest ancestral forms in which shell structures can be recognized are composed of nacre and simple prisms of aragonite. It has been suggested (Taylor, J. D., 1973) that the simple-prism-and-nacre combination originally arose spontaneously as a consequence of the precipitation of calcium carbonate contemporaneously with organic matrix under a certain set of physicochemical conditions. Subsequently, because of some selective advantage in this structural combination (Taylor, J. D., and Layman, 1972), this condition became stabilized.* In the foregoing discussion, we imply that simple aragonitic prisms represent an altered form of nacre resulting from alternating processes of shell deposition and dissolution. Assuming this to be the case, we suggest that the evolutionary scheme proposed by Wise (1970a,b) be extended backward one step. We propose a gradual change (not necessarily evolutionary in a genetic sense) within certain ancestral molluscan lines from simple aragonitic prisms to columnar [*Vertikalschichtung* of Schmidt (1923)], then row stack, and, finally, sheet [*Treppen* and *Backsteinbau* of Schmidt (1923)] nacre. It is also interesting to note that if such structural changes have occurred, aragonitic (myostracal) prisms associated with the sites of muscle attachment may represent vestiges of an early ancestral shell structure. Inasmuch as such structural changes may be correlated with oxygen tension, a detailed analysis of relationships between ambient oxygen concentrations and various shell structural types within certain Recent and fossil molluscan superfamilies may eventually prove useful in determining dissolved oxygen gradients in present, as well as ancient, marine environments (Lutz and Rhoads, 1977).

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* For an alternative view on the evolution of shell structures, see Chapter 2.

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