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CONSTITUENCY AND ORIGINS OF CYCLIC GROWTH LAYERS IN PELECYPOD SHELLS

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By

Richard McNeil Barker

B.S. (American University) 1960

Dissertation

Submitted in partial satisfaction of the
requirements for the degree of
Doctor of Philosophy in Paleontology

in the
Graduate Division
of the
University of California, Berkeley

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Approved:

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ABSTRACT

Growth layers occurring in shells of 98 species of pelecypods were examined microscopically in thin section and as natural and etched surfaces. Study began with shells of eleven species known from life history investigations to have annual cycles of growth. Internal microstructural features of the annual layers in these shells provided criteria for recognition of similar, apparently annual shell increments in eighty-six of eighty-seven other species. All of the specimens feature growth laminae, commonly on the order of 50 microns in thickness. The specimens from shallow marine environments show either a clustering of growth laminae related to the formation of concentric ridges or minor growth bands on the external shell surface. Based on observations of the number of growth laminae and clusters per annual-growth layer, it was hypothesised that the subannual increments may be related to daily and fortnightly (and in some cases monthly) cycles in the environment.

The hypothesis has been substantially developed through observations on Recent pelecypods. Experiments with marked specimens living in natural environments revealed that shell growth is usually interrupted for several days or weeks following a disturbance of the pelecypod. The interruption induced by notching the shell margin is clearly recorded by the formation of an erratic ring (viz, disturbance ring). Allowing for hiatuses due to marking operations, shell growth data on their concentric ridges or minor growth bands have a fortnightly periodicity. No obvious relationships were observed between phases of the lunar cycle and the formation of concentric shell sculptural elements. A statistical correlation between ridge formation and the advent of a new or full moon was detected in a serial study of a population of *Chione undatella*, Cholla Bay, Mexico. Attempts to raise pelecypods in aquarium tanks were mostly unsuccessful due to unfavorable chemical conditions of the seawater and an inadequate food supply. More instructive results were obtained with *Kellia suborbicularis*, a vagrant smooth-shelled form adapted to euxinic environments. Specimens that had formed fluorescent growth lines while exposed to tetracycline formed growth laminae at

the rate of one per day. The same periodicity was evident for specimens that had grown shell while living under different combinations of illumination cycles and artificial tides. None of these marked specimens formed clusters of growth laminae correlative with the experimental cycles.

Guided by mechanical principles, several functions were inferred for concentric ridges and minor growth bands as they occur on the shell as a whole and as they influence the configuration of the ventral margin. Available ecological data suggest that these functions may be important in the adaptation of species to passive burrowing to shallow depths in tidal flat substrates, and also that survivorship may be increased if the ventral margin of the shell is ridged during spring tide. While this tends to explain synchronization of ridge building with new and full moons, and persistent monthly cycles apparent in twelve percent of the species with clusters of growth laminae sampled in this study invite some other explanation.

A major result of this investigation is the recognition of annual and subannual growth layers in shells of extinct species. Few of the fossils provided unbroken sequences of growth layers useful in determining periodicities. Moreover, since it is evident that the growth rhythms are endogenous, the mere presence of a cyclic clustering of growth laminae does not necessarily carry accurate information about regular cycles in the environment. For species that are adapted to tidal flat dwelling may also be represented in the neritic zone where tidal phenomena are comparatively weak. Also, it is a generally known feature of biorhythmicity that the periodicity may decrease or increase unless regulated by an external stimulus. Study was confined, therefore, to species known from independent geologic evidence to have grown their shells under littoral or near-littoral conditions. The resulting data suggest that the days and months have been increasing gradually through the past 270 million years of geologic time. No attempt is made to draw a precise pattern of change, since a scarcity of suitable well-preserved material has obviated analysis of a significant number of samples.

Possible applications of the paleogrowth method in the fields of paleoecology and paleoclimatology are discussed.

I. INTRODUCTION

General Significance and Need for the Study

Investigations of growth rates and longevity have demonstrated that some pelecypod species form certain increments of shell on a one-per-year basis. These annual growth layers provide a basis for measuring the periodicities of finer shell increments. The author (Barker, 1964) reported that growth layers in the shells of at least some species are grouped into a hierarchy suggestive of relationships to tides and other environmental cycles. As the recognition of annual and subannual growth layers in fossil shells facilitates the study of growth in relation to environmental cycles in past geologic ages, paleoecology is furthered by data pertaining to life span, rate of growth, mortality, seasonal cycle of recruitment, local environment, and climate.

Numerical relationships between daily and fortnightly growth periodicities would provide information about changes in length of day and month through geologic time. Both subjects have an obvious bearing on the history of the earth told in language as geophysical as it is biological. However, there is a need for substantiative study of Recent shell growth that would enable correct interpretations of growth layers in fossil shells. In the present investigation the internal structures of annual and subannual growth layers are examined in shells representing various living species of pelecypods. Growth experiments under laboratory and natural field conditions are reported and evaluated with respect to biological principles of growth and rhythmicity. The resulting knowledge is shown to have plausible significance in study of shells of the Late Pennsylvanian, Cretaceous, and Cenozoic ages.

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Historical

Aristotle opined that fossil shells were inorganic structures that grew in the strata enclosing them under the influences of stars and planets. Pliny records a claim that pearls are formed by a "dew" which flows from the moon into "yawning" oysters. Medieval Christianity furthered these ideas by teaching that fossils were sports of nature put into rocks by an evil spirit to corrupt the too-curious of men. Against this background, one of the most important contributions of the early Renaissance naturalist was to show that the morphological features of many fossil shells were identical to those of some living organisms. It was in this pursuit that Leonardo Da Vinci made the earliest suggestion known to the author of a relationship between the growth layers of invertebrate exoskeletons and lunar monthly and annual cycles. The Leonardo comment surviving in a notebook translated into English by Richter (1883) is quoted here in full:

> "Another sect of ignorant persons declare that Nature or Heaven created them in these places by celestial influences, as if in these places we did not also find the bones of fishes

> which have taken a long time to grow; and as if we could not count, in the shells of cockles and snails, the years and months of their life, as we do in the horns of bulls and oxen, and in the branches of plants that have never been cut in any part. Besides having proved by these signs the length of their lives, it is evident, and it must be admitted, that these animals could not live without moving to fetch their food; and we find in them no instrument for penetrating the earth or the rock where we find them enclosed."

Although it is not impossible that early farmers counted growth rings in order to estimate the ages of trees and certain animals, there is no mention of this method of age determination in the translated works of Pliny (Bostock & Riley, 1857). The method was known to naturalists of the 19th century (Woodward, 1880) who guessed at the ages of several invertebrate organisms. These guesses amounted to little more than assuming an annual significance for a particular type of growth ring. It was not until the last quarter of the century that rigorous field studies were conducted to demonstrate that annual growth is recorded in certain skeletal parts of fishes, echinoids, and gastropods (Hazay, 1881; Carpenter, 1891; Lang, 1896; and Reibish, 1899). In the present century, beginning with Belding (1910), Orton (1926), and Weymouth (1923), biologists have shown that a number of species of pelecypods form annual shell growth layers.

There have been few paleontological studies of annual growth. Paleobotanists report the recognition of apparent annual growth rings in the wood of Permian, Tertiary, and Pleistocene trees (Andrews, 1961). Dendrochronology, the detailed scientific analysis of tree rings, has revealed an almost continuous year-by-year record of climatic changes occurring in the North American Southwest during the past 3,200 years (Douglass, 1919, 1928, 1936). Annual growth has also been recognized in the growth bands of paleozoic corals (Ma, 1937; Faul, 1943; Wells, 1963, and Scrutton, 1964) and in the bones of Ceratopsian dinosaurs (Jepsen, 1964).

Biorhythmicity

More than 500 publications on the physiological and ethological rhythms of animals have been reviewed by Cloudsley-Thompson (1963). Many terrestrial organisms ranging from protist to primate are known to have solar-day (24 hours) rhythmic activities. The activities of invertebrate

animals inhabiting intertidal and oceanic beach environments are greatly influenced by the tides, typically occurring with a 12.4-hr periodicity, as well as by the alternation of day and night. Although some lunar-tide and solar-day biorhythms are "exogenous," being induced by the direct influence of environment, others are "endogenous" to the organism, since they persist under constant laboratory conditions. Only the most obvious environmental factors have been held constant in laboratory investigations: temperature, light or darkness, supply of food, immersion in constantly agitated or non-agitated seawater, and barometric pressure. Living in a constant laboratory environment over a relatively long time, the organism may show some variation in the periodicity of its rhythmic activity (e.g., 23-25 hours instead of 24 hours). Eventually, the biorhythm may become indistinct or cease entirely. However, brief exposure of the organism to a stimulus such as a flash of light or a fluctuation of temperature usually results in the reappearance of the biorhythm. Biologists have in this way demonstrated the persistence of solar-day and lunar-tide biorhythms through several generations of invertebrate animals produced and raised under constant laboratory conditions.

Some of the earlier workers entertained the idea that persistent biorhythms are induced directly by extrinsic environmental phenomena not subject to control in the laboratory. This was discredited by several experiments with pelecypods and crustaceans transported thousands of miles across time zones and cotidal lines. In a laboratory at Wood's Hole, Massachusetts, Rao (1954) observed that individuals of *Mytilus edulis* living under constant illumination, immersion, and temperature pumped seawater through their pallial cavities most rapidly when high tide occurred on the nearby coast. Under similar constant conditions in a Los Angeles laboratory, the mussels continued their rhythmic pumping of water in phase with the tidal-cycle operative at Wood's Hole. In this laboratory, after this rhythm had persisted for a period of 4 weeks, the mussels were put into a floating cage attached to a local pier. Although constantly submerged in seawater, the mussels again shifted their water pumping rhythms so that maximal pumping occurred at the time of the local high tide. Brown (1954) and Bennett (1954) reported that New England oysters, *Crassostrea virginica*, and quahogs, *Mercenaria mercenaria*, living under constant temperature and illumination in Evanston, Illinois, continued

their activity cycles in relation to the day-night and lunar-tide cycles of their original habitats. But, after a week had passed, these pelecypods resynchronized their activity rhythms with day-night and lunar gravitation in Illinois. Similar delays of resynchronization were observed in studies of solar-day and lunar-tide rhythms of locomotor activity and melanophore pigment changes in fiddler crabs, *Uca pugnax* (Brown et al., 1953, 1954). Since an exogenous biorhythm should be anticipated as resynchronizing simultaneously with translocation of the organism, the biorhythms investigated in the preceding experiments seem to be based on internal physiological mechanisms.

Cloudsley-Thompson (1963) refers to investigations in which biorhythms were shown to be independent of temperature within the ranges tolerated by the organisms. In crustaceans, at least, a biorhythm may be retarded when the organism is exposed a few hours to an extremely low temperature (near 0°C), which induces an almost complete cessation of metabolism. When the normal temperature is restored, the biorhythmic activity is resumed out of phase with the external day-night or lunar-tide cycle. The discrepancy of phase is equivalent to the time during which the organism was kept at the temperature-induced physiological zero. A number of investigators induced crustaceans and pelecypods to acquire unnatural periodicities through the influences of illumination cycles of other than 24 hours. These organisms reestablished their orginal solar-day periodicities when returned to constant laboratory conditions. More recently, Enright (1965) reported that artificial cycles of seawater agitation entrained non-tidal rhythms of locomotor activity in isopods that normally have an endogenous lunar tide rhythm. Immersed in nonagitated seawater of constant temperature and exposed continuously to light, these isopods persisted in their entrained biorhythms for 6 days.

The manner in which a biorhythm is synchronized with an environmental cycle is uncertain, for the rhythmic environmental phenomena interact so complexly as to preclude their isolation in laboratory experiments. According to Cloudsley-Thompson (1963), most investigators believe that synchronization involves several environmental stimuli, both obvious and subtle, which act through the sensory organs to time an inherited "biological clock." It is their consensus that biological clocks evolved to provide the organism with an ability to anticipate regularly recurring changes in

the environment. In some animals there may be several biorhythmic activities that normally have a lunar-tide or solar-day periodicity, but which respond similarly to the same environmental stimulus. The common modification properties of these biorhythms suggest the existence of a "master clock" or "oscillation center." Conceivably, a master clock could be timed by the general trend of variations in the environment. There are also instances of several biorhythms, with a common lunar or solar periodicity responding differently to an external stimulus, thus suggesting the existence of several independent biological clocks that are timed independently by different external synchronizers. Seemingly at odds with the consensus, Brown (1959) argues in favor of a single "zeitgeber" for all endogenous biorhythms regardless of whether there is or is not a master clock. In his opinion, the endogenous mechanism is not hereditary as an operative clock, but is entrained in the cells of the organism through the influence of an unspecified geophysical phenomenon. Cloudsley-Thompson (1963) opines that the Brown hypothesis defies rational analysis and could be tested empirically only in outer space.

However biorhythms are synchronized, organisms that have both solar-day and lunar-tide periodicities should be expected to show fortnightly variations in their rhythmic activities. This must be so, because a given phase of the tidal rhythm occurs 50 minutes later in each successive 24-hour period, such that a given day (or night) activity coincides with a low (or high) tide once every 14.76 days. Endogenous fortnightly biorhythms are known from studies of the locomotor activity of intertidal gastropods (Bohn, 1904), locomotor activity and melanophore changes in fiddler crabs, and water pumping in oysters and quahogs. Most of the organisms that were observed to have both lunar and solar rhythmic components were not studied for a long enough period of time to demonstrate the expected fortnightly periodicity. Although some nocturnal terrestrial arthropods, birds, and mammals are known to have monthly activities, continuously operative non-reproductive activity rhythms with monthly periodicities are conspicuously absent in the marine invertebrata and protista that have been studied. Monthly and fortnightly rhythms are evident in the breeding cycles of marine invertebrates (Korringa, 1947). Excepting the polychaetes that reproduce on a monthly basis, these animals tend to reproduce once or twice a year under a full moon or during the fortnightly spring tides associated with a sequence of new and full moons.

Demonstrated Annual Cycles of Shell Growth

Several life history investigations of pelecypods have included routine observations of marked specimens and comparisons of shell margins with seasons of live collection. Most of the investigators found that major growth bands delimited on the shell surface by concentric grooves are deposited in relation to an annual cycle of growth. The groove, which represents a temporary shifting of the growth vector, is formed when the mantle is constricted and the rate of shell growth minimal or zero. In the season when growth is resumed or accelerated, the mantle extends to form a growth band that is distinguished by greater size and uniformity of curvature.

Minor grooves occuring on shells of at least some species are formed when growth is interrupted for a comparatively short period of time (one or two weeks). Orton (1926) was the first to show that these interruptions may occur when the organism is removed from its substrate or place of attachment and rolled about during storms. Pelecypods may be induced to form similar "disturbance rings" in muddy water (Shuster, 1951). Orton and subsequent observers of disturbance ring phenomena found that a familiarity with the growth of a species permits distinction between the narrow, erratically occurring disturbance rings and the major grooves that are formed annually.

In all studied species that lived in Temperate areas (Table 1), a season of rapid shell growth alternates with a season of reproduction in which many individuals of a species release gametes synchronously. Assuming that spawning is followed by a lengthy period of mantle constriction, and that shell growth is of sufficient magnitude to leave a deposit of megascopic size, it would follow that a major groove results as a "scar," as it were, of spawning. However, the records of observations listed in Table 1 provide scant evidence of a relationship between spawning and the annual groove. One coincidence between spawning season and annual groove formation is found in *Aequipecten irradians* studied by Gutsell (1930) near Beaufort, N. C. During the fall, these scallops spawn and form concentric grooves. They grow rapidly in the winter and slowly in the summer. Craig (1961) has remarked that the autumnal grooves of this species are serrated as though there had been shell breakage during the time of groove formation. Since

Table 1. Seasons of groove formation (slow growth) and spawning

Species	Time of groove formation	Time of spawning	Locality	References
*Mercenaria mercenaria**	W	S	Southampton, Eng.	A.D. Ansell et al. 1964
*Protothaca staminea**	W	LW	Georgia Strait, Brit. Col.	C.M. Fraser & G.M. Smith 1928
Venerupis pullastra	W	S	Millport, Scot.	D.B. Quayle 1952
*Venus striatula**	F-Sp.	Sp.	Millport, Scot.	A.D. Ansell 1961
*Tivela stultorum**	W	S	California	F.W. Weymouth 1923
*Cardium corbis**	W	?	Calif. - Alaska	F.W. Weymouth & S.H. Thompson 1931
*Cardium edule**	W	Sp.-F	Plymouth, Eng.	J.H. Orton 1926
	W	?	North Caspian Sea	J.A. Birstein 1936
*Mya arenaria**	W	Sp.-ES	Rhode Island	A.D. Mead 1901; C.L. Newcombe 1935
*Siliqua patula**	W	S	Alaska	F.W. Weymouth, H.C. McMillin & H.B. Holmes 1925
	W	Sp.-ES	Washington	F.W. Weymouth, H.C. McMillin & H.B. Holmes 1925
*Aequipecten irradians**	W	S	Massachusetts	D.L. Belding 1910
	F	F	North Carolina	J.S. Gutsell 1930
*Pectin maximus**	W	F & S	Isle of Man, Gt. Brit.	S.F. Tang 1941; J.F. Mason 1957
Ostrea edulis	W & S	S	Fal Estuary, Eng.	J.H. Orton 1928
*Elliptio complanatus**	W	Sp.-S**	Illinois	M.R. Matteson 1948

* Specimens obtained for study

**Incubatory, fertilization in spring

S — summer F — fall LW — late winter

ES — early summer W — winter Sp. — spring

these scallops are known to migrate to and from shore on an annual basis, it is possible that shell margins could be broken during migrations related to the spawning season, thereby inducing the formation of concentric grooves. Whatever cause involved in the origins of these grooves, the events occur at the end of the annual slow-growth season, not within it. The discrepancies between spawning season and time of groove formation in the other non-oyster species (Table 1) are sufficient to obviate a direct cause-and-effect relationship.

Two growth bands per year are formed by individuals of *Ostrea edulis* living in the Fal Estuary (Orton, 1928). In the spring, when the water temperature exceeds 50-52°F and there is an abundant supply of algal flagellates, diatoms, and other food organisms, the oyster extends its mantle to secrete a thin shell outgrowth or "shoot." For a period of 1-2 months the shoot is thickened from below as successive deposits of $CaCO_3$ are laid down on the general inner surface of the shell. As the water temperature rises above 59-60°F in the summer, there is a cessation of shell growth and a concentric groove is formed. At this time the oyster undergoes gametogenesis and spawns. In the fall, when temperatures drop to 60-57°F, shell growth resumes and a second growth band is formed. The second major growth layer is completed by the formation of a second concentric groove in the winter.

Although Orton emphasized the relationship between temperature and shell growth, Yonge (1960) reports subsequent studies of this species and *Crassostrea virginica* in other localities where shell growth proceeds without a summer hiatus, provided the supply of food is adequate.

There is no evidence that the annual slow-growth period is induced by gametogenic processes. To the contrary, there are several examples in which the annual growth cycle is either present in the absence of reproduction on is absent where there is an annual cycle of reproduction. According to Tang (1941), juveniles of *Pecten maximus* form major grooves in each of the two or three winters preceding the attainment of sexual maturity. In a recent study of five Mytilid species living on the west coast of Australia, Wilson and Hodgkin (1967) found little or no evidence of a correlation between shell secretion and reproduction. Histological preparations revealed that gametogenesis occurs during a 4-to-10 month

period depending, at least in part, on the temperature optima of the species. In all five species there are one or two peaks of synchronous spawning, and in *Mytilus edulis planulatus* and *Xenostrobus pulex* these peaks are followed by several months of less intense asynchronous spawnings. Factors other than temperature are considered as responsible for the event of spawning. The Wilson and Hodgkin studies of *M. e. planulatus* indicate that these mussels grow at a practically steady rate throughout the year. Thus, a species lacking a well-defined annual cycle of shell secretion may at the same time exhibit a clear-cut seasonality of reproduction, if not of the actual spawning activity itself.

Temperature has been considered as an important factor influencing annual growth. The field studies listed in Table 1 have shown that several temperate marine species deposit shell most rapidly and have relatively long seasons of growth in the more southerly, warmer waters of their ranges. These effects of temperature have also been demonstrated in a study of *Mercenaria mercenaria* living near the warmer water outfalls of power stations in the Southampton-Poole Harbor areas (Ansell et al., 1964). Data on hundreds of individually tagged specimens drawn from a single stock indicate that a typical colder water specimen has a maximal average daily increment of 70 microns in a May to September growing season. Specimens living closer to the power station outfalls deposit shell from April to November, in which period the maximal daily average is almost three times as great. Many of the field workers suggested that positive relationships between rate of growth and temperature should exist only within a certain range of temperature characteristic of the species, and that, just as there is a minimum temperature for growth, there may be a maximum temperature above which there is no growth. Weymouth and fellow workers did not recognize this in their studies of *Tivela stultorum* and *Saxidomus nuttalli* in localities with maximal summer temperatures of from 50 to 67°F. On the Atlantic Coast of North America, *M. mercenaria* have been studied from Prince Edward Island to Bogue Sound, North Carolina, in which range the summer maxima vary from 50 to about 81°F. However, the data fail to show clearly that growth rate varies in relation to latitude (see reviews by Pratt & Campbell, 1956, and Ansell et al., 1964). The annual rate of growth is higher in Bogue Sound than in all but the Cape Cod population in New England. Ansell and others have suggested that these data reflect

a reverse relationship between growth rate and temperature combined with the effects of local factors such as supply of diatoms and other food microorganisms, substrate particle size, and salinity. However, this has not been demonstrated. What is known of the more southerly *M. mercenaria* is that they grow throughout the year and have a late summer to winter season of slow growth. This fact in itself suggests that the annual cycle of shell growth is controlled by temperature.

A reverse relationship between water temperature and shell growth is also apparent for *Aequipecten irradians* near the southern limit of its range (Gutsell, 1930). At Beaufort, these scallops grow most rapidly in the winter; whereas, on the New England coast, shell growth is maximal in summer. Thus, as *M. mercenaria* hibernates in winter to extend its range into the adverse cold of the north, at least one species is known to adjust in a converse manner to temperatures exceeding its maximal tolerance limit.

Another expression of the influence of water temperature on annual growth was demonstrated in Dodd's (1964) study of the mineralogy of the shell of *Mytilus californianus*. The shell of this species has a nacreous (aragonite) layer that is sandwiched between an inner and an outer layer of calcite. Periodically, an expansion and contraction of the mantle zone concerned with secretion of the aragonite results in an intertonguing of the nacreous and calcitic layers. Dodd presents convincing evidence that the expansion of the aragonite secretion zone occurs in the warmer months when shell growth is most rapid.

Not all observations are in support of an hypothesis that annual growth is controlled by temperature alone. Inspection of shells of clams living in tropical seas indicate that distinct major growth bands are formed, even though the annual temperature variation is only a few degrees. In cases where these major increments are similar to the annual growth layers known from field studies of temperate species (Table 1), one may at least anticipate that some of the tropical growth bands represent annual cycles. Pannella and MacClintock (1968) have shown that the growth layers of *Tridacna squamosa* are grouped into patterns correlative with fortnightly and other subannual periodicities. This hierarchic arrangement of growth layers is so regular as to make fairly obvious the annuality of the major increments. Their finding is in agreement with a study of

Tridacna gigas revealing an exact correlation between the sequence of radioactive bands and the series of atomic bomb detonations at Bikini (Bonham, 1965). It seems doubtful that temperature differences of only a few degrees would be sufficient to induce the formation of annual layers, for an equal amount of temperature variation may occur within a 24-hr period.

Application to Geology

The use of size-frequency distributions in paleoecological studies of growth, mortality, and recruitment may be complicated by the sorting and mixing of shells transported by currents. Such a death assemblage of fossils, or thanatacoenosis, must be distinguished from the in situ assemblage, or biocoenosis, which accurately represents a community of organisms. Boucot (1953) attempted to formulate the problem beginning with the assumption that the mortality rates of most invertebrate communities are highest in the first year of growth. He reasoned that regardless of changes in the rates of growth, recruitment, and mortality, both a community and its associated biocoenosis should have size frequency distributions that are right-skewed, whereas a current-sorted assemblage of shells should have a normal-size frequency distribution. Although sorting phenomena have been demonstrated in a study of Recent shells (Craig, 1967), Olson (1957) points out that not all fossil assemblages with bell-shaped size frequency distributions can be considered as current-sorted. The fossils contributed to a biocoenosis are drawn from several parts of the biozone and not all of the life process may be equivalent. Since only a few of the skeletal remains commonly survive lithification, a considerable proportion of the resulting fossil assemblage may not be accessible for sampling. Biases involved in any one of these factors of sampling could result in a bell-shaped, even normal-size frequency distribution. Craig and Oertal (1967) are of the opinion that no matter how adequate the sampling plan is designed and the allochthonous vs. autochthonous fossils are discriminated, the life processes of the species may cause further complication. Assuming various combinations of mortality, rate of growth, and recruitment factors, these workers used a computer to generate hypothetical size-frequency distributions. Their results did not confirm the earlier postulate of Boucot, in that only a few of the histograms were right-skewed, and in one case a bell-shaped histogram was

obtained. They concluded that an independent source of data on life processes is necessary for a meaningful evaluation of size-frequency distributions in fossil assemblages.

There seems to have been only one attempt to apply growth rate data to paleoclimatology. In a series of publications in the 1930's and 1940's Ma claimed that the growth rates of paleozoic corals provide evidence of climatic zones oriented differently than those that now exist. Zeuner (1952) and Nairn (1961) have expressed doubts as to whether the growth rate data reported by Ma reflect latitudinal variations of temperature, ocean currents, or local factors of growth.

The apparent daily and lunar rhythms of growth in fossil corals and pelecypods have been found to be suggestive of dynamic changes in the earth-moon system. Initial steps in this research field were taken by Wells in his presidential address to the Paleontological Society in 1962. He showed that the major band of a Scleractinian coral from Bermuda included 360 growth lines. Equipped with the knowledge that modern corals secrete CaC03 more rapidly in the day than at night, he suggested that these striae may be related to 360 diurnal growth cycles. Reporting a mode of 399 lines per growth band on the epithecae of some tetracorals of Middle Devonian age, he interpreted this as the number of days in the year for that point of geologic time. Using an age date provided independently by studies of radioactive minerals, Wells estimated that the day had lengthened at the rate of about 2 seconds per 100,000 years. This estimate agrees closely with astronomic measurements indicating a slowing of the earth's rate of rotation (Munk & MacDonald, 1960). Scrutton (1964) considered another type of cyclic increment on some tetracorals of the same geologic age to be similar to a monthly depositional cycle inferred from observations on a living species. For ten specimens this periodicity averaged 30.59, which seems to indicate that the number of days in the synodic month has also changed. There was an average of thirteen apparent monthly growth bands per major growth band, a ratio that would be anticipated, assuming a lengthening of the moon's orbital period. Barker (1964) reported that the arrangements of growth layers in certain Recent pelecypod species are suggestive of relationships to daily cycles, fortnightly tides, and annual variations of growth. Study of similar growth layers and apparent

monthly growth layers in late Cretaceous shells (Berry & Barker, 1968) yielded averages of 12.49 and 29.65 for the months per year and days per synodic month ratios, from which it was calculated that in late Cretaceous time there were approximately 370 rotations of the earth per year. Comparisons of these results with the tetracoral data suggest that the lengths of the sidereal month and the mean solar day have increased gradually during the last 375 million years. Pannella and MacClintock (1968) reported there must be a similar tendency for there to be more than 29 1/2 finer increments per monthly increment in several fossil pelecypods. Their results seem to indicate that the greatest rate of change occurred in Late Tertiary time.

Thus, geological significance of shell-growth layering seems to be emerging in current paleontological research. However, the few results reported should be taken as tentative, for only a few small samples have been examined, and there is no substantial knowledge of biorhythmic processes of skeletal growth.

The Problem

The present investigation was begun in light of the following:

1. Annual variations of growth rate and changes in the pelecypod mantle result in the formation of relatively broad concentric bands delimited by grooves or raised rings. Although many observers have reported that the annual growth layers may be distinguished from disturbance rings, useful morphological criteria have not been presented in the literature.

2. Field studies have revealed that the form of the annual cycle of growth and reproduction varies with species and climatic zone. Most of the temperate water dwellers have annual cycles of shell growth that seem to be controlled by temperature, although oysters of the same species may have annual or biannual rhythms depending on local environmental factors. The few observations that have been made of tropical species indicate that annual growth is not controlled by temperature near the equator.

3. Finer growth layers occurring as constituents of the annual growth layers of some shells have been attributed to subannual phenomena including monthly, fortnightly, and daily rhythms.

4. Many biorhythmic physiological activities seem to be based on innate biological clocks, which are in some way synchronized with environmental rhythms.

The following subjects were selected for investigation:

1. Morphology of the annual and subannual growth layers in shells of different species.

2. The manner in which the morphologic features of the growth layers originate during shell growth, and how the processes of growth may be related to the environment of the organism.

3. Feasibility of determining length of day and lunar periodicities through the study of growth layers in fossil shells.

4. Applications of the study of growth-layering to paleoecological problems.

5. Functional significances of shell growth rhythms and how they evolved.

The author carried out four types of studies:

1. Morphology. The growth layers in shells of living species of pelecypods were examined at magnifications of up to X500. The features of these growth layers were then correlated with features of the habitats.

2. Growth of marked specimens. Shell growth was followed in pelecypods living in their natural environments and in the laboratory. Laboratory experiments included exposing pelecypods to several combinations of artificial tides and illumination cycles.

3. Serial study. Pelecypods were collected from a local fauna so that the increments on the ventral margins of their shells could be compared with season of the year. In Sonora, Mexico, a species was selected for serial sampling throughout a 1-1/4 month period and on several other occasions in the period 1967-68.

4. Study of population structure. Since a large number of specimens of a single species was collected in the 1-1/4 month series, it was possible to compare the frequency distributions of shell size and number of apparent fortnightly growth layers per shell with age groups as determined from study of annual growth layers.

Methods and Materials

The light microscope is the principal instrument of shell structure study. External surfaces and oriented sections of shells were examined through a stereoscopic reflection (dissection) type microscope, providing magnifications ranging from X8 to X100. A polarizing microscope was used to study thin sections of shells at magnifications of X20 to X500. Thin sections prepared by commercial laboratories had been mounted in transparent epoxy resin with a refractive index of n = 1.540. Thin sections prepared by the author who applied the conventional glass plate method were mounted in Lakeside 70 cement (n = 1.540). Shell surfaces were also examined through the use of cellulose peels and replicas made of oil base clay and of latex rubber.

A thin metric ruler was used to measure to the nearest millimeter the lengths and heights of shells. Vernier scale callipers were not used, as this would have multiplied the time required for routine measurements and added only a negligible degree of precision to the results. Ocular and stage micrometers calibrated in millimeters and microns facilitated the microscopic measurement of shell structures.

Photomicrographs were taken through the optical system of the polarizing microscope. Whole shells and parts of shell surfaces were photographed at various magnifications using extension rings, expansion bellows, and close-up lenses.

The University of California Museum of Paleontology provided many of the Recent and fossil pelecypod shells used in this study. The author collected many shells of certain living species in San Francisco Bay and Bodega Bay and on the Baja California and Sonoran coasts of the Gulf of California. He also collected fossils from the late Cretaceous Ripley Formation, Coon Creek, Tennessee. Sedimentological sieves were

applied to search for minute shells and organisms in sandy substrates as well as to measure sedimentary particle sizes.

The computer was employed in most of the routine statistical work. Statistical methods involved in this investigation are presented in Chapters IV and VI.

Shell Structural Terminology

The shell structural terms employed in this study are adapted from the works of Bøggild (1930) and Oberling (1956). The typical bivalve shell is composed of four principal calcareous layers and a very thin surficial covering of periostracum. The innermost principal layer, termed "endostracum," is secreted by the general surface of the mantle inside the pallial line. Deposits of the pallial line and adductor muscles comprise a second principal layer termed the "myostracum." The two outermost calcareous layers together form the "palliostracum" secreted by the free edge of the outer mantle fold. The innermost component of the palliostracum is located just outside the pallial line and is termed the "mesostracum." The outermost component is secreted by a more distal part of the mantle and is termed the "ectostracum." The reader is referred to standard paleontological textbooks or to the sources cited above for the definitions of terms referring to the complex crystalline constituents (e.g., prismatic, crossed-lamellar, nacreous).

Four categories of shell surface features are recognized in the present study:

1. Radial elements (ribs, denticles, and rays) which may be:
   a. Additive. Resulting from successive deposits of $CaCo_3$ in zones of relatively rapid growth.
   b. Nonadditive. Resulting from a folding of the mantle, or otherwise related to a radial configuration of the mantle — shell.
   c. Composite. A combination of (a) and (b).
2. Concentric elements (growth layers and concentric ridges) representing episodes of shell growth.
3. Spines and nodes. Restricted in their occurrences to certain concentric and radial elements.

4. Complex elements that seem to be independent of the radial and concentric elements. Well-known examples are the oblique undulations of the shell of *Cyathodonta*, the chevron striae of *Acila*, and the pustules of some Unionid species.

II. THE GROWTH LAYERS

Annual Layers

Examination of the shells of eleven species known to have annual cycles of growth (Table 1) revealed that annual growth layers can be recognized in these shells on the basis of megascopically visible features. Internal microstructural features of these major increments provided criteria for their recognition in shells of other species (see Table 2).

Megascopic features

All specimens examined of the species listed in Table 1 have major increments defined on the shell surface as gentle undulations or as growth bands delimited by concentric grooves. These major increments are considered to be annual layers, because they are similar in overall appearances to the increments that were demonstrated to have been formed annually. In each species, the number of major increments per shell compares favorably to the reported mode of age in years. On shells that have three or more major increments, the later increments tend to be smaller, suggesting that the linear rate of shell growth decreases with age. Such a relationship between annual rate of growth and age has been demonstrated in the field studies of these species. As viewed in vertical section, most of the concentric grooves have narrow U- or V-shaped outlines and the adjacent growth bands follow similar curved planes. These grooves reflect the gradual retraction of the mantle that occurs in the slow-growth phase of the annual cycles. In some species, particularly on the parts of the shell formed later, the growth bands adjacent to a groove do not occupy similar planes of curvature, and the dorsal slope of the groove is steeper than its ventral slope. These asymmetrical L-shaped grooves may result from a sudden change in the mantle-shell relationship. The broad undulatory type of major increment occurs in the central dissoconch area on shells of *Mercenaria mercenaria* from North Carolina and Florida. Each of these undulations consists of a relatively large depressed growth band and a thinner raised ring. As these increments are followed around the shell periphery into the anterior or posterior regions, a reversal of their relative elevation takes place, such that the formerly raised ring is depressed below the growth band and forms a broad U-shaped concentric groove. This reversal also occurs as the individual ages, for the

Table 2. Taxa represented in microscopic study of growth layers

2a. Specimens showing apparent fortnightly growth layers

Taxon	Geologic age and locality	Type of shell increment
Pinnidae		
Pinna sp.	R., loc. unknown	spinose minor growth bands
Avicula sp.	R., Sumatra A7348	minor growth bands
Atrina rugosa (Sowerby)	R., Gulf of Calif. 2404	spinose minor growth bands
Isognomonidae		
Isognomon ephippium (Linnaeus)	R., Puerto, Mex. 422	minor growth bands
Mytilidae		
Volsella demissa Dillwyn	R., Stone Harbor, N. J. D3687	minor growth bands
Septifer bifurcatus (Conrad)	R., San Diego, Calif. 1668	nodes on radial ribs
Unionidae		
Unio raveneliensis	R., Lake Nicaragua, Nic. 599	equant or asym. wide ridges
Lampsilis radiata (Gmelin)	R., Philadelphia, Pa. 550	minor growth bands
L. hydrianus Lea	R., Claiborne Parish, La.	equant or asym. wide ridges
Obliquaria reflexa (Rafinesque)	R., Ala. 396	equant or asym. wide ridges
Spondylidae		
Spondylus crassisguama Lamarck	R., loc. unknown	spinose asym. wide ridges
S. princeps Broderip	R., loc. unknown	spinose asym. wide ridges

Table 2a. Continued

Taxon	Geologic age and locality	Type of shell increment
Crassatellidae		
Eucrassatella kingicola Lamarck	R., Australia 68	equant ridges
E. digueti Lamarck	R., Mex. D3703	equant ridges
Crassatellites washingtonensis Weaver	Olig., Lincoln Fm., Wash. A9	equant ridges
Crassatella tallavignesi Deshayes	Eoc., Paris Basin B6717	equant ridges
Pholadidae		
Barnea costata Linnaeus	R., Corpus Christi, Fla. 496	protrusive ridges and nodes
Zirfaea gabbi Lowe	R., San Francisco, Calif. D3696	protrusive, asym. narrow, and equant ridges
Corbulidae		
Corbus fimbriata Cuvier	R., South Pacific 107	asym. wide ridges
Myacidae		
Mya arenaria Linnaeus	R., Pt. Isabel 7107	minor growth bands
Platyodon sp.	R., Bolinas, Calif. D3704	asym. narrow ridges
Corbiculidae		
Corbicula fluminea Müller	R., Napa R., Calif. D3705	protrusive ridges
Arcidae		
Arca incongrua Say	R., Vera Cruz, Mex. 492	nodes
Anadara ovalis Bruguière	R., Stone Harbor, N. J. D3687	nodes

Table 2a. Continued

Taxon	Geologic age and locality	Type of shell increment
Cucullaeidae		
Cucullaea (Cucullaea) labiata (Solander)	R., Sumatra S165	asym. wide ridges
Idonearca vulgaris (Morton)	Cret., Gulf Coast, UCMP D3701, D3710 and USNM Coll.	equant to asym. wide ridges
Glycymeridae		
Glycymerus lacertosa Wade	Cret., Ripley Fm., Coon Ck., Tenn., D3710	equant ridges
Lucinidae		
Lucina floridana Conrad	R., Sarasota Bay, Fla. 1706	equant ridges
Phacoides annulata Reeve	R., San Pedro, Calif. 2388	asym. wide ridges
P. californicus Conrad	R., Monterey Bay, Calif. 2395	equant to asym. wide ridges
Codakia orbicularis Linnaeus	Plio., Fla. B4085	equant ridges
Lucina subundata Hall and Meek	Cret., Cody Shale, Greybull, Wyo. D3709	minor growth bands
Tellinidae		
Tellina bodegensis Hinds	R., Tomales Bay, Calif. A4215	asym. wide ridges
Mactridae		
Mactra sp.	R., New Brighton, N. Z. B6374	asym. wide ridges
M. solidissima Dillwyn	R., Stone Harbor, N. J. D3687	minor growth bands and asym. wide ridges

Table 2a. Continued

Taxon	Geologic age and locality	Type of shell increment
Cardiidae		
Cardium corbis Martyn	R., Puget Sound, Wash. B356	nodes
C. indicum Lamarck	R., China 78	minor growth bands, spinose on dorso-posterior
Serripes groenlandicus Bruguière	R., Banks Isl., Can. B1363	minor growth bands to asym. wide ridges
Carditidae		
Venericardia sp.	R., Persian Gulf A4324	nodes
Cardita floridana Conrad	R., Sarasota Bay, Fla. 1706	asym. narrow to protrusive ridges
Veneridae		
Venus striatula (da Costa)	R., Britain 98	asym. wide and equant ridges
Mercenaria mercenaria (Linnaeus)	R., Maine D3688, N. J. D3687, N. C. D3690, Fla. D3692	asym. narrow to protrusive ridges
Chione (Chione) californiensis Broderip	R., Baja Calif. D3698, Cholla Bay, Mex. D3699, Pleist., Punta Cholla, Mex. B1394	protrusive ridges
C. (C.) undatella (Sowerby)	R., Cholla Bay D3699, Baja Calif. B7844, Pleist., San Pedro, Calif. 2388	protrusive ridges
C. (C.) cancellata Linnaeus	R., N. C. D3689, S. C. D3691, Fla. D3692, Plio., Fla. B3565	protrusive ridges

Table 2a. Concluded

Taxon	Geologic age and locality	Type of shell increment
C. (C.) succincta Valenciennes	Pleist., Newport, Calif. A2609	protrusive ridges
C. (C.) spissa Broderip and Sowerby	R., Tauranga, N. Z. 1542	equant to asym. narrow ridges
C. (Anomalocardia) subrugosa Sowerby	R., Baja Calif. 2897	asym. wide ridges
Protothaca staminea Conrad	R., Calif. 2392, 2396, D3693, D3695, D3697, Wash. 7162, Alaska B7055	asym. narrow and protrusive ridges
P. fructifraga Sowerby	R., Cholla Bay, Mex. D3699	protrusive ridges
Saxidomus nuttalli Conrad	R., Bodega Bay, Calif. D3693	equant to asym. narrow ridges
Dosinia ponderosa Gray	R., Cholla Bay, Mex. D3699	asym. wide ridges
D. dunkeri (Philippi)	R., Cholla Bay, Mex. D3699	asym. wide ridges
Pitar alternatus (Broderip)	R., San Blas, Mex. 3406	asym. narrow and protrusive ridges
P. callicomatis (Dall)	R., Baja Calif. D3702	asym. wide ridges
P. roseus (Broderip and Sowerby)	R., San Blas, Mex. 3406	asym. narrow ridges
P. dione Linnaeus	R., San Blas, Mex. 3406	protrusive ridges and spines
P. (Hysteroconcha) lupanaria Lesson	R., Guaymas, Mex. A9712, B839	protrusive ridges and spines
Meretrix sp.	Eoc., Paris Basin, France	asym. wide ridges
Astartidae		
Astarte alaskensis Dall	R., Puget Sound, Wash. 2400	equant ridges

2b. Specimens showing apparent monthly growth layers

Taxon	Geologic age and locality	Type of shell increment
Pteriidae		
Pinctada radiata Leach	R., loc. unknown	minor growth bands
Pectinidae		
Aequipecten acuticosta Zicten	Jur., Blockley, Eng. A-6310	minor growth bands
Trigonidae		
Trigonia thoracica Morton	Cret., Ripley Fm., Coon Creek, Tenn. D-3701	nodes on radial ribs
Pandoridae		
Pandora trilineata Say	R., New York, N. Y. 134	minor growth bands
Myalinidae		
Myalina subquadrata Shumard	Penn., Wayland Fm. Brownwood, Tex. D3706	minor growth bands
Ostreidae		
Crassostrea gigas (Thurnberg)	R., Tomales Bay, Calif. D3707	minor growth bands
Cardiidae		
Dinocardium robustum (Solander)	R., Port Bolivar, Tex. D-3067	nodes
Veneridae		
Chione (Gnidiella) gnidia Broderip and Sowerby	R., Cholla Bay, Mex. D3699	protrusive ridges
Irus lamellifera Conrad	R., Monterey Bay, Calif. 2395	asym. narrow to protrusive ridges

2c. Specimens showing combined fortnightly and monthly growth layers

Taxon	Geologic age and locality	Type of shell increment
Mytilidae		
Mytilus edulis Linnaeus	R., San Francisco Bay, D3708 Bodega Bay, Calif. D3693	minor growth band
Pectinidae		
Lyropecten subnodosus Sowerby	R., San Marau Isl. A36631	occasional minor growth band
Crassatellidae		
Crassatella vadosus (Morton)	Cret., Ripley Fm., Coon Creek, Tenn. D3701, D3710	equant ridge

2d. Specimens lacking evidence of lunar growth rhythms

Taxon	Geologic age and locality	Type of shell increment
Nuculidae		
Acila castrensis (Hinds)	R., Vancouver Isl, Can. 1607	finer increments indistinct
Solemyidae		
Solemya (solemya) australis Lamarck	R., Australia 68	growth laminae not clustered
Mytilidae		
Lithophaga sp.	R., Guaymas, Mex. A4200	finer increments indistinct
Mytilus californianus Conrad	R., Bodega Head, Calif. D3694	minor growth band lacks finer increments
Unionidae		
Elliptio complanatus (Many other Unionid species from the Mid-Western U. S. also having smooth shells were not studied microscopically)		
Pectinidae		
Pecten maximus Linnaeus	R., Europe 66	finer growth layers not clustered
P. diegensis Dall	R., loc. unknown	finer growth layers not clustered
P. varius Linnaeus	R., So. England 145	spinose rings lack distinct finer growth layers
Aequipecten irradians Lamarck	R., Buzzards Bay, Mass. 146	finer growth layers not clustered
Pecten texanus Roemer	Cret., Grayson Fm., Roanoke, Tex. A-5031	finer growth layers not clustered

Table 2d. Continued

Taxon	Geologic age and locality	Type of shell increment
Limidae		
Lima squamosa Lamarck	R., Micronesia, Oceania 124	nodes lack distinct finer growth layers
Anomiidae		
Anomia simplex d'Orbigny	R., Aransas Bay, Tex. A7419	finer growth layers indistinct
Arcidae		
Arca umbonata (Lamarck)	R., Galveston, Tex. D-3190	ridges lack distinct finer growth layers
Glycymeridae		
Glycymerus sp.	R., loc. unknown	growth laminae not clustered
G. pectinata (Gmelin)	Plio., Caloosahatchee Fm., West Palm Beach, Fla. B4085	growth laminae not clustered
G. veatchii major Stanton	Paleoc., Lodo Fm., Torrey Hills, Calif. A9717	growth laminae not clustered
Leptonidae		
Kellia suborbicularis Montagu	R., Duxbury Reef, Bolinas, Calif. D-3704	growth laminae not clustered
Tellinidae		
Macoma nasuta (Conrad)	R., Bodega Bay harbor, Calif. D3693	growth laminae not clustered
Sanguinolaridae		
Sanguinolaria nutallii (Conrad)	R., Bodega Bay harbor, Calif. D3693	growth laminae not clustered

Table 2d. Concluded

Taxon	Geologic age and locality	Type of shell increment
Donacidae		
Donax gouldii Dall	R., Long Beach, Calif. 2407	growth laminae not clustered
Mactridae		
Mactra semisulcata Lamarck	Eoc., Paris Basin, Cloez Coll.	growth laminae not clustered
Tresus nuttallii (Conrad)	R., Bodega Bay harbor, Calif. D3673	growth laminae not clustered
Cardiidae		
Laevicardium elatum Sowerby	R., loc. unknown	growth laminae not clustered
Clinocardium nuttallii Conrad	R., Bodega Bay, Calif. D3693	growth laminae not clustered
Veneridae		
Tivela stultorum Mawe	R., Pismo Beach, Calif. D3700	growth laminae not clustered
Transennella tantilla Gould	R., Bodegá Bay harbor, Calif. D3693	growth laminae not clustered

later-formed major increments of the larger shells consist of concentric grooves and growth bands that are continuous around the periphery. In North Carolina, this species does not cease to deposit shell in the slow-growth season; thus the undulatory type of major increment is related to growth that is continuous throughout the year.

The major shell increments of *M. mercenaria* are also characterized by the spacing (or thickness) of finer increments occurring within them. The finer increments forming the growth bands are more widely spaced (thicker) than are those which occur adjacent to or within the concentric grooves or rings. This cyclic variation in the spacing of the finer increments may become less distinct in the later-formed major increments, and in some cases the finer increments that follow a groove are spaced almost equally. These features suggest a prolonged season of no shell growth. Indeed, the growing seasons of at least three species (*Tivela stultorum, Siliqua patula,* and *M. mercenaria*) are known from observations in the field to become shorter as the individuals become older (Weymouth, 1923, Weymouth et al., 1925, and Ansell et al., 1964).

Internal structure

As viewed in thin section, the concentric grooves of the two Pectinid species are related to partings of a foliated mesectostracum. These partings are sometimes colored with a brown substance that may be traced into a concentration of periostracum within the groove on the shell surface. In the nine species representing the Veneridae, Cardiidae, *Mya*, and *Siliqua*, concentric grooves or rings rest upon translucent slow-growth layers that leave a relatively uniform extinction pattern between crossed Nicols (see Plates 1-3). The thickness of the slow-growth layers near the exterior of the shell range from 1/4 mm in *Cardium edule* to 1 cm in *Mercenaria mercenaria* from Florida and North Carolina. In the mesectostracum, the slow-growth layers have a crossed-lamellar or a nacreous or homogeneous structure. Material deposited on the mesectostracum during the season of rapid growth is more opaque and has an irregular extinction pattern. These rapid growth layers vary in crystalline structure from imperfectly crossed lamellar to prismatic.

In all eleven species, the slow- and rapid-growth layers are most distinctly expressed in the mesectostracum and in the endostracum portion of the hinge. Although these growth layers may be traced into the

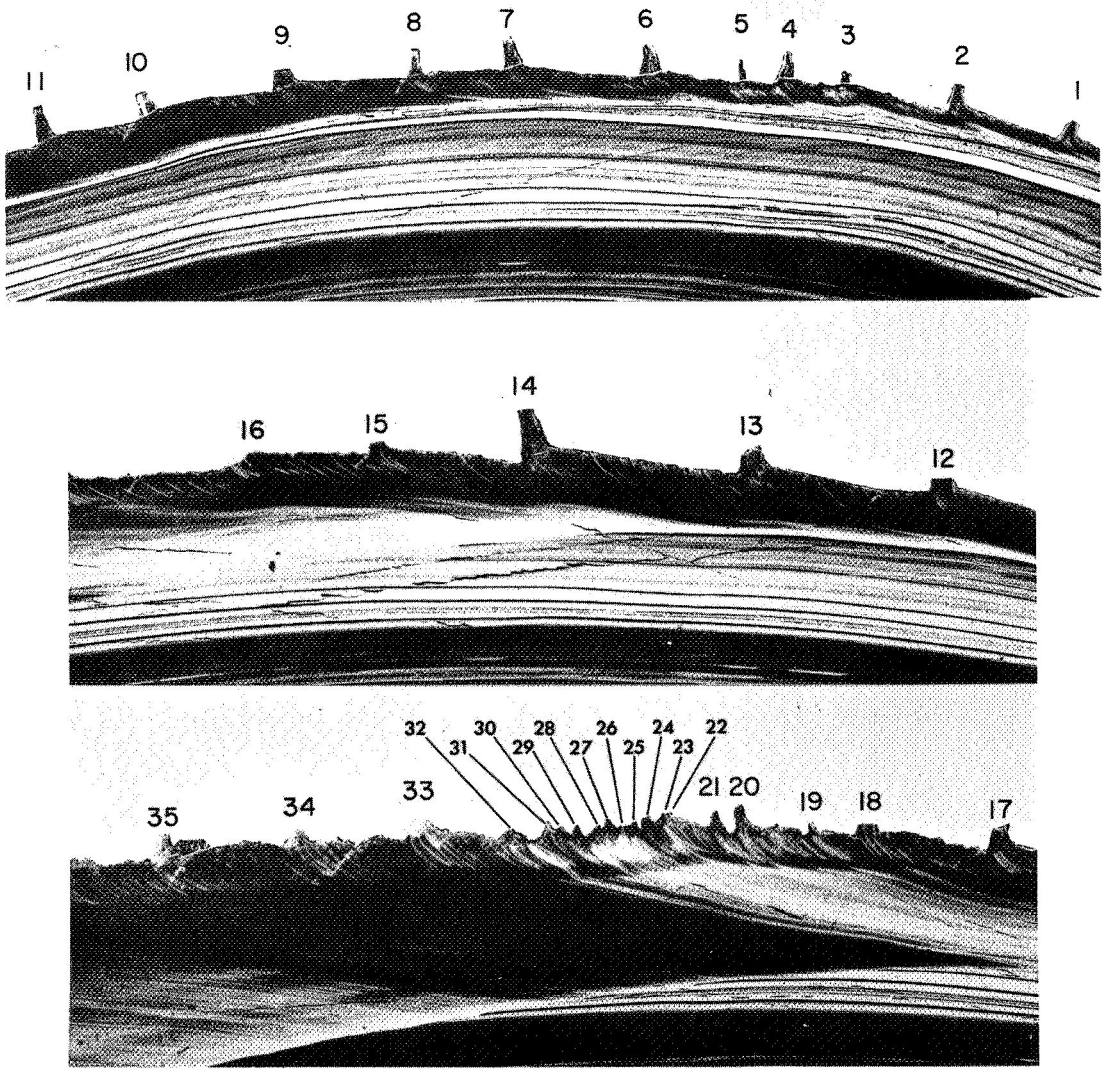


Plate 1. *Mercenaria mercenaria* (Linnaeus). Radial dorso-ventral thin section. Traverse begins near umbo (ridge 1) and ends with concentric ridge 35. Second-formed annual slow-growth layer occurs between ridge 19 and ridge 31 (see lower part of plate). Recent, Bradenton, Florida. Ordinary light X11.

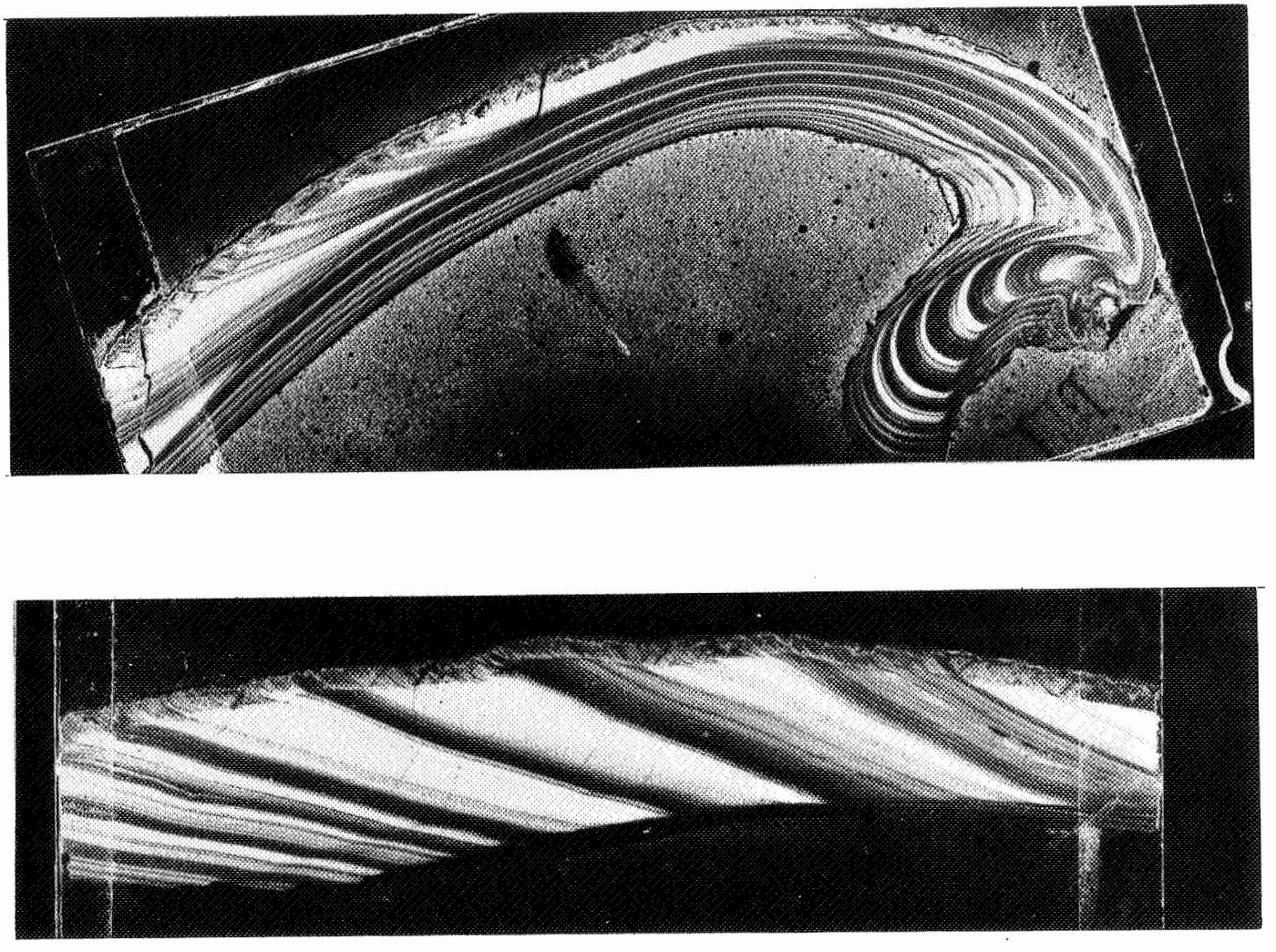
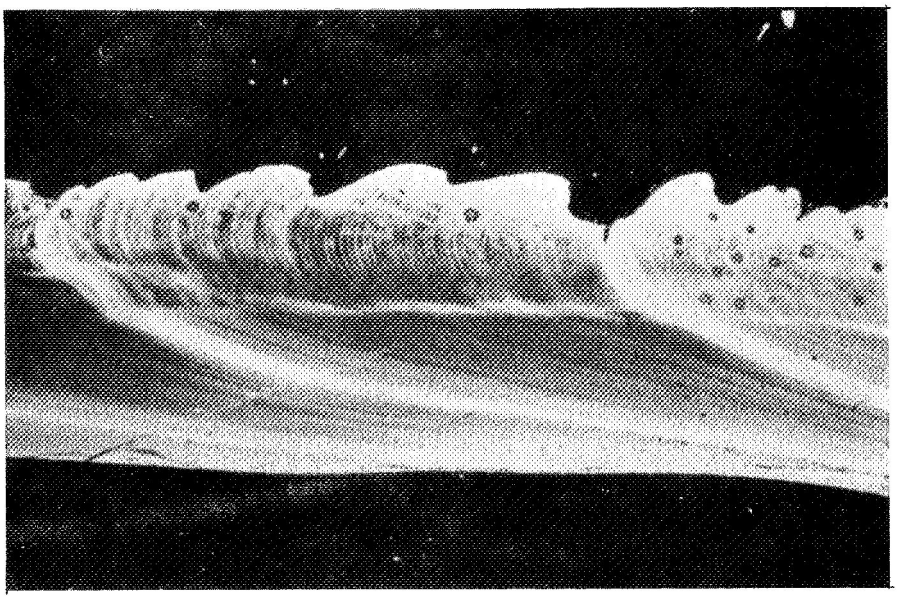
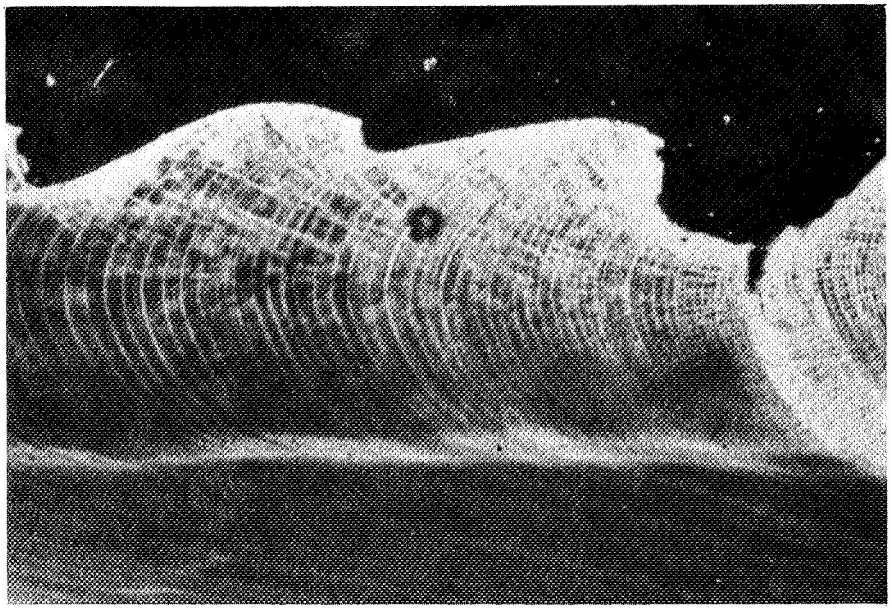


Plate 2. *Mercenaria mercenaria* (Linnaeus). Annual growth layers in radial thin section. Recent, Bogue Sound, N. C. Negative photomicrograph (printed directly from thin section) X4.



(1) Two slow-growth groove deposits appear as brightly illuminated growth layers X29.



(2) Enlargement, concentric ridges shown at lower magnification in (1)X73.

Plate 3. *Venus striatula* (da Costa). Recent, Great Britain. Radial thin section, crossed Nichols.

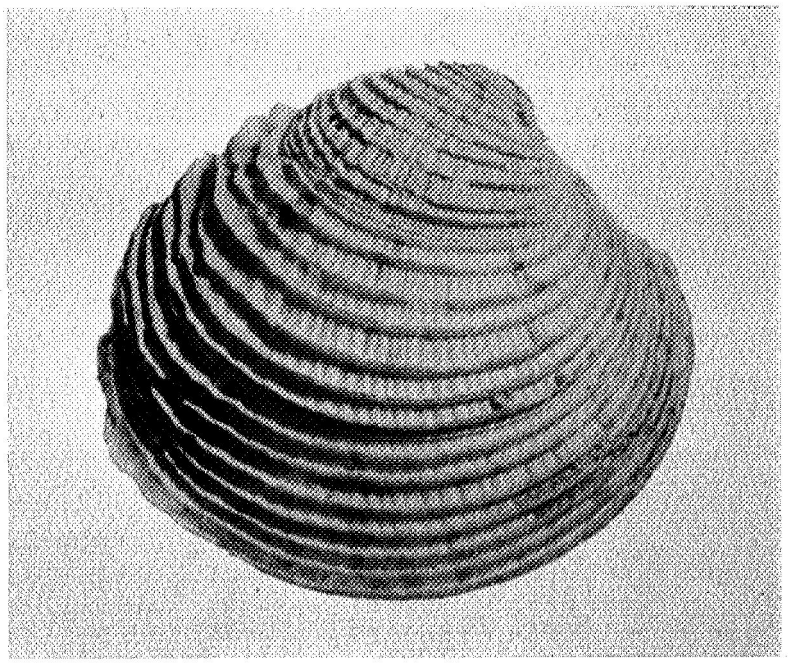
myostracum, they become very indistinct in the dissoconch endostracum of most species. Exceptions to this may be found in some shells of *Mercenaria mercenaria* in which the growth bands are pigmented through all major shell layers.

Occurrences of annual layers in other species

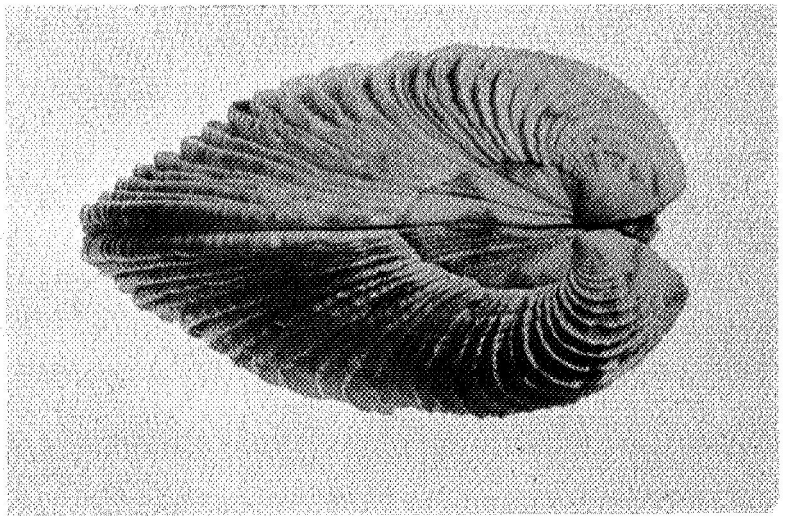
Many other pelecypod species have major shell increments similar to the annual layers that have been described. In all of these species, the number of major increments per shell seems compatible with these increments having been formed annually. The most distinct annual layers that have been recognized occur on the shells of species of the crossed-lamellar group, especially the Veneridae (e.g., see Plates 1-6:1). The concentric groove or ring is associated with the deposition of a translucent, almost optically uniform slow-growth layer that is gradually transitional to a semiopaque, optically irregular, rapid-growth layer. Although some specimens lack a strong surficial expression of annual layers, thin sections reveal distinct alternations of the slow- and rapid-growth layers.

Annual layers recognized in study of several *Pectinids, Unionids, Pinnids,* and *Volsella* most closely resemble those that were observed in *Aequipecten irradians* and *Pecten maximus*. The concentric grooves are narrow and V-shaped. They are related to mesectostracum partings that are often filled or streaked with a brown optically isotropic substance similar to the *periostracum*. In the *Unionids* and *Volsella*, these partings are usually traceable into the *endostracum*. Grooves with U-shaped or L-shaped outlines occur on shells of *Lyropecten*. These grooves are also related to partings of the mesectostracum. Finer increments are very indistinct or not present in thin sections of the preceding nacro-prismatic shells. Viewed as growth striae on the surface of the Pectinid shells, the finer increments are usually not rhythmically spaced in relation to the major growth bands and concentric grooves.

Although the author has not emphasized the study of species with nacro-prismatic shells, some of them may have sublayer imbrications similar to those that are formed annually by *Mytilus californianus*. However, it is not possible to predict the taxonomic groups in which these structures occur, since *Mytilus edulis* lacks the sublayer and may attain a large size without forming major increments of any kind. Nevertheless, a remarkable example of a rhythmically imbricated endostracum was observed

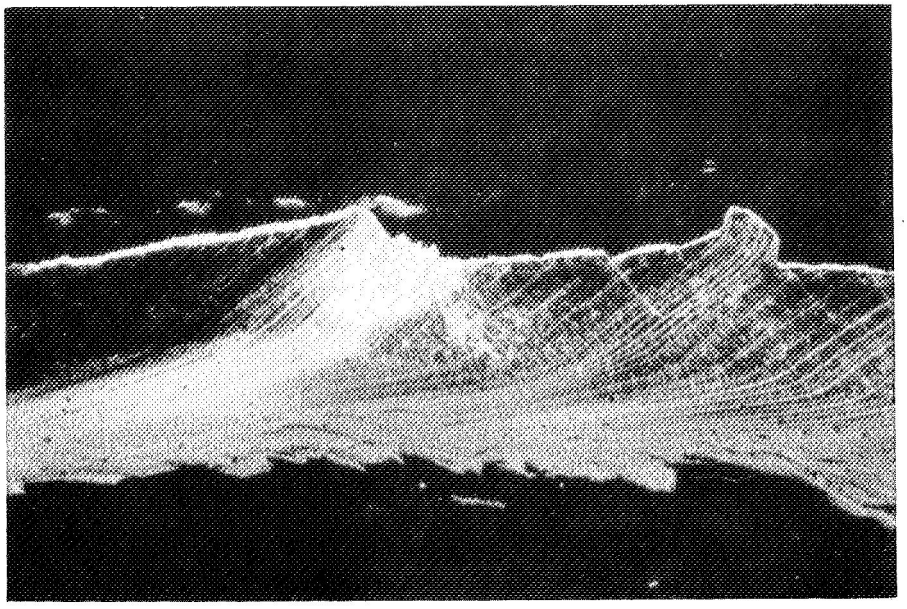


(1) Dissconch of right valve

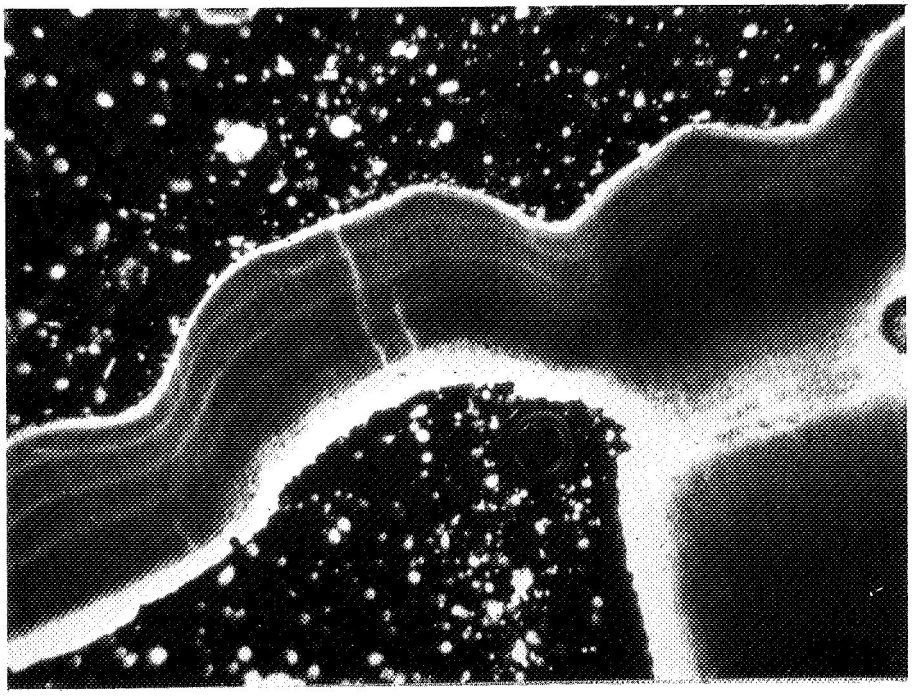


(2) Anterior view tracing grooves of dissconch into lunule.

Plate 4. *Chione undatella* (Sowerby). Concentric grooves related to decreases in spacing of concentric ridges. Recent, Cholla Bay, Sonora, Mexico X2.



(1) Winter slow-growth layer between crossed Nichols. Radial thin section X24.



(2) Horizontal thin section of ridge on ventral margin. Crossed Nichols X87.

Plate 5. *Chione undatella* (Sowerby). Recent, Cholla Bay, Sonora, Mexico.

Plate 6.

(1) *Chione cancellata* (Linnaeus). Radial thin section showing translucent groove deposit and flexure of the mesectostracum boundary beneath a concentric ridge. Recent, Bradenton, Florida. Crossed Nichols X29.

(2) *Mercenaria mercenaria* (Linnaeus). Growth laminae in the ectostracum (upper right) and in the mesostracum (lower left). Recent, Bradenton, Florida. Radial thin section, plane polarized light X285.

(3) Thin section of pelecypod shell fragment in sandstone. Paleocene, Meganos Fm., Byron Quad., California. Crossed Nichols X70.

(4) *Aequipecten acuticostia* Zicten . Clusters of growth striae on shell surface. Middle Jurassic, Blockley, Gloucester, England X4.

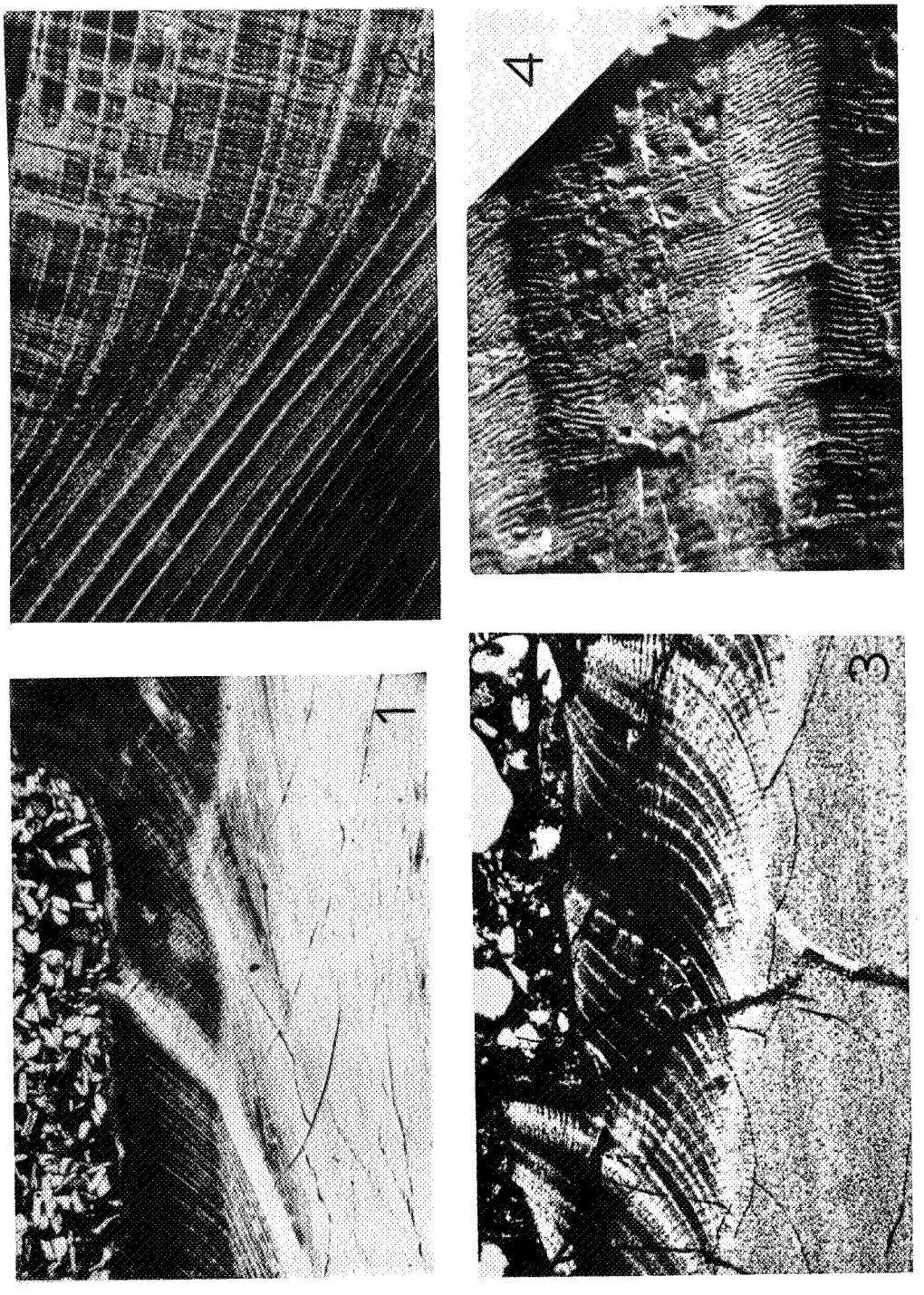
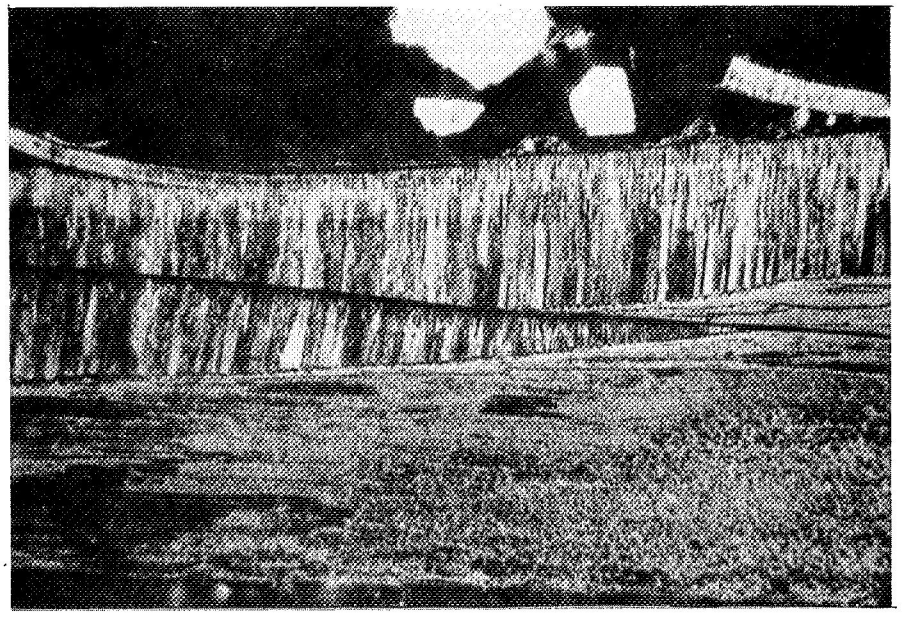


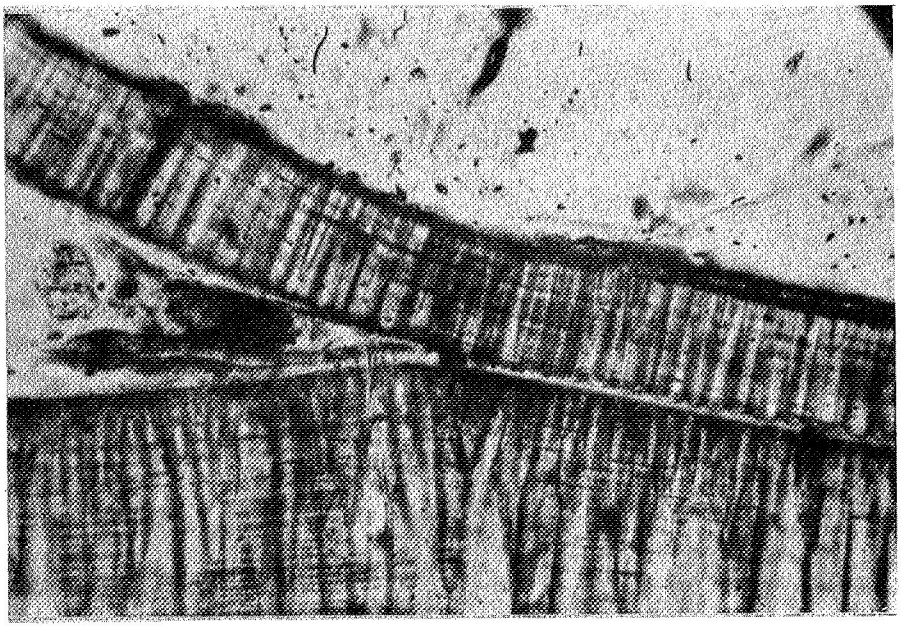
Plate 6.

in *Pinctada radiata* (see Plate 7). In this species, distinct growth layers connect the imbrications with raised concentric rings on the shell surface. In the mesectostracum, each growth layer consists of a 200- to 300-micron-thick deposit of prismatic CaCO3 and a 5-to 10-micron-thick sheet of brown translucent conchiolin. The conchiolin sheets are continuous with partings of the nacreous endostracum. Most of the growth layers are gently curved in the outer part of the ectostracum and overlap one another at relatively wide distances within growth bands on the shell surface. Periodically, two to four growth layers are deposited that terminate within a millimeter of one another, thus forming a raised concentric ring. As observed on the surface of the shell, the growth layers forming the growth rings have a crowded appearance. These growth layers are related to inward movement of the locus of the myostracum and contraction of the endostracum. Growth layers deposited after the growth rings are related to outward movement of the locus of the myostracum and expansion of the endostracum. It is clear that the formation of a major growth ring involves a contraction of the middle and inner mantle folds. Since the growth layers forming the growth rings are less extensive than those forming the growth bands, it is evident that the area of the outer mantle fold also decreases during growth ring formation. Assuming that the growth layers represent equivalent units of time, the growth rings are interpreted as forming when the volumetric rate of CaCO3 secretion per unit area is relatively low. The linear rate of shell growth appears also to be relatively slow when the growth rings are formed, because two to four growth layers forming a growth ring extend the shell only a fraction of the distance that it is extended by the addition of only one growth layer to a growth band. The major increments of *P. radiata* are similar to the annual growth layers observed in study of species with crossed-lamellar shells, consisting of slow-growth layers associated with mantle constriction and rapid-growth layers associated with active growth of the mantle.

The only Recent oyster included in this study is *Crassostrea gigas*. A medium or large shell of this species commonly has four to six major growth bands delimited by L-shaped concentric grooves. These grooves appear to result from a sudden change in the mantle-shell relationship. They are formed by translucent laminae that are visible in all of the major shell layers. As viewed in vertical section, these translucent laminae vary in thickness from 1 mm in the ectostracum to 1/2 mm in the mesostracum



(1) Imbricationoy prismatic and nacreous layers. Crossed Nichols X24.



(2) Minor growth band on surface of shell in upper right corner of (1). Plane polarized light X160.

Plate 7. *Pinctada radiata* Leach . Recent, loc. unknown. Radial thin section.

and outer parts of the endostracum. Their thicknesses within the myostracum are on the order of 5 to 10 microns. The growth bands are built of much finer (< 0.1 mm) translucent laminae intercalcated with chalky deposits that are opaque in thin section. Similar to the slow-growth layers formed annually in other pelecypods, the major translucent layers of *C. gigas* have extinction patterns that are more regular than those of the rapid-growth layers.

Judging from the shapes of the major increments and finer laminae, the shell is enlarged continually throughout the formation of a growth band. Evidence that the major increments are deposited annually is provided by comparisons of specimens obtained from a commercial oystery in Tomales Bay, California. Some of the oysters collected in the winter and spring had major translucent laminae on their shell margins. Other specimens in the winter and spring samples appeared either to have been in the initial stage of forming a growth band or to have recently completed forming one. None of the summer and fall specimens had translucent laminae on their shell margins. The fall specimens appeared to have been in the most advanced stage of the growth band formation process. Although the evidence is slight, it seems adequate enough to indicate that the growth bands are formed in the summer and parts of the fall and spring, and that the major translucent laminae are deposited in the winter or spring.

Mytilus edulis is the only pelecypod examined that was found to be lacking in major increments referable to an annual cycle of shell growth. A small proportion of the specimens observed in the San Francisco Bay and Bodega Bay harbors have concentric grooves regardless of shell size. In vertical section, these grooves are L-shaped as though resulting from a sudden change in the mantle-shell relationship. They are commonly related to an obvious breakage of the shell. On specimens collected or observed in the field in different seasons of the year, no relationship between the proximity of grooves to shell margins and seasons of the year could be recognized. It is evident that these grooves may be formed in any season of the year, whenever the shells are broken.

Erratic Growth Rings

Three types of minor concentric growth rings occur erratically with respect to the annual layers of the shells examined:

1. Surficial ring. This structure is a concentric mass of periostracum that is not expressed in the ectostracum.
2. Micro-groove. This type of groove is occasionally filled with a mass of periostracum. It is usually related to a fine (5-50 microns) translucent growth layer or parting of the mesectostracum. In some shells, this translucent growth layer has inclusions of detrital sand.
3. Shell repair ring. This is a large groove adjacent to a crinkling of finer growth layers deposited on areas of shell breakage. It is related to a translucent growth layer in the mesectostracum.

As seen on the shell surface with the unaided eye, the surficial thickenings of the periostracum and the micro-grooves resemble annual grooves. The differing magnitudes of the most distinct micro-grooves and the annual slow-growth layers are also obvious in this section (see photomicrograph *Mercenaria mercenaria*, Plates 2, 8). Within each of the twelve annual slow-growth layers of the shell there are one or two translucent growth layers that are traceable to micro-grooves on the shell surface. Quartz sand grains occur in the micro-groove deposits of annual slow-growth layers Nos. 3, 7, 8, and 9.)

Growth Layers of Daily Magnitude

Finer growth layers occurring several hundred times per major increment are considered to have a daily periodicity of formation. These apparently daily increments are here referred to as *growth laminae*. In shells of some species, such as *Mercenaria mercenaria*, there may be close to 360 or 365 growth laminae per annual layer. Other shells may have lesser numbers of growth laminae per major increment, perhaps due to interruptions of shell growth during the slow-growth season. In no case have more than 365 growth laminae been observed within a major increment.

The growth laminae are most distinct within parts or all of the palliostracum, depending on species. The other major shell layers appear



Plate 8:1. *Mercenaria mercenaria* (Linnaeus). Sand grains enclosed in mesostracum. Direction of growth to lower left (normal to growth layers). Recent, Bogue Sound, N. C. Plane polarized light X50.

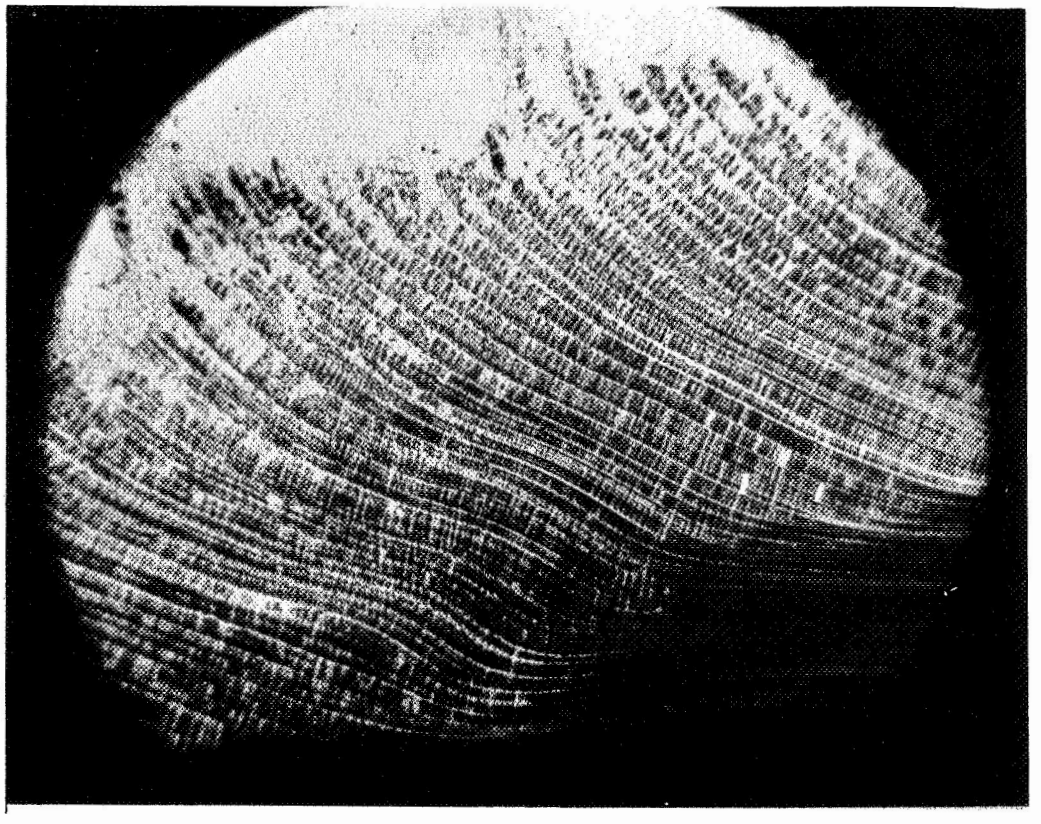


Plate 8:2. *Mercenaria mercenaria* (Linnaeus). Concentric ridges and troughs in thin section of pigmented shell. Recent, Bradenton, Florida. Plane polarized light X64.

to be lacking subannual growth layers that could be related to daily deposition. The myostracum, which is secreted by the adductor and pallial attachment muscles, lacks growth layers assignable to the category of the unit growth lamina. Fine growth lines are barely detectable in the endostracum where shell growth is considerably slower than in the extrapallial region. The same applies to dorsal parts of all of the major layers. The following descriptions of growth laminae pertain to the dissoconch mesectostracum.

In the Pteriacea, the growth laminae are defined by obvious partings of the prismatic mesectostracum (Plate 7:2). Each growth lamina is composed of segments of the nonfoliated prisms that have almost normal extinction patterns. In the Pectinidae, growth striae that are spaced at intervals of 100-300 microns on the shell surface are related to dark growth lines that have thicknesses of about 30 microns. As the magnification is increased to X200 or X300, these dark areas are seen as twistings of tiny foliated structures adjacent to a fine parting of the mesectostracum. Growth laminae are either indistinct or not present in thin sections of shells of other nacro-prismatic and foliated pelecypods that were examined.

In shells of the complex-lamellar pelecypods, the growth lamina is complex, consisting of two component layers:

1. Translucent layer that transmits light through sections that are as thick as 30 microns.
2. Series of semiopaque layers intercalcated with lighter layers that are usually quite opaque in sections more than 20 microns thick.

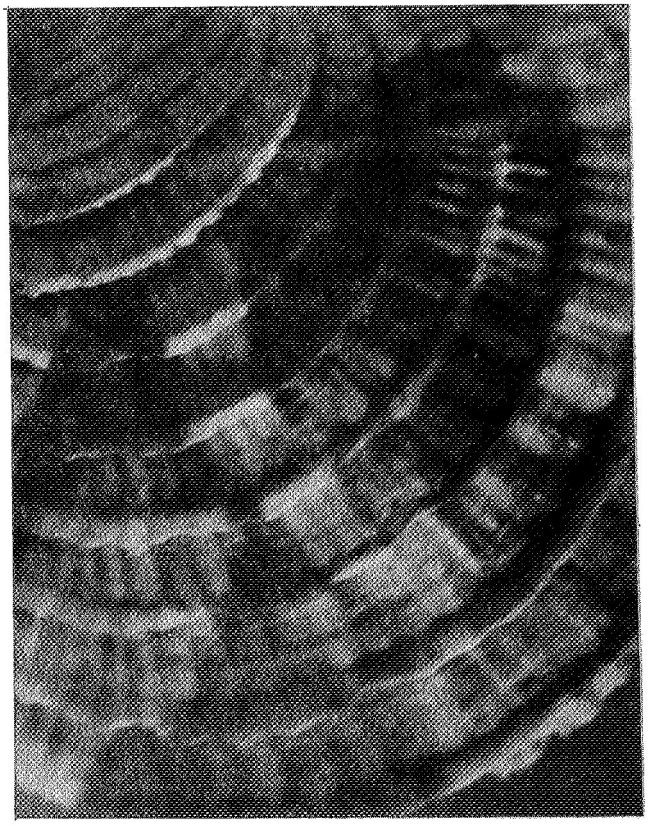
In reflected light, the translucent component has a vitreous luster and is gray or bluish gray, whereas the semiopaque component has a chalky appearance. The alternation of these components may be seen upon shell surfaces that have been treated with dilute acids or caustics. Untreated surfaces are covered by the thin periostracum which superimposes its crenulations on the underlying ectostracum surface. Treatment of the dissoconch with a 2% solution of acetic acid for a few minutes, followed by rinse in water or a wetting agent usually releases filmy shreds of

periostracum. The calcareous shell surface exposed by this treatment shows with low incidence illumination a series of imbricated growth laminae (Plates 9-11). The steplike appearances of these growth laminae are due to the relative resistance of the translucent component.

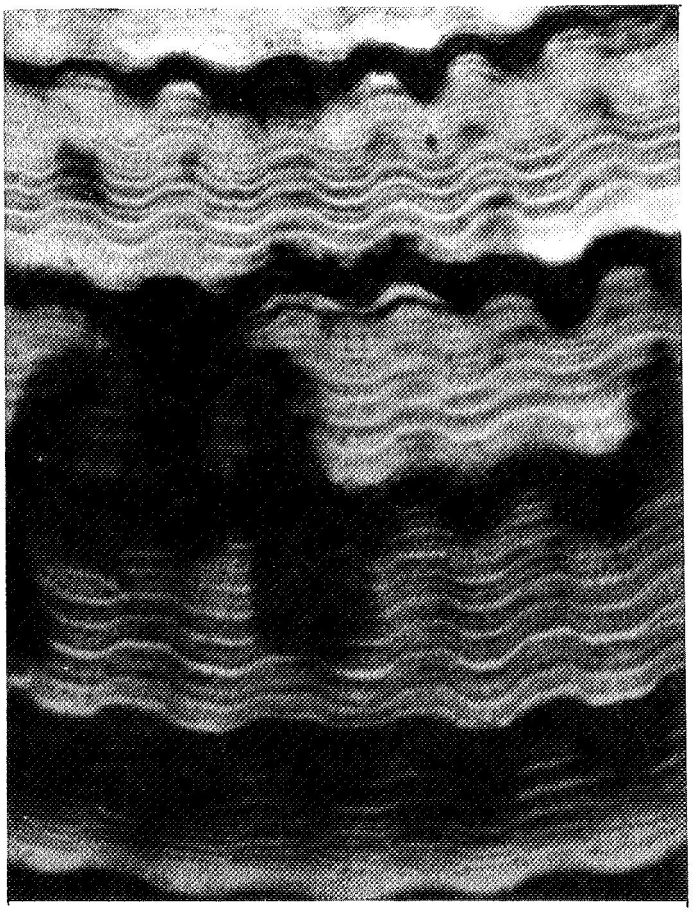
Where the shell surface has been etched to an extreme, so that the radial prisms and the denticular structures become dominant, growth laminae are indistinct. Thin section preparation must also be tempered to an optimum if the growth laminae are to be observed clearly in the ectostracum. Finer lines occurring within the semiopaque and translucent layers become increasingly apparent as the section is thinned. At the same time, contrasts between the light and dark components of the growth lamina become weaker and a variety of patterns may be seen within the unit growth lamina. On grinding to thicknesses well below 20 microns, an almost uniformly transparent film of CaCO3 may be eventually obtained. This super-thin section shows a rectangular grid, one set of lines corresponding to the boundaries of the prisms and the other set to the partings along planes of deposition. The number of partings per growth lamina in the ectostracum varies from one to four. As the growth lamina pass into the mesostracum, there is an abrupt merging of the partings and the ultrafine units they delimit. Examples of the resulting mesostracum growth laminae are shown in photomicrographs of thin sections of *Mercenaria* and *Crassatella* (Plates 6:2 and 12). It is in the dissoconch mesostracum of most shells that the growth laminae are most distinct and regular. This is not so for shells that have homogeneous structured mesostracum (e.g., *Pitar*).

Process of daily secretion

How the growth laminae are secreted may be inferred from morphological and ethological considerations. The ectostracum and periostracum are secreted by the more external parts of the outer mantle fold. Since the outer lobe is normally withdrawn when the valves are closed, additions to these major shell layers are made only when the clam has opened its valves under favorable or almost favorable conditions. Related to feeding and respiration in littoral forms, valve opening is likely to be most frequent during high tide. However, valve movements can also be sporadic. It is



(1) Untreated surface of shell with pigmented areas X10.



(2) Surface after treatment with acid; reveals steplike growth laminae X25.

Plate 9. *Chione undatella* (Sowerby). Recent, Cholla Bay, Sonora, Mexico.

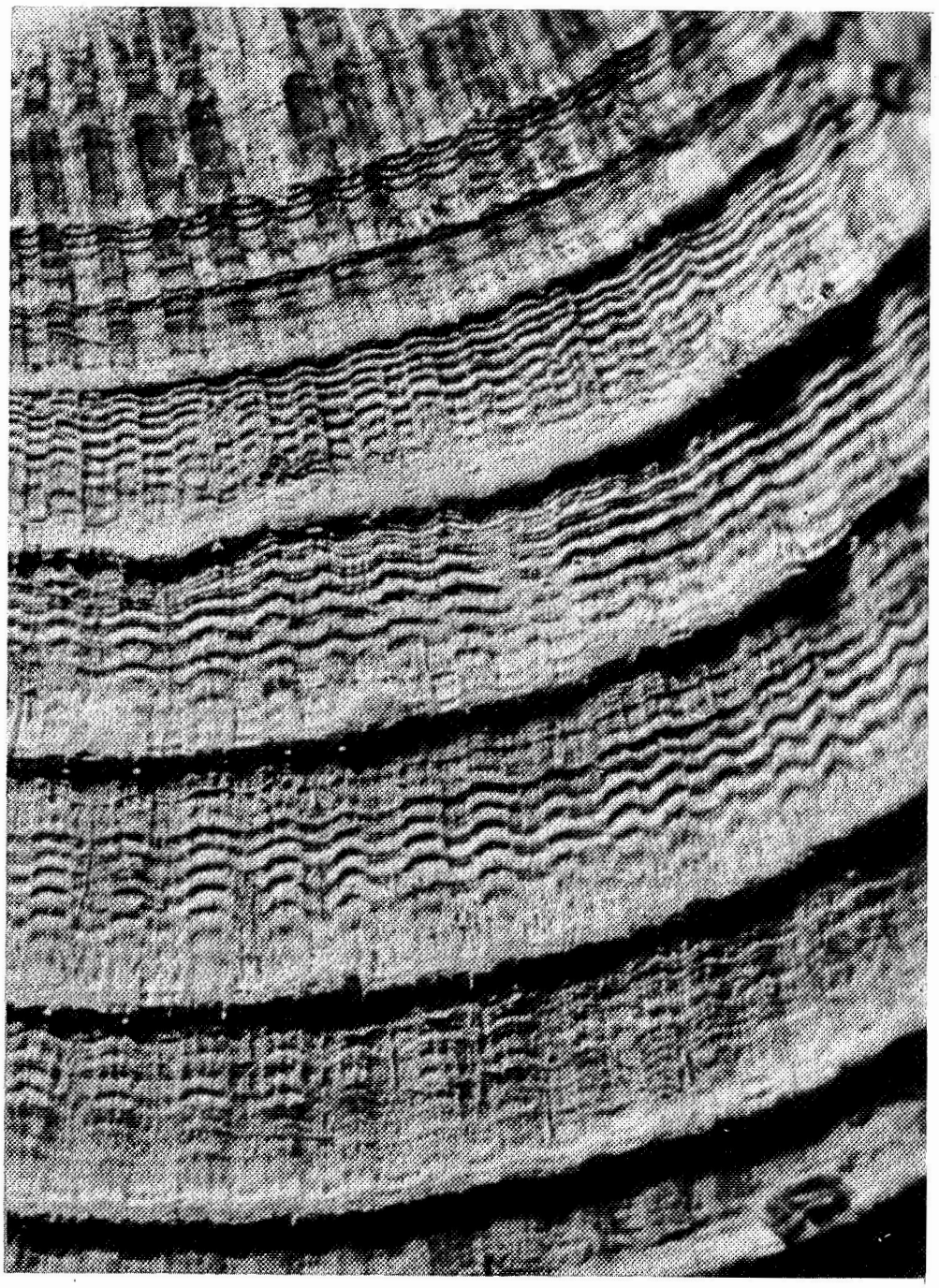


Plate 10. *Chione californiensis* Broderip . Imbrication of growth laminae forming concentric ridges and troughs on etched surface. Recent, Cholla Bay, Sonora, Mexico X12.

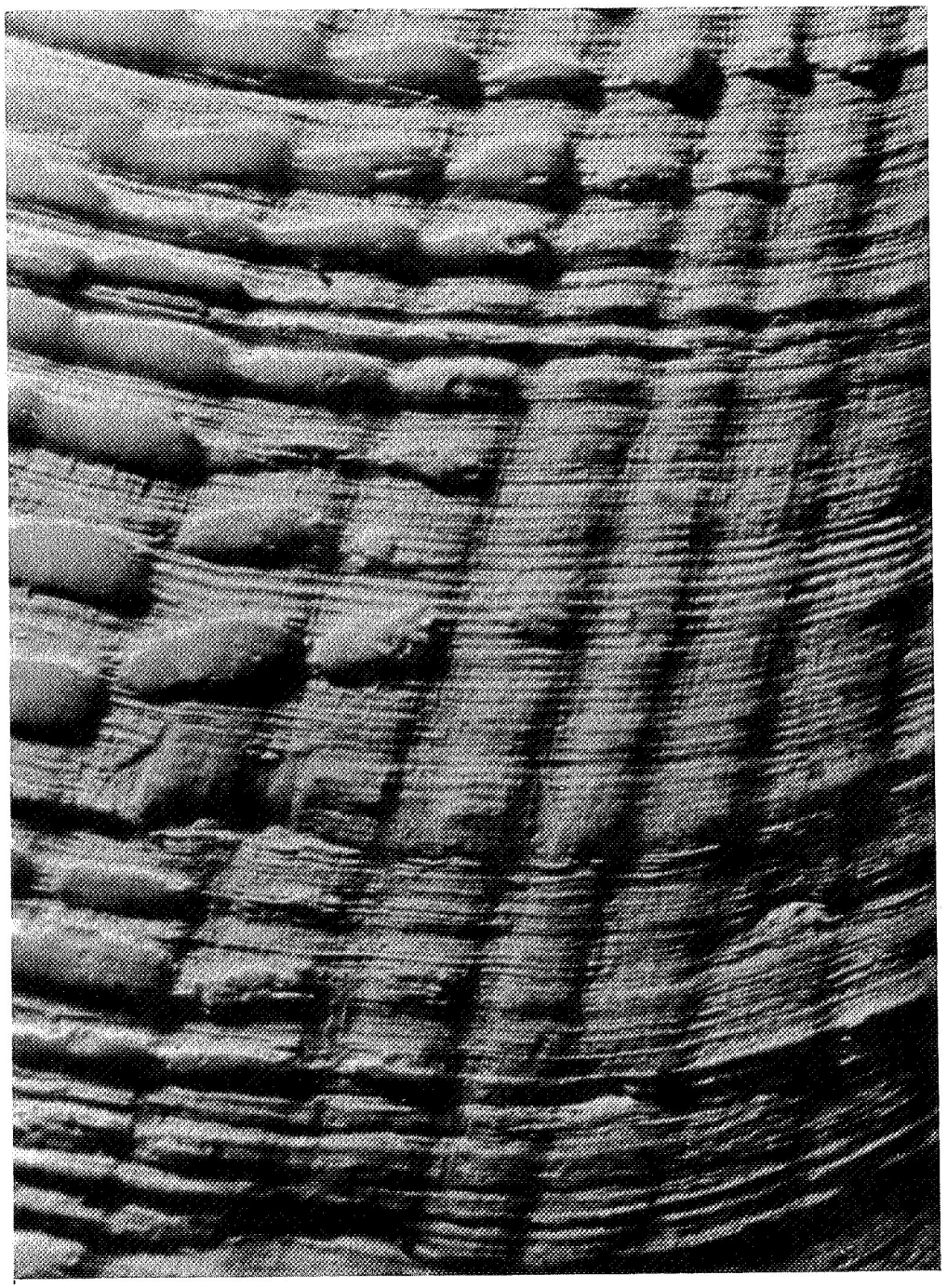
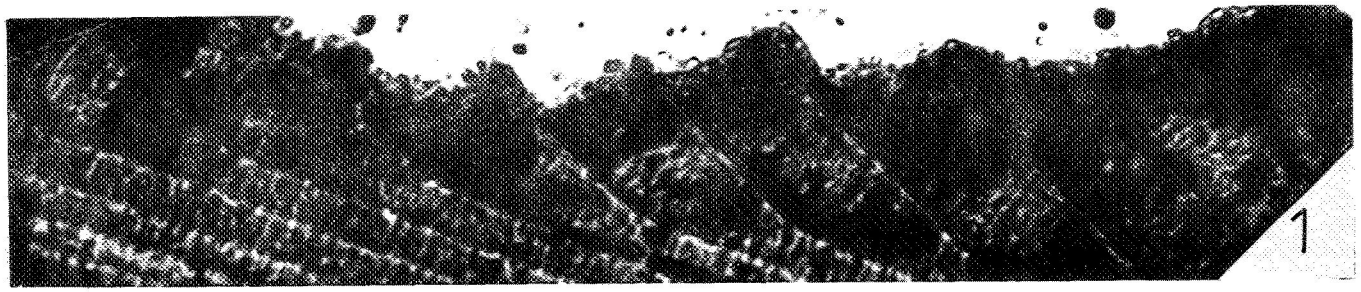
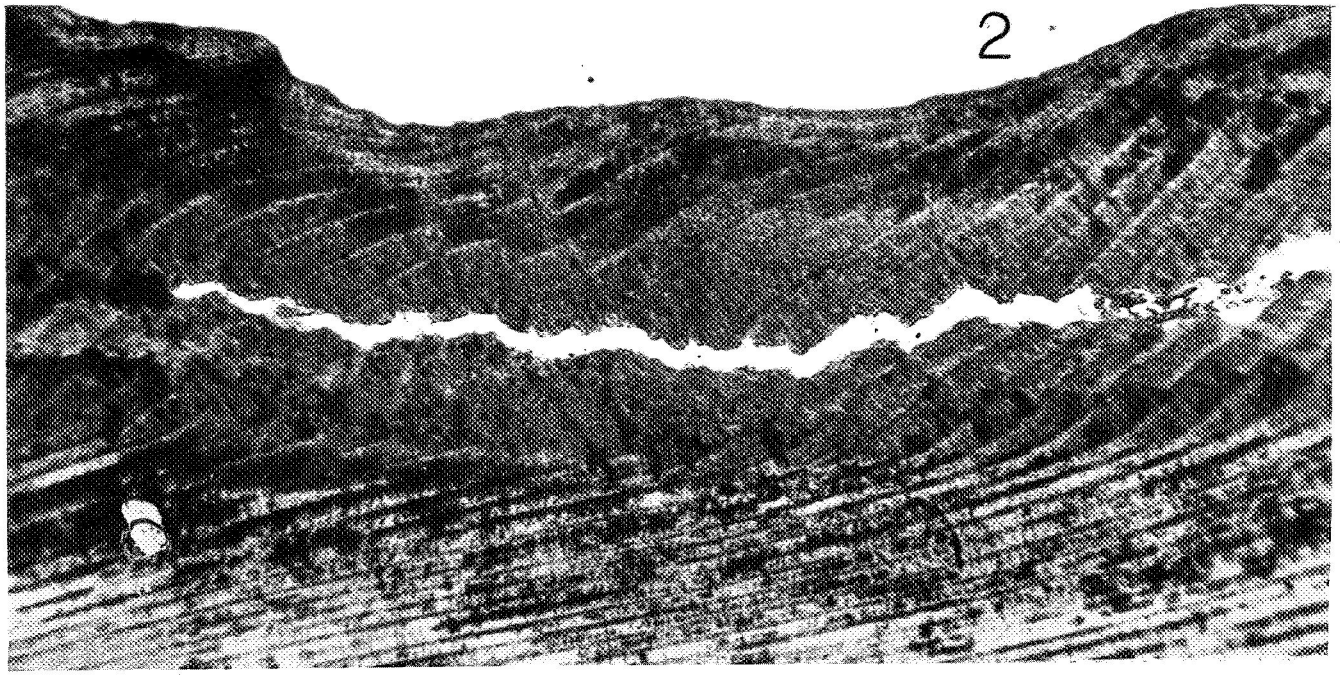


Plate 11. *Protothaca fructifraga* (Sowerby). Growth laminae forming concentric ridges and troughs on etched surface. Recent, Cholla Bay, Sonora, Mexico X13.





(2) Growth laminae and two concentric ridges X117.

Plate 12. *Crassatella vadosus* Morton . Late Cretaceous, Ripley Fm., Coon Creek, Tennessee. Radial thin section, plane polarized light.

known that the outer lobe of the mantle is equipped with photoreceptive cells that trigger the valve closing mechanism (Kennedy, 1960). Sudden movement of a shadow cast by another organism or some other object may induce the clam to retract its siphons and mantle. Also, defecation and elimination of irritants are accomplished by sudden contractions of the adductor and pallial muscles. These are everyday activities, and it seems obvious that a number of interruptions of deposition may occur within a daily cycle of addition to the ectostracum. I suggest that these breaks in deposition are the partings that occur within the translucent and the semiopaque components of the complex-growth lamina. The mesostracum, which is secreted by a more static part of the outer fold, should have a less distinct expression of these events. In fact, partings of the growth laminae are rarely observed in this layer, and then they are easily distinguished from the growth laminae.

While it is possible that the simple growth lamina observed in the Pteriacean and Pectinid specimens could result from exposure of the organism at one of the diurnal low tides, the species that have been sampled are most common in subtidal environments. It seems more likely that the simple growth lamina is related to a day-night cycle that is not affected by tidal activity.

As the complex growth lamina occurs in shells that are known to be entirely composed of aragonite, the greater opacity of the semiopaque component layer must be due to a greater scattering of light by an irregular array of crystalline constituents. Since irregular aggregations of crystals are related to conditions of rapid crystallization, the semiopaque layer is interpreted as resulting from a period of rapid secretion of $CaCO_3$ during either the day or the night. The simple growth lamina has evidence of only one episode of secretion that may occur in the same phase of the day-night cycle as the rapid secretion of the semiopaque layer.

Fortnightly and Monthly Growth Layers

In the shells of many marine and at least some nonmarine species, the growth laminae are commonly clustered several times within an annual layer, thus forming larger growth layers that have periodicities that are

Of many shells representing perhaps fifty species of the Unionacea, minor growth bands were observed only in *Lampsilis radiata*. These minor growth bands number from ten to twenty-five per major shell increment and consist of growth layers of prismatic CaC03 sandwiched between sheets of conchiolin, which are continuous with the periostracum. The organic growth layers form flexible frills that may extend as much as 1 mm above the general shell surface. Growth laminae occurring within the minor growth bands are indistinct whether viewed in thin section, polished vertical section, or on natural and etched surfaces. That the minor growth bands of these *Lampsilis* shells represent a fortnightly rhythm of shell growth is weakly suggested by their grouping within the major shell increments.

Most of the Pectinid species lack shell increments referable to monthly or fortnightly rhythms, although some shells of *Lyropecten subnodosus* show an occasional distinct minor growth band comprised of fifteen or thirty growth striae.

The least distinct minor growth bands that have been observed occur on the periostracum and ectostracum surfaces of shells of *Mytilus*. These increments are not visible in thin section. On shells of *M. edulis* from the eastern shore of San Francisco Bay, there are commonly thirty or slightly less than thirty growth striae within the minor growth bands. Occasionally, these minor growth bands are subdivided into equal halves by a relatively weak imbrication of the shell surface. In the harbor of Bodega Bay, individuals of this species tend to form only fifteen striae per minor growth band, but may also form an occasional minor band with thirty growth striae. If these minor growth bands are related to monthly and fortnightly cycles, the relationships are variable with environment. *M. californianus* forms annual layers that include four or five minor growth bands. Evidence of a subannual growth cycle is lacking in this species. Similar minor growth bands related to clusters of thirty growth striae occur on fossil Mytilid shells from the Tertiary of California. Some of these shells also have major increments in which there are commonly twelve or thirteen minor growth bands.

neither annual nor diurnal. Judging from the number of apparent daily growth layers included in the clusters, and from the number of clusters per annual layer, many of these periodicities may be either fortnightly or monthly. Related to variations in the mantle-shell relationship, the clusters of growth laminae are expressed on the shell surface as minor growth bands or as concentric ridges that are spinose in some species. (For list of the species in which these shell increments have been observed, see Table 2.)

Minor growth bands

These structures are defined on the shell surface by imbrications. The steplike appearance of the minor growth band indicates that the mantle moves inward from the former shell margin to occupy a new position that is maintained during the formation of the next minor growth band. In the shell of *Crassostrea gigas*, the imbrication is related to a 100- to 300-micron-thick, translucent growth layer. A contrastingly porous and chalky minor growth band is formed during a period of mantle-shell stability. This growth band is on the order of a millimeters in thickness. These growth layers have an extremely complex configuration and it is difficult to trace them within the shell. In the endostracum of the dissoconch, many of the translucent growth layers anastomose, and the intercalated chalky layers are discontinuous. The translucent growth layers intersect the myostracum at low angles and rise into the mesostracum at higher angles. In the mesostracum, near its boundary with the myostracum, the translucent growth layers are relatively thick and distinct. In the outer part of the mesostracum, these growth layers are thinner and less distinct, and occasionally, they anastomose or become semicontinuous. At the shell surface, the chalky layers wedge out and the translucent growth layers overlap one upon another to form a compact translucent ectostracum. The growth layers of the dissoconch endostracum may be traced into a translucent deposit of the ligamental support, where they are particularly regular and distinct.

Megascopic study of the shells of oysters from Tomales Bay sheds light on the origins of the growth layers seen in thin section. On the internal shell surfaces of specimens collected in the midst of forming

minor growth bands, the chalky deposits have a spotty distribution inside the pallial line. Evidently, the growth band deposits are wedgelike due to lateral discontinuities of secretion. Specimens collected at full moon appear to have fully completed, minor growth bands on their ventral shell margins. However, due to a lack of freshly collected specimens available for purchase from the oystery in other phases of the lunar month, this observation by itself is insufficient evidence that the minor imbrications and translucent growth layers are formed at full moon. It has been possible to count the number of minor growth bands per annual increment in the ligamental support region of the endostracum and in the adductor muscle scar region of the mesostracum. In both positions, there are commonly twelve or thirteen minor growth band deposits in the second-formed annual layer. Later-formed annual layers have fewer (6-8 common) minor growth band deposits. Considering that shell growth is interrupted for a period of several months after the second year, and that this annual hiatus increases as the organism grows older, the minor growth bands of this species could be formed on a monthly basis.

Major increments and minor growth bands similar to those of *C. gigas* have been observed in thin sections of fossil shells of *Gryphaea*. Many of the major increments have twelve or thirteen minor growth band deposits.

Minor growth bands on shells of *Pinctada radiata* are related to growth layers consisting of prismatic CaC03 deposited on sheets of conchiolin. Thirty or less partings occur within each prismatic growth layer (see Plate 7). Since these partings define simple growth laminae considered as daily increments, the minor growth bands may be formed on a monthly basis. In the shells examined, all the apparently complete major shell increments have eleven or twelve minor growth bands, which suggests that the major shell increments are annual and the minor growth bands, monthly. Similar minor growth bands were observed on shells of the Pinnidae. However, in these species there are often fifteen striae per minor growth band and the number of minor growth bands per major shell increment commonly is between twenty and twenty-five. These minor growth bands are more likely to have a fortnightly periodicity of formation.

Concentric ridges

Concentric ridges and interspaces, or troughs, occur on the shells of many intertidal and neritic marine species of Taxodont and Eulamellibranch pelecypods. Distinct concentric ridges and troughs also occur on the nonmarine shells of at least three Unionid species and in many Corbiculidae. The following types of ridges are defined:

1. Equant. Ridges and troughs of similar sizes and shapes, and including almost equal or equal numbers of growth laminae (e.g., see Plates 12:2, 13:1)

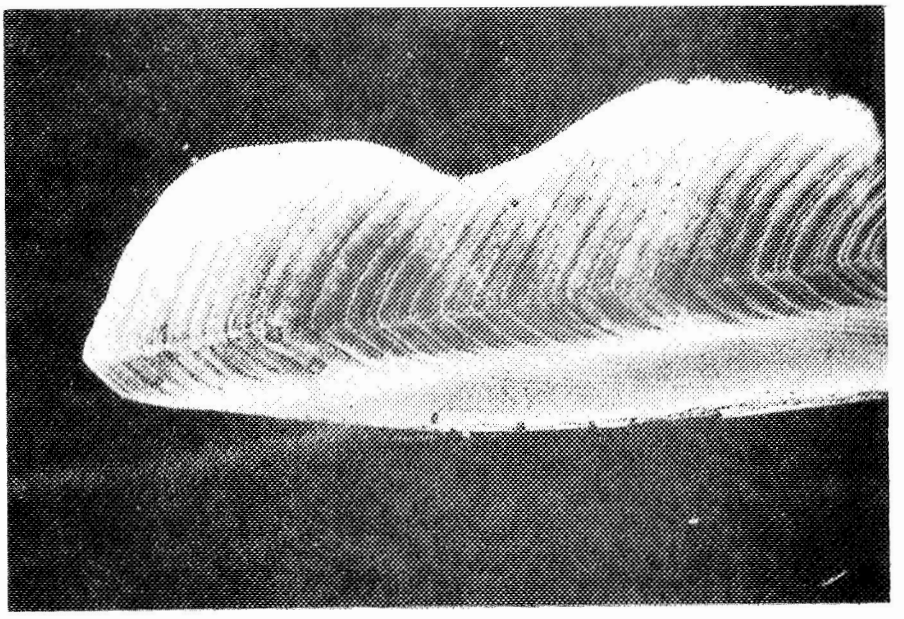
2. Asymmetric. Either the ridge or the trough is relatively narrow and includes only a few growth laminae (Plates 3, 14:1-2).

3. Protrusive. Extremely prominent, widely spaced ridges formed by relatively thin growth laminae. Most protrusive ridges occupy an almost flat plane that seems to be tangential to the ventral margin (e.g., *Chione undatella taberi*, Plates 4, 5:1, and *Mercenaria mercenaria*, Plate 8:2. Some protrusive ridges are recurved as in *Zirfaea gabbi* (Plate 13:2) and may overlap one upon another to form furls as in *Chione californiensis* (Plate 15:1).

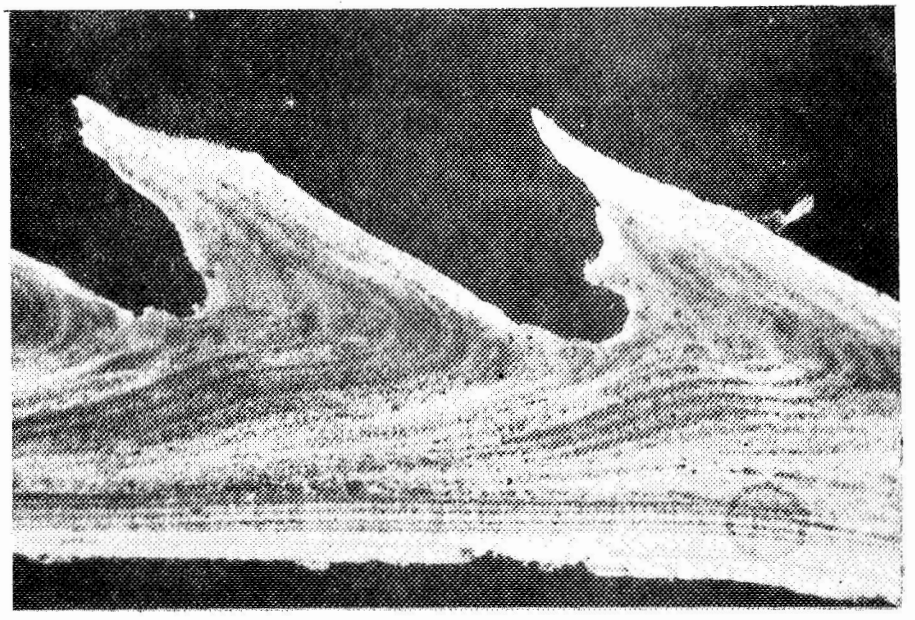
In thin section, the equant or asymmetric ridges are rarely associated with a slight outward projection of the mesostracum, and the growth laminae forming adjacent ridges and troughs are of similar thicknesses. The relatively thin-growth laminae forming the protrusive ridges are usually related to a fairly large outward projection of the mesostracum. These imbrications are commonly nacreous in the predominately crossed-lamellar mesostraca of many Veneridae.

Various combinations of these types of concentric ridges may occur on a single shell. Generally, the protrusive ridges are preceded in ontogeny by a number of narrow asymmetric ridges, and these ridges are preceded by a number of equant or wide asymmetric ridges. In many species, these ontogenetic variations of ridge shape are gradual and there may be a number of ridges with transitional shapes that are difficult to assign to one of the three categories defined above.

The Crassatellid specimens have ridges only of the equant type. These ridges are indistinct on the larger shells (Plate 16:1). In some species,



(1) Chione *(Anomalocardia) subrugosa* Sowerby . Equant concentric ridges in radial thin section. Recent, Gulf of California. Crossed Nichols · X24.



(2) *Zirfaea gabbi* Lowe . Protrusive ridges in radial thin section. Recent, San Francisco Beach, California. Crossed Nichols · X59.

Plate 13.

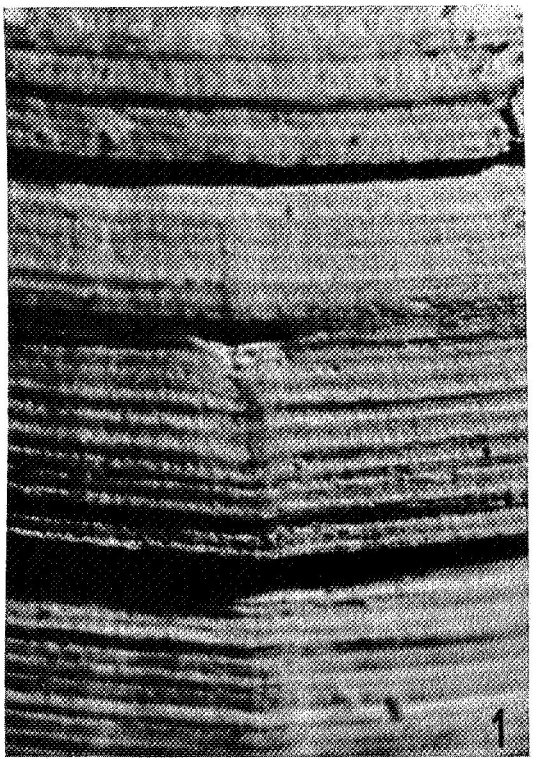
Plate 14.

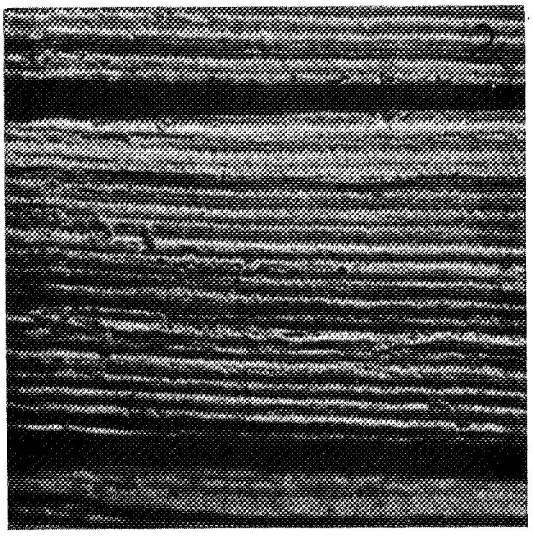
(1), (2) *Idonearca vulgaris* Morton . Closeup view of specimen illustrated in Plate 9. (1) Shows disturbance related to inclusion of foreign body and a finer disturbance ring representing some other interruption of growth X7. (2) The fourth-formed major growth band comprised of 20 concentric ridges followed by a groove in which there are 5 ridges X6.

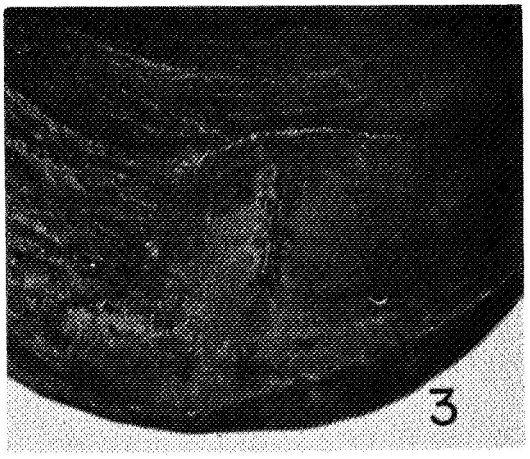
(3) *Mytilus edulis* Linnaeus . Disturbance ring related to repair of shell. Living specimen, Bodega Bay harbor X2.7.

(4) *Protothaca staminea* Conrad . Disturbance ring related to chipping of ectostracum on ventral margin, October 5, 1967. Specimen recovered on December 16, 1967. Bodega Bay harbor X4.7.

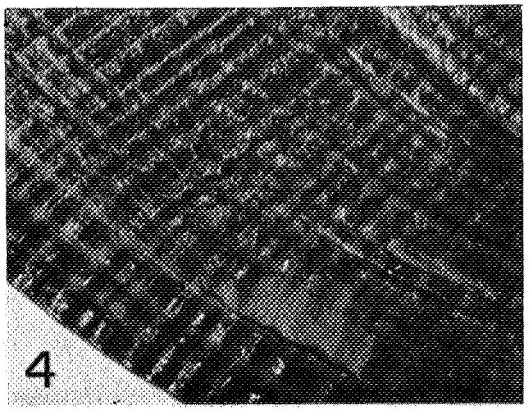
(5) *Idonearca vulgaris* Morton . Radial thin section of mesectostracum showing growth laminae in clusters of fifteen. Late Cretaceous, Ripley Fm., Coon Creek, Tennessee. Plane polarized light X100.

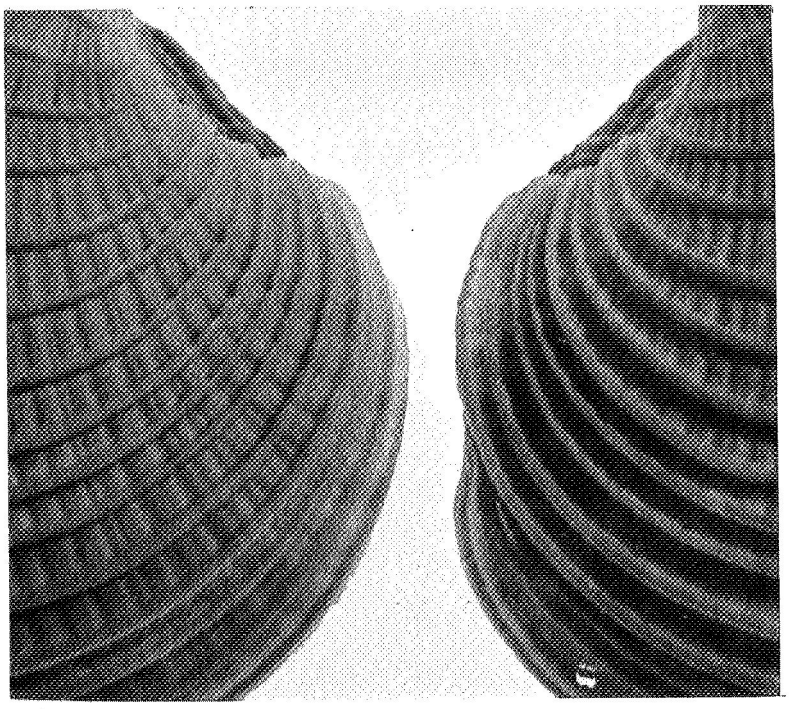

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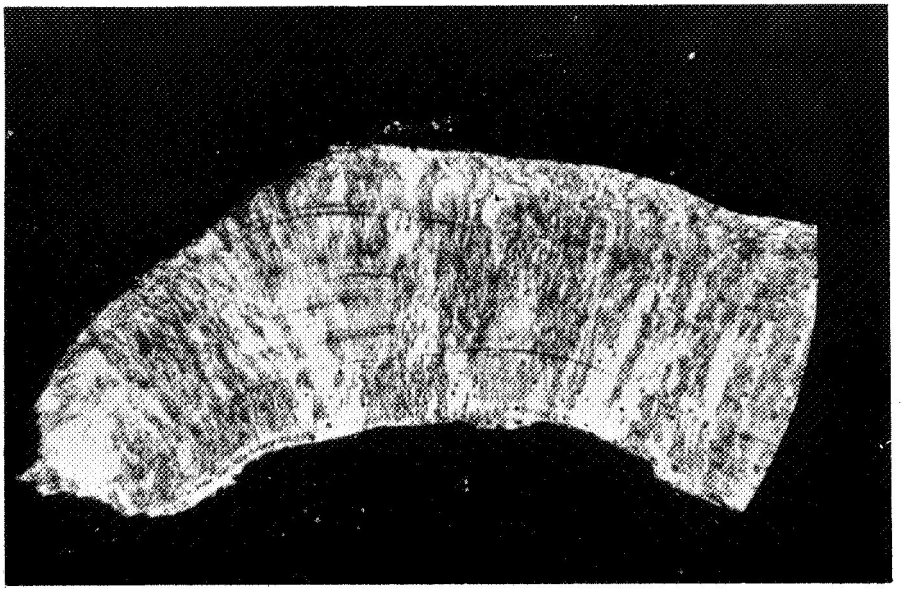

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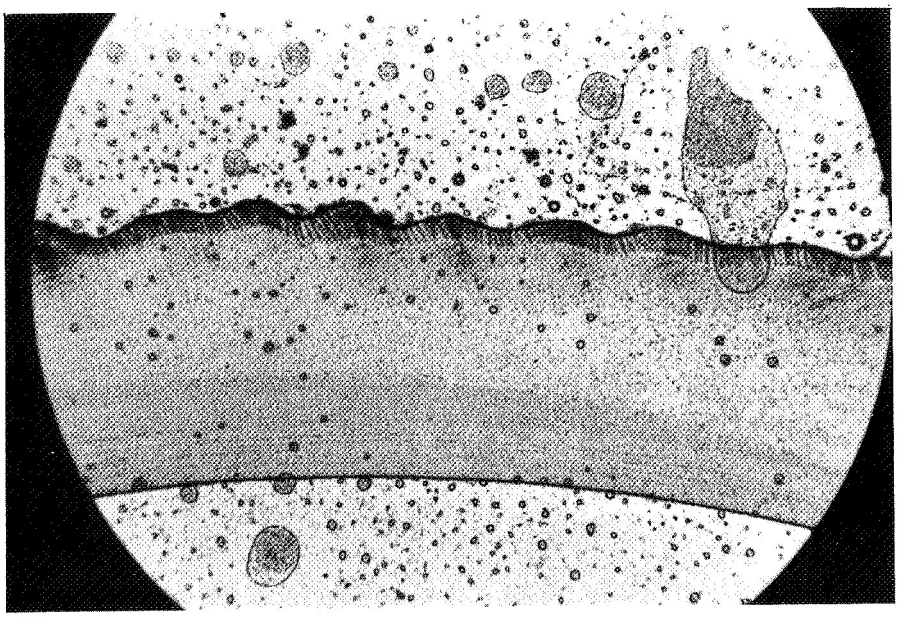


(1) *Chione californiensis* Broderip . Lateral discontinuities of concentric ridge and trough increments on left valve. Collected alive in Cholla Bay, Sonora, Mexico, Nov. 17, 1967, X10.

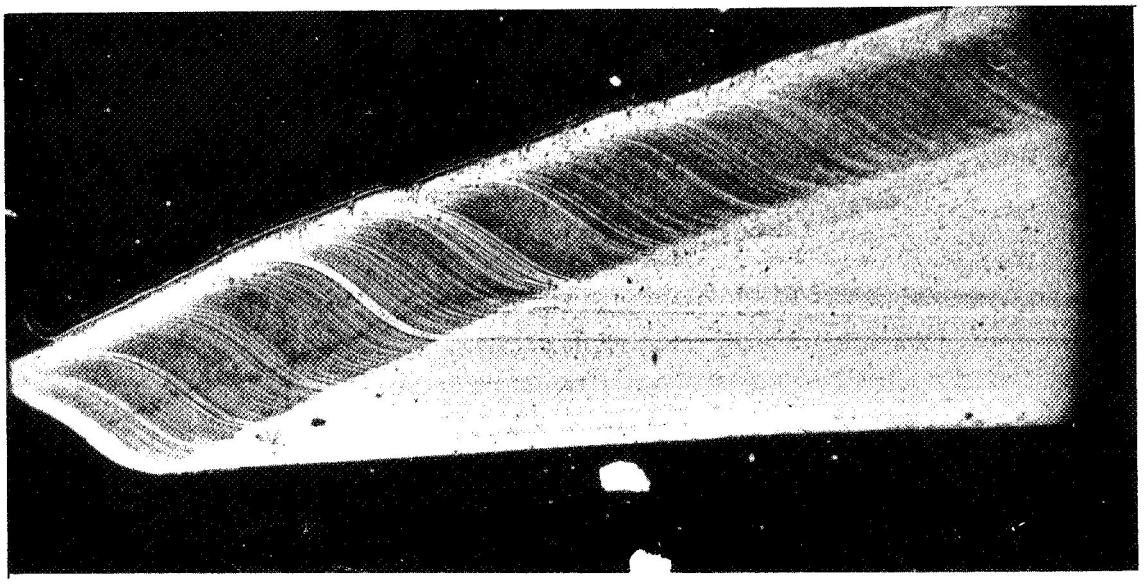


(2) *Spondylus crassisguama* Lamarck . Cross section of calcareous spine. Thin section normal to long axis of spine, near distal end of spine. Recent, Gulf of California. Crossed Nichols X25.

Plate 15.



(1) *Eucrassatella digueti* Lamarck . Radial thin section of ventral portion of shell. Recent, Gulf of California. Crossed Nichols X38.



(2) *Unio raveneliensis*. Recent, Nicaraugua. Radial thin section. Plane polarized light. X38.

Plate 16.

the concentric ridges may have one shape on the posterior of the shell and another shape on the anterior. Although this lateral variation of ridge shape may be gradual, as in many of the Veneridae and Tridacnidae, extremely abrupt transitions of ridge shape occur on the midlines of Pholad shells and on the dorso-posterior portions of many Pitarine shells. Where ridge formation is confined to a number of radial ribs or folds, e.g. in the beaded sculptures of *Cardium*, the ridges are node-like. The nodes of adjacent ribs can usually be correlated by tracing discrete growth laminae across radial furrows.

In most species with non-beaded shells, the ventral margin has either a ridge or trough that is continuous around the shell periphery. These laterally continuous ridges and troughs thus represent episodes of growth affecting the entire margin of the shell. In most species with beaded shells, all the ribs terminate at the ventral margin in the same phase of the node-trough growth cycle, thus showing that the clusters of growth laminae forming the nodes and troughs are laid down during episodes of $CaCO_3$ addition to the entire shell margin. At least some species form ridges that are laterally discontinuous or which become merged where there are lateral discontinuities of the troughs (e.g., see Plates 15:1, 17). Since discontinuous ridges and troughs occurring on the ventral margins of shells appear to be complete as compared with earlier formed discontinuous ridges and troughs, they are interpreted as forming when shell growth is confined to only a portion of the margin.

Mergings of concentric ridges are extremely frequent on certain parts of the Pitarine shell. In *Pitar* (*Hysteroconcha*) *lupanaria*, for example, the ratio of continuous-to-discontinuous troughs is, when rounded off, 1 to 1. More than three-quarters of these discontinuities occur on the antero-ventral portions of a large shell. Although the occurrences of these discontinuities are identical on the left and right valves of individual specimens, the sequence of occurrence varies between specimens from the same locality.

Lateral discontinuities of growth are extremely erratic and rare in the writer's collection of more than 800 specimens of *Chione undatella*. There are only thirteen individual specimens bearing any discontinuous

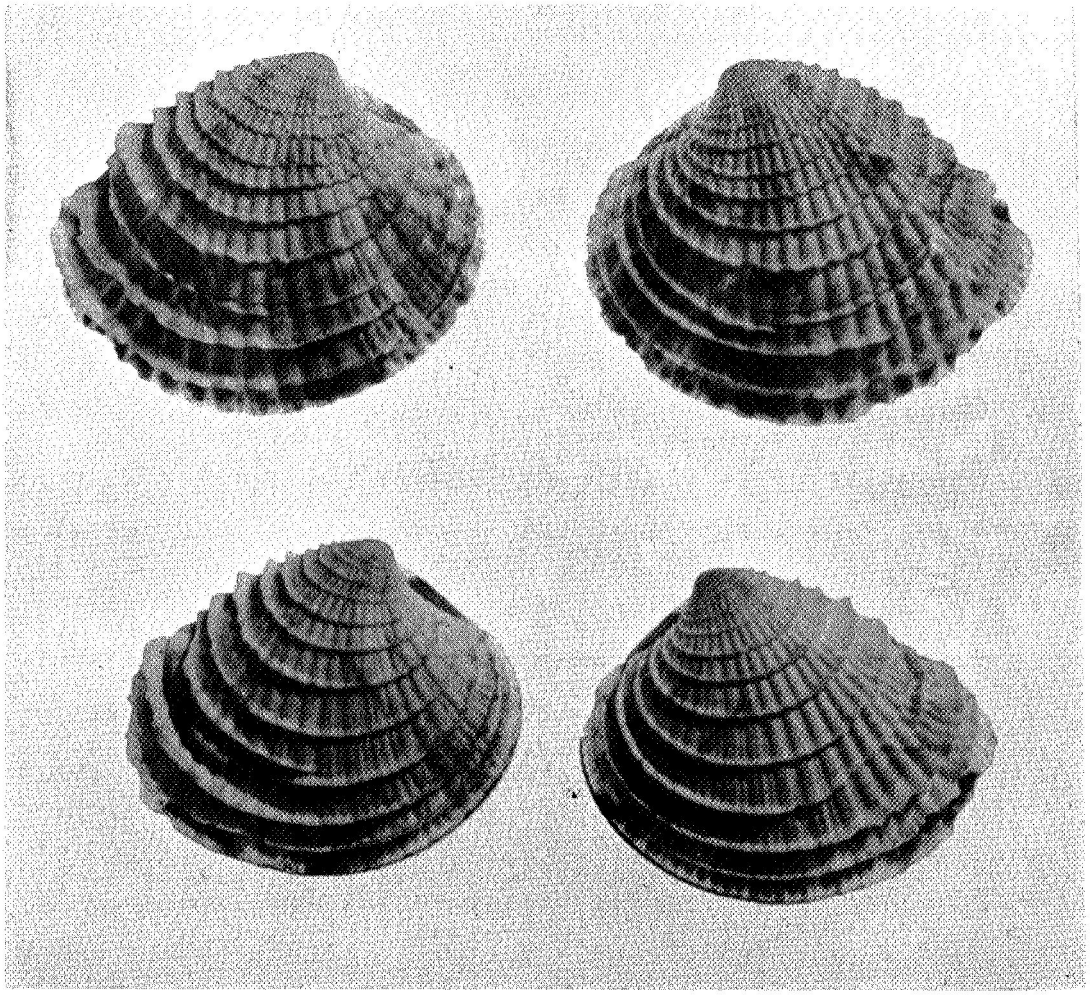


Plate 17. *Chione undatella* Sowerby . Paired valves of two specimens with lateral discontinuities of the ridge and trough increments. Recent, Cholla Bay, Sonora, Mexico X3-1/3.

ridges. Eleven of these specimens have discontinuous ridges that match on both left and right valves. Two specimens have a discontinuous ridge on the left valve and none on the right valve. None of the specimens has discontinuous troughs.

In contrast to the two above examples, laterally discontinuous ridges and troughs occur with moderate frequency on both left and right valves of *Dosinia ponderosa*. None have been observed on shells of the related *D. dunkeri*.

The preceding observations show that lateral discontinuities of shell growth are complexly related to individual variations within species (e.g., *C. undatella*) as well as to specific (*Dosinia* species) and higher (*Pitarinae*) taxonomic groupings.

Process of formation — The fact that concentric ridges are composed of ectostracum indicates that they are formed when a part or all of the outer fold of the mantle is raised above the level of the shell margin represented by the concentric trough. Most equant and asymmetric ridges and troughs represent changes in the areal extent of the edge of the outer mantle fold that does not affect the mesostracum. Gradual continuous raising and lowering of the mantle edge could result in the formation of an equant ridge and trough. A sudden oscillation of this secretory zone followed by a period of stability would produce a narrow ridge and a wide trough. Protrusive ridges represent an extreme of the sudden oscillation type of ridge-building. Since these ridges are related to imbrications of the mesostracum, the entire outer fold must be expanded during ridge formation.

Obvious factors that may be involved in the expansion of the mantle include periodic spurts of tissue growth, changes of osmotic pressure within the tissues, variations in the rates of CaC03 secretion along the mantle-shell surface, and variations in the rate of secretion by the outer mantle fold as a whole. More than a few combinations of these factors could be conceived as producing the features of the concentric ridges.

Temporal rhythm — Provided that the ridge formation process has periodicity, the spacing of concentric ridges would depend upon the rate of shell growth. A temporal rhythm of growth thus may be indicated where

the ridge spacing varies cyclically in relation to the slow and rapid growth layers that are formed annually. On many of the shell species studied, the concentric ridges are most closely spaced within the slow-growth layers. An exemplary relationship is shown in *Mercenaria mercenaria* (Fig. 1). Measured from ridge to ridge along the general shell surface in the second-formed annual layer, the spacing is maximal at 2.5 mm in the rapid-growth layer and minimal at 0.1 mm in the slow-growth layer. This relationship is obvious in all of the ten annual layers of the specimen. In many species represented mostly by shells from northerly waters, cyclic variations of ridge spacing are distinct only within two or three earlier-formed annual layers. These annual layers have relatively thick, slow-growth deposits. The later-formed annual layers of these shells are smaller and are marked by extremely thin, slow-growth deposits that lack ridges. The features of these annual growth layers suggest that growth is interrupted rather than slowed during most of the inactivity season. In some species that attain fairly large sizes without having formed any annual layers, many of the shells of common sizes may lack any crowding of ridges. There are many instances of this among the Chioninae and Pitarinae.

Fortnightly periodicity — In most of the marine shells studied, the number of growth laminae occurring within a concentric ridge and an adjacent trough is commonly fourteen or fifteen. Considering the growth laminae as daily increments, the tendency for there to be fourteen or fifteen growth laminae per ridge-formation cycle is suggestive of a fortnightly periodicity. This periodicity is also evident in the number of concentric ridges per major shell increments considered as practically complete records of annual growth. A Florida specimen (Plate 1) *of M. mercenaria* shows this clearly. There are approximately twenty-four or twenty-five ridges in each of annual layers Nos. 2-5, where No. 2 begins with the first-formed slow-growth deposit. Annual layers Nos. 6-10 have progressively fewer ridges, which should be expected to result from a progressive lengthening of winter hiatus during old age. The ridge periodicity on this Florida specimen has a value ranging from 14 to 16 days. Much of the variation indicated by this range is operational, for it is usually a subjective decision as to which ridge delimits the boundary between one annual layer and another on this specimen.

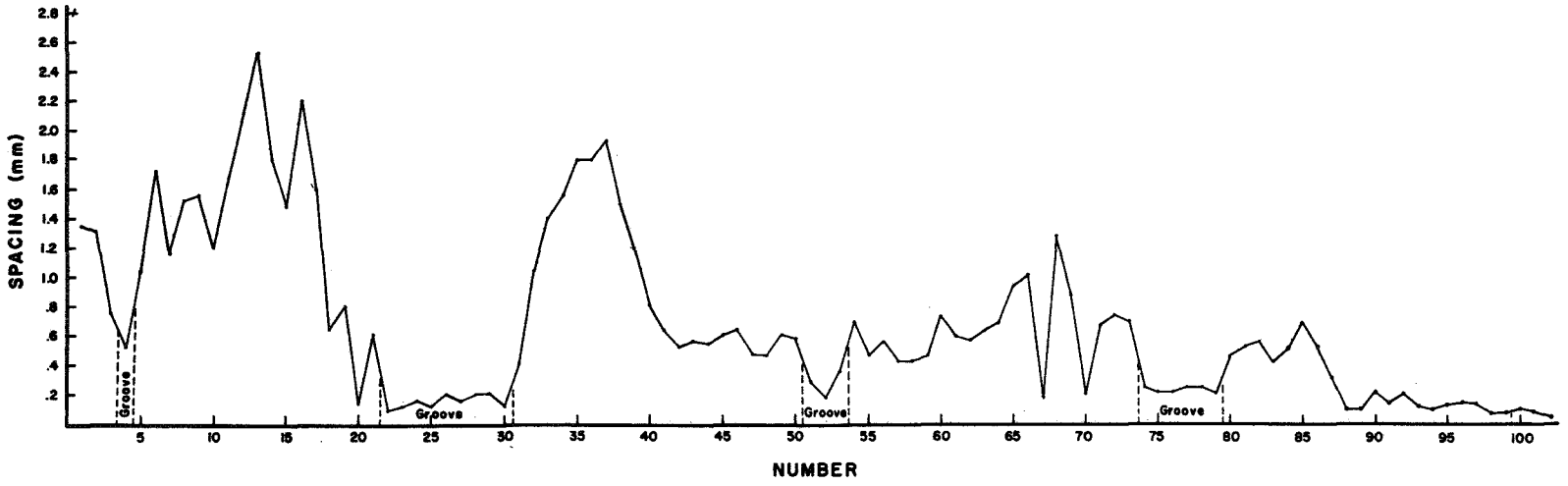


Fig. 1. Spacing of concentric ridges and slow-growth groove deposits in *Mercenaria mercenaria*.

The effect of subjectivity may be reduced greatly when the ridges are counted continuously across a number of contiguous annual layers. Estimated in this way, the ridge periodicity averages 98 ridges per 4 years, or 24.50 ridges per year. This average is equivalent to 14.91 days, which is close to the expected fortnightly periodicity of 14.76. Most pelecypod shells do not provide such a strong suggestion of a fortnightly periodicity as measured in ridges per annual layer. In many species, the growth band occurring before the first-formed, slow-growth deposit contains only a few ridges, the second annual layer (slow-growth deposit No. 1 and the growth band following it) has twenty-four or twenty-five ridges, and the successively later-formed annual layers have progressively fewer ridges. One exception to the warm temperate *Mercenaria* are some shells of *Idonearca vulgaris* from the late Cretaceous Ripley Formation. On these shells there are commonly twenty-four to twenty-six concentric ridges within each of the first three or four major increments. This ratio persists into major shell increments Nos. 5-7 of some specimens (Plate 18).

Monthly periodicity — A few of the species examined (Table 2b) have concentric ridges and troughs that are comprised of approximately thirty growth laminae. Following the hypothesis of a daily rhythm of growth lamina secretion, the ridges of these specimens appear to be formed with a periodicity approximating the 29 1/2 day synodic month. This measurement of the ridge periodicity is compatible with the numbers of ridges per annual layers recognized on the shells, provided that annual growth involves a season of hiatus that lengthens in the later years of the organism. On the larger shells of *Chione gnidia* the first growth band and groove deposit include ten to twelve ridges and may be followed by one or two annual layers with fewer ridges. Available specimens of *Irus lamellifera* show a sequence of ten to twelve ridges, terminated at the ventral margin by a slow-growth deposit. The other species of Table 2b tend to have six to ten ridges (or nodes) in the first annual layer and considerably fewer in the later-formed annual layers.

Combined fortnightly and monthly periodicities — The only example of this so far encountered is *Crassatella vadosus* from the late Cretaceous Ripley Formation. Major increments on the shells of this species are

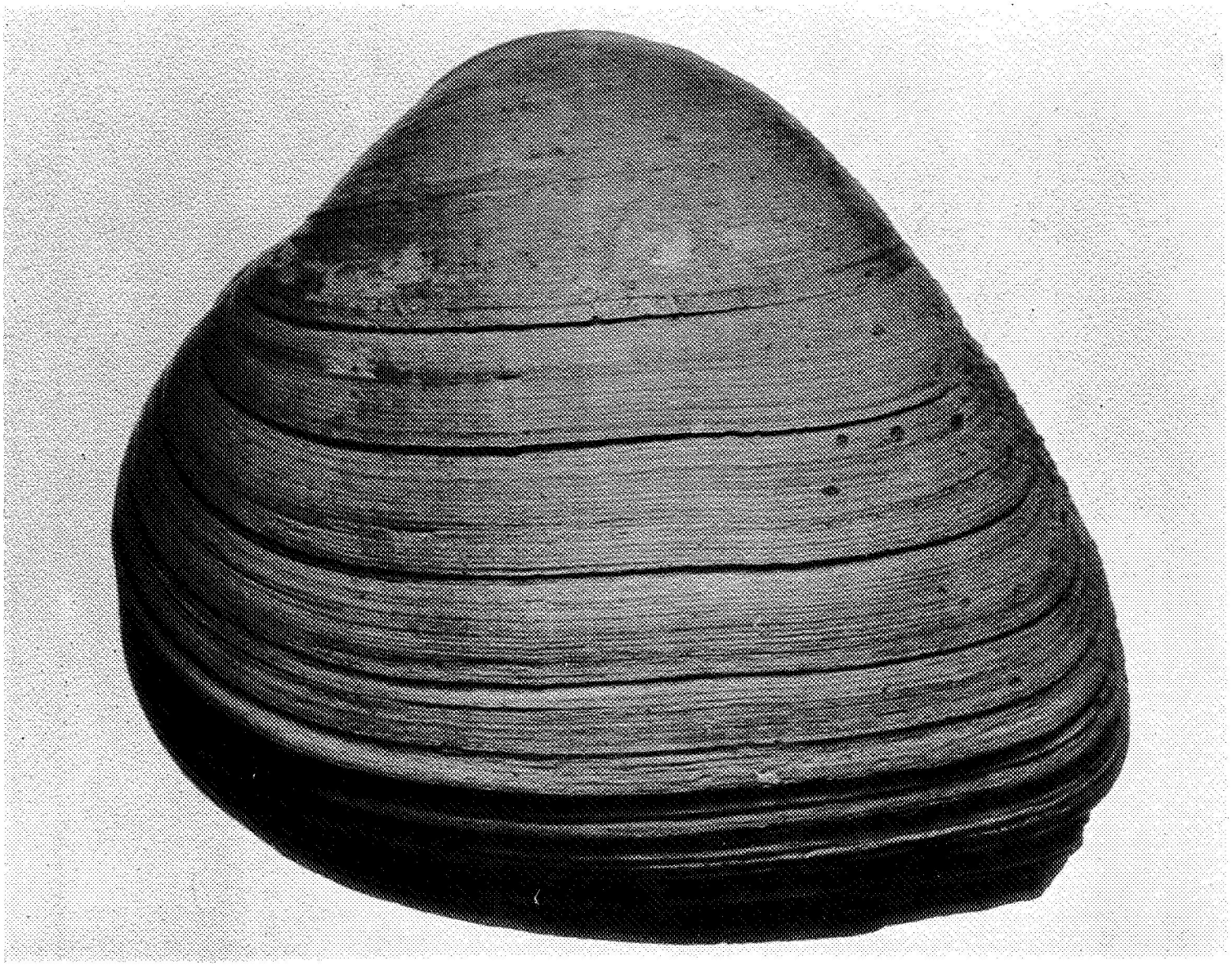


Plate 18. *Idonearca vulgaris* Morton . Major growth bands and concentric grooves. Late Cretaceous, Ripley Fm., Coon Creek, Tennessee X2 1/2.

similar in both external and internal structure to the annual layers of recent pelecypod shells. The first-formed growth band has ten to fifteen equant ridges that increase in size. This growth band is followed by a narrow concentric groove in which there are no ridges. Considering the major increment defined by the first growth band and groove as an annual deposit, the ridges seem to have been formed with a subannual periodicity that is less than monthly. On a few specimens, the first growth band is sufficiently well-perserved for surface study of growth laminae, which number fourteen to fifteen per ridge-and-trough increment. Each growth lamina consists of a translucent component and a semiopaque component. It has been shown that surface contrasts between these parts of the growth laminae are well-developed where there has been abrasion of the shell. Thus, similar to the daily shell deposits recognized in studies of modern shells, these growth laminae are regarded as showing that the ridges of the first growth band were in most cases formed with a 14- or 15-day periodicity. In the second and later-formed growth bands, ridges of low and high relief alternate, so that each high-relief ridge is preceded and followed by a low-relief ridge. There are commonly thirty growth laminae involved in the alternation of a high ridge and a low ridge (Plate 12:2). There are eight to ten alternations in the second growth band and lesser numbers in the later-formed growth bands. Thus, measured in relation to the daily and annual deposits recognized in study of these shells, the ridges that were formed in the second and later years of growth show evidence of combined monthly and fortnightly periodicities.

Deviations from predominant periodicities — In the species with apparent fortnightly rhythms of shell growth, the number of growth laminae per ridge and trough increment may occasionally be as low as eleven or as high as twenty-seven. Variations from the apparent monthly periodicity are less extreme, ranging from twenty-six to thirty-two. In light of laboratory studies made of other types of biorhythms, these deviations from the predominately 14-15 and 29-30 day rhythms of concentric ridge formation could result from temporary modifications of biological clocks. It is perhaps less obvious that these deviations could result from occasional microhiatuses of growth. For example, three growth laminae usually make up a narrow asymmetric or protrusive ridge. In a species

that has a 15-day periodicity of ridge formation, a ridge thus accounts for 3/15 = 1/5 of the cycle as compared with 12/15 = 4/5 for a trough. Assuming that a hiatus of 3 days occurs randomly with respect to the ridge-and-trough secretion episodes, the organism would fail to form a ridge in approximately one-fifth of these instances. In this case, the following numbers of growth laminae could be deposited in a period of 29-1/2 days: 3 (first ridge formed) + 12 (first trough formed) + 0 (second ridge omitted) + 12 (second trough formed) = 27 growth laminae. These twenty-seven growth laminae would comprise one ridge and one trough. Prolongation of the hiatus would subtract from the number of growth laminae deposited during the trough episode and there would result a ridge-and-trough increment containing a lesser number of growth laminae. A brief hiatus occurring wholly within a part of the trough episode would produce a number considerably lower than fifteen. It is at least conceivable that almost all of the extreme deviations from a predominate periodicity of ridge formation may reflect hiatuses. Efforts to verify this by correlating microgrooves on the shell surface with anomalous numbers of growth laminae were partly successful in that the regular fourteen to fifteen and twenty-nine to thirty lamina clusters lack evidence of hiatuses in growth. Only a few of the ridge-and-trough increments that have anomalously high or low numbers of growth laminae feature microgrooves.

Spines

Consisting of ectostracum or of mesectostracum, the spines of pelecypod shells appear to be formed by outgrowths of the outer mantle fold that are curved around an axis oriented at large angles to the shell surface. In general, the spines occur along certain radial lines of the shell and are related to episodes of concentric ridge or minor growth band formation. Three types of spines have been studied:

1. Tubular. Crescent shaped, hollow, open ventrally and distally. Example: *Pinna*.
2. Toothlike. Circular, compact, sharply tapered, often open at base of ventral surface. Example: *Pitar*.
3. Tusklike. Oval, compact, moderately tapered, usually covered over the entire ventral surface. Example: *Spondylus*.

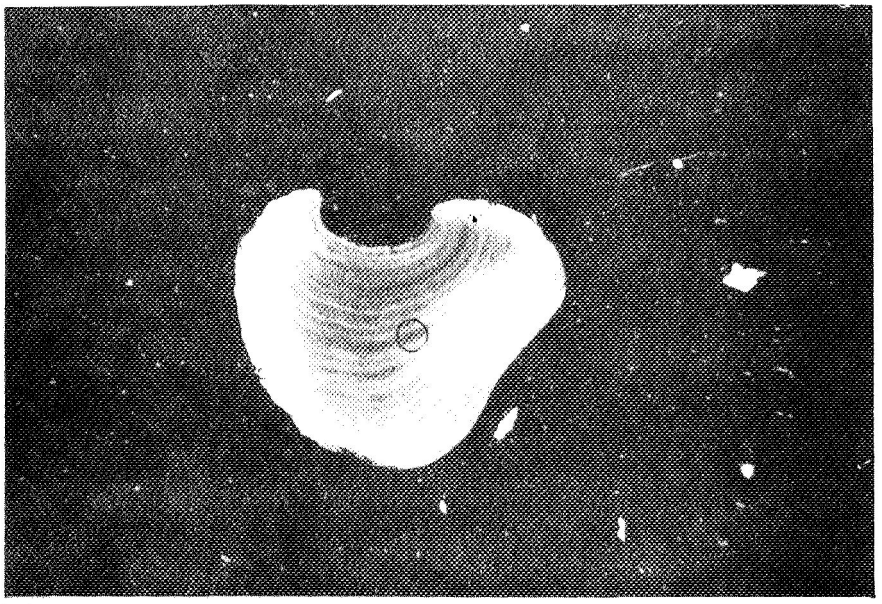
Of the spinose Pinnid shells examined, none had major increments, and all of them lacked growth laminae that were sufficiently distinct for accurate determinations of minor growth band periodicities. Nevertheless, it seems likely that the spinose minor growth bands of many or all Pinnid shells may be formed with the same 14-15 day periodicity that is apparent for the minor growth bands of non-spinose species studied.

The toothlike spines of *Pitar* have rather straight dorsal surfaces formed by a few growth laminae deposited during episodes of concentric ridge formation. The ventral surfaces of these spines are curved, being thickened basally by less protrusive, gently folded, growth laminae deposited during episodes of trough formation. In cross section, the basal ends of the spines show eight to fifteen growth laminae (Plate 19). Cross sections located near the pointed ends of the spines show three or four growth laminae that are evenly spaced. The process of spine formation which seems to be expressed in these structural features involves an episode of extreme mantle protrusion and folding, followed by a longer episode of gradual retraction and unfolding of the mantle. This process does not seem to be controlled by a simple biochronometer in the Pitarinae. For example, on shells of *Pitar* (*Hysteroconcha*) *lupanaria* from Guaymas and *P. dione* from San Blas, Mexico, the spines are related to every second, third, or fourth concentric ridge. On shells of these species from other localities in the Gulf of California, the spines are related to every fourth, fifth, or sixth ridge. These observations on the formation and occurrences of toothlike spines in Pitar are suggestive of an interaction between three factors: (1) a fortnightly rhythm of mantle expansion (as in the formation of concentric ridges), (2) temporal and spatial factors involved in ontogeny, and (3) geographic factors either of subspeciation within local population or of environmental influences on the growth of individual organisms.

Smaller toothlike spines occur on the dorso-posterior rays of *Cardium indicus* and on certain rays of Spondylid shells. However, in these species, each concentric ridge is related to the formation of one or more spines. The spines thus seem to be formed on a fortnightly basis.



(1) Plane polarized light



(2) Crossed Nichols

Plate 19. *Pitar (Hysteroconcha) lupanaria* Lesson. Cross section of calcareous spine. Thin section oriented parallel to shell surface at base of spine. Direction of growth is down. Recent, Gulf of California X26.

In the *Spondylus princeps* and *S. crassisquama* shells examined, each apparent fortnightly growth band is related to a concentric ring of tusklike and toothlike spines. The spines are complexly related to radial shell elements in *S. princeps*: over the dissoconch, there are several radial rows of large (3-5 cm) tusklike spines, and between each of these rows there are two or three rows of smaller (0.3 — 1.0 cm) toothlike spines. Almost all the growth laminae in a minor growth band are included in the formation of the basal parts of the tusklike spines occurring in the ring. The distal ends of these spines are thinner and consist of four to five growth laminae (Plate 15:2). The smaller toothlike spines are nearly circular and consist of five to seven growth laminae.

A few species of the Unionacea form toothlike spines that are few in number and occur sporadically in relation to the concentric and radial shell elements. Several other Unionid species form irregularly shaped shell pustules that are similarly erratic in their occurrences.

III. GROWTH EXPERIMENTS

Growth in the Natural Environment

Mytilus edulis

Harbor of Bodega Bay — On July 26, 1967, two dozen invididuals of this species were marked for study of shell growth through several fortnightly tidal cycles. The specimens so selected were attached to the timbers of a wharf at an elevation intermediate between the common low and high tides. They were marked by carving a notch in the shell margin at the anterior end. During the first week the specimens were observed to have already secreted shell two or three days after marking. The increment formed in the first week consisted of a concentric groove that was about 1/4 mm in breadth and a 1/4 to 1/2 mm post-groove increment. Many of the specimens were lost during the third and fourth weeks, perhaps due to a weakening of their byssal attachments at the time of marking. On September 22, after 57 days of growth, only two specimens could be recovered. These specimens were taken to the laboratory for study under the microscope.

The interruption of growth due to the marking of one of the valves was expressed as a concentric groove on the surfaces of both right and left valves of the two specimens. Growth striae marking post-groove increments were indented where they enveloped the marginal notch. The indentations of the growth striae decreased as more of them were added, until a uniformly curved shell margin was reestablished. Although the striae forming the concentric grooves were related to a sudden change in shell curvature, they were not expressed in the internal structures of the shells. One of the specimens had increased its length from 30 to 37 mm, and the other had grown from 17 to 32 mm. Minor growth bands occurring on the 15-mm increment of the smaller specimen were relatively broad and low in relief. On both of the specimens, the 57-day increment included four minor growth bands.

These results indicate that the minor growth bands of *M. edulis* are formed at the average rate of one per fourteen days. Considering that two days must be allowed for the post-marking period of no shell growth, this measurement is modified to give 59/4 = 14.75, which agrees almost

exactly with the period of the fortnightly tidal cycle. The relationship between growth rate and minor growth band spacing suggests that the decrease of spacing which occurs with age may result from a gradual decrease in the linear rate of shell growth.

San Francisco Bay — Observations on the growth of *Mytilus* in this area was the unexpected outcome of an early attempt to raise marked specimens of other species. On April 4, 1964, thirty-four shallow burrowing clams were planted in a 30 by 11 by 11 inch box located on a tidal flat north of the City of Berkeley dump. This box had a wooden floor and sides of nylon window screen on a wooden frame. The box was buried in the mud substratum to a depth of nearly 30 inches. A pair of 2-by-4-inch wooden posts 4 feet long, were bolted to the diagonal corners of the box. These posts extended 1 foot below the bottom of the box and 2 feet above the top of the box. During the spring high tides (full or new moon), the posts were submerged; whereas during neap tides, several inches of the posts were usually exposed above the surface of the water. At low tides, the box itself was usually exposed above the water level during all the fortnightly tidal cycle. In mid-July 1964, the box was examined and found to lack any trace of the planted specimens, and green algae and small barnacles were growing on the posts. In mid-September, the test box was examined again and juveniles of *M. edulis* were found attached to the barnacles. These mussels were not disturbed until November 20, 1965. At that time, the posts were found to be greatly weakened by the activities of boring organisms. The posts were then removed and taken to the laboratory for study of the mussels.

Thirty-six individual mussels were found on the posts. All were alive when collected. They varied in length from 10 to 42 mm (Table 3). Although an almost rectangular frequency distribution of shell length was apparent, there were suggestions of three modal classes centered on 19-20 mm, 25-26 mm, and 35-36 mm.

Three specimens were so encrusted with barnacles that their growth bands were obscured. The other thirty-three specimens had from two to fourteen fairly distinct minor growth bands per shell. On most of the shells, some of the minor growth bands could be subdivided into a pair of smaller bands.

Table 3. *Mytilus edulis* shell measurements, San Francisco Bay

Specimen	Length (mm)	Number of minor growth bands per shell	Occurrences of concentric grooves
1	42	14	—
2	40	12	9/3
3	40	12	9/3
4	37	(covered with barnacles)	—
5	37	11	11/
6	35	13	10/3
7	37	11	9/2
8	35	9	—
9	33	(covered with barnacles)	?/3
10	34	12	10/2
11	32	11	—
12	33	12	10/2
13	30	10	—
14	28	14	—
15	30	12	10/2
16	26	12	8/4
17	27	12	10/2
18	25	9	—
19	26	8	—
20	26	10	6/4
21	24	12	—
22	23	11	—
23	21	(covered with barnacles)	—
24	20	7	—
25	19	9	—
26	20	4	—
27	20	5	—
28	19	6	—
29	17	5	—

Table 3. Concluded

Specimen	Length (mm)	Number of minor growth bands per shell	Occurrences of concentric grooves
30	18	7	—
31	18	7	—
32	16	6	—
33	16	4	—
34	17	4	—
35	11	3	—
36	10	2	—

Twelve of the larger (26-42 mm) specimens had a concentric groove that is related to a crinkling of growth striae. On nine of these specimens the groove was followed by two or three minor growth bands. Two other specimens had a groove followed by four minor growth bands; one specimen had a groove on its margin. Between six and ten minor growth bands were formed before the groove on these specimens.

The preceding data are compatible with the hypothesis of a monthly cycle of minor growth band formation. The extreme variation of shell size and number of minor growth bands per shell may indicate that some of the smaller individuals were much younger than those first observed in September 1964. Only the larger specimens bearing the greatest numbers of minor growth bands per shell could have lived and formed shell during a larger part or all of the 14-month interval. Specimen No. 1 (Table 3) is the largest and has a total of fourteen minor growth bands. Since the shell of this specimen could not be older than 14 months, the minor growth bands must have been formed at the average rate of one per month. Specimens Nos. 2 and 3 could have formed their minor growth bands on a monthly basis during December 1964 to November 1965 (twelve growth bands in 12 months), and so on; with the smaller specimens having the fewest minor growth bands being the youngest.

The concentric grooves on the shells of the specimens are identical to the repair marks formed in the Bodega Bay experiment. Since the number of minor growth bands formed after these grooves varies from zero to four, individual shells must have been broken at different times during the summer and fall of 1965. Collisions with pieces of wood and other floating debris would be sufficient to have induced the formation of these disturbance rings. Such debris is abundant on the tidal flats and shores of San Francisco Bay.

Protothaca staminea

Individuals of this species bearing reference marks on their shells were raised in their natural environment during the summer, fall, and winter of 1967. The specimens used in this experiment were obtained from a sandy cobble bed on the north shore of Bodega Bay harbor. All were forming growth bands when taken for study. Each specimen was marked by

carving a notch in the ventral margin of its shell and returned to marked positions in the substrate. The following three series of observations were made in this experiment:

1. Ten specimens varying in length from 30 to 56 mm were marked and planted during the first week of August. All these specimens were found when the site was revisited 2 weeks later. Two of the larger specimens (55 and 56 mm in length) had died. None of the surviving specimens had resumed shell growth beyond the reference marks. These specimens were returned to the substrate. Only five marked clams were recovered on August 30. Again, there were no signs of shell growth. The specimens were returned to the substrate for a third time. None of the specimens could be found in mid-September.

2. Six specimens were marked and planted in the first week of August. Five were found when the site was revisited in the first week of September. One had formed a concentric groove followed by a concentric ridge and trough. Four clams had concentric grooves on the ventral margins of their shells. The five specimens were returned to the substrate. None of them could be found on October 5.

3. Seven specimens were marked and planted on October 5. These specimens were not disturbed by the author until December 16, at which time only two could be found. One specimen 48 mm in length had formed a concentric groove. The other specimen had formed a concentric groove and an increment which increased its length from 40 to 42 mm. Measured parallel to height, this increment is 3 mm in breadth. This 72-day increment includes four ridges and three troughs. The concentric grooves resulting from the marking of the specimens are about 1/8-mm in breadth and are partly filled with a deposit of periostracum. As seen in thin section, these grooves are related to a growth layer of translucent CaC03 that passes through the mesectostracum. On the smaller specimen growth laminae deposited beyond the groove are slightly indented in the notch area.

This experiment showed that the removal and marking of the clam commonly results in a hiatus of growth of about 20 days. The large older clams are the most affected by these operations. There is commonly no shell growth during the first 2 weeks following the marking of the shell. Later, perhaps in the third week for most younger clams, a translucent slow-growth layer of CaC03 is laid down on the mesectestracum. While the mantle is constricted relative to its normal expanded condition, a mass of periostracum is built up on the groove forming the surface of the slow-growth layer.

With regard to the periodicity of the concentric ridges of *P. staminea*, one specimen formed a complete ridge and trough unit 35 days after its shell had been marked, and another specimen, which was undisturbed after marking for a period of 72 days, formed four ridges and three troughs. Allowing 20 days for an initial hiatus due to the marking operation, these measurements suggest that the ridges are formed with a periodicity of about 15 days.

Chione undatella

On the afternoon of April 12, 1967, thirty live specimens of *C. undatella* were collected from the south bank of the main drainage channel in Cholla Bay, Sonora, Mexico. These specimens were cleaned with tissue and left to dry in the shade so that the shell surfaces could be marked with a waterproof black ink. On the morning of April 13, a felt-tip marking pen was used to mark the antero- and mid-ventral margins of these specimens. To guard against possible losses of reference marks through abrasion, the last-formed concentric ridge of each specimen was also blackened by inking and the ink marks allowed to dry 2 hours in the shade. The specimens were then planted in a shelly, coarse sand located in the center of a 35-ft triangle marked by three sign posts on the south side of the drainage channel.

During the next 2 weeks the area was inspected but not entered by the author. Considerable agitation of the substrate occurred with each tidal cycle. On April 21 and 28, uncommonly strong winds resulted in storm waves that scoured holes to depths of as much as 2 feet in the test site. On May 8, the specimens within the test area were collected

again. Only seven marked individuals were recovered. Although the marks were spotty, they were sufficient to serve as reference points. Two of the larger specimens had failed to deposit shell layers beyond these marks during the 25-day period (see Table 4). Four specimens had added shell beyond the marks on the concentric troughs of their ventral margins and appeared to be in the process of forming concentric ridges. One specimen had increased the size of its marginal trough but had not formed even the rudiments of a ridge.

Thus two of seven marked specimens were not depositing CaC03 during this period. These are larger specimens, each with more than twenty concentric ridges on its shell. By analogy with results obtained in study of shell growth in species living in Northern California, such a hiatus would be expected to follow a period of exposure. Generally, the older individuals are most affected by a disturbance. Data on the smaller, younger specimens show that the ridge-formation cycle cannot have a periodicity that is far different from the 25-day period of this experiment. Allowing for an initial hiatus in shell growth of about 10 days, this periodicity could be 15 days.

Attempts to repeat this experiment over longer periods of time in the remainder of 1967 and in the early part of 1968 were unsuccessful due to losses of the stakes marking the planting areas. In June 1968, marked specimens were planted in positions related to a bifurcation of a distinct second-order drainage channel and in pockets of sand on a distinctive rock outcrop in the main channel. These areas were revisited on September 3, 1968, but none of the marked specimens could be found.

Richmond Laboratory

During the period Summer 1965 through Winter 1966, the first shell growth experiment under laboratory conditions took place in facilities at the Space Sciences Laboratory, in the University of California Warehouse at Richmond, California. The goal of this experiment was to test for influences of light cycles and simulated tides on rhythmic shell secretion by pelecypods. Description of the experimental apparatus and observations of temperature and other environmental factors are given in the Appendix.

Table 4. Shell growth observed in *Chione undatella*

Antero-posterior length (mm)	Dorso-ventral height (mm)	Marginal increment marked on 4/13/67	Addition to shell during the 25-day period (4/13-5/8)
25	21	trough	none
22	20	ridge	none
11	10	trough	addition to the marked trough
15	13	trough	addition to the marked trough, followed by a ridge
16	14	trough	
18	14	trough	
17	14	trough	

Observations on temperate-water dwellers

On July 13, 1965, over 30 specimens of *Protothaca staminea* were collected from the cobble-sand shores of Tomales Bay, California. It was anticipated that this species would be successful in the aquaria, as the water temperature of its natural environment would be similar to that of the seawater in the laboratory. Three dozen specimens of *Mercenaria mercenaria* were purchased from a fish market in San Francisco. Since these specimens had been transported by airplane from New England, these hard shell clams were less likely to survive. All specimens of these two species were marked by carving a notch in the ventral margin of the shell and were distributed among the aquarium tanks. Care was taken not to damage the mantle. The next day, several had died and a few appeared to be dying. Twenty-eight of the healthiest looking specimens of each species were selected for the experiment and redistributed among seven tanks so that there were four specimens of each species in each tank. It was possible to group the *P. staminea* so that the specimens of each tank ranged in length from 2 to 6 cm. The *M. mercenaria* were less variable in size, their lengths ranging from 5 to 7 cm in each tank. Each test animal was situated on its dorsal slope so that any air trapped inside the mantle cavity would be released when the clam opened its valves. Within a few hours after they had been planted in the substrates, many of the specimens of both species opened their valves, extended their siphons, and appeared to be pumping water. On the next day, it was observed that all specimens had completely burrowed into the substrates and were pumping water through siphons that extended upward from the sand.

A survivorship record for these experimental organisms is given in Table 5. More than 50% of the *P. staminea* had died by the end of the second week and mortality was 100% by the end of the fifth week. None of these specimens had deposited shell beyond their marginal notches. Mortality was slower with *M. mercenaria*; about 90% of the specimens survived into the sixth week. On November 21, some 4 months after the experiment had begun, there were only six of the original twenty-eight *Mercenaria* specimens living in the system. Again no evidence of shell growth during any part of the 4-month period could be found.

Table 5. Mortalities of pelecypods in the Richmond Warehouse, July through November 1965

	Aquarium tank							Aquarium tank						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
	Mercenaria mercenaria							*Protothaca staminea*						
July 13														
14			X											
16														
27								XXX	XX	XXX	XX	XX	XX	XX
29														x
Aug. 1													X	
8								**Chione californiensis*						
9														
16				X	X									
22	X													
24			X											
28						X								
29				X										
31														
Sept. 2														
6														
8														
10						X								
21													X	
23														
28	XXX		XX			XX								
29				X										
Oct. 2									X					
8								X						
12														
16										XX				XX
19		XX			X		XXX							

* 10 surviving *P. staminea* replaced by 28 *C. californiensis* on August 8.

Table 5. Concluded

	Aquarium tank							Aquarium tank						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
Oct. 25									X		X			
30											X	X		
Nov. 2								X			X			
10								X		X		X		
13														
16										X				
Survivors on Nov. 21, 1965:	0	2	0	1	2	0	1	1	2	0	1	2	3	2

Observations on Chione californiensis

At the time when the *P. staminea* mortality had climbed to almost 100% and none of the *M. mercenaria* showed any signs of shell-growth, the author decided to introduce another species. In early August, forty individuals of *Chione californiensis* were collected in the Bay at La Paz, Baja California. These specimens were kept in seawater contained in a styrofoam box during transport by airplane to the laboratory in Richmond. On August 8, within 20 hours after they had been collected, twenty-eight of these specimens were marked by notching the ventral margin and distributed four per tank. All specimens became active during the first hour and appeared to be functioning normally. On August 9, approximately half of these clams had burrowed into the substrates, but not as deeply as the other species, and it was possible to observe the notches in their shell margins without disturbing them. The specimens that had not changed their initial positions were those of the non-tidal tanks (tanks 6 and 7). The larger specimens in tidal tanks (1, 2, and 3) had evidently attempted to burrow, but failed, because they were found lying on their sides. These same specimens failed to burrow or to locomote an appreciable amount during the experiment. In contrast, the smaller specimens in both the tidal and non-tidal tanks were the most active.

The specimens of *Chione* had a 100% survivorship until September 21 when the first fatality was discovered (Table 5). From that time onward, there was an average mortality of about one death every 3 days. The specimens were examined during times when the tanks were illuminated, but in no case was there a suggestion of shell growth. The experiment was terminated on November 21, at which time the eleven survivors were examined in detail under a binocular microscope. There was no evidence of any secretion beyond the notches in the shell margins.

The twelve specimens of *C. californiensis* that were not put into the experimental aquaria were kept alive in the styrofoam box. For 8 months, all survived and continued to pump water through their extended siphons. The tight lid on this box prevented evaporation, and there were no changes or additions to the seawater originally obtained from the Bay of La Paz. Eleven of these specimens were marked on August 8 by means of two methods. Six specimens were treated with a seawater solution of

alizarin Red-S for a period of 12 hours. This exposure to alizarin resulted in a purple staining of the shell. Five other specimens were marked by carving notches in the ventral margins of their shells. Only one specimen was measured and the features of its ventral margin were noted. Despite the 100% survivorship of these specimens, none had deposited an appreciable amount of shell when inspected on November 21. They were left in the box with the original seawater until early summer 1966. All survived, but no evidence of shell growth was found.

Starvation as a cause of mortality

Study of the specimens surviving in the aquaria until November 21 revealed that their viscera were shrunken as compared with the "full" appearances of specimens dissected at the beginning of the experiment. This reduction of visceral volume could not have been an osmotic effect, because the seawater remained at 29 $^{o}/_{oo}$, which is within the range of salinities known to occur commonly in the natural habitats of *Mercenaria mercenaria* and *Protothaca staminea*. Thus, shrinkage of the viscera must have resulted from a loss of visceral mass. Since there is no evidence that any of the clams spawned while living in the aquaria, loss of visceral mass may indicate that the organisms survived by consuming fatty materials stored within their own tissues. Starvation is thus suggested as a principal cause of mortality in this experiment.

Starvation could result from inefficient respiration for normal metabolism. However, the rapid rate of seawater circulation and the frequent aeration of this water seem to preclude stagnation that would have interfered with normal respiration. Evidence of an oxygenated state in the seawater is provided by the pH measurement (pH = 7.0) considered as normal for natural seawater, and by lack of any foul-smelling gases such as H_2S. Less direct evidence is drawn from study of the shells of clams living in the aquaria. Biologists have demonstrated a tendency for pits to be formed on the interiors of pelecypod shells as a result of anaerobic glycolysis (Dugal, 1939). None of the *Chione californiensis* and *Protothaca staminea* used in this experiment had pits on the interiors of their shells, suggesting that these specimens had been respiring normally. The interiors of many of the *Mercenaria* specimens were faintly pitted as though there had been some resorption of shell. However,

individuals of this species that had died within 24 hours after the experiment commenced also featured pits on the interiors of their shells, which suggests that some or all of the pits may have formed during dry shipment from New England. While there is no strong evidence of inhibited respiration during the experiment, there are at least some indications of oxygenated seawater favoring normal respiration

With regard to the food supply, experimental growth of *Chlamydomonas* showed that the nutrient-rich solution prepared from fertilizer gave rapid growth of algal flagellates only under direct sunlight. Regardless of the concentration of the nutrients in the bulk seawater, it seems certain that the lighting factor by itself resulted in algal growth that was insufficient to support the pelecypods.

The water temperatures involved in this experiment are comparable to summer water temperatures reported by U. S. Coast and Geodetic Survey stations located within the geographic ranges of *M. mercenaria* and *P. staminea*. Only with *C. californiensis* could there be a reasonable doubt that temperatures between 20 and 25°F would permit normal metabolism and growth. Had these temperatures been adverse for the latter species, the failures of the other species to form shell in the aquaria remain to be explained in terms of other factors that might be generally adverse.

One may suppose that the seawater did not contain toxic concentrations of metallic salts, because all the apparatus in contact with the seawater consisted either of glass or nonreactive plastics (mostly PVC, but including some polyethylene and nylon). There is no indication that the *Chlamydomonas* culture medium may have been toxic, as the introduction of this culture was not related to a change in rate of pelecypod mortality. Although it is conceivable that the concentrations of chemical trace elements might not have met the requirements of *M. mercenaria* and *Chione californiensis*, this is almost certainly not the case for *Protothaca staminea* which occurs naturally in sandy cobble beds on the shores of San Francisco Bay. In the light of available information, such chemical factors seem indaquate to explain the observed mortality in all three species.

Although the preceding evaluations of the most obvious factors in the laboratory environment have not been exhaustive, inferences based on the available information suggest that an inadequate food supply caused starvation of the pelecypods.

Bodega Marine Laboratory

During the spring of 1966, preparations were made to raise pelecypods under controlled environmental conditions in the University's marine biology laboratory at Bodega Head, California. Facilities provided for this study included a lightproof room with concrete walls and a chemically inert pipe supplying seawater pumped in from the nearby ocean. Aquarium apparatus assembled in this room followed the mechanical designs that proved to be successful in the earlier experiment at Richmond. Throughout a 2-1/2 year period, pelecypods were given reference marks and kept alive under various conditions of illumination and darkness and simulated tides. As before, the principal goal was to determine whether or not rhythmicities of shell growth are modifiable under the influences of different illumination cycles and simulated tides (see description of apparatus and observations of environmental factors in Appendix).

Pelecypods dormant in the laboratory environment

Several species of pelecypods known to have hierarchic groupings of growth layers in their shells were marked for growth in the controlled rhythm aquaria and in other aquaria of the laboratory. Although some of the clams survived for long periods of time, none of them formed normally calcified shell and most of them apparently added no material to their shells. Details are given below.

Shallow burrowing Venerid species — In February 1966, the twelve *Chione californiensis* that were originally collected in the Bay of La Paz on August 7, 1965, and kept alive in a styrofoam box were put into running seawater aquaria of the Bodega Laboratory. Although seawater flowed through the aquaria for more than 4 months, none of these specimens had deposited shell material when examined in June 1966. These specimens were moved into the simulated environmental rhythm aquaria. Twenty-eight specimens of *Protothaca staminea* collected in

Bodega Bay Harbor were introduced at this time. These specimens were marked by notching the ventral margins of their shells. Each specimen was planted in a sand-filled pint-sized polyethylene container. The containers were distributed in the aquaria so that each aquarium had a specimen of *Protothaca*. Planted in similar boxes, the specimens of *Chione* were put into the non-tidal, tidal, nonilluminated, and illuminated aquaria. All of the *Chione* specimens died sometime during September to November, 1966. *Protothaca* fatalities occurred steadily until the growth experiments were terminated on January 19, 1968, at which time there were thirteen survivors. None of the specimens of either species added CaC03 to the margins of their shells. Sections of the shells revealed no evidence of a slow-growth increment on surfaces located inside the pallial line. The *C. californiensis* had survived for a total of 1-1/4 years without growing shell. The *P. staminea* were in a similar state of dormancy for 1-1/2 years.

Macoma and Transenella — In September 1966, two more shallow burrowing species of Bodega Bay Harbor were introduced to the experimental aquaria. Twenty-eight *Macoma nasuta* were marked by notching of the ventral shell margin and another twenty-eight individuals of this species were stained in red alizarin. Each aquarium received a notched specimen and a stained one. Since these clams are moderate burrowers that feed on detritus obtained through their long inhalant siphons, they were laid on the floors of the aquaria. Several hundred individuals of *Transenella* were stained in red alizarin. Most of these tiny clams were on the order of 2 or 3 mm in size. They were distributed among the containers filled with sand in the aquaria. All of the *Macoma* specimens died during the following 2 weeks. At the same time, many *Transenella* fatalities were detected, and in later months no living individuals of this species were found in the aquaria. None of the empty valves of either species in the aquaria showed evidence of growth beyond the reference marks.

Deep burrowers — Tresus nuttallii and *Saridomus nuttallii* live in burrows on the sandy tidal flats of Bodega Bay Harbor. On July 15, 1967, a small and a large specimen of each species were obtained and marked on the ventral shell margin with indelible ink. The four marked specimens

were then buried in a narrow aquarium filled to a depth of 1 foot with sand. They were oriented as they had been found in nature, but with parts of them accessible to view against the glass. Incoming seawater was supplied by an overhead jet located at one end of the aquarium. An overflow pipe located at the other end of the aquarium was adjusted to maintain the water level a few inches above the surface of the sand. All four of the clams lived in this aquarium for several months and at all times appeared to be healthy. However, the larger *Tresus* died on September 19, and the other three died in the next 2 months. None had formed shell beyond the ink marks on the ventral margins.

Mussels — Mytilus californianus from the rocky shore of Bodega Head, and *Mytilus edulis* from pilings of Bodega Bay Harbor were put into the large (30 gal.) aquarium during the spring and summer of 1967. The specimens were marked by notching of the ventral shell margin and placed on or between rocks in the aquarium. On each occasion, the mussels survived for a week or two and secreted byssal threads. There was usually a tiny extension of the periostracum beyond the notches in the shell margins, but the main layers of the shells received no additions of $CaCO_3$. The same results were obtained with mussels living in other aquaria in the laboratory.

Pelecypods given concentrated food media

Algal culture — From November 1967 to summer 1968, pelecypods lived for periods of from 1 week to 2 months in a small (1-1/2 gal.) aquarium supplied with rich algal culture (see Appendix). Some of these were local species and had suffered little exposure during transport to the laboratory. Others were collected on the shores of the Gulf of California and had spent 1 to 2 days in a bucket of wet sand. Each specimen had its ventral shell margin notched or marked with indelible ink. None of the clams secreted $CaCO_3$ over these marks. Attempts to raise pelecypods in this aquarium with algal culture are grouped chronologically into the following:

1. November 1967. Five specimens of *Chione undatella* from Cholla Bay, Sonora, Mexico were marked by notching of the ventral margin. A thermostat and heater maintained the temperature of the water at 75°F. All died during the following 3 weeks.

2. December 1967. Three specimens of *Protothaca staminea* from Bodega Bay Harbor were marked with ink. The water temperature remained constant at 75°F. The clams died within 2 weeks.

3. January 1968. Three specimens of *C. undatella* and a specimen of *Chione californiensis* from Cholla Bay were marked by notching of the ventral margin. The *C. californiensis* died within a week. Two of the *C. undatella* specimens died in February, and the third died in May 1968.

4. May 1968. Two specimens of *P. staminea* were marked with ink; three *Mytilus edulis* from Bodega Bay Harbor and one *Mytilus californianus* from Bodega Head were marked by notching their ventral shell margins. The aquarium heater was turned off until June 10, and the water temperature ranged from 60 to 68°F. The mussels died within 2 weeks. *Protothaca* survived until mid-June.

5. June 1968. Five specimens of *C. undatella* were marked either with ink or by notching of ventral margin, and one specimen of *C. californiensis* was marked by notching its ventral shell margin. The temperature was controlled at 78°F. All specimens died in July.

From August to September of 1968, a different method of raising pelecypods in the artificial food-rich medium was attempted. Pelecypods were placed in a 30-gallon aquarium filled with a rich *Chlamydomonas* culture. Owing to changes in chemicals available for use as nutrients, the 25 gallons of additional culture medium that was prepared contained only the phosphate of sodium, pyradoxine, sodium nitrite, and ammonium chloride. EDTA was eliminated from this preparation because the author felt that this sequestering agent might actually inhibit the calcification processes of the organisms. The algal culture was grown in the 30-gal. aquarium under constant illumination by fluorescent "plant-gro" light. It was aerated and kept at a constant temperature of 74°F. In the first week of September, pelecypods and gastropods from Cholla Bay were put into the aquarium containing about 28 gallons of rich algal culture. These specimens were: six *Chione undatella* clams, two *Chione*

californiensis clams with *Crucibulum* limpets attached, three *Dosinia dunkeri* clams, and four *Cerithium stercumuscarum* snails. The shell margins of all these specimens were marked with indelible ink. All the gastropods died within a week. Although the writer was not present in the later part of September to mid-November, colleagues reported that the pelecypods had died sometime in mid-October. No evidence of growth was found when the empty shells were examined in November.

Infusoria — Although this food medium had no influence on the survival of *Protothaca staminea* and *Macoma nasuta* in aquaria, specimens of *Mytilus californianus* were kept alive for as long as 3 months in finger bowls supplied with infusoria. At intervals of 1 to 3 days, each container was given a change of seawater and a 100-cc portion of an infusoria culture. This infusoria culture had been prepared from natural seawater and green algae and contained a variety of micro-organisms. Fragments of kelp were mixed with seawater contained in a large flask. The flask was situated near a window where it was under direct sunlight in the afternoon. Within a period of 2 weeks, the seawater in the flasks became dark greenish brown in color. Microscopic study of this infusion revealed great numbers of tiny flagellates, *Stylonychia* (30-60 microns) and much smaller ciliates, and clumps of bacteria. Throughout this experiment the surviving mussels were active during times of high tide on the nearby coast from which they had been collected. The infusoria-rich seawater in the finger bowls became lighter in color during these activity periods, whereas similar preparations in containers lacking mussels retained the greenish brown color for as long as 2 weeks. Microscopic study of microorganisms in water samples drawn from the containers after a high tide in the natural environment indicated that the number of microorganisms present per unit volume decreased markedly from the number present in time of low tide. Apparently, the mussels were ingesting microorganisms during the high tide periods.

Many of the mussels added material beyond the notches that had been carved in the margins of their shells. The shell material that was added was a soft extension of the periostracum. These increments were not calcified as they did not effervesce in dilute hydrochoric acid.

Measurements of the increments formed by mussels given infusoria are shown in relation to conditions of light and darkness and other data in Table 6. The data indicate that the rate of growth was independent of illumination and that it was greater for the smaller and younger individuals than for the older. Little or no growth was observed after the first few weeks.

Some specimens were kept in finger bowls to which infusoria culture was not added. The seawater in the bowls was changed regularly. These animals secreted only a faint increment of periostracum.

Experimental growth of Kellia suborbicularis

Juveniles of *Kellia suborbicularis* living in the opaqued aquaria were first observed during August 1966. These clams simply appeared in the aquaria, as though they might have come through the seawater pipes. This was confirmed in the winter of 1967 when individuals of this species living in the laboratory seawater pipes became so abundant as to interfere with seawater flow. At that time, as on subsequent occasions, many juvenile and larger individuals were removed from clogged parts of the laboratory seawater plumbing. Within a month the juveniles observed in the opaqued aquaria in August grew until they were several millimeters larger than the internal diameters of the inflow pipes (1.5 mm). More juveniles, less than 1 mm in size, appeared in these aquaria. Thus detected by presence of juveniles small enough to pass through the inflow pipes, there appeared to be a steady flow of individuals into the aquaria during all months of the following 2-1/2 years. Reproduction occurring within the aquaria may have contributed to the apparently continuous supply of juveniles, for this species is viviparous and the young are sheltered within the pallial cavity until they have secreted weighty calcareous shells.

Several features in the life history of this species seemed advantageous to its use in the experiment that would modify secretory rhythms through the influences of illumination cycles and simulated tides. Subtidally, this species inhabits crevices, empty shells, and bottles; on rocky shores, individuals may be found living in the vacated burrows of boring pelecypods. As it is associated with relatively euxinic environments, this species was considered likely to thrive in the silty,

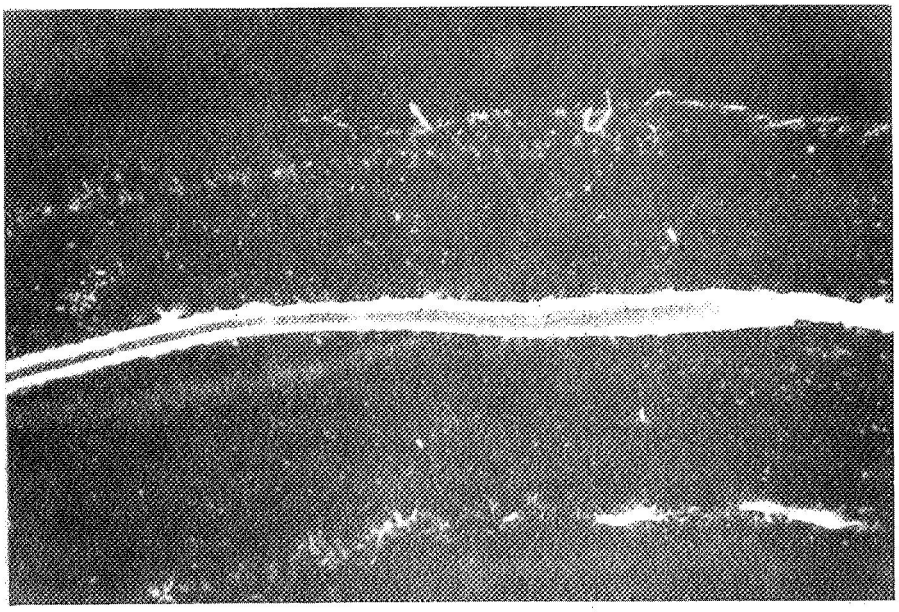
Table 6. Data on shell growth in *Mytilus californianus* in relation to light and dark

Initial length (mm)	Total size of increment (mm)			
	At week 1	At week 2	At week 6	At week 12
	Animals living under constant light			
30	1.0	1.5	2.0	2.0
32	1.5	2.5	3.0	3.0
33	0.0	1.0	—	—
48	0.5	1.0	1.0	1.0
	Animals in containers in light tight cabinet			
30	1.0	2.0	2.5	2.5
31	1.0	2.0	2.0	2.0
33	0.5	0.5	0.5	0.5
45	0.0	—	—	—
	Animals living under normal daily light-dark conditions			
29	1.5	2.5	3.0	3.5
30	1.0	1.0	1.5	1.5
33	0.5	1.0	1.0	1.0
47	0.0	0.5	0.5	0.5

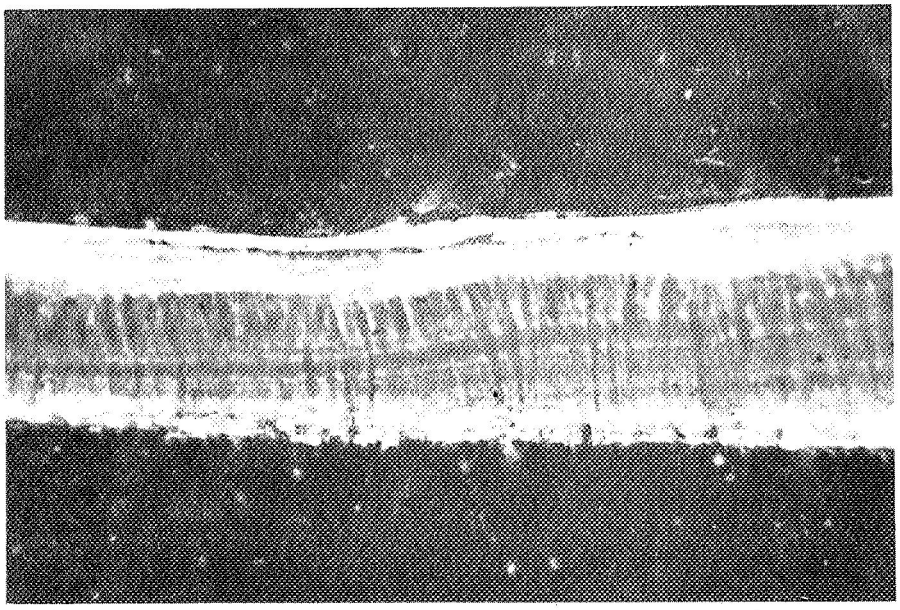
nonagitated, sulphide-rich seawater. Adaption of this species to sheltered stagnating environments seems to involve a remarkable locomotory ability as well as tolerance of chemically reducing conditions. Both small and large specimens move rapidly and can be induced to climb vertical surfaces and to move across thick deposits of silt. Because of their mobility, these clams seemed able to avoid adversities in the currents and sedimentation that might occur in the experimental aquaria. Being viviparous and negatively phototrophic, this species offered the possibility of raising clams responsive to illumination cycles from the time of zygote formation to a stage of maturity.

Despite the apparent physiological suitability of this species, some features of the shell are less favorable for purposes of this study. The thin shell is so fragile as to make thin section preparation especially difficult. Most of the thin sections that were prepared showed a granular internal structure consisting of fine (5-10 microns) particles of CaC03. A few of the thin sections showed traces of the unaltered internal shell structure, which is crossed lamellar. Growth striae spaced at 10-100 microns on the external shell surface are correlative with the growth laminae seen in thin section (Plate 20). Concentric grooves about 0.1 to 0.2 mm in breadth are present on some shells, but none were viewed successfully in thin section. Due to the high loss of internal shell structure in thin section preparation, routine study of the growth striae and concentric grooves had to be confined to shell surfaces. Acetate peels were prepared to overcome difficulties involved in study of strongly curved surfaces, but the replicas obtained were either indistinct or showed more of the underlying granular structure than the growth striae. The best results were obtained by observing the shell itself through an incident light microscope. This was facilitated by mounting the shell on a needle embedded at one end in a cylindrical mass of modeling clay.

The concentric grooves have been observed on specimens taken from cavities in mudstones at Duxbury Reef near Bolinas, California, and on specimens obtained from seawater pipes in the laboratory. In both sample groups, many of the larger shells have from one to three concentric grooves, but there are also some larger shells that lack grooves. Specimens collected in different seasons of the year at Duxbury provide



(1) X24



(2) X140

Plate 20. *Kellia suborbicularis* Montague . Radial thin section of shell (grown in laboratory at Bodega Head, California). Crossed Nichols.

no evidence of a particular season of groove formation. The grooves seem to be as sporadic in their occurrences as are the spat falls observed in the aquaria. As suggestive as this may seem, there is no firm evidence of a relationship between reproduction and groove formation. Specimens that appeared to be in the process of forming grooves did not contain juvenile clams. None of the specimens carrying juveniles had grooves located on or near their ventral margins. It is certain that at least some of the grooves result from disturbances of the organism. Specimens were induced to form identical grooves while living for a week in noncirculating seawater. It is not known, however, whether similar disturbances may occur several times during the life of an average individual living under natural conditions.

The growth striae visible on the shell surface resemble the growth laminae seen in study of Venerid and Arcid shells. The fine striae are incised below the general shell surface and have a vitreous luster. The larger intervals between the striae have a chalky appearance. Following the hypothesis of a daily secretory rhythm that was based on study of growth laminae in other species, the growth striae of *K. suborbicularis* could represent a part of a daily rhythm in which CaC03 is deposited at a relatively slow rate. The corresponding phase of the daily cycle would be, in analogy to the annual translucent groove deposit, a phase of inactivity, perhaps involving a retraction of the mantle.

Variations in the spacing of the growth striae are few and irregular on both the Duxbury and laboratory specimens. This is at least compatible with the hypothesis that a rhythmic variation in shell secretion might be induced as a direct physiological effect of a lunar monthly or fortnightly cycle in the environment. In its known occurrences, this species is protected from many tidal factors including dessication at low tide, turbulence at ebb and flood tides, and wave action at high tide. Thus, it appears that an exogenous rhythm of growth might be artifically induced if the organism were raised successfully under less sheltered conditions.

Some preliminary growth experiments during the fall of 1966 showed that this species can thrive and form normally calcified shell in the

laboratory. Near the end of 1966, a practicable technique of marking the shells had been developed, and in January 1967, a large number of specimens were obtained for the experiment. Details of the preliminary experiments and observations made during the following 1-year period are reported below.

Marking the shell for study of growth — Due to the fragility of the shell, it was not feasible to mark specimens by carving notches in their ventral shell margins. Instead, reference lines were marked in the shells through the use of chemicals (see methods discussed by Swann, 1961). Alizarin staining of the entire shell was not a useful method, for very weak concentrations resulted in death of the organism or, at the least, a condition of dormancy that lasted a week or more. A fluorescent marking technique gave better results, once a suitable nontoxic concentration had been experimentally determined.

Submerged for 12 hours in a 0.14% solution of tetracycline in seawater, the test animal concentrates this material in its mantle and other organs. The intensely fluorescent material remains visible in the tissues for a day or two, during which time a portion of it becomes incorporated in such increments as are added to the shell. Shell deposited after this fluorescent material has disappeared from the tissues lacks this intense fluorescence. Although repeated application of tetracycline at intervals of several days proves toxic for many *K. suborbicularis*, there occasionally is found an individual that survives the second treatment only 3 days after the first treatment. Such an individual may be induced to form a pair of closely spaced fluorescent lines.

Apparent daily rhythm — Through the microscope it was observed that the fluorescent lines formed by incorporation of tetracycline in the shell during a 1- to 2-day period include one or two growth striae. On specimens marked at the beginning and end of a 7-day interval, the unit of shell delimited by fluorescent lines, together with the fluorescent lines, commonly included six to eight growth striae. Similar results were obtained whether the specimens grew under constant illumination or in nearly constant darkness. These observations of growth over short periods of time showed that the growth striae are formed at the rate of one per day and that their apparent circadian periodicity of formation is independent of light cycles.

Attempts to follow growth over longer periods in miscellaneous laboratory aquaria were complicated by interruptions of seawater flow. Due to clogging of the seawater pipes and occasional mechanical troubles in the pumping apparatus, the flow of seawater was interrupted for a few hours, a day, or a week at a time. When seawater ceased to flow for more than a day, the ordinary "wet tank" aquaria, consisting of glass plates held either loosely or under tension in redwood frames, were drained, while seawater contained in plastic boxes and other non-leaking vessels became stagnant. Consequently, many organisms were dessicated or asphyxiated when the water was off. Aeration of the seawater was not very successful in preventing loss of clams. Overheating may have been a cause of death, as the general aquarium room was heated to temperatures exceeding the norm of the nearby ocean. Temperatures were lower in the closed dark room where many of the marked *K. suborbicularis* survived and formed shell. The following groups of specimens formed a significant amount of shell while living in the ordinary aquaria located in this part of the laboratory:

Group A — Specimens marked on March 9, 1967, and distributed among soft drink bottles contained in a large (about 100 gal.) non-leaking tank located beneath a "wet table." Each specimen was examined on August 22 and marked again with tetracycline. None of these specimens could be found in mid-October. The increments that were added to the shells in the March-August interval included four to six concentric grooves that may have resulted from the interruptions of seawater flow during the spring. These grooves encumbered the counting of growth striae. Despite this, the number of growth striae per 165-day increment was judged to be in the vicinity of 50 to 75 on each specimen.

Group B — Specimens in an 8-oz. jar covered with coarse nylon screen ("Lumite" window screen) and marked on August 20. The jar was situated in a wet tank near a jet of seawater. The bivalves were able to move freely within this jar and to extend their siphons through the screening. Observation on October 25 revealed that these specimens had increased their dorso-ventral heights by 2 to 6 mm. Each specimen had one concentric groove located near its ventral margin. Approximately forty growth striae occurred between the fluorescent line and concentric groove of each specimen. The number of striae occurring between the groove and

ventral margin varied from two to fifteen. As shown in Table 7, forty to fifty-five growth striae were formed during the entire 61-day period. The specimens were marked again, but died in the wet tank 2 weeks later.

Group C — Specimens in an 8-oz jar covered with fine screen (nylon stocking) and marked on June 28. These were situated next to group B in the wet tank. Although movement within the jar was unrestricted, the finer mesh screen prevented the clams from extending their siphons outside the jar. The specimens were examined and marked a second time on August 11 and a third time on October 25. They died sometime in November. During the 44 days between June 28 and August 11, one specimen was dormant and four specimens added 1 to 2 mm to their heights. There were no grooves in the formed increments, indicating that shell growth may have been continuous. On each of these specimens, the number of striae per increment ranged from forty to forty-five. During the August 11 to October 25 interval, four specimens added a millimeter to their heights. Each of these increments bore a concentric groove. The striae in these increments were too fine and indistinct for accurate counting.

Considering that concentric grooves indicate interruptions of growth, most of the preceding measurements of the rate of growth striae formation incorporate the intervals of time during which there was no appreciable shell growth. Such measurements would tend to underestimate the rate at which units of shell delimited by the striae are formed when growth is practically continuous. The apparently uninterrupted increments formed by the four specimens in group C are considered most likely to provide evidence of the periodicity of the growth striae. These specimens appeared to have secreted shell on a day-by-day basis for a period of 44 days. Allowing for errors likely to occur in the counting of fine striae on strongly curved surfaces, the approximation of forty to forty-five striae per 44 days is strongly suggestive of a daily cycle of growth.

Rate of growth — Measurements of shell growth in the preceding three groups are shown in Table 7. Height was measured parallel to the shell midline, and length was taken as the antero-posterior dimension perpendicular to height. Each measurement is considered to be accurate to the nearest millimeter. Rate of growth refers to the increase in length

Table 7. Shell growth observed in *Kellin suborbicularis*

Group A

Initial size (mm) March 9, 1967		Size (mm) August 27, 1967		Approximate rate of growth (microns per day)		Relative rate of growth (proportional change per day)	
L_1	H_1	L_2	H_2	$\Delta L/\Delta t$	$\Delta H/\Delta t$	$\Delta L/L_1\Delta t$	$\Delta H/H_1\Delta t$
2	2	9	7	42	30	.021	
4	3	11	9	42	36	.011	
4	3	11	9	42	36	.011	
6	4	13	10	42	36	.007	
6	5	11	9	30	24	.005	
11	8	18	14	42	36	.004	

Group B

August 20, 1967		October 25, 1967					
4	3	14	10	148	104	.037	.035
7	6	11	9	60	45	.009	.008
8	6	14	10	90	60	.011	.010

Table 7. Concluded

Group C

Initial size (mm) June 28, 1967		Size (mm) August 11, 1967		October 25, 1967		Approximate rate of growth (microns per day) Days 1-45		Days 46-120		Days 1-120	
L_1	H_1	L_2	H_2	L_3	H_3	$\Delta L/\Delta t$	$\Delta H/\Delta t$	$\Delta L/\Delta t$	$\Delta H/\Delta t$	$\Delta L/\Delta t$	$\Delta H/\Delta t$
11	9	14	11	15	12	67	44	13	27	33	25
12	10	14	11	15	12	44	22	13	27	25	17
13	11	14	11	15	12	22	0	13	27	17	8
13	11	15	12	16	13	44	22	13	13	25	16
14	11	16	13	17	13	44	44	13	0	25	16

or height and is expressed as microns per day. Thus defined, growth was most rapid in group B. These specimens lived in an environment with rapid seawater flow. Since the rate of flow of seawater into the tank holding group A was also rapid, differences in growth rate between these two groups may have been due to the frequent interruptions of flow experienced by group A during the spring. The growth rates of four out of five specimens in group C during a total of 120 days are lower than the lowest rate of growth in group A during 166 days. The relatively low growth rates of these group C specimens are related to their having been in a jar that was covered with a fine screen which slowed the rate of seawater circulation through the jar. The preceding observations show that the rate of shell growth is positively related to the rate and persistence of seawater circulation.

There is no evidence of a relationship between the initial sizes and measured growth rates of specimens within any of the three groups. Assuming that the initial sizes of the specimens were representative of their individual ages, the data seem to indicate that growth rate was not appreciably affected by ontogenetic factors. The strongest proof of this would involve comparing known individual ages and growth rates of specimens living in the same environment at the same time. While it is conceivable that unbroken sequences of growth striae on specimens in the three groups would provide some evidence of individual ages, the umbones of these specimens were abraded such that there could be no accurate determination of the number of striae formed before the specimens were marked. Nevertheless, the available data permit an approximation of the ranges of age in the three groups. Except for the largest specimen in group A (obtained from a seawater pipe) the specimens were found in the opaqued aquaria. Since they must have entered these aquaria through the inflow pipes, the specimens were less than 1.6 mm in maximal size sometime later than August 1966. Considering that juveniles living within the pallial cavities of parents are commonly as large as 1 mm, the specimens ranging from 2 to 6 mm in length in group A were most likely less than 6 months in age when marked in January 1967, and many specimens of groups B and C were probably less than a year in age when marked in June and August 1967. Thus, the apparent

lack of ontogenetic variation of growth rate applies only to the first year of life.

Another indication that the rate of growth was independent of ontogeny may be found in *relative* growth rate data. The relative rate of growth is useful in detecting size-related or age-related changes in the actual rate at which the organism grows. Symbolically, the relative rate of growth is the change in height (ΔH) or length (ΔL) in proportion to initial height (H_1) or length (L_1) during a certain interval of time (Δt):

$$R = \Delta L/L_1\Delta t \quad \text{or} \quad R = \Delta H/H_1\Delta t.$$

Where the actual rate of growth does not vary with respect to age or size, the relative rate of growth must, by definition, decrease with increase of age or size. As shown in Table 7 an inverse relationship between relative rate of growth and initial size is strongly evident in the data of group A and at least suggested by the data of groups B and C.

Attempt to modify secretory rhythm — On March 19, 1967, approximately 200 *Kellia suborbicularis* of various sizes were marked with tetracycline and distributed in the opaqued aquaria. Many failures of the seawater supply occurred during the next 2 months, and none of the marked specimens were found living when the aquaria were inspected in late May. Less than a hundred of the empty shells in the aquaria had the fluorescent lines that were formed in March. Judging from the apparent loss of more than 100 specimens and the common observation of *Kellia suborbicularis* crawling within the overflow pipes and drainage trough, it seems likely that many specimens had departed from the aquaria — perhaps in times of water failure and consequent stagnation within the aquaria. Some of the empty shells in the aquaria had been broken. It was found that many fiddler crabs had been living in these aquaria. Predition by crabs may have furthered the loss of the marked specimens.

Following the successes of raising *Kellia suborbicularis* in jars covered with nylon screens, a second attempt to modify the apparent daily rhythm of growth striae formation began on August 22. Twenty-nine 8-oz jars were filled with the tetracycline solution and four to five *Kellia suborbicularis* were put into each jar for a period of 12 hours. A jar

of marked specimens covered with coarse screen was put into each of the aquaria listed in Table 8. Additionally, a jar of specimens covered with the fine screen was put into one of the opaqued aquaria that had neither illumination nor simulated tides. In each aquarium tank, the marked specimens were situated within an inch of the inflow pipe.

During the next 3 weeks, the flow of seawater into the aquaria was continuous and the mechanical apparatus simulating environmental cycles operated without mishap. On September 13, the specimens were inspected, to see whether or not shell growth was underway. Observed under black light, each specimen in the filled jar that was accessible to view featured a fine (<1 mm) relatively nonfluorescent increment that followed the fluorescent line of August 22. The specimens were returned to their aquaria and left to grow over a longer period of time.

From late September to early December, there were several interruptions of the flow of seawater into the experimental aquaria. On January 19, 1968, a major mechanical problem with the pump prompted the termination of the experiment.

Results — All of the specimens originally marked on August 22 were alive when taken from the aquaria. Microscopic study of their shells under black light revealed that the length increments following the fluorescent line of August 22 varied from a mode of 3 mm in the simulated tide aquaria to a mode of 1 mm in the non-tidal aquaria. The maximum length increment observed was 5 mm, and a few specimens had not formed increments of appreciable sizes. There were no obvious relationships between the sizes of increments and the light cycles of the aquaria. Increments formed under constant illumination were similar in size to those of the nonilluminated aquaria.

From fifty to seventy growth striae occurred within the increments that were formed in each of the non-tidal aquaria. Specimens of the simulated tide aquaria had formed smaller numbers of growth striae, there being apparent a mode of between twenty and twenty-five. There were no cyclic variations in the spacing of this growth striae. All of the August 22 to January 19 increments had concentric grooves. Many of the

Table 8. Arrangement of cycles in experimental aquarium tanks of the Bodega Marine Laboratory

Number of tanks	Illumination cycles (hrs)		Period of simulated tide (hrs)
	Light	Dark	
1	12	12	8
1	12	12	16
1	12	12	30
6	12	12	—
1	12 (red)	12	—
1	12 (yellow)	12	—
1	12 (green)	12	—
1	12 (blue)	12	—
1	15	15	—
1	8	8	8
1	8	8	—
1	4	4	—
1	1/2	1/2	8
1	1/2	1/2	—
1	18	6	—
1	6	18	—
3	—	constant	—
2	constant	—	—
1	—	constant	8
1	6	6	8

specimens had formed three of these structures, a few had formed four or five of them.

Specimens contained in the two jars in the same aquarium tank grew at different rates. The specimens that lived in the jar covered with coarse screen increased their lengths and heights 1-1/2 to 2 times as rapidly as the specimens raised under fine screen (see Table 9). The fine screen (an ordinary nylon stocking) had a low permeability that impeded the circulation of seawater through the jar. Accumulation of detritus on the fine screen contributed to this effect, as the screen was completely covered by a layer of organic silt when observed on January 19. The coarse screen did not accumulate a significant amount of detritus.

Significance — In the observations of this experiment, there is the same relationship between growth rate and the water supply as was evident in the preliminary growth experiments. The greatest amount of growth occurred in the non-tidal aquaria where the seawater circulated on a continuous basis. The least amount of growth occurred in the simulated tide aquaria where the flow of seawater was regularly suspended at intervals of four to fifteen hours. Additional evidence that growth rate depended on rate of seawater flow is provided by the differing growth rates of specimens raised under fine and coarse screens in the same aquarium. Based on these positive relationships between rate of flow and rate of shell growth, one anticipates that prolonged interruptions of the seawater supply would tend to arrest growth, perhaps enough to result in the formation of disturbance rings similar to the concentric grooves observed in the August 22 to January 19 increments. Thus, the concentric grooves that were formed by the *Kellia* living through many interruptions of seawater flow are interpreted as representing periods of zero or near-zero shell growth induced by the more extensive interruptions of seawater flow.

The observed numbers of growth striae per increment do not correlate with the environmental rhythms maintained in the aquaria. If the growth

Table 9. *Kellia suborbicularis* Raised in Experimental Aquarium Tanks

Initial size (mm) September 13, 1967		Size (mm) January 14, 1968		Approximate rate of growth (microns per day)	
L_1	H_1	L_2	H_2	$\Delta L/\Delta\tau$	$\Delta H/\Delta\tau$
Animals living in jars covered with coarse screen					
5	3	8	7	23	31
7	5	10	8	23	23
7	5	10	6	23	8
8	7	12	9	31	16
12	10	15	11	23	8
Animals living in jars covered with fine screen					
10	9	13	10	13	8
11	10	13	12	16	16
11	10	14	10	23	0
12	11	13	12	8	8

striae formation process had been synchronized with any of the illumination cycles or simulated tides, the following relationships would have resulted under ideal conditions of uninterrupted growth:

Cycle (hr)	Growth Striae
1	3,097
8	387
16	193
24	129
30	103

The above relationships differ considerably in numerical value from the observed maximum of seventy striae per increment. Although hiatuses of shell growth are considered to have been sufficient to account for the obvious discrepancy, one would expect to find the greatest number of growth striae formed in aquaria having the shortest periodicities, if the simulated cycles of the environment influenced the formation of the striae. However, the growth striae varied erratically from fifty to seventy per increment in each of the non-tidal aquaria and from twenty to twenty-five in the tidal aquaria. It is evident that the growth rhythm represented by the growth striae was not modified by the environmental cycles. Unless the apparent daily rhythm of the growth striae is subject to influences not detected or controlled in this experiment, this rhythm must have an innate physiological basis. Moreover, the lack of cyclic groupings of growth striae formed during the experiment suggests that there is something in the physiological makeup of the organism that precludes the entrainment of an exogenous rhythm of shell secretion. Considering that *Kellia suborbicularis* retains tetracycline in its mantle, foot, and other organs for 1 to 2 days, the critical factor postulated may involve a budgeting of assimilation and metabolism that tends to smooth out short-term aberrations in the supply of food and seawater.

IV. GROWTH OF THE SHELL OF *Chione Undatella*

In March 1967, a population of the pelecypod *Chione undatella* (Sowerby) was located in Cholla Bay, Sonora, Mexico. The species bears distinct concentric ridges and is available in abundance on the tidal flats at the head of the Gulf of California. From April 2 to May 8, living specimens were collected on a daily basis from a sampling grid staked out in Cholla Bay. In the search for minute juvenile clams, sediments were also taken for sieve analysis. Observations on the accompanying molluscan fauna and the environment were made. The specimens were examined under a light microscope to compare increments of the ventral margin with sample dates. Measurements were made of shell size and number of concentric ridges per shell. The resulting numerical data have been processed through use of a computor providing rapid determination of conventional statistical measures. Histograms of shell size and number of concentric ridges per shell were made to show probable age groupings. Specimens collected in other seasons of 1967 and 1968 supply additional evidence in support of the inferred age groups.

Identification of specimens

Chione (*Chione*) *undatella* (Sowerby) is a tidal flat dweller common in the Gulf of California and ranging southward to Panama. The subgeneric assignment of this species follows that in the study of Pacific Coast Chioninae by Parker (1949). The most useful morphological shell differences between this species and the similar *Chionne* (*Chione*) *californiensis* were the following:

C. (*C.*) *undatella*	*C.* (*C.*) *californiensis*
Lunule faintly sculptured with concentric ridges dominant, ridges of dissoconch very thin and nearly normal to shell surface, medial cardinal tooth pointed.	Radial ribs dominant on lunule, concentric ridges of dissoconch strongly recurved one upon another, medial cardinal tooth broad and flat.

Parker (1949) established three subspecific categories for *C.* (*C.*) *undatella*:

1. *C.* (*C.*) *undatella* s.s. Medial cardinal tooth nearly straight and longer from edge of hinge plate to umbone than along edge of hinge plate.

2. *C.* (*C.*) *undatella* subsp. *simillima*. Medial cardinal tooth of right valve curved anteriorly and elongated parallel to the edge of hinge plate.

3. *C.* (*C.*) *undatella* var. *taberi*. Even, widely spaced, concentric ridges, surface colorations, flat valves, dentition intermediate between (1.) and (2.).

The specimens collected in Cholla Bay include 808 individuals identified as the variety *taberi*. These specimens have medial teeth that are certainly not elongate parallel to the edge of the hinge plate. On comparing these specimens with Parker's illustrations, it was observed that the concentric ridges of *C.* (*C.*) *undatella* s.s. are much more closely spaced. Most of the specimens have color patterns that are so variable that no two individual patterns could be considered identical. The valves are flat, a typical length to thickness (both valves) being 39:20 = 1.95 as compared with the dimensions of the type *taberi* of 39:19 = 2.05. These characters are similar to those of the variety *taberi* and differ from the other known subspecies. For the sake of brevity, they will be referred to as *C. undatella* in this study.

Features of Cholla Bay

Cholla Bay is a part of the southern end of Bahia del Adair located near Puerto Penasco on the Sonoran coast of the Gulf of California (Fig. 2). Grossly described, the borderlands consist of granitic peaks to the south, basaltic mountains and terraces to the north, and a desert playa to the east. A fossiliferous sandstone of Quaternary age forms the south shore of Cholla Bay. This sandstone is partly concealed on the north shore, mostly by sand dunes, to a lesser extent by talus, and in at least one place by waterlain deposit of bones, pumice, and locally derived rock fragments.

The tides of Cholla Bay are of the diurnal type, with two complete tidal cycles each 24.8-hour (lunar day) period. The extreme low-tide is practically flush with the regional shoreline on either side of the

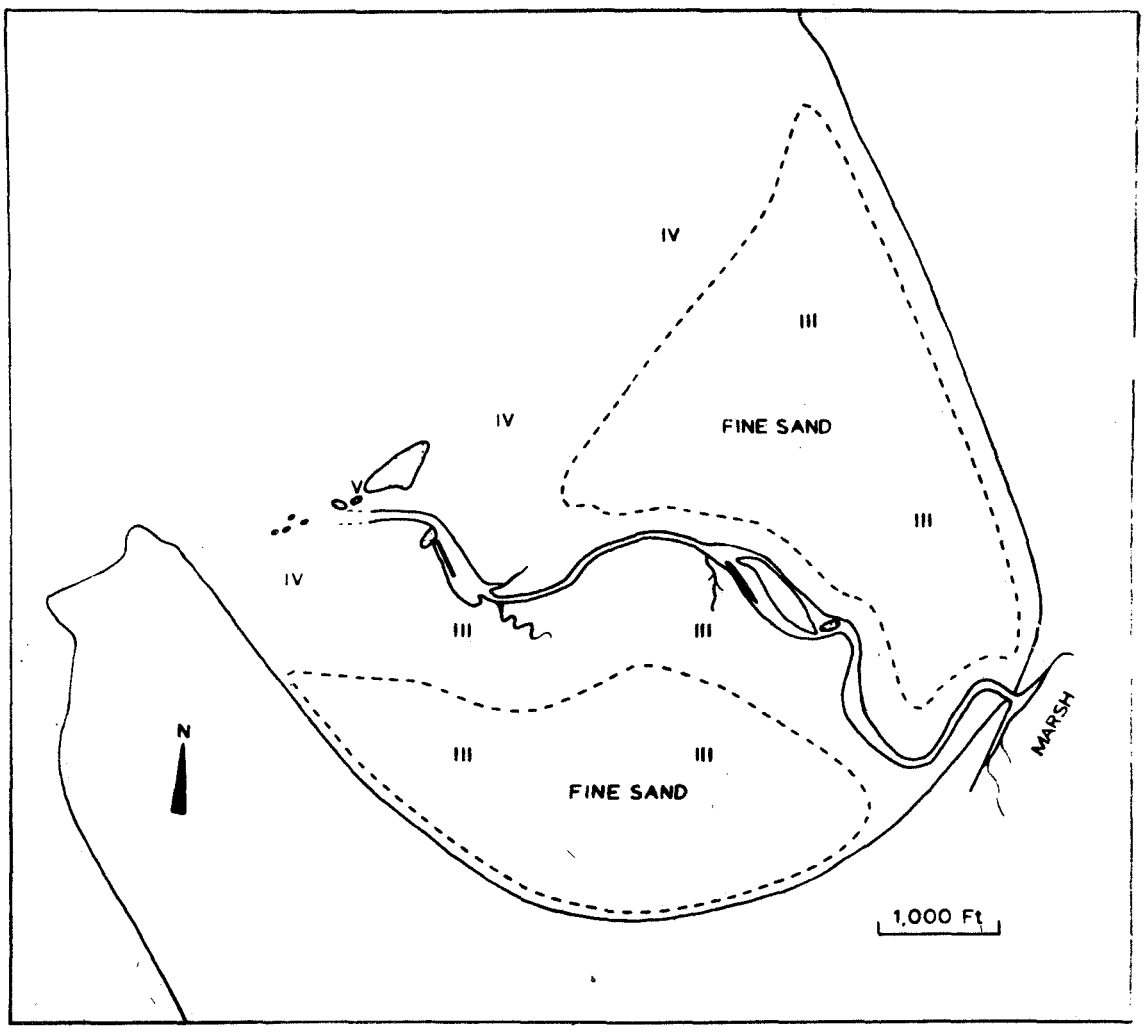


Fig. 2. Map of Cholla Bay, Mexico. Sampling area shown as a solid black line oriented parallel to main drainage channel. Roman numerals refer to molluscan fauna (see text).

mouth of Cholla Bay. High tides commonly travel a distance of 1-1/4 miles to the marine marsh at the head of the bay. Spring tides have been known to extend a mile or two beyond the marsh. Thus, Cholla Bay consists of tidal flats that are scoured twice a day by tides having a lateral range of 1-1/4 to more than 3 miles. Numerous drainage channels course through these tidal flats to accomodate the strong ebbtides. These drainage channels merge with a major drainage channel referred to be local inhabitants as "The Estero" or "The River Jordan".

There are no permanent freshwater streams flowing into Cholla Bay. Considering that the town of Puerto Penasco is supplied with water from deep wells located several miles to the north, it seems doubtful that there is any appreciable influx of groundwater from the surrounding desert. According to the inhabitants, there is seldom any rain in the summer and only minor precipitation in the winter. Although exact precipitation records are not available for Cholla Bay, Roden (1958, 1964) reported an average precipitation of 30 cm for the state of Sonora. Roden's salinity data show a minor annual variation of 36.0 $^{o}/oo$ in the spring and summer and 35.6 $^{o}/oo$ in the winter.

Mean surface water temperatures in the Puerto Penasco area vary from a summer high of 31.2°C to a winter low of 14.9°C and compare almost exactly with a few measurements of temperature at a depth of 10 m (Roden, 1964). A series of measurements of temperature taken by the author in Cholla Bay during April 1967 revealed almost as much variation at the diurnal level. Noon air temperatures were about 22 to 26°C, whereas lows of 15 to 16°C were observed at midnight and before sunrise. Water temperatures varied in relation to the air temperature, although the ranges observed were smaller. Tide pools and water in the main drainage channel in the head-region were warmest (24 to 25°C) when low tide was an hour or two before noon. In the mid-region and at the mouth of the bay, water in the main drainage channel had a noon temperature of 23 to 24°C. At night, tide pools and water in the channel cooled to 15°C.

Winds in the Gulf of California follow a seasonal pattern that may be expressed in both the water currents and the phytoplankton. Gentle breezes blow from the southeast in summer, whereas the winter winds are

northeasterly and have greater velocities. Fall is the season of hurricanes from the southeast, and spring is a season of very strong winds of variable direction. According to Roden (1958), these prevailing winds induce an upwelling of colder, saltier, nutrient-rich bottom waters. He suggests that upwelling should be greatest along the coast of Baja California in the winter, because the winter winds tend to blow the surface waters of the Gulf away from the head-region and towards the southeast. On the Sonoran coast, upwelling sould be expected to occur in the summer when prevailing winds would be moving surface water in a northwesterly direction. However, Roden believes that there is a need for more evidence to verify this suggested seasonal cycle of upwelling.

Phytoplankton may increase in numbers in relation to upwellings in the Gulf of California, according to Round (1967). Bahia de Adair occupies a major portion of Round's phytoplankton zone No. 4, which is characterized by "tropical" species of diatoms, tintinnids, dinoflagellates, and silicoflagellates. This zone has a rather low productivity of phytoplankton in comparison with other zones in the Gulf. Round attributes this low productivity to the influence of the Colorado River. However, Roden (1958) states that the salinity of the surface waters of the Gulf increases northward in all seasons, with there being no evidence of a dilution effect. Whatever the variations in distribution of the phytoplankton may prove to be, Round's data for the Puerto Penasco area are suggestive of a summer abundance correlative with upwelling in that area. Thus, there is at least some evidence of a seasonal cycle of phytoplankton productivity related to differences in upwelling induced by summer and winter winds. It seems probable that this annual cycle may be very important to the suspension feeders living in Cholla Bay.

Sediments

The sediments of Cholla Bay are here divided into two categories:

1. Sediments of the shoreline, minor in areal extent and practically devoid of bivalves
    a. Well-sorted, coarse-grained sand mixed with cobbles and pebbles derived from borderland

b. Medium-grained sand

2. Tidal flat deposits, widespread and rich in mollusks

   a. Nearshore fine-grained ("muddy") sand
   b. Medium-grained sand located midway between (2a.) and (2c.), rich in sand-sized shell fragments.
   c. Main drainage channel deposit of shells and larger shell fragments in a matrix of coarse-grained sand.

Samples of the tidal flat sediments were taken for sieve analysis and microscopic study. In sampling, a 3-1/2-inch vial was pushed into the substrate to gather sediment down to a depth of 3 to 3-1/2 inches. Vials of sediment were taken from the approximate centers of tidal flat deposits in the western quarter of the Bay. Organisms, shells, and shell fragments larger than 1 cm were removed from these samples. If this had not been done, a few large organisms or shells in a sample of sand would have resulted in a multi-modal size frequency distribution.

The three samples were soaked in freshwater to remove brine, and then allowed to dry in the open air. Each dried sample was weighed on a torsion balance to the nearest gram. A standard set of sedimentological sieves and a shaker were used to wet seive each sample into seven fractions retained on the following sieves: #5 mesh (opening 4 mm), #10 (2 mm), #18 (1 mm), #35 (0.5 mm), #60 (0.25 mm), #120 (0.125 mm), and #230 (0.063 mm). These fractions were dried in open air and weighed. Clay and silt-sized sediments that passed through the #230 sieve were discarded with the water. The weights of these finer-than-sand fractions were determined by subtracting the sum of the sand fractions from the weight of the original sample.

The data (see Table 10) show that the median sieve sizes of the samples are in agreement with field observations of sediment coarseness, the sand of the drainage channel being about three times coarser than the nearshore sand. Coefficients of sorting seem to show that sorting increases towards the shore. The coefficients of geometrical quartile skewness indicate that most of the sorting evident in these sample-size frequency distributions occurs in the finer sizes.

Table 10. Mechanical analysis of sediment samples

Sample	Sieve #	Size (mm)	Wt. (gm.)	%	$\sum$%
Matrix of	4	8.0	11	4.2	4.2
main	5	4.0	22	8.5	12.7
drainage	10	2.0	34	11.1	23.8
channel	18	1.0	48	18.5	42.3
(2a)	35	0.5	42	16.2	58.5
M = 0.36 mm	60	0.25	34	13.1	71.6
So = 3.01 mm	120	0.125	32	12.4	84.0
Sk = 0.77 mm	230	0.063	27	10.4	94.4
	<230	<0.063	9	3.5	97.9
Medium	5	4.0	5	1.1	1.1
grained	10	2.0	10	2.2	3.3
sand	18	1.0	22	4.8	7.1
(2b)	35	0.5	51	11.2	18.3
M = 0.22 mm	60	0.25	93	20.4	38.7
So = 1.50 mm	120	0.125	249	54.7	93.4
Sk = 1.39 mm	230	0.063	16	3.5	96.9
	<230	<0.063	9	2.0	99.9
Nearshore	10	2.0	1	0.4	0.4
sand	18	1.0	1	0.4	0.8
(2c)	35	0.5	2	0.8	1.6
M = 0.105 mm	60	0.25	12	5.0	6.6
So = 1.41 mm	120	0.125	74	31.0	37.6
Sk = 1.03	230	0.063	126	52.7	90.3
	<230	<0.063	23	9.6	99.9

To obtain a visual estimate of the constituency of these samples, the fractions were spread on graph paper ruled in millimeters and examined with a binocular microscope. The drainage channel sample consists of approximately 60% detrital grains and 40% bioclasts, whereas more than 98% of the nearshore sample may be detrital. The medium-grained sand (2b) appears to have an intermediate constituency of 90% detrital grains and 10% bioclasts. Thus, it appears that the finer-grained, well-sorted sediments have the greater proportion of detrital material.

In all three samples, fractions coarser than 1 mm consist largely of disarticulated juvenile clam shells and molluscan shell fragments. The only articulated bivalves found belong to a species of *Tellina*. Molluscan skeletal parts belonging to other groups, including scaphopods, are rare. Fragments of calcareous bryozoa and plates of barnacles are common in these fractions. A few fish scales, jaws, and teeth, and a few calcareous worm tube fragments were found.

Bioclastic fractions finer than 1 mm and coarser than 1/4 mm are as much foraminiferal as they are molluscan. No articulated bivalves were found in this size range. Fractions finer than 1/4 mm appear to be entirely detrital.

The preceding observations form a basis for infering local sedimentation regimens. Most of the bioclasts are of local molluscan origin, with a small amount of skeletal debris assignable to neritic species. Bioclastic and detrital sediments are coarsest in the main drainage channel where the tidal currents have greater velocity and turbulence. Relatively poor sorting would be expected to result from the trapping of finer particles in crevices between the abundant empty shells.

Molluscan fauna

Berry (1956) was the first to report that the mollusks of Cholla Bay occur in several ecological zones that are characterized by abundances of individuals belonging to certain species. Based on Berry's study, these zones are summarized below by the Roman numerals shown on the map (Fig. 2).

I. *Salicornia-Melampus* Zone. Region of flat sloughs covered with the haline plant *Salicornia* and shells of the pulmonate *Melampus*.

II. Estero. Lower three-quarters of the main drainage channel and most of its tributaries. Bivalves: *Protothaca grata, Protothaca fructifraga, Chione californiensis, Chione undatella*, and *Heterodonax bimaculatus*. Some gastropods of Zone III and *Crucibulum* attached to *C. californiensis*.

III. Tidal flats adjacent to the main drainage channel. Bivalves: *Dosinia dunkeri, Cyclinella singleyi, Chione gnidia, Chione pulicaria, Chione californiensis, Macoma indentata, Macoma pacis, Cryptomya californica*, several species of *Tellina* and *Apolymetis*. Gastropoda: *Neritina luteofasciata, Cerithium stercumuscarum, Polinices uber*, two species of *Nassarius, Melongena, Cerithidea*, several turrids, conids, and terebras.

IV. Outer strand. Bivalves: *Dosinia ponderosa, Megapitaria squalida*, and *Laevicardium elatum*. Gastropods: *Strombus gracilior, Melongena patula, Murex erythrostoma, Muricanthus nigritus*, species of *Crepidula* attached to the muricids, *Calyptrea* and *Crucibulum* attached to empty bivalve shells, several conids and terebras.

V. Fossiliferous reef exposed at extreme low tide at the mouth of Cholla Bay. Dominant mollusk: *Cerithium stercumuscarum*. Other gastropods: *Anachis, Turbo fluctuosus, Calliostoma, Tegula, Eupleura*, and some fusinids. *Neosimnia* and the bivalve *Pteria* attached to gorgonian corals.

Factors controlling zonation.— All species of Zone III are most abundantly represented in the lower three-quarters of the bay near the main drainage channel. These features, along with the progressive changes in species composition of the fauna, led Berry to suggest that differences in immersion and exposure control zonation. As observed by this writer, the tidal flats of the head-region are exposed for about 6 hours at low tide. During this period, the ebbtide currents in the main drainage channel decline to practically zero and the tributaries are drained. Heating, stagnation, and dessication occur in the head-region

at this time. Farther down the main channel, ebbtide currents are swifter and more turbulent, persisting through almost the entire period of low tide. Near the mouth of the Bay, tidal flats are exposed for no longer than 1 or 2 hours, and the tributary channels are usually full of water throughout the tidal cycle. On the basis of these observations, the writer agrees with the suggestion that zonation is controlled by conditions of immersion and exposure. The abundance of shallow burrowing bivalves and other mollusks in the main drainage channel is considered to reflect a lesser amount of water fouling, temperature change, and dessication during low tide. The suitability of this environment for bivalves is evidenced by the common occurrence of exposed live *Chione californiensis* covered with microscopic algae and one or two limpets as well as marks of limpet attachment, and live *Chione undatella* bearing encrustations (Plate 21).

Occurrence of C. undatella.— Individuals are most commonly found nestling between larger shells in the coarse sand matrix of the shelly main channel deposit. Shell colorations tend to camouflage the clam on the salt and pepper background of sands, composed mostly of granitic rock fragments and dark heavy minerals. Individuals lacking shell colorations are less well camouflaged on detrital sand, but they are the better camouflaged where the substrate is composed mostly of shell fragments. The clams occur in clusters distributed irregularly in the main channel. Where clustered, the population density is of the order of five per square foot. The clusters occur without any obvious relationship to local variations of substrates within the zone. No indication of a consistent relationship between shell coloration, clustering of individuals, and variations of substrate composition was observed. It seems apparent that the several polymorphic forms of this species are equally well adapted to the microenvironments of Zone II. This would seem to be a favorable factor for the bivalves, since the substrates and microenvironmental conditions of the main channel are subject to change during tidal scour, and this change may be extreme during storms.

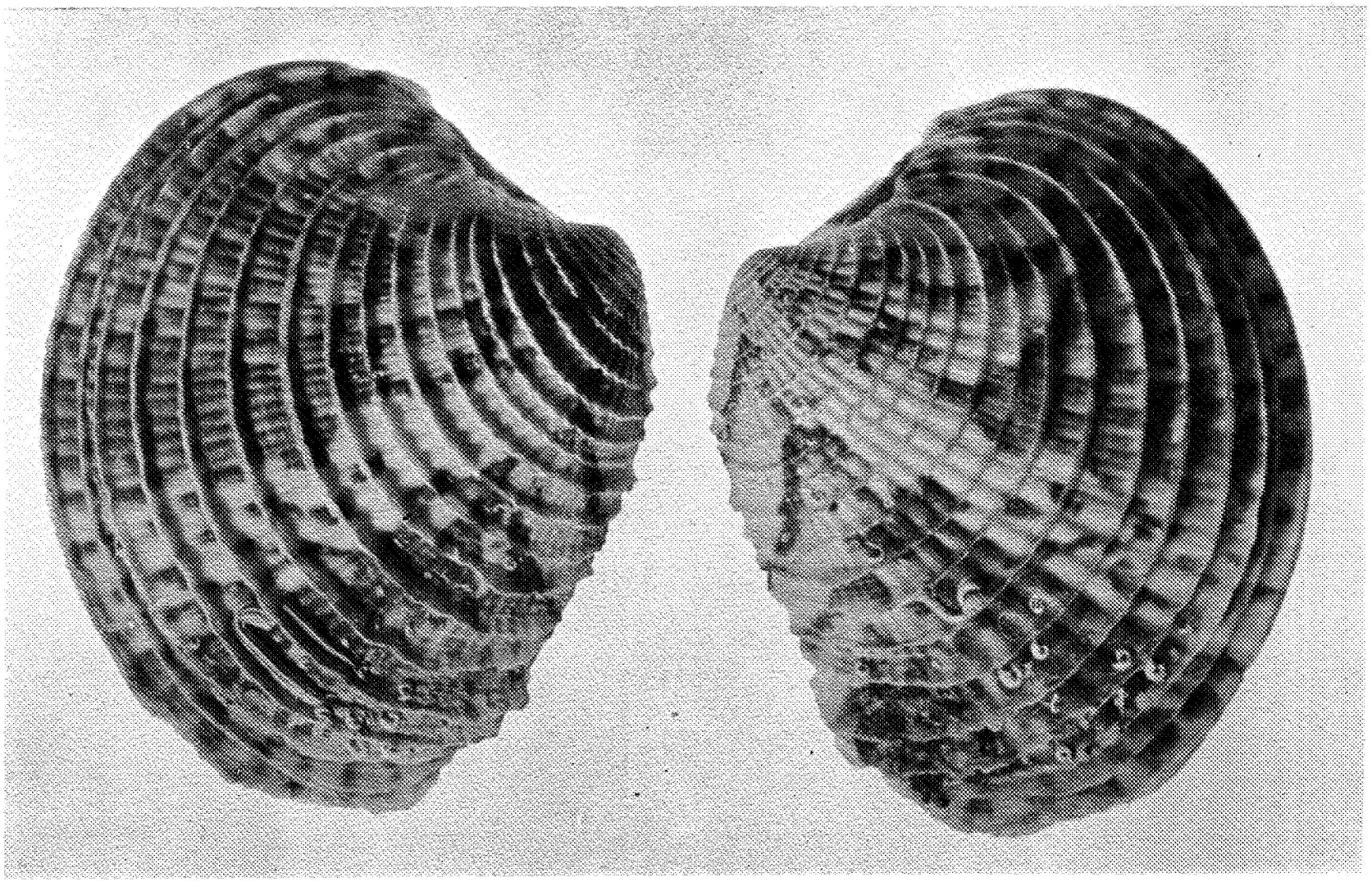


Plate 21. *Chione undatella* (Sowerby). Shell of specimen collected alive, encrusted with algae and other microorganisms. Recent, Cholla Bay, Sonora, Mexico X4-1/2.

Burrowing ability — Field observation shows that *C. undatella* rarely occurs with any part of its shell exposed except when there has been a scouring of the substrate by fortnightly spring tides. However, this species is a shallow burrower, at least when it is feeding. In comparison with *Gnidiella* and *Protothaca* (see Plate 22), both of which are known to burrow more deeply, its pallial sinus accomodates a rather short pair of siphons. Since the pallial sinuses of *C. californiensis* and *C. undatella* have practically the same relative depth, the anterior end of the typically smaller *C. undatella* must be buried to a lesser depth at time of feeding. Shallowness of burrow and lesser weight would tend to render the average individual more susceptible to tidal scour. The usual concealment of *C. undatella* is difficult to explain unless it is correlated with a superior burrowing ability. Observations on the burrowing activities of these clams support this inference. When individuals of differing sizes were placed on their sides on the tidal flat, only a few of the larger specimens failed to right themselves and begin to burrow. Under the same conditions, only a few smaller specimens of *C. californiensis* could right themselves and burrow. From these observations, *C. undatella* seems most likely to escape the scouring action of flood and ebbtides by moving deeper into the substrate. Such vertical movement, together with an ability to re-establish a burrow, would explain the frequent concealment of this short-siphoned species.

Occurrences of gastropods — The gastropod zonation involves substrate factors in addition to immersion-exposure conditions. *Cerithium stercumuscarum* occurs in great numbers on the tidal flats and in the main channel. During low tide, individuals move along the surface of the tidal flat as though sifting the sediments for minute particles of food. Shortly before the beginning of flood tide, these vagrant invidivuals attach themselves to shells or any available object. Individuals living in the main channel are much less active, clinging to stable objects and moving little throughout low tide. The densest population occurs on the "reef" of Zone V. In addition to the Bay mouth sandstone outcrop observed by Berry (1956), sandstone has been

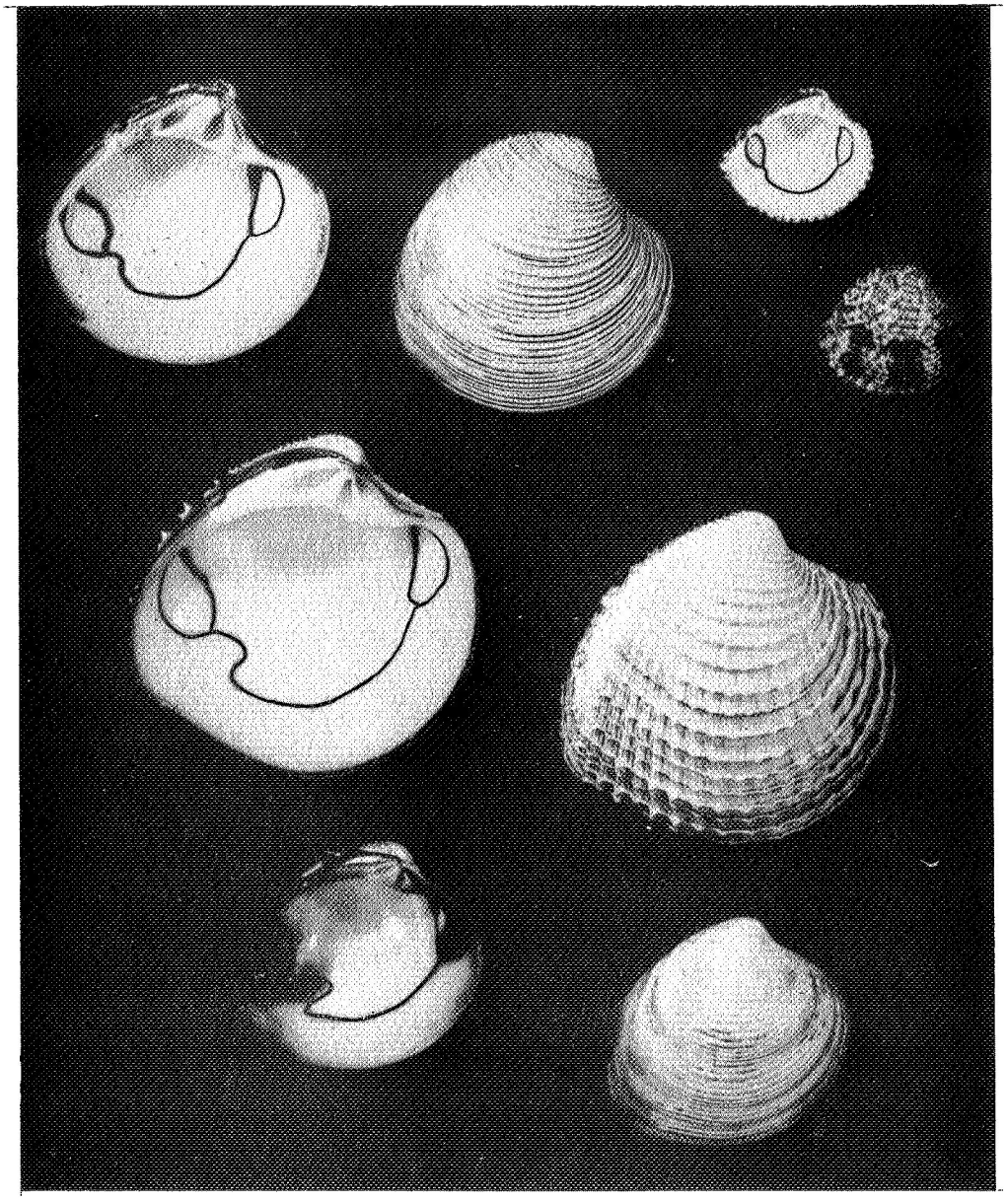


Plate 22. Chionids of Cholla Bay. Upper left: *Chione californiensis* (Broderip). Upper right: *Chione undatella* (Sowerby). Middle: *Chione gnidici* (Broderip & Sowerby). Lower: *Protothaca fructifraga* (Sowerby) approximately X1/5

intermittently exposed elsewhere in the main channel. One outcrop is located 750 feet east of the bay mouth outcrop. A dense population of *C. stercumuscarum* was observed on this outcrop during all major seasons of the year. In the head of the Bay there is another outcrop of sandstone that is devoid of living gastropods. It seems evident that the population density of this species depends on both the proximity to the open Gulf and the stability of the substrate.

The habits of some vagrant gastropods are cyclical in some aspects, related to tides in most species, and to both tidal and diurnal cycles in nocturnal species. *Nassarius versicolor*, perhaps the second most numerous gastropod of Cholla Bay, becomes active at the beginning of low tide in different parts of the tidal flats and the main drainage channel. At the approach of high tide, this animal burrows into the sands of the tidal flats or into the coarse sand matrix of the channel. *Olivella* and *Oliva* are more complex in their habits, being active and ubiquitous throughout Cholla Bay during nightime low tides. During the day, these Olivids are found buried a few inches beneath the surfaces of the tidal flats. Observations of other gastropod species are few in number, but it seems probable that many of these species may be most actively engaged in searching for food when the tide is low.

Predators on bivalves in Cholla Bay — Larger individuals of *Dosinia ponderosa*, Laevicardium elatum, *Protothaca grata*, *Chione gnidia*, and *Chione californiensis* are exploited by man. Predation on *C. undatella* is more difficult to prove. Predation by the blue crab was observed on an everyday basis, but in each case the thin-shelled *Macoma* was the prey. Usually, the swift moving crab would depart with clam grasped firmly. Occasionally, an individual would move rapidly towards me, and on two such occasions it was possible to obtain the bivalve. The shell of one of these specimens was articulate but had been broken in several places. The valves of the other specimen were broken and spread apart, and much of the viscera of the clam was missing. Empty *Macoma* shells, broken in similar patterns occur in the channel deposits. However, very few of the empty *Chione* shells have the same fractured appearance. Attempts to experimentally feed the blue crab on *Macoma* and *Chione* failed.

Gastropods would seem to be more likely to prey upon the Chionids. Species of *Busycon* and some other carnivorous snails are able to use their apertural lips to pry open bivalve shells, and the strong apertural lip of the relatively thin shell of *Murex* is reported to have the same prying function in feeding on the massively shelled bivalve *Arca* (Colton, 1908). It is generally well-known that carnivorous gastropods such as *Urosalpinx* and *Polinices* may use abrasive radulae and acid-secreting glands to bore holes through bivalve shells (Keen, 1958).

Shells with holes indicative of predation by boring carnivores are rare in Cholla Bay. One of the 808 *C. undatella* specimens collected alive has an incomplete borehole that is very circular. Located on the umbone and positioned midway between a pair of concentric ribs, this hole penetrates only half of the shell thickness. If it is assumed that a gastropod was in the process of attacking this bivalve at the time of collection, or that an attack occurring before this time was unsuccessful, then the proportion 1:808 would suggest that few boring predators are active, or that they rarely attack this species, or both.

Shells with diagnostically broken margins would be common among the remains of clams eaten by crush and pry predators such as *Busycon* and *Murex*. From casual observations on empty shells in the field, it is estimated that between 5 and 20% of the dead *C. undatella* shells have chipped ventral margins. Attempts to feed *Melongena* and *Murex* on *C. undatella* were inconclusive. However, these gastropods and several others in Cholla Bay do have shells similar to those described by Colton (1908) as predators on bivalves. The occurrences of chipped margins on an appreciable number of empty *C. undatella* shells strongly suggest that gastropods contribute to the bivalve mortality.

According to Olsson (1956), *Olivella* feeds on small organisms including bivalves smaller than 10 mm, and several species of *Oliva* seize and ingest whole a variety of larger prey including *Olivella*. Experimental evidence of Olivid predation in Cholla Bay is inconclusive. Specimens of *Oliva* and *Olivella* could not be induced to feed on Chionids, even when the flesh of these clams was exposed. Dissection of the

snails revealed no bivalve shell parts in the stomach contents. Although the shallow burrowing bivalves of Zones II and III are accessible to the Olivids, a thick Chionid shell would be a severe test of the digestive capacity of any predator. Probably, the Olivids seek out more readily digestible prey (e.g., the thinner shelled species of *Macoma* and *Tellina*, or non-mollusks).

Nassarius versicolor is very abundant in Cholla Bay. It is a rapidly moving scavenger with remarkable sensory powers. During the low tide of April 21, 1967, thousands of these small green snails were observed as they converged on a pile of fish heads and intestines discarded an hour earlier by fishermen. The snails were moving up a tributary channel in three neat columns about 150 feet in length. Movements of other individuals in the main drainage channel were also in the direction of this carrion, regardless of whether the snails were up-current or down-current from the tributary mouth. Similar mass movements but on a smaller scale were observed each day at low tide.

Individuals of *N. versicolor* quickly locate bivalves with broken shell margins. To feed on such an injured clam, the snail inserts its proboscis through the break in the shell. As many as five of these snails were found inside a *C. californiensis* with large breaks in the ventral margin. From early spring to mid-summer, many large specimens of *C. californiensis* were found with strips of decaying mantle protruding from their shells. Attached to the margins of these shells, there were specimens of *N. versicolor* feeding on the decaying tissues.

N. versicolor is considered a scavenger feeding on organic detritus in various states of decomposition. This snail is also considered an opportunistic predator in that it seeks out injured clams having exposed soft parts. Since this opportunistic predator is extremely abundant, it is regarded as probably the most important predator on Chionid bivalves in Cholla Bay.

Internal Structure of the Shell of Chione undatella

Principal layers, growth laminae, and concentric ridges

The endostracum is homogeneous, being almost transparent and colorless, and having an almost uniform extinction pattern when rotated between crossed nicole. The palliostracum is constructed of columns of aragonite that extend outwards from the innermost part of the mesostracum to the shell surface. Structural variations along the lengths of these columns are useful in characterizing the two components of the palliostracum:

1. Ectostracum. A thin layer in which the columns are extremely undulose and fibrillar.
2. Mesostracum. A thicker deposit in which the columns are either nacreous or crossed-lamellar.

Superimposed upon these columns are growth laminae that can be traced to the lines of growth on the shell surface. The number of partings per growth laminae in the ectostracum varies extremely. As the growth laminea pass into the mesostracum, there is an abrupt merging of the partings and the ultrafine units they delimit. It is in the mesostracum that the growth laminae are most distinct and regular. The other principal layers appear to be lacking in growth laminae.

The growth laminae are mutually parallel and straight within the inner and middle parts of the mesostracum. Nearing the mesectostracum boundary, there is a recurving of the growth laminae, and at the shell surface they dip in the ventral direction at moderate angles close to 45 degrees. There is a tendency for the columns to be oriented normal to the growth layers in the mesostracum and a weaker tendency for this orientation in the ectostracum. Thus, the columns dip ventrally at angles close to 45 degrees in the mesostracum, become practically parallel to the shell surface in the center of the ectostracum, and dip dorsally at low angles nearest the shell surface.

The protrusive concentric ridges are built of relatively thin growth laminae that are associated with nacreous columns in the mesostracum. Growth laminae forming the interspaces, or troughs, between the concentric ribs are associated with crossed-lamellar columns in the mesostracum, except where there may be a major concentric slow-growth groove deposit of nacreous CaC03. It is commonly observed that

three growth laminae form a ridge and ten to twelve growth laminae form a trough. In accord with the general hypothesis of this study, the tendency for there to be fifteen growth laminae per ridge-trough increment is suggestive of a daily cycle for the growth laminae and a 14 to 15 day cycle for the concentric ridges.

Radial ribs and denticles

Crenulations of the ventral margin appear as radial ribs on the external shell surface and as denticles on the internal shell surface. These ribs and denticles are visible on the dorsal and ventral surfaces of the concentric ribs. Denticles formed beneath the flat areas between concentric ribs eventually are buried by the inner portion of the mesostracum. Variations of growth lamina shape or thickness are small in the mesostracum, if the thin section is oriented reasonably parallel to the radial ribs. When the section is cut at a high angle to these ribs, as in a longitudinal section cut parallel to length, or at the umbone where the radial ribs are sharply curved, the growth laminae are crenulated in relation to the ribs and denticles.

On many shells, some of the crenulations of the margin are marked with splotches of red-brown gray, and sometimes blue. Occasionally, the marginal colorations are so consistently related to the external surfaces of certain radial crenulations as to produce a rayed marking. Thin sections of these ray-marked radial ribs reveal a consistent coloring of the ectostracum and outer parts of the mesostracum. However, the most common type of marking is splotchy. The splotches occur irregularly with respect to occurrences of concentric ribs.

Major increments

Some of the larger *C. undatella* shells show major growth bands delimited on the surface by one or more concentric grooves. The grooves occurring on the dissoconch appear to be 0.25 to 0.50 mm in width and depth, respectively. On closer inspection, it is observed that the groove structure is an imbrication of the shell surface, such that the curved planes of the adjacent growth bands are about one-fourth to one-half mm apart. In thin section, the concentric grooves of the dissoconch correspond to translucent, nacreous growth layers ranging in thickness from 20 to 100 microns in the ectostracum to about 5 microns in the

mesostracum. These groove deposits are lacking or not visible in the endostracum. The grooves are traceable from the dissoconch into the lunule where they are very distinct. In thin sections oriented so that they include the lunule, the grooves are related to fine (about 3-5 microns) translucent growth lines. On the escutcheon, the grooves are not always distinct and are difficult to observe in thin section.

The growth bands are composed mostly of semiopaque CaC03. In the ectostracum, the growth bands are entirely fibrillar. In the mesostracum, the growth bands are crossed-lamellar except where they include nacreous tongues related to concentric ridges. The concentric ridges vary in their spacing, depending on position within the major increments. The earliest-formed (umbonal) ridges are closely spaced, whereas ridges located in the middle of the first-formed growth band are more widely spaced. Nearing the first-formed groove and immediately following it, several ridges are again closely spaced. Ridges included in the later growth bands tend to be equally spaced. The number of ridges per major growth band varies within and between specimens. However, on all of the specimens having several major increments, there is a progressive decrease in the number of ridges per band in the later bands. These major increments are morphologically similar to the annual growth layers formed by the species of Table 1, especially those of *Venus striatula*, *Protothaca staminea*, and *Cardium corbis*.

Minor concentric rings

Two types of minor concentric growth rings have been observed:

1. Microgrooves. Formed by one or two growth laminae elevated or depressed in relation to the general shell surface; irregular in their occurrences.
2. Reduced concentric ridges. Low in relief and abnormally thin; many occurrences are adjacent to the major concentric grooves.

These minor concentric rings are not expressed as growth layers in the internal structure of the shell.

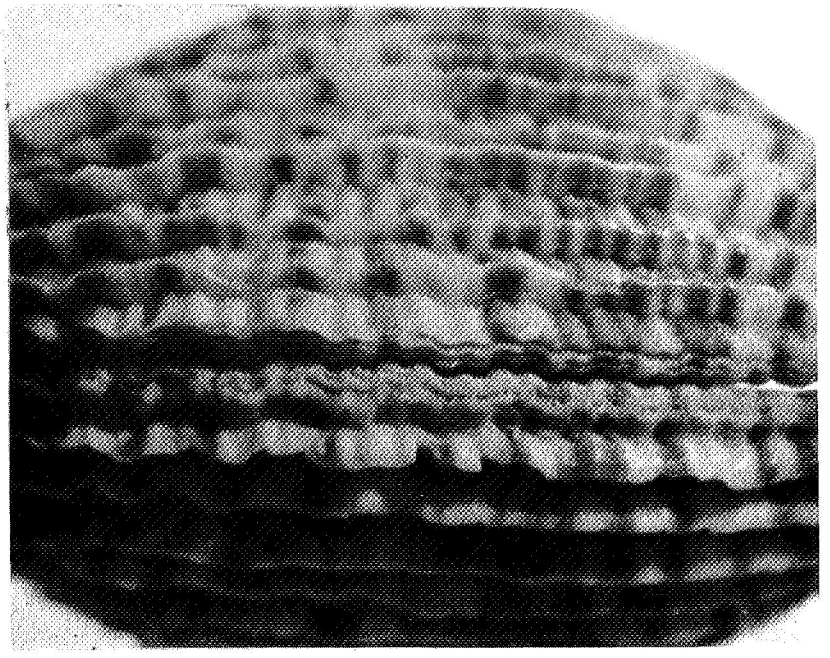
Major Increments Related to Annual Growth

The hypothesis that the major increments of the shell of *C. undatella* are related to an annual cycle of growth has been tested through the comparison of ventral margins of shells collected in different seasons.

The samples used for this serial study were taken from the main drainage channel between April 2 and May 8, 1967; August 23-24, 1967; November 17, 1967; and January 21, 1968. Sampling in the spring of 1967 followed a plan designed for the day-by-day serial growth study. The other samples consist of specimens collected randomly during the other intervals.

The ventral margin of each shell was examined through a reflected light microscope and assigned to either the groove or growth band category. Regardless of its thickness, the translucent component of the major increment is most distinct were it can be observed between two adjacent growth bands. On the ventral margin, the translucent component appears as a shelflike groove or lip that is depressed below the general external surface of the dissoconch (Plate 23:1). The shallowest marginal grooves are formed on moderate size or small specimens with less than twenty concentric ridges. A few of the smaller shells with grooved margins have dissolution pits (Plate 23:2). Since a very shallow marginal groove is difficult to distinguish from the growth band preceding it, one anticipates that a number of smaller specimens actually in the marginal groove category may erroneously have been assigned to the growth band category. Although these errors do not preclude the recognition of an annual cycle through study of serial samples, it is to be expected that the proportion of specimens assigned to the marginal groove category could be much less than 100% even though the entire population might be in a season of groove formation.

Observations of grooves and growth bands are given in Tables 11a-e. Notation for a specimen bearing a growth band comprised of eighteen concentric ridges followed by a groove and a second growth band with six ridges is 18/6. The summary data are presented below.





(2) Pits on interior surface of shell. Specimen collected alive from bank of main drainage channel, May 7, 1967, X4 1/2.

Plate 23. *Chione undatella* (Sowerby). Recent, Cholla Bay, Sonora, Mexico.

Table 11. *Chione undatella* shell measurements

Cholla Bay, Sonora, Mexico

Legend of Tables 11a-e

Notation: V.M. - ventral margin
R - ridge on ventral margin
T - trough on ventral margin
/ - occurrence of major concentric groove

Lunar cycles: April 2-May 8, 1967 (11a) - see Fig. 5 for phases of lunar month, Fig. 6 for Guaymas tidal curve.

August 23-24, 1967 (11b-c) - samples collected 3-4 days past full moon.

November 11, 1967 (11d) - sample collected at full moon.

January 21, 1968 (11e) - sample collected 6 days past full moon.

Table 11a

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
Day 1	30.000	26.000	33.000	T	
	26.000	22.000	24.000	T	
(April 2)	22.000	19.000	20.000	T	
N = 6	22.000	17.000	19.000	T	
	18.000	15.000	18.000	T	
	18.000	14.000	20.000	T	
Day 2	29.000	27.000	15.000	T	
	19.000	15.000	17.000	R	
(April 3)	19.000	16.000	16.000	T	
N = 19	17.000	14.000	19.000	T	
	13.000	11.000	15.000	R	
	20.000	17.000	19.000	R	
	20.000	16.000	16.000	T	
	19.000	16.000	13.000	T	
	18.000	15.000	12.000	T	
	17.000	14.000	15.000	T	
	13.000	10.000	16.000	R	
	10.000	9.000	13.000	T	
	23.000	19.000	20.000	R	
	20.000	17.000	21.000	R	
	16.000	14.000	15.000	R	
	17.000	15.000	15.000	T	
	15.000	12.000	14.000	R	
	13.000	10.000	13.000	R	
	10.000	8.000	14.000	R	
Day 3	24.000	18.000	24.000	T	
	24.000	20.000	20.000	T	
(April 4)	25.000	21.000	29.000	T	
N = 18	21.000	20.000	17.000	T	17/
	18.000	15.000	18.000	T	
	17.000	14.000	16.000	T	
	16.000	14.000	23.000	T	
	43.000	31.000	24.000	R	
	31.000	28.000	33.000	T	
	17.000	15.000	20.000	T	18/2

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
	23.000	19.000	18.000	T	
	21.000	18.000	21.000	T	
	21.000	17.000	21.000	R	
	19.000	15.000	15.000	R	
	18.000	15.000	16.000	T	
	17.000	15.000	23.000	T	
	17.000	13.000	18.000	T	
	13.000	11.000	13.000	T	
Day 4	33.000	27.000	29.000	T	
(April 5)	33.000	30.000	36.000	T	
	23.000	22.000	18.000	T	
	22.000	20.000	20.000	T	
	22.000	21.000	24.000	T	
N = 29	20.000	17.000	22.000	T	
	18.000	15.000	17.000	T	
	17.000	14.000	17.000	T	
	16.000	13.000	17.000	T	
	15.000	13.000	16.000	T	
	15.000	12.000	16.000	R	
	15.000	13.000	17.000	T	
	14.000	12.000	15.000	T	
	14.000	12.000	16.000	T	
	15.000	13.000	21.000	R	
	12.000	11.000	17.000	R	
	13.000	10.000	17.000	T	
	11.000	9.000	20.000	R	
	11.000	10.000	14.000	T	
	9.000	8.000	17.000	T	
	11.000	10.000	13.000	T	
	10.000	8.000	15.000	T	
	11.000	9.000	15.000	T	
	8.000	7.000	14.000	T	
	9.000	7.000	15.000	T	
	10.000	9.000	14.000	T	
	34.000	30.000	40.000	R	
	29.000	25.000	34.000	T	
	25.000	22.000	20.000	T	
Day 5	38.000	31.000	29.000	T	
	26.000	22.000	28.000	T	
(April 6)	26.000	22.000	24.000	T	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
	19.000	15.000	16.000	R	
	18.000	15.000	16.000	T	
	17.000	13.000	22.000	R	
N = 22	22.000	20.000	30.000	T	
	22.000	19.000	22.000	R	
	29.000	25.000	29.000	T	
	27.000	22.000	26.000	R	
	21.000	18.000	19.000	R	
	20.000	16.000	23.000	T	
	19.000	16.000	21.000	R	
	18.000	15.000	21.000	T	
	17.000	14.000	21.000	T	
	15.000	12.000	16.000	T	
	13.000	12.000	18.000	T	
	15.000	12.000	16.000	T	
	13.000	11.000	14.000	T	
	10.000	7.000	12.000	T	
	19.000	16.000	22.000	T	
	11.000	10.000	16.000	T	
	36.000	30.000	20.000	T	
	23.000	21.000	23.000	T	14/6/3/
	19.000	12.000	16.000	T	
	14.000	12.000	16.000	T	
	13.000	11.000	16.000	T	
	12.000	10.000	17.000	R	
	10.000	7.000	12.000	T	
	11.000	9.000	9.000	T	
	11.000	10.000	14.000	R	
	10.000	8.000	14.000	T	
	10.000	8.000	13.000	T	
	8.000	7.000	14.000	R	
	24.000	20.000	33.000	T	
	20.000	15.000	15.000	T	
	15.000	12.000	19.000	R	
	14.000	11.000	17.000	T	
	10.000	9.000	12.000	T	
Day 7	22.000	19.000	16.000	R	
(April 8)	20.000	18.000	16.000	R	
	22.000	19.000	18.000	R	
	20.000	16.000	16.000	T	14/2

Table 11a Continued
CHIONE UNDATELLA SHELL MEASUREMENTS
CHOLLA BAY, SONORA, MEXICO, APRIL 2 – MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
	20.000	18.000	16.000	T	15/1
	18.000	15.000	17.000	T	13/4
	19.000	17.000	19.000	T	16/3
N = 23	16.000	13.000	18.000	T	
	16.000	13.000	15.000	R	
	16.000	12.000	16.000	T	7/9
	15.000	12.000	14.000	T	
	12.000	10.000	14.000	R	
	11.000	9.000	14.000	R	
	12.000	10.000	15.000	T	
	10.000	8.000	12.000	R	
	10.000	9.000	15.000	T	
	10.000	8.000	14.000	R	
	8.000	7.000	13.000	R	
	35.000	29.000	30.000	R	18/12/
	25.000	22.000	22.000	T	20/2
	24.000	21.000	26.000	T	
	23.000	19.000	10.000	T	
	21.000	19.000	18.000	T	
Day 8	33.000	29.000	28.000	R	
(April 9)	29.000	25.000	29.000	R	
	23.000	20.000	18.000	R	
	23.000	20.000	18.000	T	
	24.000	20.000	20.000	T	
N = 29	22.000	18.000	18.000	T	
	21.000	16.000	16.000	T	
	22.000	19.000	19.000	T	
	21.000	17.000	16.000	T	
	20.000	17.000	19.000	R	
	20.000	17.000	20.000	T	
	19.000	15.000	18.000	R	
	16.000	14.000	18.000	T	
	20.000	17.000	20.000	T	
	19.000	16.000	17.000	R	
	17.000	14.000	20.000	T	
	17.000	14.000	15.000	T	
	17.000	15.000	17.000	R	
	14.000	12.000	17.000	T	
	15.000	12.000	13.000	T	
	14.000	12.000	16.000	R	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS
CHOLLA BAY, SONORA, MEXICO, APRIL 2 – MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
	14.000	11.000	14.000	T	
	12.000	9.000	13.000	T	
	12.000	10.000	17.000	T	
	11.000	10.000	14.000	T	
	11.000	9.000	14.000	T	
	10.000	9.000	9.000	R	
	11.000	9.000	15.000	R	
	6.000	5.000	11.000	T	
Day 9	42.000	38.000	50.000	R	
(April 10)	30.000	26.000	28.000	T	
	27.000	22.000	20.000	T	
	20.000	16.000	21.000	T	
N = 18	20.000	16.000	18.000	R	
	18.000	16.000	18.000	T	
	18.000	15.000	17.000	T	
	18.000	14.000	16.000	T	
	15.000	12.000	11.000	R	
	15.000	12.000	13.000	R	
	16.000	14.000	13.000	T	
	8.000	7.000	11.000	T	
	12.000	11.000	12.000	T	
	13.000	11.000	16.000	T	
	13.000	10.000	19.000	R	
	19.000	16.000	15.000	R	
	11.000	10.000	16.000	R	
	10.000	9.000	14.000	R	
Day 10	18.000	15.000	19.000	R	
	16.000	13.000	18.000	T	
(April 11)	14.000	12.000	16.000	T	
	15.000	12.000	16.000	T	
N = 7					
	14.000	11.000	16.000	R	
	13.000	11.000	14.000	T	
	12.000	10.000	14.000	T	
Day 11	16.000	13.000	16.000	T	
	25.000	22.000	25.000	T	
(April 12)					
	20.000	16.000	19.000	T	
N = 22	16.000	13.000	14.000	R	
	20.000	20.000	19.000	R	
	21.000	20.000	20.000	T	
	15.000	12.000	15.000	T	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
	24.000	20.000	20.000	R	
	18.000	15.000	19.000	T	
	16.000	13.000	18.000	T	
	12.000	10.000	15.000	R	
	14.000	12.000	12.000	R	
	12.000	11.000	15.000	R	
	13.000	12.000	17.000	T	
	16.000	14.000	19.000	T	
	10.000	9.000	12.000	T	
	11.000	10.000	17.000	T	
	9.000	8.000	16.000	T	
	7.000	6.000	11.000	T	
	7.000	6.000	11.000	R	
	7.000	6.000	10.000	R	
	7.000	6.000	15.000	R	
Day 12	21.000	12.000	20.000	T	
	20.000	16.000	22.000	R	
(April 13)	20.000	17.000	15.000	T	
	21.000	20.000	21.000	T	
N = 25	20.000	18.000	18.000	R	14/3
	30.000	26.000	27.000	T	
	22.000	17.000	18.000	T	
	20.000	16.000	21.000	T	
	17.000	13.000	21.000	T	
	19.000	15.000	17.000	T	
	16.000	13.000	16.000	R	
	15.000	12.000	17.000	T	
	20.000	16.000	21.000	T	
	16.000	12.000	17.000	R	
	17.000	13.000	16.000	T	
	11.000	9.000	12.000	R	
	22.000	16.000	17.000	R	
	21.000	17.000	20.000	R	
	20.000	16.000	18.000	T	
	19.000	16.000	19.000	R	
	19.000	15.000	20.000	R	
	17.000	13.000	14.000	T	
	16.000	12.000	15.000	T	
	15.000	12.000	19.000	T	
	11.000	9.000	13.000	T	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
Day 13	24.000	20.000	22.000	R	
(April 14)	23.000	18.000	20.000	T	
	21.000	18.000	17.000	T	
	18.000	15.000	23.000	R	
N = 32	19.000	16.000	21.000	R	
	19.000	15.000	15.000	R	
	20.000	15.000	20.000	T	
	23.000	18.000	18.000	T	15/3
	20.000	16.000	23.000	T	
	19.000	15.000	20.000	T	
	18.000	15.000	20.000	T	
	19.000	17.000	20.000	T	
	18.000	15.000	16.000	T	
	20.000	16.000	20.000	T	
	18.000	16.000	20.000	T	
	14.000	12.000	18.000	T	
	14.000	11.000	17.000	T	
	17.000	13.000	18.000	R	
	15.000	12.000	14.000	T	
	14.000	12.000	16.000	T	
	12.000	10.000	15.000	R	14/1
	14.000	11.000	16.000	T	
	12.000	10.000	15.000	R	
	14.000	12.000	9.000	T	
	11.000	10.000	15.000	R	
	10.000	8.000	14.000	R	
	10.000	9.000	15.000	T	
	11.000	9.000	15.000	T	
	9.000	7.000	15.000	T	
	7.000	6.000	13.000	R	
	14.000	11.000	15.000	T	
	12.000	9.000	16.000	T	
Day 14	22.000	10.000	22.000	R	
	22.000	17.000	21.000	T	
(April 15)	22.000	17.000	20.000	R	
N = 24	39.000	35.000	37.000	T	
	20.000	16.000	21.000	R	
	21.000	17.000	19.000	R	
	21.000	17.000	22.000	T	
	19.000	14.000	17.000	T	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
	19.000	15.000	17.000	T	
	20.000	16.000	17.000	T	
	17.000	15.000	20.000	T	
	20.000	17.000	18.000	R	
	21.000	17.000	22.000	T	
	18.000	14.000	15.000	T	
	15.000	12.000	19.000	T	
	20.000	16.000	19.000	T	
	19.000	15.000	17.000	T	
	18.000	15.000	19.000	R	
	18.000	14.000	22.000	R	
	14.000	12.000	17.000	R	
	23.000	19.000	21.000	R	
	22.000	18.000	19.000	T	
	22.000	12.000	17.000	R	
	19.000	15.000	19.000	T	
	22.000	18.000	25.000	T	
Day 15	21.000	17.000	16.000	T	
(April 16)	20.000	16.000	20.000	R	
	19.000	15.000	16.000	R	
N = 33	19.000	15.000	21.000	R	
	15.000	13.000	19.000	R	
	22.000	19.000	29.000	T	
	20.000	15.000	22.000	T	
	20.000	17.000	24.000	R	
	21.000	18.000	22.000	T	
	21.000	17.000	22.000	T	
	20.000	19.000	20.000	T	
	20.000	16.000	18.000	T	
	21.000	18.000	18.000	T	
	20.000	15.000	17.000	R	
	20.000	16.000	16.000	R	
	22.000	17.000	20.000	T	
	16.000	13.000	16.000	R	
	16.000	13.000	19.000	T	
	17.000	13.000	19.000	T	
	17.000	15.000	18.000	R	
	18.000	15.000	15.000	R	
	17.000	13.000	15.000	R	
	17.000	14.000	15.000	T	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
	17.000	13.000	19.000	T	
	15.000	13.000	16.000	R	
	14.000	12.000	15.000	R	
	14.000	11.000	16.000	T	
	14.000	11.000	13.000	T	
	12.000	10.000	16.000	T	
	13.000	10.000	13.000	T	
	12.000	10.000	13.000	T	
	11.000	9.000	17.000	R	
Day 16	21.000	17.000	20.000	T	
(April 17)	21.000	18.000	22.000	R	
	21.000	17.000	17.000	T	
	15.000	12.000	14.000	T	
N = 29	18.000	15.000	19.000	R	14/1
	19.000	17.000	17.000	R	
	17.000	14.000	22.000	R	
	17.000	14.000	20.000	T	
	21.000	18.000	26.000	T	26/
	19.000	15.000	18.000	T	16/2
	18.000	15.000	15.000	T	
	19.000	17.000	18.000	T	
	15.000	13.000	17.000	R	
	17.000	14.000	20.000	T	
	18.000	15.000	18.000	T	
	16.000	13.000	22.000	T	22/
	13.000	11.000	17.000	T	
	16.000	13.000	18.000	T	
	15.000	12.000	20.000	T	
	15.000	12.000	13.000	R	
	14.000	12.000	22.000	T	20/2
	13.000	10.000	17.000	T	
	16.000	13.000	17.000	R	
	16.000	13.000	17.000	T	
	16.000	13.000	16.000	T	11/5
	14.000	12.000	14.000	T	
	12.000	10.000	15.000	T	
	16.000	13.000	17.000	T	
	16.000	13.000	21.000	T	
Day 17	41.000	36.000	31.000	T	
	26.000	22.000	28.000	T	28/

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS
CHOLLA BAY, SONORA, MEXICO, APRIL 2 – MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
(April 18)	26.000	23.000	32.000	T	
	22.000	18.000	17.000	R	16/1
	22.000	19.000	23.000	T	
N = 43	22.000	19.000	19.000	R	
	19.000	16.000	22.000	R	
	19.000	17.000	21.000	T	
	16.000	13.000	17.000	R	
	22.000	18.000	22.000	T	
	20.000	18.000	20.000	R	11/9
	20.000	17.000	20.000	T	
	17.000	14.000	20.000	R	
	18.000	15.000	18.000	T	
	18.000	15.000	21.000	R	
	16.000	12.000	15.000	T	
	17.000	14.000	19.000	T	
	15.000	12.000	14.000	T	
	17.000	14.000	18.000	T	17/1
	17.000	14.000	16.000	T	13/3
	20.000	18.000	18.000	R	17/1
	12.000	14.000	16.000	R	
	16.000	12.000	14.000	R	
	12.000	11.000	14.000	T	
	10.000	9.000	11.000	T	
	21.000	18.000	24.000	T	
	21.000	18.000	29.000	T	29/
	20.000	17.000	19.000	T	
	20.000	16.000	22.000	T	
	21.000	17.000	19.000	T	
	18.000	15.000	19.000	T	
	19.000	15.000	19.000	T	
	19.000	15.000	22.000	T	
	17.000	14.000	18.000	T	
	12.000	14.000	15.000	T	
	16.000	13.000	22.000	T	
	13.000	11.000	17.000	T	
	13.000	11.000	19.000	T	
	14.000	12.000	14.000	T	
	12.000	10.000	15.000	R	
	19.000	16.000	19.000	R	15/1
	19.000	16.000	19.000	T	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
	10.000	8.000	13.000	R	
Day 18	27.000	22.000	26.000	T	
	22.000	19.000	23.000	R	
(April 19)	24.000	20.000	21.000	R	
	21.000	17.000	18.000	T	18/1
N = 24	21.000	16.000	20.000	R	17/3
	21.000	17.000	24.000	T	
	20.000	16.000	19.000	T	
	19.000	17.000	23.000	T	
	17.000	14.000	18.000	R	
	19.000	15.000	18.000	R	
	16.000	13.000	21.000	R	
	19.000	15.000	19.000	R	
	19.000	15.000	23.000	T	
	15.000	14.000	14.000	T	
	17.000	15.000	16.000	T	14/2
	16.000	12.000	17.000	T	
	16.000	11.000	19.000	T	
	13.000	11.000	13.000	T	
	12.000	10.000	17.000	T	
	22.000	17.000	23.000	T	
	12.000	9.000	15.000	T	
	12.000	9.000	16.000	T	
	11.000	10.000	13.000	R	
	9.000	7.000	16.000	T	
Day 19	18.000	15.000	18.000	R	
	18.000	14.000	20.000	R	
(April 20)	16.000	13.000	20.000	T	
	15.000	12.000	16.000	T	13/3
	12.000	12.000	17.000	R	
N = 20	14.000	11.000	17.000	T	14/3
	12.000	11.000	20.000	R	
	11.000	10.000	19.000	T	16/3
	12.000	9.000	13.000	T	9/2/2
	11.000	9.000	18.000	T	
	10.000	9.000	16.000	T	
	14.000	13.000	20.000	T	
	15.000	12.000	21.000	T	
	14.000	11.000	23.000	T	
	17.000	14.000	19.000	T	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ribs per shell	V.M.	Ribs within major increments
	19.000	15.000	24.000	T	
	19.000	16.000	22.000	T	
	19.000	18.000	19.000	T	
	21.000	17.000	22.000	T	
	23.000	20.000	20.000	R	17/2/1
	22.000	18.000	21.000	T	
Day 20	21.000	19.000	25.000	T	
(April 21)	23.000	19.000	24.000	T	
	22.000	18.000	23.000	T	
	19.000	16.000	20.000	T	
N = 32					
	16.000	14.000	21.000	T	
	18.000	13.000	19.000	T	
	13.000	12.000	20.000	T	
	12.000	11.000	18.000	T	
	16.000	14.000	21.000	T	
	14.000	11.000	18.000	T	
	9.000	8.000	14.000	T	
	9.000	9.000	20.000	R	
	10.000	9.000	19.000	T	
	10.000	9.000	17.000	T	
	10.000	9.000	18.000	T	
	9.000	8.000	14.000	T	
	11.000	10.000	18.000	T	
	10.000	9.000	17.000	T	
	9.000	7.000	15.000	T	
	10.000	8.000	17.000	T	
	9.000	7.000	18.000	T	
	11.000	9.000	16.000	T	
	9.000	8.000	12.000	T	
	11.000	9.000	16.000	T	
	7.000	5.000	15.000	R	
	7.000	6.000	14.000	T	
	36.000	31.000	31.000	T	
	28.000	25.000	25.000	T	
	24.000	20.000	21.000	T	
	18.000	17.000	16.000	R	
	15.000	13.000	17.000	T	
Day 21	29.000	24.000	32.000	T	
	22.000	19.000	22.000	R	
(April 22)	19.000	17.000	18.000	T	

Table 11a Continued
CHIONE UNDATELLA SHELL MEASUREMENTS
CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ribs per shell	V.M.	Ribs within major increments
N = 23	20.000	16.000	18.000	R	
	20.000	17.000	20.000	R	
	19.000	15.000	21.000	T	
	20.000	16.000	18.000	T	
	18.000	14.000	19.000	T	
	18.000	15.000	20.000	T	
	14.000	12.000	13.000	T	
	14.000	11.000	16.000	R	
	9.000	8.000	14.000	T	
	13.000	11.000	17.000	T	
	13.000	11.000	17.000	T	
	11.000	10.000	15.000	T	
	11.000	9.000	13.000	T	
	15.000	11.000	17.000	T	
	28.000	24.000	30.000	T	
	17.000	14.000	13.000	T	
	14.000	11.000	12.000	R	
	11.000	8.000	16.000	T	
	12.000	11.000	15.000	T	
	11.000	9.000	14.000	T	
Day 22	30.000	24.000	29.000	R	20/9
	20.000	17.000	18.000	T	17/1
(April 23)	16.000	13.000	16.000	T	
	21.000	17.000	17.000	T	
	19.000	16.000	17.000	T	
N = 16					
	22.000	19.000	20.000	R	16/4
	20.000	16.000	17.000	T	
	17.000	13.000	17.000	R	
	18.000	14.000	18.000	R	
	18.000	15.000	20.000	T	
	15.000	12.000	17.000	T	
	14.000	11.000	16.000	R	
	13.000	10.000	12.000	T	
	14.000	12.000	16.000	T	
	12.000	10.000	20.000	T	
	11.000	10.000	16.000	T	
Day 23	16.000	13.000	20.000	T	
	12.000	11.000	15.000	R	
(April 24)	14.000	12.000	18.000	T	
	17.000	14.000	20.000	T	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ribs per shell	V.M.	Ribs within major increments
N== 24	17.000	15.000	25.000	T	
	19.000	16.000	18.000	R	
	17.000	14.000	18.000	R	
	18.000	15.000	21.000	T	
	18.000	15.000	17.000	T	
	19.000	15.000	19.000	T	
	20.000	17.000	18.000	R	
	20.000	17.000	20.000	T	
	19.000	15.000	19.000	T	
	20.000	17.000	19.000	R	
	23.000	20.000	25.000	T	
	27.000	23.000	22.000	R	21/1
	12.000	10.000	18.000	T	
	15.000	12.000	22.000	T	
	14.000	12.000	20.000	R	
	16.000	13.000	18.000	T	
	18.000	15.000	18.000	T	
	19.000	15.000	21.000	T	
	21.000	18.000	19.000	T	
	24.000	20.000	25.000	T	
Day 25	21.000	17.000	18.000	R	
(April 26)	26.000	23.000	24.000	R	
	25.000	20.000	18.000	R	
	24.000	20.000	19.000	R	
N = 50	21.000	18.000	20.000	R	
	22.000	18.000	21.000	R	
	20.000	17.000	23.000	T	
	19.000	16.000	13.000	T	
	20.000	17.000	21.000	R	
	20.000	17.000	20.000	R	
	19.000	16.000	20.000	R	
	19.000	16.000	20.000	T	
	22.000	18.000	19.000	R	
	19.000	15.000	20.000	R	
	18.000	15.000	21.000	R	
	18.000	15.000	21.000	R	
	17.000	14.000	15.000	T	
	19.000	15.000	17.000	T	
	18.000	15.000	17.000	T	
	17.000	14.000	17.000	R	

Table 11a Continued
CHIONE UNDATELLA SHELL MEASUREMENTS
CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ribs per shell	V.M.	Ribs within major increments
	16.000	13.000	17.000	T	
	25.000	22.000	21.000	T	
	23.000	19.000	18.000	T	
	22.000	18.000	22.000	T	
	20.000	17.000	21.000	T	
	18.000	16.000	19.000	R	
	19.000	16.000	23.000	R	
	15.000	14.000	17.000	T	
	16.000	13.000	20.000	R	
	13.000	10.000	16.000	T	
	12.000	11.000	16.000	R	
	11.000	9.000	13.000	T	
	13.000	12.000	15.000	T	
	13.000	11.000	17.000	T	
	12.000	10.000	17.000	T	
	11.000	10.000	14.000	R	
	12.000	10.000	16.000	T	
	11.000	9.000	15.000	R	
	11.000	9.000	11.000	T	
	11.000	9.000	14.000	R	
	9.000	8.000	16.000	T	
	35.000	30.000	27.000	R	
	16.000	12.000	15.000	T	
	16.000	12.000	17.000	T	
	13.000	11.000	12.000	T	
	15.000	12.000	16.000	R	
	13.000	11.000	14.000	T	
	13.000	11.000	18.000	R	
	12.000	10.000	16.000	T	
	9.000	7.000	15.000	T	
Day 26	20.000	17.000	21.000	R	17/4
(April	18.000	14.000	19.000	R	
	17.000	13.000	18.000	R	
27)	25.000	22.000	27.000	T	4/22/1
	13.000	11.000	17.000	T	12/5
N = 38	13.000	11.000	18.000	R	
	21.000	20.000	30.000	R	4/25/1
	20.000	19.000	19.000	R	
	22.000	20.000	19.000	R	17/2
	20.000	18.000	19.000	T	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ribs per shell	V.M.	Ribs within major increments
	18.000	15.000	20.000	R	
	22.000	18.000	23.000	T	23/
	22.000	19.000	21.000	R	14/3/4/
	18.000	16.000	21.000	R	18/3
	20.000	17.000	19.000	R	
	15.000	13.000	14.000	T	
	15.000	13.000	18.000	T	
	15.000	13.000	15.000	T	
	16.000	14.000	17.000	T	14/3
	16.000	13.000	17.000	R	
	17.000	15.000	18.000	R	
	15.000	13.000	15.000	T	11/4
	16.000	14.000	14.000	T	
	14.000	12.000	16.000	T	
	12.000	10.000	13.000	T	
	12.000	11.000	14.000	T	
	12.000	10.000	16.000	T	
	13.000	11.000	15.000	R	
	10.000	9.000	13.000	T	
	13.000	12.000	14.000	R	
	12.000	10.000	15.000	R	
	13.000	11.000	18.000	T	
	11.000	9.000	20.000	R	
	11.000	9.000	18.000	T	
	12.000	10.000	16.000	T	
	10.000	8.000	13.000	T	
	16.000	14.000	22.000	T	
	18.000	15.000	19.000	T	18/1
Day 27	34.000	30.000	33.000	T	
(April 28)	23.000	20.000	23.000	T	
	24.000	20.000	22.000	R	
	22.000	19.000	20.000	R	
N = 35	21.000	18.000	19.000	T	
	22.000	19.000	22.000	T	
	22.000	18.000	17.000	T	
	21.000	18.000	18.000	T	
	21.000	18.000	20.000	T	
	20.000	17.000	16.000	T	
	21.000	18.000	19.000	T	
	17.000	15.000	14.000	T	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ribs per shell	V.M.	Ribs within major increments
	29.000	26.000	22.000	R	
	25.000	20.000	20.000	R	
	24.000	20.000	24.000	T	
	22.000	19.000	21.000	R	
	20.000	18.000	21.000	R	
	19.000	16.000	21.000	R	
	21.000	18.000	15.000	R	
	18.000	15.000	21.000	T	
	19.000	15.000	20.000	R	
	20.000	18.000	20.000	T	
	18.000	15.000	14.000	T	
	19.000	16.000	21.000	R	
	19.000	16.000	15.000	R	
	19.000	16.000	19.000	T	
	18.000	15.000	17.000	R	
	23.000	20.000	23.000	R	
	18.000	16.000	21.000	R	
	19.000	16.000	20.000	T	
	17.000	14.000	14.000	T	
	18.000	15.000	20.000	T	
	17.000	14.000	17.000	T	
	17.000	15.000	21.000	R	
	14.000	12.000	15.000	R	
Day 28	27.000	22.000	24.000	T	
	25.000	20.000	23.000	R	
(April 29)					
	23.000	20.000	18.000	R	
	21.000	17.000	16.000	R	
	20.000	17.000	17.000	T	
N = 20	19.000	16.000	19.000	R	
	19.000	17.000	18.000	T	
	18.000	14.000	18.000	T	
	18.000	15.000	15.000	T	
	19.000	16.000	19.000	T	
	18.000	15.000	17.000	R	
	19.000	16.000	16.000	R	
	16.000	14.000	18.000	R	
	19.000	16.000	18.000	R	
	13.000	11.000	17.000	R	
	16.000	13.000	16.000	T	
	13.000	11.000	13.000	T	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ribs per shell	V.M.	Ribs within major increments
	12.000	10.000	16.000	T	
	10.000	9.000	13.000	R	
	9.000	7.000	13.000	T	
	27.000	23.000	19.000	R	
Day 29	23.000	20.000	23.000	T	
(April 30)	19.000	16.000	19.000	T	
	19.000	15.000	19.000	T	
	18.000	15.000	17.000	T	
	14.000	12.000	14.000	T	
N = 20	22.000	18.000	22.000	R	
	23.000	20.000	21.000	R	
	20.000	17.000	23.000	T	
	21.000	18.000	20.000	T	
	21.000	17.000	21.000	R	
	21.000	19.000	16.000	T	
	20.000	16.000	15.000	R	
	19.000	15.000	21.000	T	
	21.000	17.000	19.000	T	
	19.000	17.000	16.000	T	
	18.000	15.000	17.000	T	
	17.000	13.000	17.000	T	
	17.000	13.000	19.000	T	
	16.000	14.000	20.000	R	
Day 31	13.000	10.000	17.000	T	
(May 2)	10.000	7.000	17.000	T	
	11.000	8.000	15.000	R	
N = 20	20.000	17.000	20.000	T	
	20.000	16.000	17.000	R	
	16.000	12.000	14.000	R	
	19.000	15.000	19.000	R	
	20.000	18.000	23.000	T	
	9.000	7.000	16.000	T	
	12.000	11.000	22.000	T	
	12.000	10.000	18.000	R	
	13.000	11.000	17.000	R	
	13.0	11.0	17.0	R	
	12.000	10.000	16.000	T	
	16.000	14.000	18.000	T	
	27.000	24.000	25.000	R	
	13.000	11.000	13.000	T	
	14.000	12.000	17.000	T	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
	14.000	12.000	21.000	T	
	16.000	13.000	18.000	R	
	25.000	22.000	24.000	T	
Day 33	22.000	18.000	24.000	T	22/2
(May 4)	22.000	20.000	28.000	T	
	12.000	11.000	15.000	T	
N = 10	10.000	9.000	17.000	T	
	13.000	11.000	15.000	T	
	8.000	6.000	11.000	R	
	10.000	9.000	12.000	T	
	15.000	12.000	20.000	R	20/
	13.000	10.000	18.000	T	
Day 34	26.000	22.000	20.000	T	
(May 5)	12.000	11.000	15.000	T	
	20.000	16.000	14.000	T	
N = 21	21.000	17.000	18.000	T	
	20.000	17.000	14.000	T	
	22.000	17.000	21.000	T	
	21.000	18.000	17.000	T	14/3
	22.000	18.000	18.000	T	
	24.000	20.000	22.000	T	
	25.000	20.000	23.000	R	
	30.000	26.000	32.000	R	
	32.000	28.000	33.000	T	
	21.000	17.000	20.000	T	
	22.000	18.000	18.000	R	
	12.000	10.000	17.000	T	16/1
	13.000	10.000	15.000	T	14/1
	13.000	10.000	14.000	T	
	15.000	12.000	14.000	T	
	21.000	18.000	25.000	R	
	16.000	14.000	20.000	T	
	22.000	19.000	22.000	T	
Day 35	21.000	18.000	19.000	T	
(May 6)	17.000	13.000	18.000	T	
	14.000	12.000	12.000	R	
	19.000	17.000	20.000	T	
N = 22	20.000	17.000	20.000	T	
	19.000	16.000	20.000	R	
	16.000	12.000	16.000	T	

Table 11a Continued
CHIONE UNDATELLA SHELL MEASUREMENTS
CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
	13.000	12.000	17.000	T	
	20.000	16.000	18.000	T	
	20.000	18.000	16.000	R	
	18.000	16.000	20.000	R	19/1
	14.000	12.000	15.000	T	
	16.000	13.000	18.000	T	
	18.000	16.000	17.000	T	
	18.000	14.000	23.000	R	
	16.000	13.000	21.000	T	
	15.000	12.000	15.000	T	
	25.000	20.000	29.000	R	
	26.000	20.000	29.000	T	
	28.000	24.000	25.000	T	23/2
	17.000	14.000	18.000	T	
	21.000	19.000	19.000	R	
Day 36	20.000	15.000	18.000	T	
(May 7)	15.000	12.000	19.000	T	
	14.000	11.000	15.000	R	
	12.000	10.000	18.000	T	
N = 26	11.000	9.000	14.000	T	
	19.000	16.000	18.000	T	
	15.000	17.000	13.000	T	
	14.000	10.000	18.000	T	
	11.000	10.000	18.000	T	
	20.000	17.000	16.000	T	14/2
	18.000	15.000	20.000	T	
	17.000	12.000	15.000	T	
	12.000	10.000	18.000	T	
	22.000	19.000	21.000	T	
	19.000	16.000	19.000	T	
	18.000	14.000	20.000	R	
	16.000	13.000	20.000	R	
	22.000	18.000	24.000	T	
	23.000	19.000	23.000	T	
	19.000	17.000	19.000	T	
	18.000	14.000	17.000	T	
	17.000	13.000	23.000	T	
	24.000	20.000	23.000	T	
	21.000	17.000	18.000	R	
	20.000	18.000	21.000	R	

Table 11a Continued

CHIONE UNDATELLA SHELL MEASUREMENTS

CHOLLA BAY, SONORA, MEXICO, APRIL 2 - MAY 8, 1967

Sample	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges in major increments
	19.000	15.000	15.000	R	
Day 37	26.000	22.000	21.000	T	
	23.000	19.000	24.000	T	
(May 8)	18.000	16.000	19.000	T	
	16.000	13.000	21.000	T	
N = 11	14.000	12.000	16.000	T	
	18.000	15.000	20.000	R	
	15.000	12.000	16.000	R	
	13.000	11.000	19.000	T	
	13.000	11.000	18.000	T	
	11.000	9.000	18.000	R	
	12.000	10.000	15.000	T	

Table 11b. *Chione undatella* Shell Measurements

Cholla Bay, Sonora, Mexico, August 23, 1967

Specimen	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges within major increments
1	28	23	27	R	20/7
2	27	23	20	R	
3	27	24	16	T	12/4
4	31	25	23	R	
5	29	26	29	R	24/5
6	27	22	24	R	17/7
7	28	24	28	T	23/5
8	26	23	28	R	
9	29	25	22	T	17/5
10	31	26	24	R	18/6
11	26	23	21	T	15/6
12	25	24	27	T	22/5
13	26	22	26	R	25/1
14	23	20	21	T	
15	24	20	23	T	
16	28	24	27	R	21/6
17	28	27	26	R	21/5
18	29	25	27	R	
19	25	21	26	R	
20	25	21	23	R	
21	26	22	21	T	
22	27	22	26	T	21/5
23	23	18	23	T	
24	31	25	23	T	18/5
25	26	22	26	R	20/6
26	26	22	23	R	12/9
27	25	21	21	R	
28	22	19	22	T	
29	19	17	18	T	15/3
30	24	20	23	T	

Table 11c. *Chione undatella* Shell Measurements

Cholla Bay, Sonora, Mexico, August 24, 1967

Specimen	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges within major increments
1	25	21	22	T	14/8
2	25	22	23	T	
3	29	25	26	R	19/7
4	30	24	28	R	22/6
5	27	24	26	T	18/8
6	28	22	22	T	16/6
7	24	21	24	T	20/4
8	29	24	25	T	20/5
9	25	21	23	T	19/4
10	23	21	24	R	
11	24	20	25	R	20/5
12	22	19	23	T	18/5
13	27	24	26	T	16/10
14	27	22	20	T	15/5
15	23	20	23	R	18/5
16	21	19	21	R	16/5
17	20	17	22	R	17/5
18	26	22	27	R	21/6
19	24	19	21	R	
20	28	23	26	T	18/8
21	22	18	21	T	
22	21	19	24	R	
23	32	22	24	R	19/5
24	23	20	20	T	
25	25	22	21	T	
26	23	20	22	T	
27	22	19	22	R	17/5
28	31	28	23	R	19/4
29	30	25	24	R	20/4
30	30	26	23	R	18/5
31	28	24	22	T	17/5
32	26	23	22	T	18/4
33	27	24	25	T	
34	25	21	21	T	16/5
35	25	21	24	R	18/6
36	22	19	20	R	
37	31	27	24	R	19/5
38	25	20	20	T	
39	22	18	18	T	
40	17	15	23	R	

Table 11d. *Chione undatella* Shell Measurements

Cholla Bay, Sonora, Mexico, November 11, 1967

Specimen	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges within major increments
1	31	27	27	T	15/12/
2	34	29	26	R	14/12/
3	32	28	26	R	14/12/
4	30	22	24	R	12/12/
5	28	21	20	T	
6	33	27	30	R	18/12
7	34	31	29	R	18/11/
8	30	25	25	R	25/
9	30	24	30	T	30/
10	30	26	28	T	28/
11	31	27	33	R	33/
12	22	19	20	R	16/4/
13	25	23	24	R	12/12/
14	24	20	19	T	
15	24	20	16	R	
16	32	22	40	R	27/13/
17	29	23	28	R	18/10/
18	25	21	21	T	
19	22	18	16	R	
20	21	18	16	R	
21	26	23	22	R	
22	26	22	27	T	17/10/
23	26	22	28	R	
24	20	17	17	T	
25	21	18	18	R	14/4/
26	21	20	19	R	
27	22	19	19	T	
28	16	11	13	R	
29	17	14	17	T	
30	16	14	16	R	

Table 11e. *Chione undatella* Shell Measurements

Cholla Bay, Sonora, Mexico, January 21, 1968

Specimen	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges within major increments
1	38	32	27	T	27/
2	30	27	28	T	28/
3	30	27	25	R	20/5
4	31	27	23	T	23/
5	30	25	23	R	23/
6	31	27	23	T	23/
7	29	26	28	R	28/
8	25	21	20	R	20/
9	24	22	20	T	20/
10	22	20	23	R	
11	22	19	22	T	17/5/
12	20	18	18	T	
13	23	19	19	R	
14	18	16	14	R	
15	18	16	18	T	
16	17	14	15	T	
17	15	13	13	T	
18	13	11	16	T	
19	12	11	19	T	13/6/
20	17	13	19	T	
21	15	12	16	T	
22	16	13	17	T	
23	13	10	14	T	
24	10	9	15	T	
25	8	7	13	T	
26	39	28	29	R	18/11/
27	34	30	30	R	30/
28	35	31	33	R	33/

Winter sample (January 21, 1968) — Fourteen of the twenty-eight specimens have one or more complete major increments. Each of these fourteen specimens has a groove on its ventral margin. The non-groove specimens bear an average of 16.4 concentric ridges per shell and average 16.0 mm in length.

Spring sample (April 2-May 8, 1967) — Twelve of the thirty-four daily samples disappeared before the author became sufficiently familiar with the morphology of the major increments to carry out a systematic study of marginal grooves. Preliminary observations on the specimens are not counted. The twenty-two remaining samples that are counted include 521 specimens. Of these, sixty-five specimens have one or more major increments. Sixteen of the specimens have grooved margins. On the 49 specimens with non-groove margins, the final groove is commonly followed by one to three concentric ridges. Specimens without grooves commonly have seventeen or eighteen concentric ridges per shell and average close to 18 mm in length.

Summer sample (August 23-24, 1967) — None of the seventy specimens show any signs of groove formation on their ventral margins. Most of these specimens are large (mean length: 25.8 mm) and have more than twenty concentric ridges (mean: 22.9 ridges per shell). Forty-four of them bear one moderately deep groove commonly followed by four to six (mean: 22.9 ridges per shell). Forty-four of them bear one moderately deep groove commonly followed by four to six (mean: 5.47) concentric ridges.

Fall sample (November 17, 1967) — Twelve of the thirty specimens have two growth bands, and on eleven of these specimens the second-formed growth band is followed by a grooved ventral margin. There are commonly ten to thirteen (mean: 10.3) concentric ridges within the second-formed growth bands of these specimens. Four of the thirty specimens feature one growth band followed by a grooved margin. Fourteen of the thirty specimens do not show any grooves; these specimens have an average of 18.5 concentric ridges and average 21.9 mm in length.

From the above observations, it appears that groove formation is most common in mid-winter and less common during the spring and fall. No evidence of groove formation was found in the summer sample. It is also apparent that the number of concentric ridges occurring within the growth band that follows the most recently formed groove increases from

April to November. Thus, additions of ridges to the shell occur during a growing season comprised of the spring, summer, and fall. Since the groove deposits are usually less than 1/100 as thick as the growth bands, the rate of shell growth must be considered as minimal during groove formation, and maximal in the spring to fall season when the growth bands are formed. The hypothesis of an annual cycle of shell growth is in accord with this evidence. It seems evident that this cycle has two phases that are expressed in the morphology of major increments:

1. Active, or rapid growth phase. Represented by growth bands that are predominately semiopaque and uniformly curved. Commonly, the first-formed growth band may be subdivided into three parts interpreted as forming in three different seasons:

    a. Spring or early summer. Umbonal sequence of moderately thick growth laminae and moderately spaced concentric ridges

    b. Summer. Center of growth band featuring widely spaced concentric ridges and thick-growth laminae.

    c. Fall or early winter. Thin growth laminae and closely concentric ridges occurring near the first-formed groove.

Cyclic variation in the thicknesses of the subannual increments (growth laminae and ridge-trough units) are weakly or not at all evident in the later-formed growth bands. These later-formed growth bands become successively thinner. Since the thicknesses of their subannual component increments are comparable to those located in the center of the first-formed growth band, the later-formed growth bands are interpreted as representing only portions of the rapid growth phase. Accordingly, the observed decrease in the number of ridges per each successive growth band is interpreted as resulting from a progressive shortening of the active growth season during old age.

2. Inactive, or slow-growth phase. Represented by nacreous groove deposits composed of extremely thin growth laminae. Depression

of this slow-growth layer into the palliostracum beneath the external shell surface indicates that the free edge of the mantle is somehow reduced in size during the season of inactivity. Lack of related variation in the myostracum suggests that a similar constriction does not occur in the main portion of the outer fold of the mantle. Occasional traces of the slow-growth layer in the endostracum probably result from a change in the rate of secretion.

Annual Growth in a Warmer Environment

Provided the annual growth cycle of *Chione undatella* is controlled by water temperature, individuals living in a warmer environment would tend to have seasons of active shell growth that are either longer or shorter, depending on the temperature optimum in this species. Considering the concentric ridges to represent fortnightly cycles of shell growth, any changes in the length of the growth season would be expressed in the numbers of concentric ridges occurring within the annual growth bands. It is also anticipated that the inactivity season of a population living in a warmer environment occurs during a different part of the year than in Cholla Bay. In consequence of this the concentric groove representing the inactivity season would be formed in a season different from that of the Cholla Bay population. To test for these postulated temperature effects, the author examined the major increments occurring on thirty out of thirty-three specimens from Coyote Cove, Concepcion Bay, Baja California. These specimens were collected in early February 1961 and were deposited in the Recent mollusk collection of the U.C. Museum of Paleontology. Each specimen consists of two matching valves and is assumed to have been alive when taken in Coyote Cove. Observations of major increments, concentric ridges, and shell lengths and heights of the specimens are listed in Table 12. The data are summarized for interpretation below of their significances regarding the postulated effects of temperature.

Twenty-two of the specimens have a single concentric groove that is followed by zero to nine (average: 3.5) ridges. Eight other specimens have two concentric grooves, the second-formed groove being followed by zero to four (average: 2.4) ridges. Assuming that the concentric ridges are formed with a 15-day periodicity, it is calculated that most of the

Table 12. *Chione undatella* Shell Measurements

Coyote Cove, Concepcion Bay, Baja California

Collected by N. Schlosser, 1961 (UCMP B-7844)

Specimen	Length (mm)	Height (mm)	Ridges per shell	V.M.	Ridges within major increments
1	38	33	39	R	34/5
2	38	33	34	R	31/3
3	36	34	36	T	36/
4	43	40	41	R	31/10/
5	36	32	35	T	25/7/3
6	39	37	40	T	38/2
7	41	38	40	R	37/3
8	43	40	44	R	41/3
9	37	32	31	T	25/6
10	38	35	32	R	17/14/1
11	38	32	30	T	26/4
12	39	38	37	T	
13	39	37	35	T	27/5/3
14	35	32	32	T	27/5
15	37	35	34	T	8/24/2
16	36	32	32	T	27/5
17	39	35	38	T	18/16/4
18	33	30	31	R	30/1
19	39	34	38	R	15/20/3
20	34	31	31	T	31/
21	35	32	26	R	21/5
22	32	28	25	T	
23	35	31	37	T	33/4
24	40	37	50	R	47/3
25	35	33	36	T	27/9
26	35	32	27	T	24/3
27	35	32	35	R	29/3/3
28	36	31	33	R	28/5
29	32	28	36	T	34/2
30	35	30	33	R	30/3
31	33	30	30	T	27/3
32	33	28	20	T	17/3
33	32	31	26	R	

twenty-two one-groove specimens had completed forming their grooves and were in a season of active shell growth during the middle of December 1960. It is likewise calculated that most of the two-groove specimens had entered their third growing season in early January 1961.

Among all of the specimens that have one or two grooves, the number of concentric ridges per first-formed growth band varies from eight to forty-seven. There are three to twenty-four ridges in the second-formed growth bands of the specimens with two grooves. Allowing 15 days for each ridge-formation cycle, these data are interpreted to indicate that the length of the growing season varies extremely with the individual clam. Consequently, it is not possible to determine the time at which groove formation was most commonly initiated prior to February 1961. Nevertheless, the second inactivity season in the life history of an individual seems to have been longer than the first one, for on the average there are twenty-eight ridges in the first-formed growth band and 12.4 ridges in the second-formed growth band.

In the preceding summary of the data, the time at which active growth is resumed after a winter hiatus was calculated as occurring about 3 months earlier in Concepcion Bay than in Cholla Bay. This difference is related to the apparently warmer winter of Concepcion Bay. Seawater temperatures taken at a depth of 10 m in both of these areas (Roden, 1958) are practically the same in the months of April, June, and August, whereas the February data indicate that seawater in the mouth of Concepcion Bay is 8.5°F warmer than seawater near the mouth of Cholla Bay. Although comparable measurements of temperature in the two areas are not available for the other months of the year, it seems probable that the flood tide waters of Cholla Bay are considerably colder throughout most or all of the winter than those of Concepcion Bay. The longer inactivity season of the Cholla Bay population is thus related to a colder winter. It has been mentioned that increased plankton productivity due to upwelling of nutrients may occur on the Baja California coast during the winter and on the Sonoran coast during the summer. Annual growth seems to be independent of these variations in the food supply. The available data suggest that the annual growth cycle of *C. undatella* is controlled by temperature as it is in many other pelecypod species inhabiting temperate marine environments.

Serial Study

Experimental growth of marked specimens of *C undatella* showed that the rate of ridge formation is on the order of one per 25 days or less. Based on the number of growth laminae occurring within the ridge-trough increments, it was hypothesised that the ridges are formed with a 14-15 day periodicity. Is there a relationship between ridge formation and a certain phase of the fortnightly tidal cycle? To obtain data bearing on this problem, a series of daily samples of *C. undatella* was collected from April 2 to May 8, 1967. A total of 808 specimens were obtained from the coarse shelly sands of a 300-by 3-ft area located on the south bank of the main drainage channel. The west end of this strip is 30 feet from the sandstone outcrop shown in Fig. 2. Throughout this area the substrates are similar to those of sediment sample A (Table 10). The entire sampling area was exposed at low tide and flooded at high tide at least once a day during all but 3 days of the sampling period. On these 3 days (April 25, May 1, and May 3) the low tide of the daylight hours was insufficient to uncover the area. Once tidal flow had commenced, the lag time in flooding of the east and west ends of the area was only 10 to 20 minutes.

Samples were also taken outside of the above sample area, so that shell morphology could be compared with differences in the sediments. On May 5, 6, and 7, samples were collected along three traverses oriented perpendicular to the drainage channel. Specimens were obtained from circular areas 1 foot in diameter spaced at intervals of 15 feet along these traverses. On May 4, 5, and 8, specimens were collected at random in the center of the main drainage channel. No samples were collected on either April 25 or May 1 and 3.

Each specimen was examined with respect to fullness and color of visceral mass within a few hours after collection. Epsom salts were used to relax many of these animals so that the soft parts could be observed without damaging the shell. The shells of these specimens were cleaned in soapy water, rinsed, dried, and packed in tissue for more detailed study in the laboratory. Some specimens were examined without the use of Epsom salts. For these observations, it was necessary to pry the valves apart. These specimens were preserved *en toto* in ethyl and isopropyl alcohols.

Morphological Features Studied

The 808 specimens were systematically examined in the laboratory at Bodega Head. Shell lengths and heights were measured with a ruler to the nearest millimeter. Using a X20 microscope, concentric ridges were counted, and the character of the margins were noted with respect to the ridge-trough cycle. From these measurements, apparent growth rates and shape indices were derived. Together with tidal data obtained from the U.S.C.G.S. table for Guaymas, Mexico (U.S.C.G.S., 1967) and the dates of sample collection, the specific variables in this study are:

1. Length. Measured along the antero-posterior axis.
2. Height. Measured parallel to midline (perpendicular to length) from umbone to ventral margin.
3. Number of concentric ridges per shell. Counting begins with the first sharply defined concentric ridge, which seems to correspond to the first "secondary ridge" of the dissoconch in Carriker's terminology (Carriker, 1961).
4. Low tide. Lowest tide of a given day.
5. Tidal range. Algebraic difference between the lowest low tide and the highest high tide of a given day.
6. %T. Percentage of specimens in a sample with concentric troughs or interspaces (as opposed to ridges) on their ventral margins.
7. Day number. Days in the period of the experiment (April 2-May 8) were numbered consecutively from one to thirty-six.
8. Length/height ratio. Computed as variable (1) divided by variable (2), this ratio is considered to be proportional to the elongateness of the shell.
9. Length/number of concentric ridges ratio. Computed as variable (1) divided by variable (3), this ratio tends to measure the average increase in shell length per unit time. It is thus distinct from the average linear rate of shell growth that is obtained by dividing the arc length of the partly coiled shell by the time required for its growth.

10. Height/number of concentric ridges ratio. Computed as variable (2) divided by variable (3), this ratio approximates the average increase of height per unit time, where height is again distinct from the distance between ventral margin and umbone measured in a coiled line along the shell surface.

Statistical computations

Computations were made with the University's DCS 7094 computer using a series of programs in the STATPAK library. The statistics computed are listed below under subheadings.

Arithmetic mean —

$$\bar{x} = (1/N)\ (\Sigma x).$$

Standard deviation (maximum likelihood estimate) —

$$S_x = (1/N)\ \Sigma(x_i - \bar{x})^2.$$

The means and standard deviations computed for the total sample of N = 808 shells are listed in Table 13. Daily means and standard deviations are shown in Table 14.

Kolmogorov-Smirnov "D" statistic —

$$D = \text{maximum } |F_o(x) - S_n(x)|.$$

$F_o(x)$ is the theoretical cumulative normal distribution that has the same mean and variance as the sample frequency distribution $S_n(x)$. Similar to the well-known chi-square test, the "D" statistic is used to test for the "goodness of fit" of the sample frequency distribution to a normal one. The sample frequency distribution differs from normal at the 0.05 level if D exceeds 0.0479 for N = 808, or 0.233 for N = 34. According to Siegel (1956), this test is always more powerful than the chi-square, because individual samples are emphasized and a smaller amount of information is lost through the combining of categories.

In conjunction with the above test, the computer was used to plot histograms showing both the sample and the theoretical frequency distribution [i.e., $S_n(x)$ and $F_o(x)$]. Most of the sample frequency distributions

Table 13. Statistics of Individual Shell Measurements

(*Chione undatella*, Cholla Bay, April 2-May 8, 1967, N = 808)

Variable	Arithmetic mean	Standard deviation
1	17.5366	5.2681
2	14.6419	4.5585
3	18.4250	4.2384
4	−.2703	.4128
5	2.8825	.6360
6	66.7844	11.3495
7	18.5167	9.7317
8	1.2016	.0775
9	.9528	.2007
10	.7945	.1713
11	1.7297	.4128
12	2.8194	.3036
13	2.6369	.3089
14	2.8899	.2148
15	1.0331	.2295
16	4.1871	.1695
17	2.7137	.7357
18	.1816	.0634
19	−.0705	.2125
20	−.2530	.2157
21	.5189	.2438

Table 14. Daily means of shell measurements(*Chione undatella*, Cholla Bay, April 2 through May 8, 1967)

	1	2	3	4	5	6	7	8
1.	22.670	18.830	22.330	-.500	3.100	100.000	1.000	1.212
2.	17.260	14.470	15.680	-.500	3.000	47.000	2.000	1.201
3.	21.390	17.720	20.500	-.400	2.700	83.000	3.000	1.203
4.	17.070	14.790	19.520	-.300	2.000	83.000	4.000	1.164
5.	19.770	16.500	20.950	-.100	2.300	71.000	5.000	1.205
6.	15.290	12.470	16.470	.100	2.100	75.000	6.000	1.235
7.	17.610	14.910	16.700	.400	1.800	57.000	7.000	1.188
8.	17.690	14.860	17.210	.100	2.100	66.000	8.000	1.195
9.	18.060	15.280	18.220	-.100	2.400	56.000	9.000	1.186
10.	14.570	12.000	16.140	-.300	2.700	71.000	10.000	1.215
11.	14.360	12.450	16.140	-.400	2.900	59.000	11.000	1.158
12.	18.600	14.840	18.160	-.400	3.100	64.000	12.000	1.265
13.	15.910	13.030	17.220	-.400	3.100	68.000	13.000	1.221
14.	20.580	16.460	19.880	-.300	3.100	58.000	14.000	1.264
15.	17.670	14.420	18.180	-.300	3.000	58.000	15.000	1.228
16.	16.690	13.830	18.240	-.400	3.100	76.000	16.000	1.210
17.	18.230	15.490	19.300	-.500	3.200	57.000	17.000	1.181
18.	17.500	14.210	18.830	-.500	3.100	68.000	18.000	1.238
19.	15.500	13.050	19.200	-.300	2.900	75.000	19.000	1.190
20.	14.630	12.530	18.750	0.000	2.800	91.000	20.000	1.172
21.	16.440	13.610	17.830	.300	2.300	78.000	21.000	1.212
22.	17.500	14.310	17.880	-.300	2.900	69.000	22.000	1.223
23.	18.130	15.170	19.170	-.700	3.400	71.000	23.000	1.196
24.	17.180	14.360	17.840	-1.000	4.000	52.000	25.000	1.199
25.	15.870	13.660	17.920	-.900	4.000	55.000	26.000	1.168
26.	20.600	17.570	19.570	-.700	3.800	54.000	27.000	1.175
27.	17.700	14.800	17.200	-.400	3.400	50.000	28.000	1.196
28.	19.750	16.500	18.900	-.100	3.000	70.000	29.000	1.201
29.	20.480	17.050	19.620	.200	2.400	81.000	31.000	1.207
30.	15.000	12.800	18.400	.600	1.800	80.000	33.000	1.184
31.	14.950	12.450	18.050	.800	1.700	55.000	34.000	1.215
32.	18.680	15.640	19.320	.400	2.100	68.000	35.000	1.198
33.	17.540	14.500	18.680	.100	2.500	77.000	36.000	1.218
34.	16.270	13.640	18.820	-.200	2.900	73.000	37.000	1.196
X	17.563	14.653	18.432	-.2059	2.7794	68.412	18.147	1.204
S	2.037	1.651	1.395	.3985	.5875	11.922	10.680	.024

of individual shell measurements (N = 808) differ significantly from normal at the 0.05 level.

There are two exceptions: length and height (Figs. 3 and 4). The same results were obtained for plots of the means of the daily samples (N = 34). When logarithms of the daily means were tested, it was found that the distributions of all variables except day number are not significantly different from normal. The following variables were derived in this transformation:

12. Log (daily mean of length)
13. Log (daily mean of height)
14. Log (daily mean of number of ridges per shell)
15. Log (daily mean of tidal range)
16. Log (%T)
17. Log (day number)
18. Log (daily mean of length/height)
19. Log (daily mean of length/number of ridges per shell)
20. Log (daily mean of height/number of ridges per shell)
21. Log (low tide + 2), where 2 is added to each datum to avoid negative numbers.

Covariance —

$$C_{xy} = (1/N)\ \Sigma(x_i - \bar{x})\ (y_i - \bar{y}).$$

Pearson product moment correlation coefficient —

$$r_{xy} = C_{xy}/S_x S_y.$$

Sample correlation coefficients for the daily means of the twenty-one variables are shown in Table 15. Pearson's standard table (Crow et al., 1960) was referred to in testing for the significance of r. The null hypothesis of this test is that r does not differ from zero at the 0.05 level of significance. Before this null hypothesis can be rejected, the sample correlation coefficient must exceed 0.073 for N = 808, or 0.338 for N = 34. The test is valid only if the frequency distributions of x and y can be considered as normal at the 0.05 level.

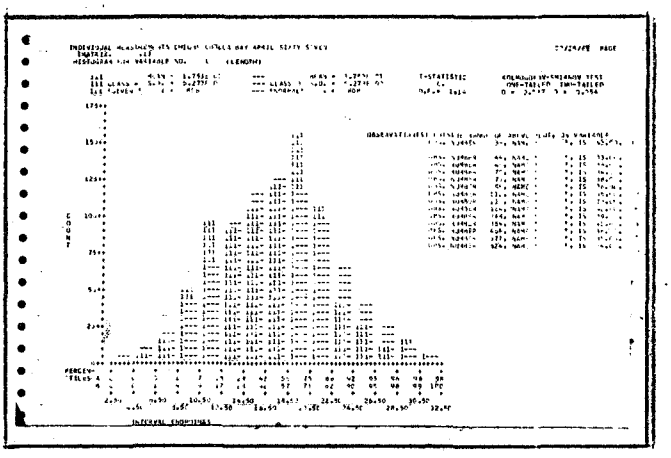


Fig. 3. Computer Output: Histogram of shell length.

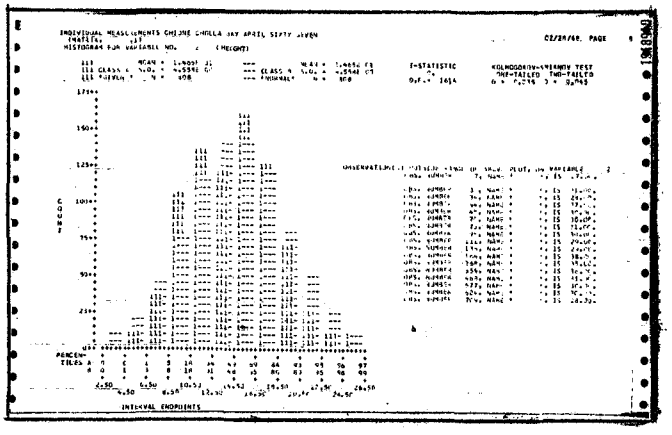


Fig. 4. Computer Output: Histogram of shell height.

Table 15. Sample correlation coefficients

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	1.000	.986	.702	-.205	.198	.135	-.167	.236	.734	.705	-.205	.998	.984
2	.986	1.000	.715	-.210	.190	.139	-.156	.073	.704	.715	-.210	.982	.998
3	.702	.715	1.000	-.081	.068	.536	.043	.037	.034	.025	-.081	.684	.701
4	-.205	-.210	-.081	1.000	-.904	.209	.248	.062	-.208	-.216	1.000	-.210	-.216
5	.198	.190	.068	-.904	1.000	-.310	.087	.009	.205	.196	-.904	.203	.196
6	.135	.139	.536	.209	-.310	1.000	-.093	-.015	-.330	-.347	.209	.103	.108
7	-.167	-.156	.043	.248	.087	-.093	1.000	-.089	-.279	-.269	.248	-.155	-.144
8	.236	.073	.037	.062	.009	-.015	-.089	1.000	.286	.056	.062	.244	.076
9	.734	.704	.034	-.208	.205	-.330	-.279	.286	1.000	.972	-.208	.750	.718
10	.705	.715	.025	-.216	.196	-.347	-.269	.056	.972	1.000	-.216	.720	.728
11	-.205	-.210	-.081	1.000	-.904	.209	.248	.062	-.208	-.216	1.000	-.210	-.216
12	.998	.982	.684	-.210	.203	.103	-.155	.244	.750	.720	-.210	1.000	.985
13	.984	.998	.701	-.216	.196	.108	-.144	.076	.718	.728	-.216	.985	1.000
14	.689	.701	.998	-.073	.069	.528	.079	.037	.017	.007	-.073	.673	.689
15	.218	.203	.083	-.908	.992	-.258	.050	.047	.220	.200	-.908	.222	.208
16	.109	.108	.520	.231	-.331	.994	-.069	.007	-.351	-.376	.231	.081	.081
17	-.316	-.320	-.123	.184	.130	-.219	.912	-.040	-.334	-.342	.184	-.295	-.299
18	.237	.074	.037	.065	.007	-.013	-.086	1.000	.287	.057	.065	.245	.077
19	-.133	-.139	.047	.433	-.272	-.013	.614	.047	-.229	-.243	.433	-.127	-.136
20	.712	.718	.030	-.229	.205	-.346	-.272	.070	.975	.999	-.229	.727	.733
21	-.175	-.186	-.067	.988	-.916	.258	.181	.093	-.178	-.195	.988	-.180	-.192

	14	15	16	17	18	19	20	21
10	.007	.200	-.376	-.342	.057	-.243	.999	-.195
11	-.073	-.908	.231	.184	.065	.433	-.229	.988
12	.673	.222	.081	-.295	.245	-.127	.727	-.180
13	.689	.208	.081	-.299	.077	-.136	.733	-.192
14	1.000	.082	.515	-.078	.037	.060	.012	-.061
15	.082	1.000	-.277	.099	.045	-.284	.210	-.902
16	.515	-.277	1.000	-.169	.009	.004	-.372	.282
17	-.078	.099	-.169	1.000	-.039	.421	-.340	.131
18	.037	.045	.009	-.039	1.000	.051	.071	.097
19	.060	-.284	.004	.421	.051	1.000	-.243	.398
20	.012	.210	-.372	-.340	.071	-.243	1.000	-.208
21	-.061	-.902	.282	.131	.097	.398	-.208	1.000

Type I correlation — Variable (7) and the log of the daily mean of (7) are by definition rectangular in distribution. Where either of these variables is the y of an x,y regression, the slope of the regression line is tested for significance (Crow et al., 1960). The slope of x,y from the sample is

$$b = (S_y/S_x) \quad (r).$$

For the significance test, the "t" statistic is calculated from b, the standard error of estimate ($S_{y/x}$), and the standard error of b:

$$t = \frac{b - B}{S_b} \quad .$$

The null hypothesis holds that the slope of the regression line does not differ from zero at the 0.05 level of significance (i.e., the real slope, B, is zero). The null hypothesis is rejected if $|t|$ exceeds 1.96 for N >120, or 2.03 for N = 34.

Other statistical measures and tests have been applied where necessary. They are described below where appropriate.

%T vs. sample date

In order to establish any statistically significant variation in %T, it is desirable to use as many specimens as possible for each point plotted. Consequently, the samples have been grouped by threes and the resulting %T values taken as representative of the mid-points of their groups.

As shown in Fig. 5, there are three peaks in %T centered on April 6, April 21, and May 6, and two lows centered on April 12 and April 28. Two questions are posed with respect to the significance of the cyclic variation of %T shown in this graph. First, is variation in %T significantly non-random with respect to time? Second, are the differences between the peaks and lows of %T in this graph significant?

To answer the first question, the X^2 (chi-square) test for randomness (see Crow et al., 1960, and Molina, 1942) has been applied to the %T data. This test compares the sample distribution with a theoretical Poisson distribution that has the same arithmetic mean and standard deviation.

The mean and variance of the Poisson distribution are equal and are computed as the number of events *r* divided by the total number of time intervals or counts *N*. Here we are concerned with the average number of concentric ridges forming per sample day, and hence r is the total number of ridges found on the ventral margins of 808 specimens, and N is the number of sample days; i.e., 34. Thus, the mean is 31.59. All steps in computing χ^2 are given in Table 16. Theoretical relative frequencies listed in Column 3 of this table were obtained from a standard statistical reference (Molina, 1942). The sample classes have been so grouped that the e_i values of column 4 are 5 or greater than 5. If the computed χ^2 of 5.52 exceeds this limit, the null hypothesis is rejected. Thus, there is no statistical support of the hypothesis that occurrences are random with respect to time.

The second question is answered through comparisons of the 0.95 confidence limits shown in Fig. 5. The confidence limits of the first and second peaks overlap with the upper limit of the first low, indicating that there is a greater than 5% risk of error in accepting the cycle defined by these points. There are only forty-three specimens included in peak #1 and sixty-eight specimens in low #1. According to statistical tables (see Crow et al., 1960) at least 100 specimens would have to be included in these data before the confidence limits would be narrow enough not to overlap. The lack of significance is thus related to an inadequate number of specimens within these data. Low #2, which includes 129 specimens, has confidence limits that do not overlap those of the adjacent highs (#2 and #3). The apparent difference between this low and the adjacent highs is significant, and there is a less than 5% risk of statistical error in accepting the cycle defined in this part of the %T graph.

Despite the small number of specimens included within peak #1 and low #1, these points are at least compatible with the regular cycle of %T that is defined by statistically significant differences between the other highs and lows. It seems reasonable to consider all of the data in attempting to determine the periodicity of this cycle. The centers of the peaks appear to be spaced at intervals of 15 days. The same amount of time separates the apparent centers of the two lows. From the center of peak #1 to the center of peak #3 there are two complete

Table 16. Poisson test for randomness of ridges

X ridges per sample	n_i = actual number of occurrences of X		Theoretical relative frequency of χ in one day	e_i = theoretical number of χ in one day		$(n_i - e_i)^2/e_i$
0-5	1		0.	0.		
6-10	1		0.	0.		
11-15	0	16	.0009	.03	14.41	.176
16-20	4		.0190	.06		
21-25	4		.1221	4.15		
26-30	6		.2990	10.17		
31-35	6		.3637	12.37		3.296
36-40	1		.1745	5.93		
41-45	7	12	.0504	1.71	7.96	2.052
46-50	3		.0084	.29		
51-55	1		.0009	.03		
>56	0		0.	0.		

$$X^2 = \sum_{i=1}^{3} \frac{(n_i - e_i)^2}{e_i} = 5.524$$

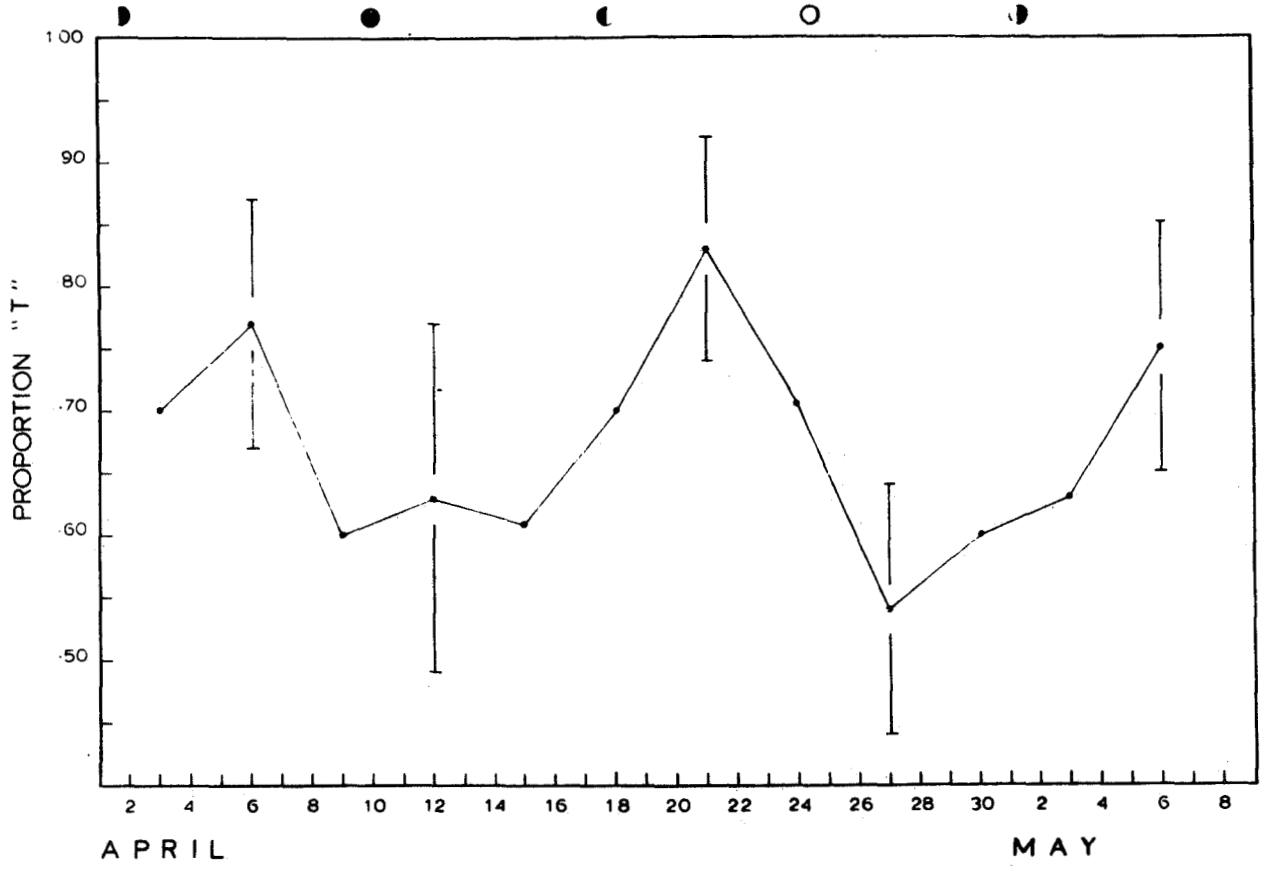


Fig. 5. Proportion of *Chione undatella* forming troughs compared with sample data.

cycles spanning a period of 30 days. No matter how the periodicity is read from this graph, it appears to be very close to 15 days.

Alternatives for interpretation of the %T cycle

Provided each individual forms a concentric ridge once each fortnight and this activity coincides with a new or full moon, the graph of %T would consist of a simple oscillation from highs approaching 100% to hear-zero lows. The observed variation of %T differs from such an idealized curve. Although its highs and lows are consistently related to certain parts of the fortnightly tidal cycle (see Fig. 6), the range of variation is rather small (55 to 85%) and somewhat irregular. A number of complicating factors may be postulated to explain these features of the %T curve. On the one hand, it could be hypothesized that the %T cycle may have resulted, for example, from operational biases related to observational error, tidal influences on sampling, or stratification of the sample population with respect to ridged margins. An alternative hypothesis is that the %T cycle does relfect a 15-day cycle upon which is superimposed the influences of wintering individual clams that are not actively secreting CaC03, genetic variants, and individuals at variance with the general trend because of environmental differences within the sampling area. Grouped under topic headings that follow below, these sources of variation are discussed in light of the data provided by this study.

Observational error

The writer believes it unlikely that the shape of the %T curve could in large degree result from a difficulty in distinguishing between concentric ridges and troughs. The sharply defined ridges of *C. undatella* are spaced at intervals of about 1 mm. Since the one-fifteenth part of a millimeter occupies a major portion of the field of view at a magnification of X60, the discrimination of a ridge from a trough should be easy. Only in a minority of the 808 specimens could there have been a problem in distinguishing between the end of a ridge and the beginning of a trough (or, vice versa). Furthermore it would be expected that these errors are of a random nature, tending to cancel out in the large sample. It seems clear that this source is inadequate to account for an observable amount of variation in the %T graph.

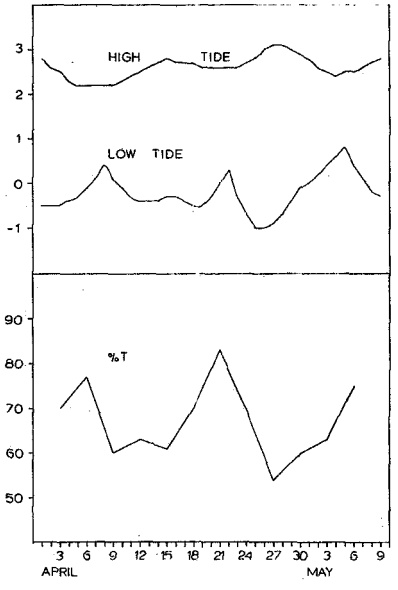


Fig. 6. Guaymas tidal curves compared with %T data of Cholla Bay, Mexico.

Seasonal hiatus and %T

From the morphology of the major increments considered to have been formed annually, it has been inferred that the older individuals of *C. undatella* undergo a longer winter hiatus than do the younger clams. If it is assumed that individuals enter a season of little or no shell growth in different weeks, then different increments would be present on the margins of inactive, wintering individuals. With regard to the number of growth laminae per ridge-trough unit, the trough most commonly includes a larger part (about four-fifths) of the ridge-trough unit. Therefore, if wintering begins at different times for different individuals of this species, most of the wintering individuals would be found with troughs on their ventral margins. From this condition, there would result a bias towards higher values of %T in a series of samples collected during the winter season. Such a bias could account for at least some of the difference between the observed oscillation of %T from highs of 85 to lows of 55 and the idealized 0 to 100 curve. The data of this study are analyzed below with respect to this possibility.

Long-term trend in %T — Provided the irregularity of the observed %T curve reflected the presence of wintering individuals in the daily samples, then this irregularity should have decreased in the later samples as more of the hypothesized wintering clams became active. There is only a faint suggestion of this trend in the %T graph. The correlation statistic b, for %T vs. day number, is negative, as would be expected, but its numerical value is too low for significance at the .05 level. Therefore, if any long-term trend is superimposed on the 15 day cycle of %T, it cannot be detected with a confidence of 0.95 as %T vs. day number in the April 2 to May 8, 1967 series.

However, some evidence of such a long-term trend may be drawn from observations on specimens collected at random in the main-drainage channel near the site of the April-May collection during other seasons of the year. As shown in Table 11 and in Fig. 5, the %T associated with full moon in June and November are much lower than the %T observed under full moon in April. %T associated with the post-full moon conditions in August seems to indicate a steeper rise than the one observed under the

post-full moon conditions of April. %T for January is close to the corresponding datum of April, which would be expected if there were as many individuals wintering in January as there were in April. The points for these summer, fall, and winter seasons are too few in number to permit a statistical test of significance. Nevertheless, the data are at least compatible with the prediction of a non-skewed %T cycle in the hypothesised growing season.

Correlation with specimens considered as older — Further evidence of such a cycle may be found in the log-log plots of the shell data for the spring of 1967 (Table 15). There is a significant correlation between %T and the number of concentric ridges per shell ($r = 0.515$). since the ridge-trough cycle has been demonstrated to have a 15-day periodicity, this correlation approximates a relationship between age and %T. This relationship tends to substantiate the hypothesis that some of the skewness of the %T vs. time graph resulted from the influence of older individuals that were still wintering in the April 2 to May 8 interval. There is also a significant correlation between %T and the mean length per number of ridges per shell ($r = -.350$). Length per number of ridges per shell has been defined as an approximation of the rate at which an individual adds to its shell along the antero-posterior axis during the growing season. If it is assumed that the more slowly growing individuals undergo a relatively long season of inactivity, this relationship provides another indication that %T was influenced by the presence of wintering specimens.

Shell formation in April and early May — The major increments provide an interpretative basis for determining the number of specimens engaged in the shell secretion process during the Spring of 1967. This determination depends primarily on the assignment of the ventral margin increments to either the slow-growth or rapid-growth phases of the annual growth cycle. However, the slow-growth deposits are so thin that their recognition on ventral margins cannot be considered as certain in all cases. In order to minimize the amount of error that results from occasional misidentifications of margin increments, a second criterion is obtained from the average sequence of ridges per annual band. The first-formed major band of a typical shell includes, on the average,

sixteen ridges. Band No. 2 tends to have half as many ridges and the later bands have fewer ridges. Putting these averages together into a statistical sequence, the data of the 420 specimens in the twenty-two daily samples that were studied for grooves yield an average of 16.9 ridges added to the shell in year I, 8.8 in year II, 4.5 in year III, and 4.0 in year IV. In many cases, the ridge-per-band sequence of an individual should resemble the preceding averaged sequence, because the averages for the different age groups are unimodal. Therefore, where the ventral margin lacks a groove deposit because there has been no growth at all, the probability of its proper assignment to the slow-growth phase may be increased in many cases by reference to the averaged sequence. For example, consider a shell that has one major groove located between band No. 1 and band No. 2. If the number of ridges included in band No. 2 is close to one-half the number of ridges in band No. 1, say 20/12, it seems likely that band No. 2 is practically complete. Conversely, if the number of ridges in band No. 2 is low, say 20/2, then it would seem probable that the specimen had just begun its growing season. Obviously, some difficulties are presented by specimens that have intermediate numbers of ridges in their marginal bands. Should a specimen with the sequence 16/6 be interpreted as being in the season of slow-growth? At the end of the growing season? Actually, this problem is rarely encountered in the April 2 to May 8 data. Of the fifty-seven specimens bearing one groove each, fifty-three of them have from zero to five ridges in band No. 2. Since the complete year II growth bands have an average of 8.8 ridges, the forty-one specimens with one groove followed by one to five ridges (Table 17) could have entered their second growing season when collected. Twelve specimens with one groove and four of the ten specimens bearing two or more grooves have distinct grooves on their ventral margins. These twenty-two specimens (Table 18) are assigned to the slow-growth season category. Four of the other six specimens with two or more grooves have from one to three ridges following the second-formed groove, and thus appear to have been in the active growth season. Two of the six have four and six ridges following the second-formed groove, thus appearing to have been inactive.

The preceding assignments of specimens are totaled to obtain an estimate of the number likely to have been forming shell at the time of collection. Of the sixty-six groove-bearing specimens, twenty-one of

Table 17, *Chione undatella* specimens with major increments considered to have been forming in Cholla Bay, April through May, 1967

Date	*Ridges within major increments*	*Number of ridges per shell*	Date	*Ridges within major increments*	*Number of ridges per shell*
	41 Specimens less than 1 year in age				
April			April		
4	18/2	20	24	21/1	22
8	14/2	16	27	17/4	21
	15/1	16		12/5	17
	13/4	17		17/2	19
	16/3	19		18/3	21
	20/2	22		14/3	17
13	14/3	17		11/4	15
14	15/3	18		18/1	19
	14/1	15	May 4	22/2	24
17	14/1	15	5	14/3	17
	16/2	18		16/1	17
	20/2	22		14/1	15
	11/5	16		19/1	20
18	16/1	17		23/2	25
	17/1	18	7	14/2	16
	13/3	16			
	17/1	18			
	15/1	16			
19	18/1	19			
	17/3	20			
	14/2	16			
20	13/3	16			
	14/3	17			
	16/3	19			
23	17/1	18			
	16/4	20			
	4 Specimens surviving 2nd winter				
April					
20	9/2/2	13			

Table 18. Specimens of *Chione undatella* with major increments considered to have been inactive in Cholla Bay, April through May, 1967

Date	Ridges within major increments	Ridges per shell	Date	Ridges within major increments	Ridges per shell
	8 Specimens less than 1 year in age				
April			April		
4	17/	17	17/	22/	22
5	18/	18	27	23/	23
	20/	20	May 4	20/	20
	17/	17			
	21/	21			
	4 Specimens between 1 and 2 years in age				
April					
5	29/	29			
17	26/	26			
18	28/	28			
	29/	29			
	4 Specimens 2 years in age				
April					
8	7/9	16			
	18/12	30			
18	11/9	20			
23	20/9	29			
	4 Specimens 3 years in age				
April					
5	25/7/4	36			
7	14/6/3	23			
	20/7/6	33			
27	14/3/4	21			
	1 Specimen 4 years in age				
April					
5	25/7/4/4	40			

them (equivalent to 32%) have been considered as being in the season of slow or zero growth. Assuming that the 354 non-groove specimens collected in the same period were in the season of rapid growth, the data available suggest that 5.2% of the specimens in the total sample were wintering.

Percentage forming shell based on study of specimens collected in August, 1967 — Forty-five of the seventy specimens feature one groove followed by a number of concentric ridges (Tables 11b-c). These grooves have been interpreted as resulting from a season of slow or zero shell growth in the winter of 1967. The ridges occurring between these grooves and the ventral margins are considered to have been formed in the post-winter season of active growth. Based on the fortnightly periodicity of the ridge formation cycle, each of these ridges should represent a fortnight; i.e., 14.77 days. Therefore, the number of ridge occurring between the winter groove and shell margin, multiplied by 14.77, approximates the number of days before August 23-24 that the individual began its season of active growth. The median number of post-winter ridges is 5/6 which compares closely to the arithmetic mean of 5.74 ridges. These averages indicate that about half of the specimens were wintering as late as early June.

There is some evidence to show that the August specimens represent ridges per shell groups that were dominant or moderately common in the spring sample. In the August sample, the growth band preceding the 1967 winter groove includes, on the average, 18.2 ridges. Since this average correlates almost exactly with the mean of 18.4 ridges per shell obtained from study of the 808 specimens in the spring sample, the forty-five specimens in the August sample are considered as belonging to the age group that was most common in the spring sample population. The twenty-five specimens of the August sample that do not have any grooves average 22.2 ridges per shell. Counting back to the center of the April-May sample interval at the rate of 14.77 days-per-ridge cycle, it is calculated that these specimens belong to an age group that averaged 13.5 ridges per shell. Shells bearing 13 or 14 concentric ridges are moderately common in the spring sample (see Fig. 7).

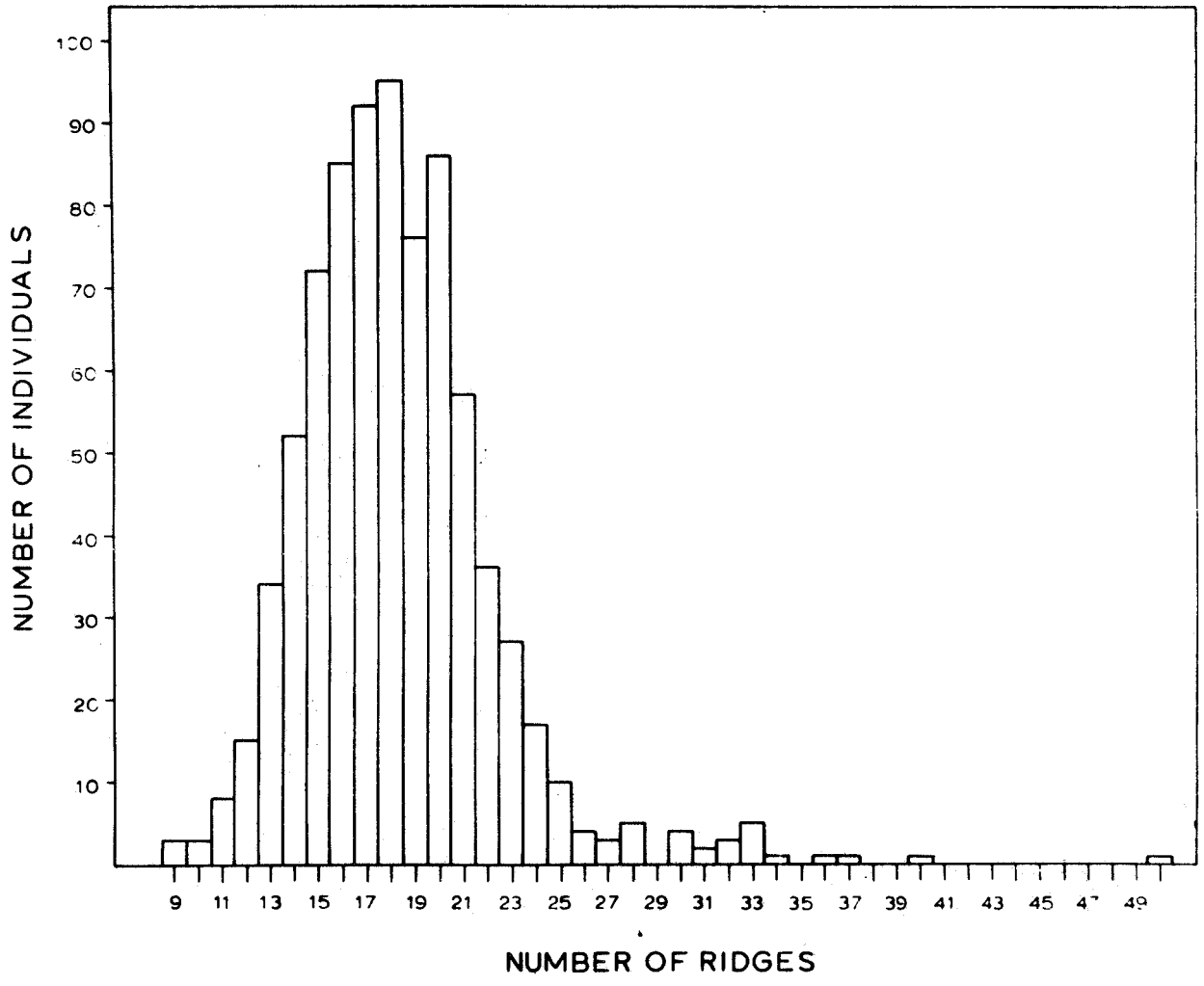


Fig. 7. Histogram of number of ridges per shell of *Chione undatella* collected in Cholla Bay, April 2 through May 8, 1967.

On the basis of the preceding extrapolations, it seems probable that estimates of %T in the spring series of samples may have been influenced by unrecognized wintering individuals most commonly bearing eighteen concentric ridges.

Significance of seasonal growth hiatus — Several suggestions of an influence of winter hiatus on %T have been detected. However, attempts to estimate the percentage of the sample population likely to have been wintering yield conflicting results. The estimate that depends on recognition of marginal grooves seems most liable to error, because the grooves that are formed by individuals having less than twenty concentric ridges tend to be weakly incised and are difficult to recognize on shell margins. Extrapolation of growth records of the August specimens suggests that a little more than half of the spring population were wintering. Most of the August specimens considered to have been forming grooves in the spring would have had eighteen ridges at that time and therefore would not necessarily have been recognized as wintering. The highs of the %T curve depart from the idealized 100% by 15% and the lows differ from the idealized zero by 55%. If all of the differences of %T were assumed to result from the presence of wintering specimens, then the percentage would be considered as 15 + 55 = 70. The percentage extrapolated from the August sample seems to be compatible with this estimate.

Tidal controlled sampling bias

It is conceivable that clams living at one site may be forming concentric ridges during a certain phase of the lunar cycle, while during that same time the individuals living at another site are forming troughs. If the collecting of individuals in a daily sample is in some way influenced by the tidal cycle, then the proportions of specimens from the different sites could be controlled or at least influenced by the phase of the fortnightly cycle at the time of sampling. A cyclic variation of %T could reflect such a tidally controlled bias of sampling of a stratified population. The following alternative hypotheses are considered:

1. Individuals wintering with concentric ridges on their margins were so positioned as to predominate in samples taken during spring tides; dormant individuals with troughs on their margins were sampled mostly at neap tides.

2. Several geographically stratified groups of clams were forming ridges at different times and different rates.

3. Several geographically stratified groups of clams were adding ridges to their shells at different times but at a common rate.

The first alternative hypothesis would explain the observed April-May %T cycle regardless of the rate of ridge-trough formation. Since it has been estimated that a little more than half of the population may have been wintering in the spring of 1967, this hypothesis would seem tenable.

The second alternative hypothesis predicts a random variation of %T, provided the number of asynchronous, geographically stratified groups of clams is large. This cannot be, for the %T cycle observed in April-May 1967 has a probability greater than 0.95 of being non-random variation. On the other hand, a small number of asynchronous, geographically stratified groups would result in a polymodal %T graph. There is a faint suggestion of a minor peak located within the first low of the April-May graph. However, it has been shown that the difference between this low and the second low that does not have a minor peak is insignificant at the 0.05 level. Since there is no other indication of irregular polymodality on this graph, the second alternative hypothesis is considered insufficient as an explanation of the observed %T cycle.

The third alternative hypothesis proves to be tenable if one assumes that the several groups were adding ridges at the rate of one every 15 days. The need for this assumption is demonstrated in the following example.

Let us assume that the common rate of ridge addition is one per 20 days instead of one per 15 days. In this case, the time of ridge formation within a group would occur 5-1/4 days later with each successive fortnight. The hypothesis predicts a tendency for a group of clams, say group A, to predominate over another group, say group B, in the sample taken at spring tide, and for group B to predominate over group A at neap tide. If ridge formation is common in group A during the first spring tide, then the %T of that sample will be low. The time of the next spring tide (14.77 days later) would not coincide with the time of the next ridge formation in group A. There would result a very high %T observation at the time of the second spring tide, because both groups of clams would be

forming troughs at that time. A decrease in %T would not be observed until ridge formation occurred in group A (about 5-1/4 days later). It is thus theoretically demonstrable that the rate of ridge formation would be expressed as the periodicity of the resulting %T graph. Provided the observed %T cycle is to be explained by the third alternative hypothesis, the rate of ridge addition to the shell must be about one every 15 days.

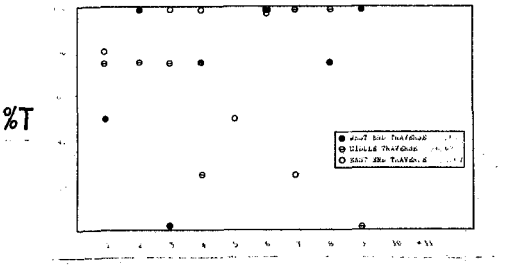
Proceeding with this assumption, sampling bias with respect to groups of clams such as the hypothesised groups A and B could conceivably produce a 15-day cycle of %T that would lack 100% peaks and 0% lows. A sufficiently large number of these groups of clams would so decrease the amplitude of the %T variation as to make it appear random. However, the number of these hypothesised groups included in the April-May data would seem insufficient to have randomized the %T variation, for the %T cycle has a probability greater than 0.95 of being non-random.

Thus, the third hypothesis seems tenable, assuming that (a) the rate of concentric ridge addition to the shell is one per 15 days and (b), only a few stratified asynchronous groups were sampled.

Both hypotheses of tidal controlled sampling bias considered as tenable predict that variations in %T are related to the tidal cycle and to sample position. Attempts to correlate these variables are described below.

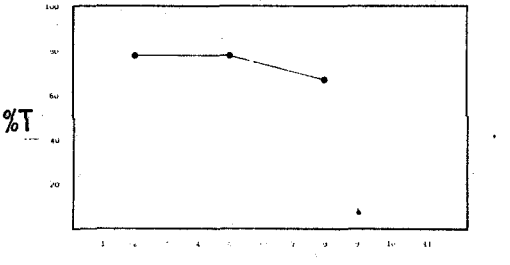
Statistical comparison of %T, tides, and sample position — A tendency for lows of %T to coincide in time with the lows of the low tides is weakly apparent in Fig. 6. However, the shapes of these curves are different. This difference has been measured by analysis of linear regression of the %T data on the tidal data. The sample correlation coefficients are low and statistically insignificant.

A similar lack of correlation is seen in the plot of %T vs. position perpendicular to the length of the main drainage channel (Fig. 8a). Variations are extreme and erratic along these traverses, and the number of specimens ranges from only one to five for each point. To decrease scatter, %T data of equivalent positions in these traverses have been combined and grouped by threes. The results (Fig. 8b) show little deviation from a mean of 74%. The slope (b) of this regression is 0.207, which yields a



Position (Interval 15 feet)

(a) Ungrouped data



Position (Interval 15 feet)

(b) Traverses combined and data grouped by threes

Fig. 8. %T vs. position in traverses across main drainage channel in area of serial sampling.

"t" of 0.742, which is below the critical value of 12.706.

The above statistical tests show that the %T graph as a whole cannot be explained by variation of tidal level or sample position. Rather, it appears that a majority of the *C. undatella* form their ridges during the new and full moon phases, when tidal range is maximal and the diurnal low tides are at their fortnightly extremes. Variations of %T at other phases of the cycle deviate significantly from the tidal curve and remain to be explained in reference to non-tidal factors.

Synchrony of concentric ridge building and %T

Correspondance between the observed %T and the idealized cycle of %T depends on the simultaneousness of ridge construction within the *C. undatella* population. Three sources of asynchrony are postulated as incluencing the amplitude of the %T cycle:

1. The time required for the formation of a concentric ridge may vary with the individual.
2. Although most individuals form their ridges near the time of new or full moon, the exact days on which ridge building begins or ends vary from one individual or group of individuals to another.
3. Within the population there may be a group of individuals tending to form their ridges in relation to another phase of the fortnightly cycle.

It has been observed that the number of growth laminae within a concentric ridge varies from one to five. It would follow from the hypothesis of a daily periodicity of growth lamina deposition that ridge building takes place within 1 to 5 days. However, such deviations are extremely rare, occurring with a frequency of about one in ten. This source of asynchrony would thus account for a minor amount of difference between the observed %T and the idealized cycle.

The other two postulates suggest the possibility of a relationship between %T and age groups or sample position. However, the data of this study reveal no suggestion of a correlation between ridged margins and size or number of ridges per shell. Nor is there a significant correlation between %T and sample position. If asynchronous deviants are assumed to be frequent in the sample population, they must be considered as likely

to occur in one age group or sample position as in another. Rather, individual variation seems most likely to control asynchronous ridge building. How much this variation may influence %T cannot be determined from the available data.

Distribution of Age Groups

A morphological parameter that is known to have some relationship to the age of the individual organism provides information that is useful in studies of population structure. Usually, a frequency distribution of size or weight is used to determine the number of annual age groups present in a sample population. In this determination, allowances must be made for individual differences of growth rate. Futhermore, if the determination is to provide a valid approximation of the natural population structure, it must be assumed that there is a discrete season of recruitment and a common survivorship beyond the first year. In this study of *C. undatella*, specimens with annual increments and finer time-significant growth layers provide a separate source of information about longevity and survivorship. Inferences drawn from both sources are compared in order to test for the consistency and accuracy of the results.

Age groups expressed in histograms

In Fig. 7 it is shown that the frequency distribution of the number of concentric ridges per shell begins with a minimum of nine and rises steeply and continuously to the modal class of eighteen. Between eighteen and twenty-six ridges per shell, there is a continuous but more gradual decrease in frequency, followed by low frequency that extends to the fifty ridges per shell class. Based on the estimated 15-day periodicity of the ridge formation cycle, the modal class of eighteen ridges per shell is considered to represent a group of individuals approximately three-quarters of a year in age. Accordingly, the mininal frequencies in the twenty-five to twenty-six ridges per shell classes may represent a group of individuals about 1 year in age. If so, then recruitment of individuals with disso-conchs must have been maximal in the summer of 1966. The wide spread or, "tail" beyond twenty-six ridges per shell suggests that a much smaller number of individuals in the April-May 1967 sample were older than 1 year, although minor modes that would represent older annual groupings are not clearly defined.

Histograms of shell length and height (Figs. 3 and 4) show major peaks that seem correlative with the year I group recognized in the study of the ridges-per-shell histogram. The normal distributions computed from the sample means and variances of size measurements indicate that the principal peak of the length histogram is centered on the 16.5 to 18.5-mm class and that the peak of the height histogram is centered between the 12.5 to 14.5-mm and 14.5 to 16.5-mm classes. The midpoints of these peaks are taken as 17.5 mm for length and 14.5 mm for height. It seems valid to calibrate these size midpoints in units of ridges-per-shell, for there are significant positive correlations between the number of concentric ridges per shell and both length and height. This conversion is made by dividing the midpoints by the mean ratios of size to number of concentric ridges per shell:

$$\frac{\text{length midpoint}}{\text{mean length/ridges-per-shell}} = \frac{17.5}{0.953} = 18.4 \text{ ridges-per-shell}$$

$$\frac{\text{height midpoint}}{\text{mean height/ridges-per-shell}} = \frac{14.5}{0.795} = 18.2 \text{ ridges-per-shell.}$$

The resulting equivalents correlate exactly with the class considered as the midpoint of the first year I group on the basis of the ridges-per-shell histogram. Shell measurements occurring outside the ranges of the computed histograms suggest minor peaks that are not sufficiently distinct for delimitation of midpoints.

Specimens with annual layers

In a previous section it was reported that the number of ridges per annual layer averages 16.9 in the first layer, 8.8 in the second, 4.5 in the third, and 4.0 in the fourth. Although this statistical sequence provides a basis for evaluating the completeness of an annual layer, the averages were obtained from study of individuals of different ages. As variations in the length of the active growth season for a clam of a given age may occur from year to year, the number of ridges formed by a group of individuals of approximately the same age could deviate from the average in the statistical sequence. For example, the average of 16.9 ridges in the first-formed annual layers of individuals originating

in several different years differs from the midpoint of eighteen ridges derived from the histogram. This difference could reflect a longer than normal average growing season in 1966-1967. Consequently, the sixty-six specimens that have annual layers are divided into the following age groups derived from study of the histogram.

Year I — Forty-nine specimens with less than twenty-five ridges per shell and one groove followed by none to five ridges. These individuals show evidence of having lived through a summer and winter (1966-67).
$\bar{x}$ (ridges per shell) = 18.4.

Intermediate between years I and II — Four specimens with one groove and 26 to 29 ridges per shell.
$\bar{x}$ (ridges per shell) = 28.

Year II — Four specimens with one groove followed by nine or twelve ridges considered to have been inactive when collected, and four specimens with two grooves considered to have just begun their third season of active growth.
$\bar{x}$ (ridges per shell) = 23.1.

Year III — Three specimens with three grooves, and one specimen with sequence 20/7/6, all considered inactive.
$\bar{x}$ (ridges per shell) = 24.1.

Year IV — One specimen with sequence 25/7/4/4/, inactive, 40 ridges per shell.

Comparison of the average number of ridges per shell in group I with the first year modal class derived from the ridges-per-shell histogram shows a difference of 18.4 — 18.0 = 0.4. This difference is small in relation to the standard deviation of the ridges per shell in the annual layer estimate: s = 2.45. Application of the one-sided "t" test (see Crow et al., 1960) shows that this difference is not significant. Computed from $\bar{x}$ = 18.4, a = 18.0, s = 2.45, and N-1 = 48, the value of t is 1.14, which does not exceed the critical value of 1.68. Thus, there would be greater than 0.05 risk of error in assuming that the difference between the two values did not result from random variation. Conceivably, a number of errors could be involved, including, for example, shell growth

differences between the years sampled and consequent overlapping of age groups, and indistinctness of grooves on the margins of some individuals. Whatever the errors that are involved, their influences on the estimates of the year I midpoint tend to cancel out in a sample of N = 49 individuals. It has been demonstrated with a statistically significant sample that the magnitude of difference between estimates of the year I midpoint from the histogram and from individual shell study methods is on the order of 0.4 ridges per shell. This amount is theoretically equivalent to 6 days. The data also show an extreme overlapping of year groups II and III and the intermediate group. Ideally, the older individuals would, on the average have greater numbers of ridges per shell. However, such is not the case, for the shells intermediate between year groups II and III have an average of 28 ridges, and the shells of year groups II and III have almost the same average number of ridges (23.1 vs. 24.1). This lack of a consistent relationship between age and total number of ridges per shell of the individuals older than 1 year accounts for the lack of clear annual groupings expressed as minor peaks in the ridges per shell histogram.

With regard to survivorship, the above data for 420 specimens indicate that 2% are survivors of two winters, 1% survivors of three winters, and less than 1% survivors of four winters. Approximately 4% of the total April-May sample of 808 specimens have twenty-six or more ridges per shell. In the absence of annual layer data, these specimens would be interpreted as having ages exceeding 1 year. Thus, the two methods give almost the same estimates of the percentage in the sample surviving beyond a second winter. Although the precise separation of annual groups calls for the study of annual growth layers, survivorship data of either sort give *C. undatella* has a life span of one year. As the histogram of ridges per shell was successfully calibrated in units of shell size, histograms of shell size also provide an indication of the annuality of this species. It would be difficult to explain the agreement between the ridges per shell histogram, shell size histograms, annual layers of individual specimens, and the fortnightly periodicity of ridge formation unless this species has a normal life span of one year or less.

Spawning record

A lengthy season of effective spawning would account for the rather wide spread of the year I group seen in the ridges-per-shell histogram. Allowing 15 days for each ridge-trough cycle, the range of this histogram peak is interpreted to indicate that the year I clams may have originated 9 to 25 fortnights prior to the time of collection in spring 1967. The spawning season would thus seem to range from April to November. However, the amount of time the juvenile clam spends in the prodissoconch and dissoconch I stages must be considered. According to Carriker (1961), *Mercenaria mercenaria* begins to form its principal concentric ridges within a few weeks after metamorphosis. Although this species is not a member of the Chioninae, Carriker's observation provides the order of magnitude of the pre-dissoconch II period likely to occur in the ontogeny of *C. undatella*. Hence, it is assumed that the following calculations of time spat group origins contain an unknown but probably negligible error.

Slightly more than 74% of the shells collected daily between April 12 and May 8, 1967 have fifteen to twenty-two ridges. Forming their ridges at the rate of one each 15 days, there specimens would have originated in the summer of 1966. Shells with seventeen to eighteen ridges are the mosst frequent of all. They are considered to represent a peak in the initiation of ridge formation during late July and early August. Allowing a few weeks for completion of the pre-dissoconch II stage, a peak in effective spawning would have occurred in the previous month, i.e., in June.

Although the preceding predictions were made early in this study, attempts to verify them were unsuccessful. In no season of the year has a living *C. undatella* with less than nine concentric ridges been found in samples from various parts of the tidal flats and drainage channels. Nevertheless, spawning must have occurred in 1967, for small individuals with 10 or 12 concentric ridges are present in all samples collected in 1968. These observations are difficult to explain unless it is assumed that the early juveniles are distributed unevenly in the bottom sediments. Only a few dozen kilograms of sediments have been screened and examined for juveniles. Perhaps examination of much greater quantities of sediments is necessary to locate their whereabouts. Obviously such a sedimentological search for juvenile *C. undatella* in Cholla Bay would be very time consuming and seems to be the least promising approach.

Inspection of the larger specimens collected in different seasons of the year has shown no evidence of gonad swelling in preparation for spawning. Nor is there evidence of visceral shrinkage, which is likely to occur in the aftermath of spawning. Not all bivalves may be expected to present such megascopically obvious features of pre- and post-spawning activities. The gonads of a pelecypod are best examined histologically and perhaps this approach would be more productive.

Nevertheless, data on the seasonality of shell growth in *C. undatella* are consistent with a summer spawning season. In the malacological literature (discussed earlier), there is reported a tendency for the time of maximal shell growth to alternate with the season in which gametes are produced and gonads enlarge. Since the slow-growth groove deposits are most common on the margins of specimens collected in winter, it would be predicted on this basis alone that a peak of spawning occurs in late spring or early summer, perhaps in June.

V. FUNCTION AND ORIGIN OF LUNAR GROWTH RHYTHMICITY

Adaptive Significance of Concentric Elements

The fact that shell "ornament" in general is useful in characterizing species and other taxonomic categories suggests that genetic factors may be involved in the fortnightly and monthly growth rhythms recognized in study of the concentric elements of pelecypod shells. The apparent fortnightly periodicity of concentric ridge formation implies a relationship between shell growth and the fortnightly rhythm of the environment. The ecological associations of concentric shell elements provide clues to how these growth rhythms may have evolved to adapt pelecypods to certain environments. According to Nicol (1965, 1967), the species that have well-developed concentric ridges and spines are most common in shallow marine environments of the mid-temperate to tropical zones. Several writers (Nicol op. cit.; Carter, 1967; and Waller, 1969) suggest that the functions of ridges and spines in these environments involve burrowing activities, retention of moisture at low tide, and protection from predators. To surmise the possible consequences of a given type of concentric shell element in the life history of the pelecypod, these and other activities or conditions are discussed below.

Strengthening of the shell

The sturdiness of a shell is likely to be an important survival factor under forces involving the mass and thixotrophy of surrounding sediments, internal stresses resulting from contraction of the adductor and pedal retractor muscles, and collisions with shells and other objects either floating or dislodged and transported during storms. As in the use of buttresses and arches, to construct a building out of a minimum of material, the pelecypod appears to strengthen its shell through the formation of non-additive ridges and concentric ridges (*cf.* buttresses). Protrusive ridges, nodes, and spines that are thin and fragile may absorb some of the energy of dynamic force, thus protecting the underlying

shell from collisions with other objects. A thick, resilient periostracum would absorb shocks by functioning like a cushion under a hammer. It is postulated that these features of external shell sculpture or of periostracum thickness are important in the adaptation of species to the energy conditions of their environments. To test this postulate, the radial and concentric shell elements of the marine species included in this study are compared with environmental data provided by Abbot (1954) and Keen (1958). The data are presented in the following categories of life habit:

1. Passive burrowers.
    a. Shallow depths in sands and muds of the intertidal zone. Most species that have a cancellate sculpture consisting of prominent narrow or protrusive concentric ridges and some kind of radial ribs; *Donax gouldii* and *Transennella tantilla* having small, relatively thick, medium-inflated, smooth shells, and burrowing rapidly; *Tivela stultorum* with large thick, medium-inflated, smooth shell; *Mya arenaria* and *Macoma nasuta* having thin, compressed, smooth shells; and the two species of *Pitar* having concentric ridges and dorso-posterior rows of spines.
    b. Burrowing more deeply in sandy tidal flats: *Dosinia ponderosa* and *D. dunkeri* having relatively thick, compressed shells with equant to wide ridges; *Chione gnidia* with relatively thick, inflated shell, bearing fine radial ribs and protrusive concentric ridges.
    c. Neritic. Most species that have equant or wide concentric ridges and lack ribs; *Mactra solidissima* with medium-thick, medium-inflated, smooth shell; and *Pandora trilineata* with compressed, thin, smooth shell.
2. Vagrant burrowers.
    a. Shallow depth in substrate. Cardiid species with inflated, medium-thick shells bearing strong radial ribs and nodes; *Solemya australis* with thin, smooth shell.
    b. Deep in substrate. *Siliqua patula* with compressed, elongated, thin, smooth shell.

3. Permanent deep burrowers. *Tresus nuttalli* and *Sanguinolaria nuttalli* with inflated, thin, smooth shells, and *Saxidomus nuttalli* with medium-inflated, medium-thick shell bearing equant to narrow concentric ridges. These species coexist in the same tidal flat environments in Northern California.
4. Burrowers with byssal attachment.
   a. Littoral to shallow neritic: *Pinna* sp. with thin shell, bearing radial ribs and tubular spines, and *Volsella demissa* with thin shell bearing ribs.
   b. Neritic: *Cardita floridana* with medium-thick shell bearing radial ribs and narrow or protrusive ridges.
5. Attached to solid objects. These species occur as dense clusters of individuals oriented with their long axes normal to the substrate. Dynamic forces due to wave action tend to be divided among the individuals of a cluster and are directed into the shells at low angles.
   a. Rocky coast. *Mytilus californianus* with medium-thick shell, bearing a thick periostracum, radial ribs, and arched minor growth bands.
   b. Protected shore. *Mytilus edulis* similar to preceding but with weak radial ribs that are confined to a juvenile stage; *Anomia simplex* with thin, smooth shell; and *Crassostrea gigas* with thick shell, bearing flat minor growth bands.
6. Nestlers.
   a. Free living. *Glycymeris* sp. in rocky crevices of littoral and shallow neritic zones, with thick, medium-compressed, smooth shell; and *Kellia suborbicularis* with thin, smooth shell, in bottles and crevices at neritic depths and in vacated burrows in rocky shores.
   b. Attaches. *Isognomon eppupina* with thin shell, bearing radial ribs, living in clusters; *Anadara ovalis* and *Arca incongrua* with inflated, thick shells, bearing nodes and radial ribs; and *Pinctada radiata* with medium-inflated, medium-thick, smooth shell, usually in quiet neritic environments.

c. Clinging to rocks below low tide line: *Spondylus crassisguama, S. princeps* with thick, medium-inflated shells bearing wide ridges and many large spines.

7. Borers into soft rock: *Lithophaga* sp. with thin shell, bearing medium-thick periostracum and radial ribs; *Platyodon* sp. with thin shell, bearing concentric ridges; *Irus lamellifera* with medium-thick, medium-inflated shell, bearing protrusive ridges; *Barnea costata* with thin, moderately inflated shell, bearing protrusive ridges that are nodelike on radial ribs; and *Zirfaea gabbi* with thin, inflated shell bearing radial ribs and concentric ridges that are equant on the posterior and narrow and serrated on the anterior.

8. Passive nektos, or swimmers: *Lima squamosa* with thin medium-compressed shell, bearing radial ribs and nodes; occasionally seeks shelter by attaching byssal threads to rocks in crevices; six of the seven Pectinid species with compressed or medium-inflated, medium-thick shells, bearing strong radial ribs and lacking concentric elements except for scale-like nodes formed by projecting growth laminae on ribs; *Lyropecten subnodosus* with thick, medium-inflated shell, bearing strong radial ribs and minor growth bands that are arched.

In the above data, the most elaborately sculptured, thicker shells are related to relatively high-energy environments. Thin smooth shells predominate among the species with life habits that enable them to avoid exposure to strong wave action. Thus, the shell-strengthening functions postulated for the radial and concentric shell elements seem to be important in the adaptation of pelecypod species. In some of the species that are exceptional to these generalizations, shell sculpture may have one or several special functions that are more significant than adding to shell strength. This could be the case for the species that have thick, sculptured shells and the same modes of life in the same habitats as do the species with relatively fragile, smooth shells. It is also possible that the concentric and radial shell elements of some species are more vestigial than functional.

Locomotion vs. stability

Analogous to the functions of rudders and wings on torpedos and airplanes, it could be postulated that the concentric ridges of a pelecypod shell influence considerably the path of a clam plowing through a substrate. That there may be such an influence on pelecypod locomotion has not been demonstrated. In fact: the most vagrant shallow burrowers are the Cardiids, which lack concentric ridges; one of the most active species in burrowing and reburrowing several times each day is *Siliqua patula*, which has a smooth shell; and the younger, more actively moving individuals of many species lack prominent concentric ridges, which appear later in the ontogeny when the organism becomes a passive burrower. To the contrary, a ridged shell has a greater surface area than a smooth shell of the same shape and size; hence the ridges increase the friction between shell and substrate, thus functioning to hold the organism securely in a burrow. There may be a need for anchorage, as the foot organs of older individuals of many pelecypod species are small in relation to overall body size than are those of younger individuals. That the older individuals may be sedentary for long periods is supported by the author's observations of encrustations and limpet attachment marks on exposed shell surfaces of older individuals of *Chione californiensis* and *C. undatella* in Cholla Bay.

Of the three types of ridges differentiated in this study, the protrusive ridges should have the greatest potential to hold the pelecypod shell in the substrate. This is supported by the fact that the species with protrusive ridges are common intertidally, whereas many of the species forming equant or wide ridges are most common below the low tide line. It seems difficult to evaluate the relative contributions to stability in the substrate of furled and flared protrusive ridges. On the one hand, the approximately normal orientation of a thin ridge to the shell surface increases the substrate-shell contact area; but on the other hand, sediments trapped beneath furled ridges increase the specific gravity of the whole shell. Nor is this evaluation made by comparing the micro-environments of species with furled and flared ridges as in *Chione undatella* and *C. californiensis*, since the former species has a superior burrowing ability, which would alone account for greater

success in the main drainage channel. There is a lack of environmental data needed to test for relationships between habitats and the occurrences of narrow as opposed to wide asymmetric ridges.

In the Bay of La Paz, the author observed that the tubular spines of *Pinna* effectively resist upward movement of the shell. These tubular ridges are open upwards and are filled with sediments that increase the specific gravity of the shell. There can be no doubt that these effects of tubular spines are advantageous to *Pinna*, which occurs as clusters of individuals bound to the sediments and to each other at their dorsal ends by a network of byssal threads. The toothlike spines of *Pitar* occur in rows along the dorso-posterior shell margin. According to Carter (1967), these clams burrow to such shallow depths that most of the spines protrude above the substrate. Being thus subject to wave action or tidal currents. these spines may actually decrease the stability of the pelecypod. With this in mind, it seems significant that the concentric ridges of most passive shallow burrowing intertidal species become low in relief on the dorso-posterior margin and may be absent in the escutcheon. Although this lateral variation of ridges may have evolved for some other reason, it seems likely to contribute to stability in the substrate. The tusklike spines of *Spondylus* are not related to burrowing, but according to Abbot (1954) they function to wedge the shell into crevices in reefs and old wrecks.

Retention of moisture

It is conceivable that concentric ridges and radial ribs increase the amount of water adhering to the shell at low tide, thus tending to protect the pelecypod from overheating and dessication. This retention of water would be very important where the surface water is warm and where the air is either dry or warm, since these conditions result in a high rate of evaporation. Consequently, it seems advantageous for the intertidal dwelling pelecypods of warmer climates to retain water within interstices provided by shell sculpture. This function explains the predominance of the ridged form in the pelecypod faunas of warm temperate to tropical climates, whereas the functions of shell strengthening and increasing stability in the shallow burrow do not. An example of latitudinal variation in the distinctness of concentric ridges within a species may be seen in *Saxidomus nuttalli*. Burrowing deeply in tidal

flats from the Aleutian Islands to Northern California, individuals of this species have smooth shells and by virtue of this feature comprise the variety *gigantea*. Southward from Northern California to Baja California, individuals of this species form concentric ridges that are quite distinct. Although a thorough field study of this species has not been published, Abbot (1954), gathering available data, suggests that there may be a geographic gradient between the northerly and southerly forms. A similar suggestion of a cline involving a southerly increase in the distinctness of concentric ridges comes from the data on *Mercenaria mercenaria* from New England to Florida. It seems noteworthy here that extremely prominent ridges occur on the Recent shells of *M. campechiensis* from the Gulf of Mexico and on fossil shells of *M. mortoni* from subtropical or warm temperate Miocene deposits of the Chesapeake Bay region. Since temperature is the most obvious physical difference between the tidal flat or shallow neritic environments of these suggested clines, visceral heating and dessication depending on air and water temperature could be selective factors affecting the genetics of ridge formation in these species. However, there is at least one example of subspeciation involving the distinctness of concentric ridges that seems to be independent of the moisture retention function. *Protothaca staminea* s.s., a shallow burrower in various substrates of open and protected shores from the Aleutian Islands to Baja California, shows no appreciable variation in the distinctness of concentric ridges. *P. staminea* var. *ruderata*, occurring in the same habitats from the Aleutians to Puget Sound, has protrusive ridges that are comparatively more distinct. An incongruity is seen between two different species of *Protothaca: P. grata* has indistinct narrow ridges and burrows to shallow depths in the larger tidal flat drainage channels of the Gulf of California; *P. fructifraga* has distinct protrusive ridges and the same habitat. Moisture retention does not seem to be the most important function of concentric ridges for these species. Thus, the survival value of moisture retention in the interstices provides by concentric ridges varies with species and between different groups of species.

Protection against predators

A boring gastropod large enough to bore through a thick pelecypod shell would have difficulty in reaching through the profusion of spines formed by most species of *Spondylus*. The spines of *Pitar dione*,

P. lupanaria, and *Cardium indicum* are confined to the dorso-posterior margins of their shells, and it should be expected that a snail predator would simply burrow through the substrate into a position from which it could attack the nonspinose part of its prey. Spines occurring in a few rows on a part of the shell would provide some protection from skate fishes and other bottom-feeding nektonic predators. The overlapping of furled ridges on the shell surface of *Chione californiensis* have a similar effect of increasing the space between the boring gastropod and the viscera of the clam. Additional protection would result from the filling of the spaces beneath these ridges with sand. Non-furled, widely spaced ridges could provide little if any protection against boring gastropods. However, the shell-strengthening effects of any type of shell sculpture would be important in determining whether or not the shell is crushed between the chelicera of an attacking crab or the jaws of an attacking fish.

It is possible that the configuration of the ventral margin of a pelecypod shell is an important factor of susceptibility to gastropods that use the apertural lips or spines of their shells to chip and pry open their prey. A rudimentary concentric trough on the ventral margin, together with a ridge dorsal to it, form a notch on each valve. These notches are similar to the commissure. They are considered as *false catcholds* for the chip and pry predator, because they lead to a breakage of concentric ridges rather than to a forcing apart of the two valves. This must be so, because the force exerted by a lever inserted in such a notch is distributed between the ridge and the underlying shell mass. Since one valve is buttressed by the adjacent valve, the shell mass underlying the ridge is certain to be stronger than the ridge. Breakage of the ridge destroys the false catchold at the point of initial attack, which leaves the gastropod in a situation analogous to the problem of opening a rimless can with a lever-type can opener. According to Coulton (1908), a gastropod that is unsuccessful in attacking from one point on the margin immediately shifts its attack to another point. Coulton also reported that the chip and pry gastropod predators sometimes break the apertural lips or spines of their shells in unsuccessful attacks on pelecypods, and that this is followed by a retreat of the gastropod into a burrow for a period of shell regeneration. Since the

gastropod eye is primitive, it seems likely that the gastropod may often confuse the false catcholds on the ventral margin of a pelecypod shell with the true catchold (viz., the commissure). Assuming that the frequency at which a gastropod breaks its own shell is related to the number of attacks made on pelecypods, it is probable that the ratio of two false catcholds to one true catchold reduces effective chip and pry predation on a pelecypod population.

As the configuration of the ventral margin may influence its susceptibility to breakage during storms and other turbulaent events, the presence of a thin, prominent ridge on the ventral margin would, by means of absorbing dynamic forces, tend to reduce predation by snails that gain access to the body through breaks in the shell.

Nonmarine shells

There are some gross similarities between the physical factors in marine and brackish or freshwater environments. Despite the usually low amplitudes of waves and tides in most lakes and rivers, occasional storms result in considerable turbulence. Consequently, the strength of a shell and its resistance to dislodgement from the substrate would be important to the freshwater pelecypod that burrows passively to shallow depths in lake shore or river bank sands. Near the mouths of rivers, tides may have amplitudes sufficient to expose tidal flats. Pelecypods inhabiting these intertidal though brackish or freshwater environments, would benefit from any external shell sculpture during low tide. Following the adaptive significances inferred from study of shell sculpture in marine forms, at least some non-marine pelecypod species should also be equipped with radial or concentric elements. In confirmation of this, distinct concentric ridges are formed by the species of Corbiculidae inhabiting estuaries as well as inland lakes and rivers. *Corbicula fluminea*, perhaps the most common and widespread living species, was emphasized in this study. Isom and Sinclair (1963) have documented the dispersal of this species in North America. First appearing in the Columbia River Estuary, Washington, 1938, and somewhat later in estuaries of the Gulf and Atlantic coasts, the species has spread into the upper reaches of many river systems, including the Mississippi. Protrusive ridges occur on *C. fluminea* shells collected by the author in the tidal waters of the Napa River Estuary. Similar ridges were observed on

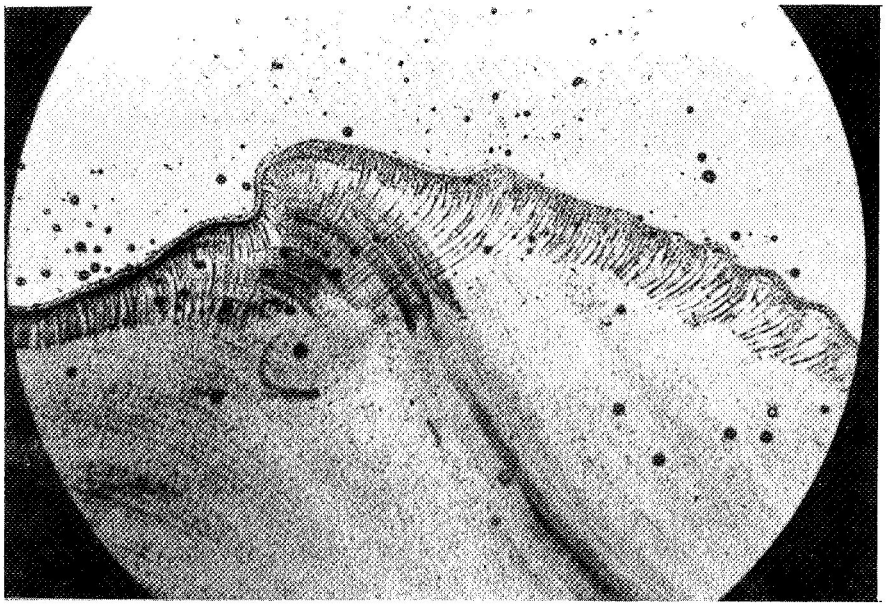
specimens collected from the Florida Everglades, at sites that are at least proximal to tidal phenomena. All of the intertidal specimens illustrated in the Sinclair and Isom monograph have distinct, apparently protrusive ridges; whereas some of the inland river specimens seem to have low relief, narrow ridges. Within this species, then, there is a suggestion of a relationship between the distinctness of the ridges and the presence of tidal activity. Perhaps further study would show that these variations reflect the genetics of balanced polymorphism, with the ridged form being predominate through natural selection in littoral environments.

The typical unsculptured Unionid shell is related to quiet river or lake environments, or to life habits other than passive shallow burrowing in shoreline sands. Most of the Unionacea either nestle among boulders and cobbles in shallow waters, or burrow in the finer sediments of relatively calm, deep-water environments. At least one species, *Anodonta cygnea*, is known to utilize its smooth elongate shell in rapid locomotion. According to Bloomer (1946), this vagrant shallow burrower migrates into shallow water during August to spawn and spends the winter in deeper water. Although there is a lack of field observation of Unionid burrowing activities, the smoothness of the typical shell seems better adapted for locomotion than stability in substrate. Whether vagrant or sessile, it should be emphasized that the Unionid shells are constructed of medium-thick resilient periostracum. These are not weak shells, and the periostracum alone seems sufficient to protect the mussel from impacts that might occur during storms or floods. As most Unionid species do not range into tidal waters, there is no need of devices for retention of water on shell at low tide. There is no evidence of freshwater fishes, crustaceans, and gastropods that crush, bore, or chip and pry apart nonmarine pelecypod shells. As summarized by Sinclair and Isom (1963), the predation that occurs involves the ingestion of whole clams by ducks and several species of catfish, sunfish, drum, and carp. The investigators analyzed the stomach contents of fish and bird predators and found only a few species of the Sphaeridae having maximal growth sizes of 4 mm or less. On examining the annual growth layers of Unionid shells, it is this writer's impression that most species attain a length of 30 to 50 mm during the first year of

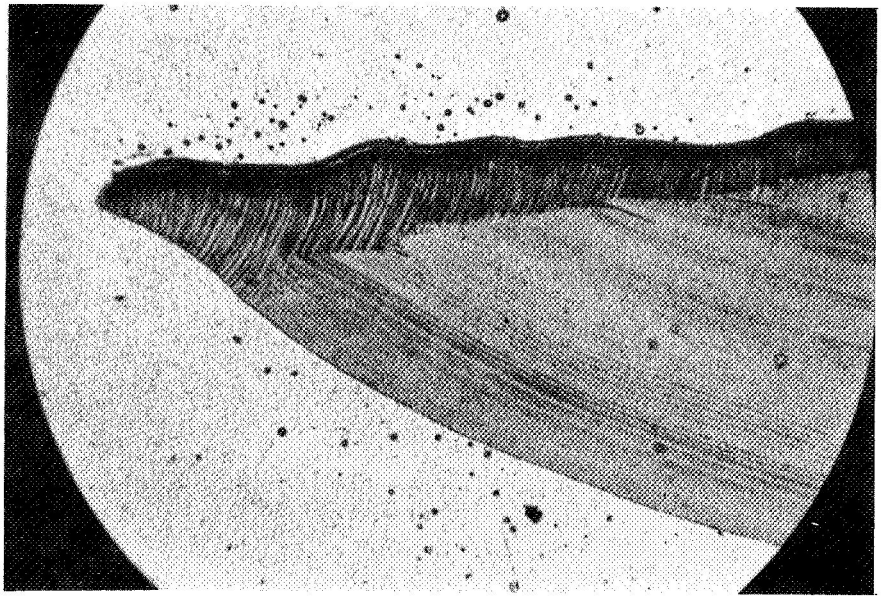
growth. As this common length is larger than the maximal sizes of clams known to be ingested by freshwater fishes and waterfowl, many species of the Unionacea may be too large in the first annual season of rapid growth to be swallowed.

Turning to the exceptional Unionid species that have external shell sculpture, the pustules occurring irregularly on shells of *Quadrula* are related to various habitats in the mid-western United States. These low relief pustules could function slightly to prevent the swallowing of the clam by predator. The pustules seem to be too low in relief to give any but a minimal stabilization in the substrate or strengthening of the shell. The midline nodes formed in each slow growth season by species of *Obliquaria* (Plate 24) are large enough to have appreciable shell-strengthening and substrate-stabilization functions. Additionally, the combination of a rapid initial rate of growth with a midline node at the end of the first season would tend to reduce predation. Four Unionid species represented in this study form equant or wide concentric ridges: *Obliquaria reflexa* from Alabama, *Unio raveneliensis* from Lake Nicaraugua, and *Lampsilis hydrianus* from Claiborne Parish, Louisiana. The Claiborne specimens are likely to have been collected in tidal waters of the Mississippi River. Locality data for the *Obliquaria* are incomplete. There is no information about the tidal range of Lake Nicaraugua available to the author. Specimens of *Lampsilis radiatus* have minor growth bands that are structurally identical to those of the marine Pteriid *Pinctada radiata*. The conchiolin component layers of these growth bands are related to concentric frills of the periostracum. As the periostracum frills resemble calcareous furled ridges of some marine pelecypods burrowing passively near the surfaces of tidal flat substrates, the frills could function to increase burrow stability, to retain miosture at low tide, and to increase the cushioning effect of the periostracum. The origins of these specimens cannot be determined exactly, but all of them are knowm to have been collected from rivers near major cities on the Atlantic coast of the United States.

It has been emphasized above that almost all of the nonmarine specimens with strong concentric ridges, periostracum frills, or minor growth bands are associated with estuaries or have a reasonable proximity



(1) Slow-growth node on midline of shell



(2) Ventral margin

Plate 24. *Obliquaria reflexa* (Rafinesque). Recent, Alabama. Radial thin section, plane polarized light X26.

to tidal phenomena. The majority of the Unionid species have smooth shells and seem to be adapted to non-tidal, freshwater environments, and perhaps to a vagrant burrowing life habit as well. These findings are compatible with the adaptive significances of concentric shell elements inferred from study of marine shell.

The Periodicities

Most of the species included in this study form concentric ridges with a predominate 14 to 15 day periodicity that is based on an innate biological clock. This clock may have evolved independently for the purpose of forming ridges, or it may be a master clock which evolved primarily for the regulation of oxygen consumption or some other primary life activity. In either case, the apparent fortnightly periodicity of ridge formation determines the configuration of the ventral margin of the shell and then may influence the survival of passively burrowing pelecypods in shallow marine environments. Three such possible functions of the ventral margin have already been discussed: (1) retention of moisture at low tide (maximum reservior between valves with ridged margins), (2) protection against shell breakage (maximal when there are ridges on the margins of adjacent valves), and (3) resistance to chip and pry predators (maximal when valve margins have rudimentary concentric troughs). Regarding the first postulated function, the exposed ventral periphery of a pelecypod in a shallow burrow is most vulnerable to heating and dessication when the tidal flat is drained to an extreme. Extreme draining of tidal flats may occur day or night during the spring tide phase of the fortnightly cycle. Hence it would be advantageous for the pelecypod to initiate ridge formation as the tidal range increases towards its fortnightly maximum, i.e. a few days in advance of the new or full moon. Conversely, as a concentric trough is formed on the ventral valve margin, the commissure is elevated above the water retained on the ventral surfaces of the pair of ridges preceding the pair of troughs, and the mantle edge is no longer protected by a film of water. In warm climates where the rate of evaporation is high, the formation of a trough on the ventral margin could be adverse to the organism unless synchronized with the neap tides that result in a lesser amount of draining of the tidal flat.

The second postulated effect involves the shock-absorbing function of the ridges. It would be most advantageous for the clam to form a ridge on each valve in preparation for the turbulent ebb and flow of spring tides. Individuals forming troughs instead of ridges at the time of maximal tidal amplitude (when ebb and flow may be turbulent) would be most susceptible to margin breakage. In some environments the mere breakage of a valve margin may not be fatal, but in Cholla Bay it was observed that individual Chionids with broken shell margins are quickly attacked by larger numbers of Nassarid snails during low tide.

The third effect, that of resisting predation by Strombid, Muricid, and perhaps other types of chip and pry predators, would be most important during spring tides when shallow burrowing peleycpods are most frequently dislodged. In order for the ridge formation rhythm to provide protection against this type of predation during spring tides, ridge formation must occur several days before full and new moons, so that each valve has a "false catch-hold" opposite to the commissure. This relationship between lunar phase and ridge formation is evident in the %T results of the serial study of *Chione undatella* (Fig. 5). Although there is no evidence of chip and pry predation in Cholla Bay, *C. undatella* occurs in other tidal flats of the Gulf of California where the Muricids and conchs may be more abundant. Comparing the observations of Berry (1956) with the present day gastropod fauna of Cholla Bay, and guided also by the comments of residents, it seems that in recent years shell collectors have reduced the numbers of ornate Muricids and conchs. Thus, only in recent years could the postulated protective function have become insignificant in Cholla Bay.

All of the functions of the fortnightly periodicity of ridge formation seem to be advantageous to the organism provided that ridge formation is initiated a few days before new and full moons. No matter how the rhythmicity evolved originally in the Pelecypoda, there is reason to believe that its synchronization with the fortnightly tidal cycle is maintained by natural selection in shallow marine and estuarine waters.

Mytilus edulis is the only species observed to have apparent fortnightly growth bands. These shell increments are so low in relief that, despite their effect of strengthening the shell as a whole, they

do not seem capable of providing the same functions on the ventral margin as concentric ridges and troughs. Tidal control of this rhythm seems more feasible if less direct, acting on a "master clock" concerned with the regulation of oxygen consumption, water pumping rate, or some other activity.

Most of the species with apparent monthly growth rhythms (Table 2b) have life habits other than shallow burrowing in the littoral zone. Three of the species inhabit subtidal environments: *Lyropecten subnodosus*, probably freeliving, *Pinctada radiata* a nestler attached to subtidal rocks, and *Dinocardium robustum* an actively vagrant benthonic cockle that attains a large size. Three species inhabit sheltered subtidal and littoral environments: *Crassostrea gigas* as dense clusters on tidal flats, each member of the cluster being firmly cemented to another shell or to some other solid object, and *Irus lamellifera* sheltered in a permanent burrow cut into soft mudstone. The functions postulated for the fortnightly ridge formation rhythm would not be significantly advantageous in a sheltered environment. Moreover, it seems obvious that these preceding six species have specialized habits enabling them to avoid or withstand many of the harmful effects of the spring tides. *Chione (Gnidiella) gnidia* seems to lack as protected a habitat; however, this species has a very heavy shell and burrows to a greater depth than most of the ridged pelecypods that have the apparent fortnightly periodicity. These characteristics seem to provide this species with protection against turbulence and predation. *Pandora trilineata* is the best example in Table 2 of a non-sheltered shallow-burrowing pelecypod with an apparent monthly rhythm of growth. These clams are more vagrant than passive and occur from above the mean low tide line to 60 fathoms. In the intertidal environment, these clams would probably be dislodged frequently during the spring tides. As their shells are thin, breakage and susceptibility to predation should be common. It is difficult to explain the lack of protection this species has unless it is ethological rather than morphological. Possibly this species is an extremely rapid burrower throughout the ontogeny, as in *Macoma nasuta*, but there is no observations reported to substantiate this.

With one or two exceptions, the monthly growth rhythms recognized in this study are associated with environments that are subtidal and/or protected from predation, tidal scour, and dessication at the low spring tide. If the biological timekeeping of this rhythm is facilitated by a special clock, the function of the monthly rhythms are not obvious. Otherwise, if the periodicity of ridge formation is based on a master clock, then one is equally uncertain as to the functional basis of the master clock unless it is primarily concerned with the timing of spawning to a single phase of a particular monthly cycle.

VI. PALEONTOLOGICAL SIGNIFICANCES OF RHYTHMIC GROWTH

Thanatacoenosis and the Normal Distribution

Study of 808 specimens collected at random from a living population of *Chione undatella* showed that the frequency distributions of shell size and number of ridges per shell differ significantly from normal. Departures from normalcy are graphically evident (Figs. 3, 4, 7) in the peakedness of the modal class and in the low frequencies drawn out over the larger or older age classes. Many of the larger, older specimens could be omitted from a small sample, in which case the histograms would tend to be more symmetrical. To test for the danger of failing to distinguish the non-normal size frequency distribution of a biocoenosis in a small sample, the sample data cards of this experiment were split into decks of differing sizes for computerized histogram analysis of shell length (variable 1). The larger deck contained 368 cards drawn from the sampling interval April 6-20, 1967. This sample accurately represented the total sample of 808 specimens in that it gave a histogram (Fig. 9) that is significantly different from normal at the 0.05 level. Smaller decks with N's of 309, 184, and 182 gave histograms (Figs. 10, 11, 12) with D values below the critical values for significant differences from normal. The means and variances of the two smaller samples (N=184 and N=182) are most dissimilar to those of the N=808 sample. These results show that a sample of 182 or 184 shells may not be representative of the available population. While it is not feasible to stipulate a minimal number of specimens required for an accurate representation of a biocoenosis, the approximate order of magnitude is closer to a thousand than to a few hundred. Thus, unless a thousand shells are collected, a biocoenosis of a community with life processes similar to those of *Chione undatella* could be confused with a sorted fossil assemblage having a bell-shaped size frequency distribution. The lack of distinct polymodality in any of the histograms generated by smaller samples suggests that a distinct bimodal or polymodal distribution does not commonly result from accidents in sampling within the test range of N=182 to 309. Provided that a sample is collected from a defined stratum (or unit of sedimentation), polymodality associated with an N of about 200 or more shells more likely would indicate the population structure of the fossil community rather than accidents in sampling or sedimentary processes.

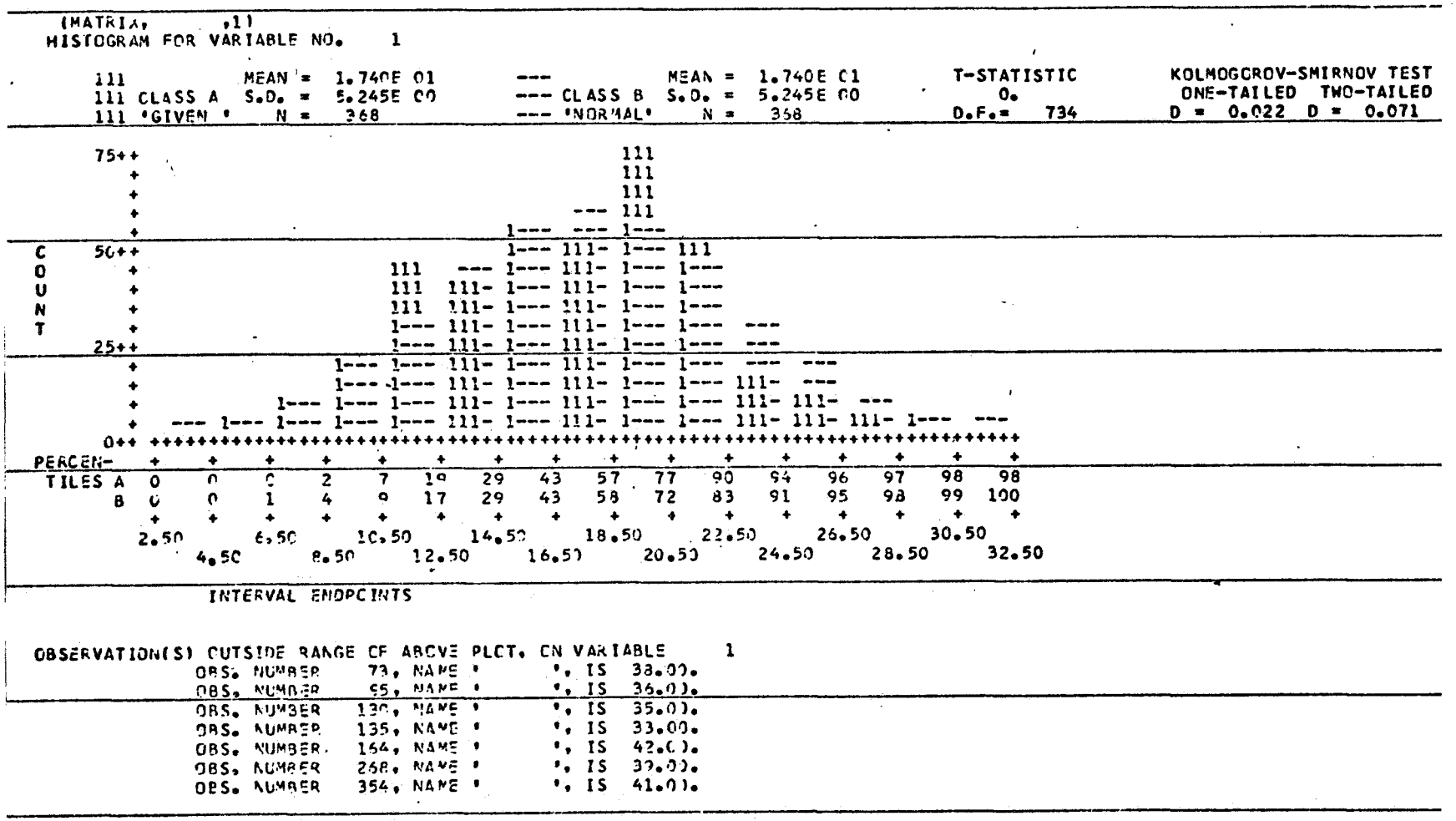


Fig. 9. Shell length, *Chione undatella*, N = 368.

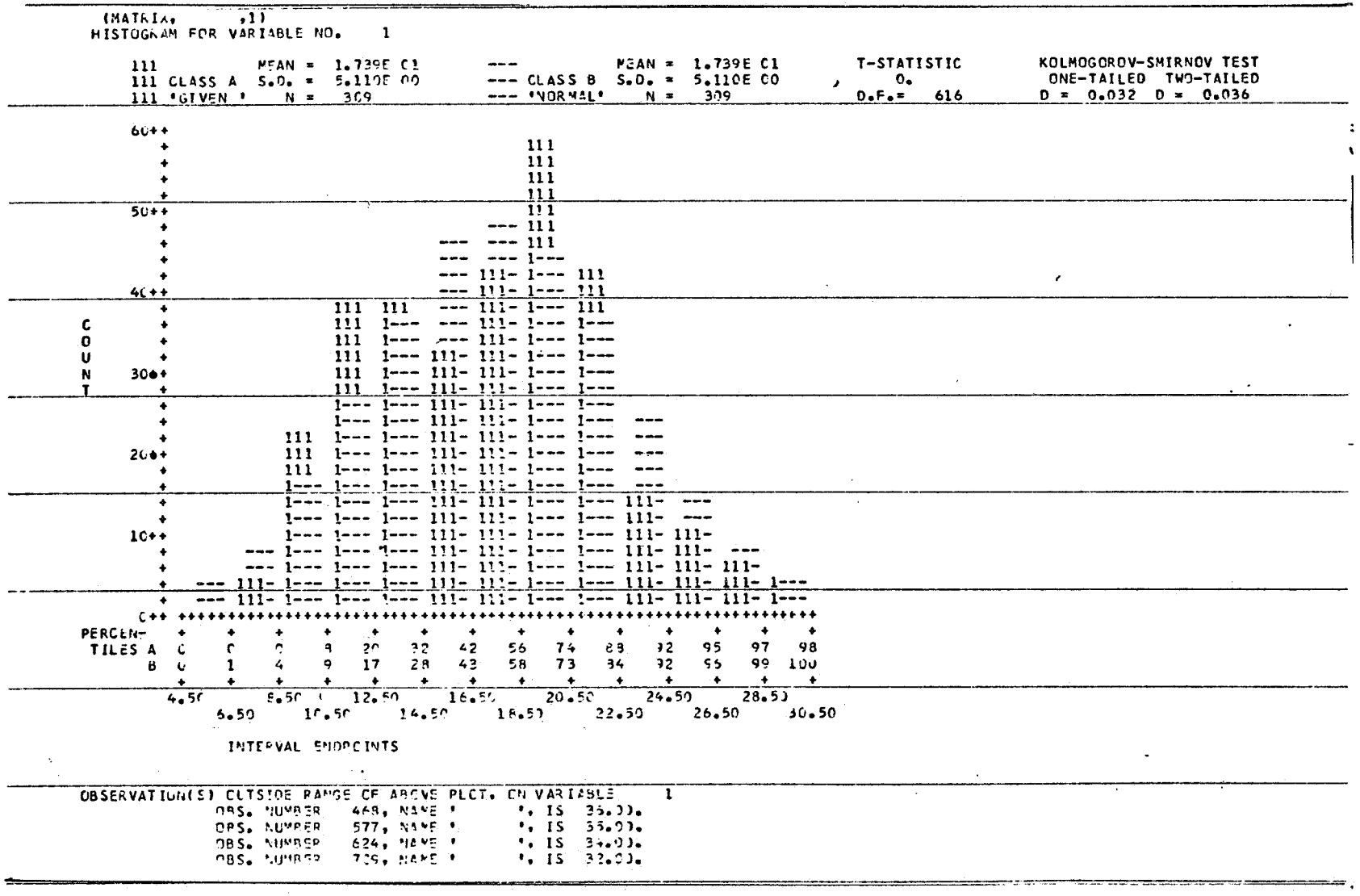


Fig. 10. Shell length, *Chione undatella*, N = 309.

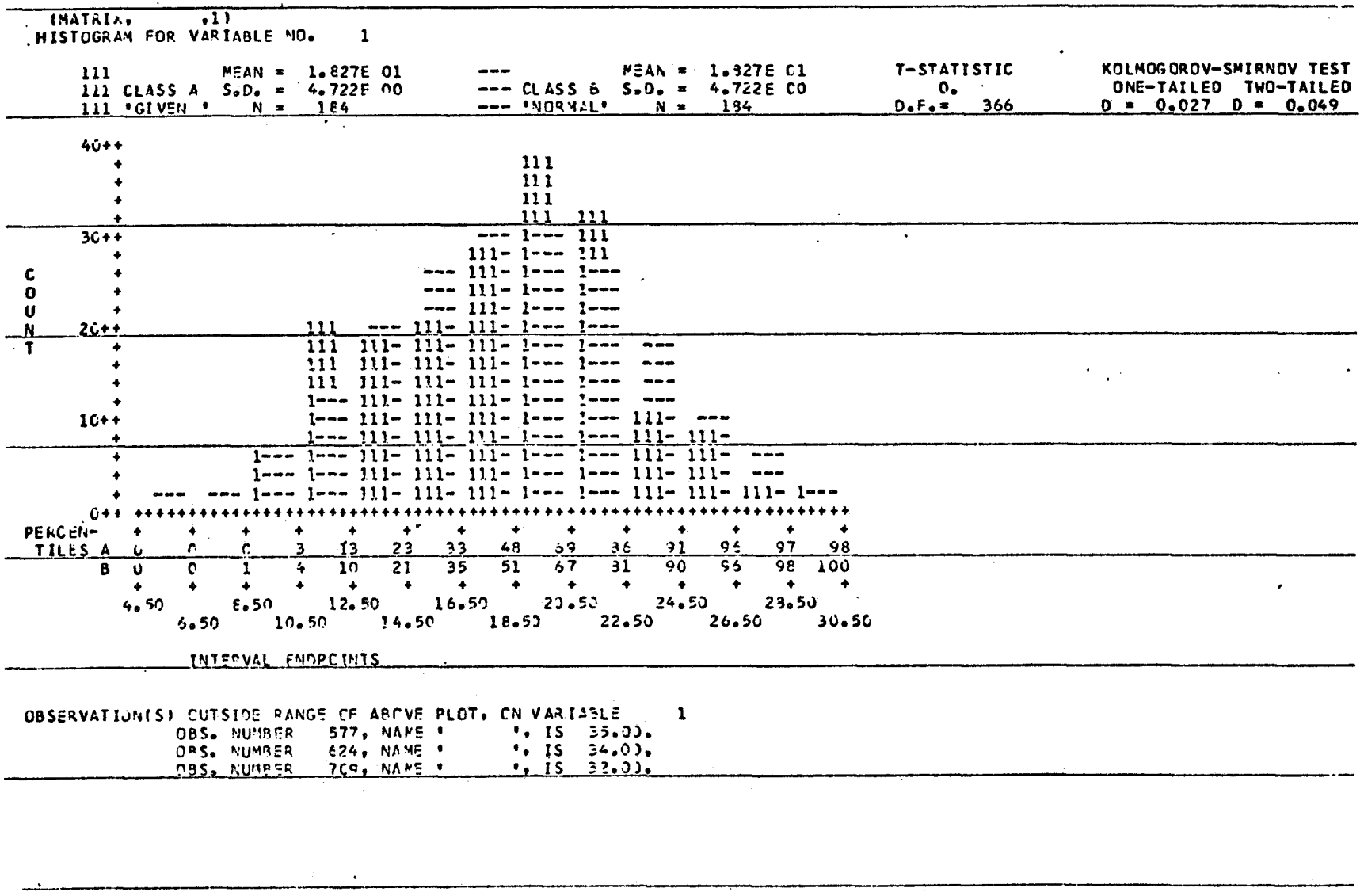


Fig. 11. Shell length, *Chione undatella*, N = 184.

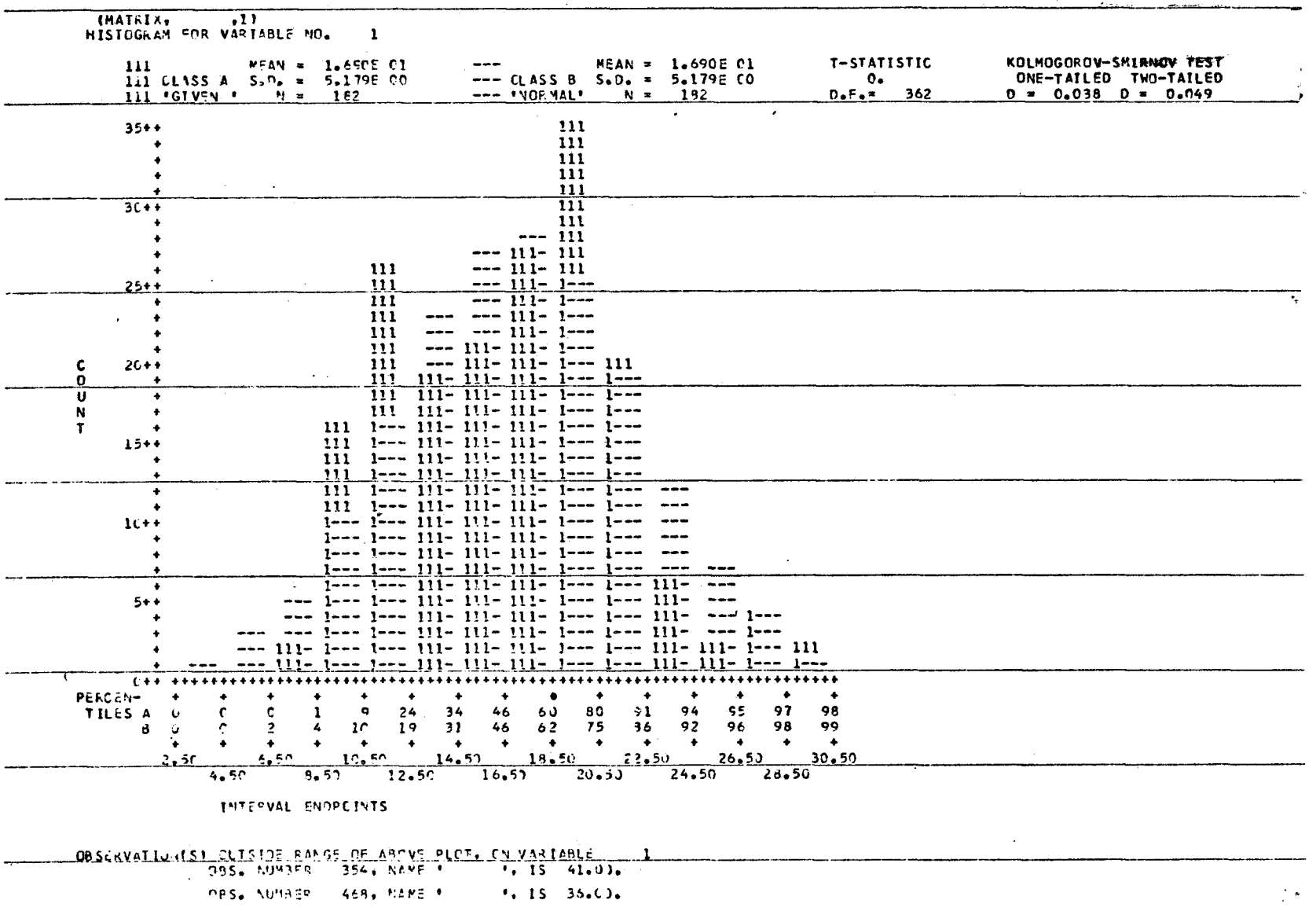


Fig. 12. Shell length, *Chione undatella*, N = 182.

Population Structure

The *Chione undatella* study demonstrated that recruitment occurs during an 8-month season with a peak month of effective reproduction in the late spring or early summer. This seasonality of recruitment was inferred from the ridges-per-shell histogram, but since it was also shown that the number of ridges per shell may be calibrated in terms of shell size, the size histograms may also serve as guides to seasonal recruitment. The frequency distribution of the age groups derived from study of the ridges-per-shell histogram is similar to the pattern predicted by the computer of Craig and Oertal (1967) for a hypothetical population in which there is a constant or nearly constant rate of recruitment, constant high rate of mortality, and a decreasing annual rate of growth. Such conditions were concluded in the author's study of relationships between annual layers and fortnightly ridge increments in the *C. undatella* shells. This agreement between ecologic theory — or its predictions — and evidence provided by the occurrences of growth layers in shells of a living species tends to validate the paleogrowth method of determining population structures.

The accuracy of estimating mortality seasons from direct study of shells depends on how accurately the marginal growth layers represent the season in which death occured. Observations of shell growth and of annual layer morphology makd it evident that a regular winter hiatus is the rule for temperate species. This hiatus varies with individual organisms and environment and may or may not be preceded by a slow growth layer. It was also observed that pelecypods exposed to unfavorable environmental conditions may suspend the shell growth for days, weeks, months, or as long as 1-1/2 years at a time, and that this hiatus may be recorded as a disturbance ring only if shell growth is eventually resumed. Consequently, the lack of a slow-growth deposit on the ventral margin of an empty shell is *not* a sure indication that the organism expired during the season of active growth, neither is the marginal slow-growth layer of an empty shell necessarily an indication that fatality occurred in the slow-growth season.

Paleoclimate

Since there is a general relationship between temperature and rate of shell growth in pelecypod species of temperate climates, one should expect to find morphological differences in the annual growth layers of

shells formed in differing climates. The rate of shell growth measured in some fashion (such as the amount of skeletal material added to the shell per unit time) is one of the most obvious measurements that could be made of a fossil shell. In several previous investigations (Weymouth, 1923, Weymouth *et al.*, 1925, 1931, Mason, 1957, Ansell *et al.*, 1964, Barker, 1964, and Clark, 1968), annual means of water temperature were correlated with the thicknesses of annual and subannual growth layers in shells of the living species *Tivela stultorum, Siliqua patula, Pecten maximus, Mercenaria mercenaria, Mactra solidissima, Chione cancellata, Anadara ovalis,* and *Pecten diegensis*. In the case of *M. mercenaria,* the author (Barker, 1964) reported that the average maximal thicknesses of growth laminae in shells from Bogue Sound, North Carolina, were numerically intermediate between averages similarly obtained in study of shells from Boothbay, Maine, and Bradenton, Florida. The author has since learned of contrary results reported by Chestnut (1952). Chestnut's data indicate that the shell growth rate in Bogue Sound is only slightly greater than in most of the New England localities and considerably lower than the average reported for Cape Cod, Massachusetts, by Belding (1931). Unlike the other investigations in which marked specimens were left undisturbed for a full year, Chestnut's data refer to marked specimens that were measured repeatedly throughout the year. These repeated observations may have interrupted growth repeatedly, thereby inducing a lower annual average growth rate. The author has since examined thin sections of additional *M. mercenaria* shells from Boothbay, Bogue Sound, and Bradenton. The same differences of growth laminae thicknesses and ridge spacing were obvious. Moreover, as shown in Table 19, the average breadths of major increments Nos. 1-5 are 50 percent greater in the Bogue Sound shells than in Boothbay shells. Differences between the Bogue Sound and Bradenton averages are so small as to be of doubtful significance. If the slight difference indicated by these data were substantiated in further study, then the postulated inverse temperature-growth relationship would appear to take place in Bradenton where the monthly average water temperature varies from 63.4°F in January to 85.6°F in July and August. These temperatures reflect a climate much warmer than that of the North Carolina coast where monthly averages vary from 58.6°F (March) to 80.4°F (August).

Table 19. *Mercenaria mercenaria* measurements of annual shell growth layers

Locality	Annual rate of growth (mm per year)						Annual mean water temperature (°F)
	Year I	II	III	IV	V	Mean	
Boothbay, Maine	6	12	10	15	10	10.6	46.1 (Portland, Maine)
	13	8	3	8	9	8.20	
	Mean (two shells): 9.40						
Bogue Sound, North Carolina	35	25	16	13	7	19.2	69.3 (Diamond shoal lightship)
	12	22	27	13	6	16.0	
	Mean (two shells): 17.6						
Bradenten, Florida	18	25	15	20	18	19.2	75.3 (St. Petersburg)
	12	26	14	13	5	14.0	
	Mean (two shells): 16.6						

Despite the preceding examples of temperature-growth relationships, however simple or complex they may prove to be, contrary results were obtained in study of shells of another species, *Protorhaca staminea*, from localities on the Pacific Coast from Auk Bay, Alaska, to San Diego, California. The thicknesses of the growth layers in these shells are so variable among individuals of a single locality as to suggest that local environmental factors have a greater influence on the annual rate of shell growth. It is conceivable that a study of large numbers of shells could reveal statistically significant relationships between the average growth rates and annual mean temperatures of the localities. However, on the basis of present knowledge, the rate of shell growth of an individual of this species has dubious climatic significance, and the same must apply to any fossil shell unless there is some reason to presume that the species had a simple relationship to temperature.

Seasonality

The presence of a continuous cyclic variation in the environmental factors affecting shell growth (seasonality), seems to be clearly expressed in the spacing of subannual growth layers formed by many temperate water dwellers. The clearest evidence of this was seen in shells of *Mercenaria mercenaria* from North Carolina, where growth in this species is known to be continuous throughout the year. The annual cycles of ridge-spacing apparent in a shell decrease in amplitude with increase of age. Amplitude variations are also apparent in comparisons of different shells from the same locality. Since these shells are of comparable sizes and ages and have a common date of live collection, the amplitude variations do not represent differences of growth between the years. It seems more likely that erraticisms in these annual growth cycles resulted from local environmental phenomena affecting the rate of shell growth. Despite these complications, a similar periodicity in the growth layering of a fossil shell would show that the organism underwent a continuous or almost continuous annual variation of growth rate.

A few other examples of continuous shell growth through two or more consecutive years were recognized in shells from subtropical and tropical seas. Annual growth in the subtropical species *Pinctada radiata* is seen as a distinct cyclic variation in the spacing of apparent monthly growth

layers forming scalelike ridges on the shell surface. The ratio of eleven or twelve ridges per cycle persists for as many as three cycles in a large shell. The Tridacnid shells have up to four annual growth layers per shell. As there are close to twenty-five apparent fortnightly shell increments in each major growth band, the growth bands seem to be nearly complete records of annual growth. The slow growth portions of the annual growth layers usually lack expression on the shell surface, but on some shells they may form weakly incised U-shaped grooves of thin, weakly raised rings as in the Florida and North Carolina *M. mercenaria*. Although the growth laminae forming the slow growth portions of the annual layers are relatively thin, as was reported in an earlier study (Pannella and Mac Clintock, 1968), no reversals were observed in the spacing of concentric ridges or in the thicknesses of growth laminae either approaching or following the slow growth layers. Instead, the successively added ridges increase *steadily* in relief and spacing, and the successively added growth laminae forming the growth bands are of uniformly increasing thicknesses. These features of the Tridacnid annual growth layers show that the organism itself regulates the rate of shell growth. The Tridacnids seem to have a quantum type of annual growth cycle, in that the steadily accelerating growth precess is abruptly interrupted for a short period of slow growth on a once a year basis. Annual growth layers considered to have been formed without a season of hiatus and having features similarly suggestive of a quantum type of cycle were seen in shells of *Cucullaea labiata*, a neritic dweller of subtropical and tropical seas in the Indo-Pacific area, and in shells of the Pinnidae from tropical waters of the Gulf of California.

The other shells examined, whether of tropical, subtropical, or temperate dwelling pelecypods, show evidence of lengthy seasonal hiatus at the end of the first or second growing season. As the successively later formed growth bands have decreasing sizes and are comprised of fewer subannual increments, the seasonal hiatus appears to increase as the organism grows older. In most of the shells from temperate waters, there is an apparent annual variation in the thicknesses of subannual increments formed in year I or in years I and II. The finer increments formed in the later years appear to be equally spaced, as though all of them are formed in the midst of the rapid growth season.

Exceptional to the preceding group are the shells of *Saxidomus*, *Zirfaea*, *Platyodon*, *Cardium*, and a few others from temperate waters that show instead a quantum type of annual growth cycle in all years of growth. The numbers of apparent fortnightly increments in the annual growth layers of these shells are commonly suggestive of continuous growth in the first 2 years. All of the tropical and subtropical shells with features of seasonal hiatus lack any evidence of cyclic variation of growth rate. Ontogentic control of growth rate is evident in some of these shells, which show a steady increase in the thicknesses of subannual increments with increase of age. Others have almost equally sized subannual increments, which could represent either internal regulation of growth rate or the lack of seasonal changes in the environment, or both.

In summary, the preceding features of annual growth layers are complexly related to the seasonality of climate and to the internal growth factors of the organism. Although there is a relationship between cyclic variations in the thicknesses of growth layers and seasonality, the lack of continuous cyclic variation of growth rate does not necessarily indicate a non-sesonal tropical climate. The quantum type of annual growth cycle may also result from internal regulation of growth rate or from a seasonal hiatus sufficient to preclude a clear record of seasonal changes of growth rate. While the data may permit the recognition of seasonality in shell growth layering, they do not provide positive criteria of tropical or subtropical climates. Hence, on the basis of present criteria, the most that may be anticipated in paleontological application is to obtain a fossil species that grew through a large enough part of the year to record seasonal changes of growth rate, if any. Judging from the observations on Recent shells, ideal timekeepers such as *Mercenaria mercenaria* are extremely rare. Many species would have to be represented in a sample of a fossil assemblage or a number of fossil assemblages before a significant indication of climate could be obtained.

Disturbance rings — Surficial erratic rings and common microgroove deposits occurring in a fossil shell would have an uncertain meaning, since they are formed by pelecypods that are exposed to various unfavorable physical and chemical conditions. Shell repair marks are more significant.

In *Mytilus edulis* and other epifaunal pelecypods, shell breakage may result from collisions with floating objects, but rocks and large empty shells churned up during a storm could also collide with an epifaunal organism. Both epi- and infaunal species may suffer shell damage during attacks by predators ranging from gastropods to elasmobranchs and bony fishes. To the author's knowledge there is no experimental information on how a non-ostreid pelecypod may form a disturbance ring containing sand and other obviously detrital particles. Oysters are known to include large amounts of detritus in their shells due to loose adhesion between mantle and shell, and, in estuary waters of variable salinity, they may form calcareous chambers filled with muddy water trapped in puckerings of the mantle (Worsnip and Orton, 1923). There are several reasons why these ostreid mechanisms do not apply to the inclusion layers observed in *Mercenaria mercenaria*: (1) there is normally a tight seal between mantle and shell, and (2) the detritus does not occur throughout the entire shell and there is no suggestion of chambering. Other means are suggested based on the morphology of the shell and available ecologic data.

On the inclusion of sand grains

Thin sections of a shell of *M. mercenaria* from Bogue Sound, North Carolina, revealed the presence of sand grains in some annual slow growth increments of the middle and inner mesostracum. The fact that these inclusions are related to a particular season of the year (slow growth layer) suggests that abnormal activities are required to enable them to move inward over the center of the mesostracum. In each of the slow growth layers with inclusions, the sand grains rest upon a common pre-inclusion growth lamina and are enveloped by a common post-inclusion microgroove deposit. In each case, the inclusion of sand grains must have occurred after the disturbance when the valves were open and the organism was on the verge of resuming shell growth. One possible explanation of the inclusions is that they resulted from extreme movements of mantle, shell, and foot organ as in the activity of a dislodged burrower. The author observed that *M. mercenaria* and other passive burrowers of medium to large sizes do not burrow easily when they are laid upon their sides on a horizontal surface. Typically, the clam moves about until it falls into a depression or abuts a larger shell or

some other object against which it may become lodged with its ventral or anterior end oriented downward into the substrate. Only in this position can a large part of the foot be inserted into the substrate for burrowing. Since it was observed in Cholla Bay that the attainment of a favorable burrowing position after dislodgement by a storm involves an extreme amount of locomotory activity, the gaping shell repeatedly drawn over the substrate could result in the deep insertion of sand between mantle and shell.

Correlation with hurricanes

There is some indirect evidence of this. Field study (Chestnut 1952) showed that the season of slow growth in Bogue Sound is during late summer and early fall. In this same season, tropical cyclones of hurricane intensities commonly sweep over the coastal sections of the Gulf and South Atlantic States. Although these hurricanes are usually little more than 100 miles in size, they persist for 1 to 4 weeks and travel hundreds of miles up the seaboard. Meteorologists (Dunn and Miller, 1964) classify them according to the speeds of their circular winds: minor, winds less than 74 mph, minimal; 74-100 mph, major; 101-135 mph; and extreme; 136 mph and higher. Most of the minor hurricanes that have occurred in the present century produced large waves causing millions of dollars of damage in Georgia and the Carolinas. It is thus probable that any of the hurricanes in Bogue Sound would be sufficient to dislodge a large number of the pelecypods burrowing there. Hurricane records (Tannehill, 1955; Dunn and Miller, 1964) were consulted to compare the sequence of inclusions in the shell with occurrences of hurricanes in Bogue Sound. The sand grains occur in annual slow growth layers Nos. 3, 7, 8, and 9. Judging from the good state of preservation of the articulated shell, its age seems more likely to be a few decades rather than a number of centuries. Even so, the records were checked as far back as the year 1700. Only one correlative sequence was found:

Date	Wind speed	Annual slow growth No.
1949, August 24	minimal	3
1953, August 13-14	minimal	7
1954, October 15	extreme	8
1955, August 12, 17	minimal	9
1955, September 19	minimal	9

In the correlation of the late summer hurricanes of 1955 with the inclusion layer in annual slow growth layer No. 9, it is assumed that shell growth ceased to occur for a period of about one month after the first hurricane, or that only one of the three hurricanes dislodged the clam. There were no hurricanes in the Bogue Sound area during the years 1950-52, 1956-59, and 1961-62. This exact correlation between hurricanes and sand grain inclusions would be improbable as mere coincidence.

Cape Hatteras storms — An alternative source for the phenomena would be the storms originating locally. Gales are produced by interactions between land breezes and warm air currents of the Gulf Stream flowing within 20 miles of Cape Hatteras. However, the longitudes of Morehead City and Cape Hatteras are 65 miles apart, and the storm waves originating near the Cape would not be as effective in Bogue Sound, which is sheltered by a 2-mile-wide barrier island. Furthermore, the Cape Hatteras storms usually occur in the winter, which precludes correlation with the inclusion of sand grains in the late summer-fall slow growth layers of the shell.

Paleontological evidence of storms? — Provided the process of sand grain inclusion has been accurately deduced, a severe storm is suggested by the occurrence of an arenaceous disturbance ring in a fossil shell. Cross correlations of apparent major storm records among several autochthonous fossil shells could thus permit the recognition of successive generations represented in the assemblage. The resulting calendar of stormy seasons and years would be important in the study of paleoclimates, for in the Recent Epoch the intensities and frequencies of tropical cyclones and other forms of atmospheric disturbances are generated by annual changes in the heating of the atmosphere and related annual fluctuations of marine currents and major air masses. Of the phenomena considered in this search for criteria of "seasonality", the process by which non-ostreid pelecypods incorporate sand in shell seems most deserving of further study.

Rate of Rotation of Earth

Study of shell growth in living pelecypods revealed several sources of error in the measurement of lunar periodicities expressed in the growth layers of shells. Occasional omissions of daily increments from the growth record not only result in an underestimation of the fortnightly (or monthly) periodicity, but may also result in an extremely high apparent periodicity measurement where the growth rhythm is related to the formation of relatively thin concentric ridges. The latter type of error is less likely to occur if study is confined to shells with equant ridges and troughs. However, these forms are associated with neritic environments. Since the fortnightly and monthly rhythms of shell growth are based on innate mechanisms, they could persist as vestigial processes in pelecypods living under non-tidal conditions. Biological experiments (discussed in Chapter I) have shown that the periodicity of a biorhythm undergoes a spontaneous change when synchronization with the environmental rhythm is no longer functional. Consequently, the actual periodicity of a growth rhythm in a non-tidal pelecypod may be a poor indication of the true lunar periodicities in the environment. The measurement of length of day in relation to the year as recorded in the growth layers of a shell suffers from similar complications. Shell growth that is continuous throughout the year seems to be rarely approximated in any of the species included in this investigation. Moreover, as the apparent daily rhythm of shell growth in at least one species (*Kellia suborbicularis*) was found to be independent of obvious environmental factors, there is the possibility of endogenous variations of the circadian periodicity in deep water or in other environments where contrasts between night and day are very weak. The ideal paleontological calendar would be a shallow water shell in which the growth layers occur with constant numerical relationships and without any signs of hiatus. Of all the Recent shells examined, shells of *Mercenaria mercenaria* from Florida and North Carolina most closely approached this ideal. These specimens thus served as objective guides for study of fossil shells.

Search for comparable fossil shells

Fortnightly rhythms of growth were recognized through study of many fossil pelecypod shells obtained from museums and in the field. Only a few of these shells are sufficiently well-perserved for studies of finer increments, and the prospects are diminished further when specimens bearing disturbance rings are extracted from the sample. Despite these limitations, the periodicities of apparent fortnightly and monthly increments have been estimated in terms of the number of included daily growth laminae. Where thin section observations have been necessary, the growth laminea have been counted in the mesostracum in order to avoid errors due to partings that are common in the ectostracum of many species. Measurements of the month in relation to the year have also been obtained from shells that appear to have been secreted on a year round basis.

Statistical method — A brief discussion of the statistical method used in obtaining the measurements seems essential, for the results depend on the basic considerations of what is to be measured and how. Where the increments are variable in shape, or for some other reason lack precisely definable boundaries, it is often the case that as many as three finer increments occupy the boundary region. To which of the adjacent larger increments should one, two, or all of the bounding finer increments be assigned? Each boundary that is delimited on this basis introduces a subjective error into the measurement. This error may be decreased if the finer increments are counted continuously through a sequence of contiguous larger increments. It may also be the case that different numbers of larger increments are sampled in the different shells. In this case, a continuous count of the finer increments through a sequence of ten larger increments provides a less biased estimate than a count through only one larger increment. This must be so, because a boundary selection error affecting the one cycle measurement by ± 0.10 would have one-tenth as much influence (± 0.01) on the ten-cycle measurement. The margin of error is critical to the study of changes in the month or day. However, in order to take into account individual differences between shells of a species, it is necessary to include all of the specimens in

the averaging. This has been possible through the weighting of measurements according to the number of larger increments sampled:

$$\bar{X} = \Sigma rb/\Sigma b^2.$$

where r is the number of finer increments (e.g., ridges), and b is the number of larger increments (e.g., bands). The standard error of one measurement of r in a total of N traverses is taken as

$$S = \left(\frac{\Sigma (r - \bar{X}b)^2}{(N - 1)} \right)^{\frac{1}{2}}$$

According to the usual principle of weighting, the standard error of the mean is inversely proportional to the square of b:

$$S_x = \frac{S}{\left(\Sigma b^2\right)^{\frac{1}{2}}} .$$

In this study, the $\bar{X}$ as defined above has been estimated for species of several time stratigraphic intervals. These estimates are averaged and the resulting means are considered to be representative of the midpoints of the intervals. Some of the observations reported in previous studies are used in obtaining estimates of the grand means. These observations are also averaged by the weighting method defined above.

The growth layers — Most of the specimens examined by this writer (see Table 20) have major bands and grooves that are similar to the annual layers known from field studies of modern bivalves. Concentric ridges or other clusters of growth laminae thicken and thin in relation to these major increments, there being evident a major cyclic variation of growth rate. Thin sections of Cenozoic and late Cretaceous specimens bearing these major increments reveal that the groove deposits are translucent and exhibit the extinction patterns considered diagnostic of slow-growth layers in shells of Recent bivalves. Many of the specimens show evidence of a relation between aging and progressive decrease in the sizes of the growth layers. In the successively later-formed major layers of these specimens there is a decrease in the number of finer increments. In

Table 20. Growth layers counted in fossil bivalves

20a. Growth laminae per cluster

Geologic age, species, and locality	Number of specimens	Number of ridges	Number of growth laminae
Pleistocene			
Chione californiensis Sandstone near Punta Cholla, Sonora, Mexico	1	16	236
		5	74
	2	10	148
$\bar{X} = 14.75$ $Sx = 0.02$		5	73
	3	7	103
		5	74
	4	8	118
	5	6	36
		4	16
Chione succincta Palos Verdes Fm., Newport Beach, California	1	4	59
		6	89
		3	46
$\bar{X} = 14.78$ $Sx = 0.15$	2	4	57
		3	45
Chione undatella San Pedro Sandstone, San Pedro, California	1	11	163
		3	43
	2	8	118
$\bar{X} = 14.77$ $Sx = 0.05$		5	73
		2	30
	3	4	59

Table 20a. Continued

Geologic age, species, and locality	Number of specimens	Number of ridges	Number of growth laminae
Pliocene			
Chione cancellata Caloosahatchee Fm., Southern Florida	1	7	105
		3	45
	2	6	89
$\overline{X} = 14.84$ Sx = 0.13	3	3	44
		3	42
Codakia orbicularis Caloosahatchee Fm., Southern Florida	1	5	74
	2	5	73
	3	4	60
$\overline{X} = 14.82$ Sx = 0.10	4	4	60
Eocene			
Meretrix splendida Lutetian, Morigny, France	1	7	105
		5	73
$\overline{X} = 14.87$ Sx = 0.13		2	30
Paleocene			
Venerid shell fragments in sandstone thin section, Meganos Fm., Byron Quad., California		4	60
		4	60
		4	59
		3	45
$\overline{X} = 14.85$ Sx = 0.06		3	44
		2	30

Table 20a. Continued

Geologic age, species, and locality	Number of specimens	Number of ridges	Number of growth laminae
Paleocene Continued		2	29
		2	29
Upper Cretaceous			
Crassatella vadosus Ripley Fm., Coon Creek, Tennessee	1	7	211
		6	177
		5	148
$\bar{X}$ = 29.65 Sx = 0.17		5	147
		5	149
		4	114
		3	89
		2	60
Glycymerus lacertosa Ripley Fm., Coon Creek, Tennessee	1	8	238
		5	148
	2	4	120
$\bar{X}$ = 29.76 Sx = 0.07		2	60
Upper Lower Cretaceous			
Lucina subundata Cody Shales, Greybull, Wyoming	1	7	208
	2	5	150
$\bar{X}$ = 29.81 Sx = 0.13			

Table 20a. Concluded

Geologic age, species, and locality	Number of specimens	Number of ridges	Number of growth laminae
Middle Jurassic			
Aequipecten acuticostia Blockley, Gloucester, England	1	3	90
$\bar{X} = 29.85$			

Table 20b. Clusters of growth laminae per major increment

	Sample	Number of major increments	Number of ridges
Upper Cretaceous			
Idonearca vulgaris	Providence Sand (9 shells)	4	99
		3	75
		3	75
		2	51
		2	50
		2	49
		1	25
		1	25
		1	24
Idonearca vulgaris	Ripley Fm., Coon Creek, Tennessee (19 shells)	6	150
		5	125
		4	100
		3	74
		3	75
		3	75
		3	76
		3	75
		3	75
		3	75
		3	75
		3	75
		2	51
		2	50
		2	50
		2	50

Table 20b. Continued

Sample		Number of major increments	Number of ridges
Upper Cretaceous Continued		2	49
		2	49
		2	50
Idonearca vulgaris	Cussetta Fm. (6 shells)	2	51
		2	51
		2	50
		2	50
		2	49
		1	26
Idonearca vulgaris	Coffee Sand (2 shells)	5	125
		3	74
$\bar{X} = 24.99$ Sx = 0.07			
Upper Pennsylvanian			
Myalina subquadrata	Wayland Fm., Brownwood, Texas (5 shells)	5	64
		3	39
		3	39
$\bar{X} = 12.82$ Sx = 0.07		3	38
		2	25

Recent bivalves, similar sequences of ridges per annual layer have been related to a progressive lengthening of the season of dormancy with increasing age of the individual.

Growth laminae and other fine units are conspicuous on the surfaces of many specimens, and in a few instances it is possible to approximate the number of striae per ridge cycle. This cursory determination is the least precise method of study. In the Cenozoic specimens, striae related to crinklings of the periostracum or to other irregular partings of the ectostracum tend to obscure the translucent and semiopaque components of the growth laminae. In all of the specimens, the sequences of growth laminae are broken by encrustations, fractures, and other surface alternations. The growth laminae were most distinctly observable in vertically oriented thin sections.

Days per month

Plio-pleistocene — Well-preserved shells of *Chione* and *Codakia* have been among the most suitable for the recognition of the apparent fortnightly and monthly clusters of growth laminae. The *Codakia orbicularis* specimens have from seven to twelve sharply incised major grooves considered as annual slow-growth layers. The number of ridges per major band varies from fifteen to twenty in the first-formed major layer and decreases in the second- and later-formed major layers. The *Chione californiansis* and *Chione succincta* specimens have fewer of the supposed annual layers, but again the number of ridges per major layer undergoes a progressive decrease in the later bands. In specimens of these three species, the concentric ridges become more closely spaced in the smaller bands of older age. These specimens thus show the seasonally discontinuous growth plan so commonly found in living bivalves. Evidently, growth occurred during only a portion of the year, with the hiatus season becoming longer as the organism grew older. In consequence, the growth laminae have been counted in several discrete bands. Shells of two species, *Chione undatella* and *Chione cancellata*, are lacking in major growth layers. The grand means of the Pleistocene and Pliocene measurements listed in Table 20 are, respectively, 14.77 ± .01 and 14.83 ± .00. Since the growth laminae counted are identical to the units considered to be formed with a daily periodicity in Recent bivalves, these figures may represent fortnightly cycles of growth equivalent to a synodic

month of 29.54 ± 0.02 days in the Pleistocene and 29.66 ± 0.01 days in the Pliocene.

Eocene — Meretrix splendida shells available for study have unbraded umbones, and it has been necessary to confine the counts of growth laminae to the mid-regions and ventral portions of the shells. These portions of the shells bear from six to nine weakly incised concentric grooves spaced about 2 to 4 mm apart. The number of grooves per shell correlates with the number of major lines of growth visible in the dorsal margins of the shells. Each growth band delimited by these grooves is comprised of two very indistinct concentric ridges or undulations. In thin section, ridges are observed to be related to clusters of about fifteen growth laminae, and the grooves are related to extremely fine (100 u) translucent deposits. If these grooves were formed annually, shell growth may have been restricted to a single month of the year during the ontogenetic stages represented. The measurement of 14.87 ± 0.08 may thus be interpreted as indicating a 29.74 ± 0.16 day synodic month. Pannella, MacClintock, and Thompson (1968) reported an average of 29.96 for a species considered as being of about the same geologic age. Simple averaging of the two means yields a grand mean of 29.83 days per month.

Paleocene — This sample consists of shell fragments in sandstone from the Meganos Fm. Coalinga, California. All of the fragments visible on the surfaces of this rock sample have similar concentric ridge features. As viewed in thin section, all of these fragments have a complex crossed-lamellar ectostracum and a narceous endostracum. The ridges are related to a spreading of the mesostracum and are usually comprised of fourteen or fifteen growth laminae (see Plate 6:3). Based on these structural features, the shell fragments seem most likely referable to a non-cancellated Venerid group. Because no differences were discovered between these fragments, they have not been considered as remains of several species. The available evidence points to similarity, and they are grouped together with the weight of a single sample. The mean is taken as an estimate of the days per fortnight, indicating a synodic month of 29.70 ± 0.12 days.

Late Cretaceous — Monthly increments in shells of *Crassatella vadosus* were examined in thin sections located on the shell midlines in the second and/or third major increments. The resulting mean number of

growth laminae per ridge cycle (Table 20) seems to reflect a synodic month of 29.65 ± 0.07 days can be made from specimens of *Glycymerus lacertosus* that is based solely on the recognition of regular groupings of growth laminae. Major growth bands occur on these latter shells, but the grooves between them are marked in the ectostracum and mesostracum as partings of the shell. These grooves are suspect with regard to their having been formed one per year. Nevertheless, the growth laminae seem to be identical to those of *C. vadosus*, in that they are alternations of translucent and semiopaque shell, and their grouping is thus suggestive of a lunar periodicity.

Averaging the preceding late Cretaceous means with means calculated from previously published measurements in three other species of about the same geologic age (Pannella, MacClintock, and Thompson, 1968), the resulting grand mean available for the late Cretaceous is 29.89 ± 0.22.

Mid-Cretaceous — The *Lucina subundata* shells lack major increments that could be considered correlative with an annual cycle of growth. Concentric ridges and numerous fine striae occur on the shell surfaces, with a total of twenty-three ridges on the larger shell and eighteen on the other. The striae range in spacing from 50 microns on the ridges to about 100 or 150 microns on the interspaces between the ridges. Recrystallization has obliterated the original structure of the shell. Despite a lack of information on the longevity of a modern representative of the Lucinid group, a life span of 23 years seems more likely to be the exception than common in Bivalvia. If the ridge formation rhythm of this species were related to any environmental cycle, its periodicity is probably lunar not annual. The striae which tend to occur about fifteen times per ridge cycle on nonabraded shells are assumed to be daily, and the average of 14.91 ± 0.04 per ridge cycle is considered to be an estimate of the synodic month.

Middle Jurassic — Striae on the surface of *Aquipecten acuticostia* are similar to those of Recent Pectinids. Approximately two-thirds of the ventral portion of the shell is sufficiently well-preserved for study, and on this portion there are three contiguous groupings of growth striae (Plate 6:4). Continuous counting of the striae in this sequence of groupings yielded an average of 30. This average could be an approximation of the days per synodic month. However, the lack of any trace of rhythmic

groupings of striae on the larger part of the preserved shell surface means that any connection there may have been between growth and the lunar cycle must have been purely exogenous.

Months per year

Late Cretaceous — Major increments with features of an annual cycle of growth are particularly distinct on the rather massive shells of *Idonearca vulgaris* from the Ripley Formation (Plates 14:1, 14:2, 18). These annual layers consist of growth bands on the order of 1 to 3 cm in size and concentric grooves about 1 mm in breadth. Typically, there are eight to twelve annual layers in a large shell, indicating that the large growth size was due to a moderately longer than average life span as well as to a rapid rate of shell growth. Although the internal shell structures are mostly altered, some thin (<100μ) translucent groove deposits were detected in thin sections of well-preserved shells. Major increments Nos. 1 to 4 (where No. 1 is the one formed in the first year) are weakly delimited by shallow L-shaped grooves. The surfaces of these earlier growth bands form a uniformly curved surface. Commonly, there are about twenty-five concentric ridges in each major increment in the sequence Nos. 2 to 4. There is no crowding of the ridges located adjacent to the grooves of these earlier major increments. The L-shaped groove structure itself consists of the ventral side of one ridge and the external surface of an adjacent ridge. These features of the major increments suggest an annual cycle in which there was a sudden change in the mantle-shell relationship accompanied by a brief slowing of secretion. Assuming that the concentric ridges were formed with a fortnightly periodicity, the tendency for there to be 24 or 25 ridges in each of the earlier major increments may indicate shell growth on a year-round basis. Later growth bands (those commonly formed after No. 4) are narrower and are delimited by relatively wide, deeply incised grooves. These grooves are V-shaped on the shell midline. On the posterior and anterior they become U-shaped and there is some suggestion of a crowding of the ridges within them. However, this apparent crowding seems to be due to the angle at which the grooves and ridges must necessarily be viewed on the shell surface, and it is their observer's opinion that the ridges within the grooves are equal in breadth to the ridges of the growth bands. It seems that, in older age, the seasonal drainage in the mantle occurred

more gradually, but without an apreciable change in rate of shell growth. As there are usually fewer than twenty-five ridges in a later major increment, the later grooves may also represent a seasonal hiatus that became longer and more strongly marked in senescence.

A few of the shells feature erratic rings (Plate 14:1). Some of these minor grooves are connected to millimeter-sized hollows in the shell surface at one or more points along a line of growth. The hollows are formed by sharp foldings of the finer increments (growth laminae and concentric ridges) in the ventral direction of shell growth. A number of increments added below the erratic ring are deformed in line with the hollows, but, as in the parallel folding of rock strata, their deformation decreases gradually with each successive increment and the lines of growth become more uniformly concentric. Similar hollows are formed by living bivalves when sand-sized particles become lodged between the mantle and shell. Other erratic rings occurring on the shells are not related to crinkling of the finer increments and may have resulted from minor disturbances not involving shell breakage or inclusion of foreign particles. The period of time represented by either type of erratic ring may be a few weeks. Assuming that the fossil disturbance rings resulted from natural disturbances of the organisms over comparable periods of time, it is to be anticipated that a major increment bearing one or more erratic rings may include fewer than the most common number of concentric ridges. Only twenty-three ridges occur in the major increment shown in Plate 14:1. Such a major increment is regarded as an incomplete record of an annual growth cycle.

Although major increments Nos. 2 to 4 commonly include twenty-four or, more often twenty-five ridges each, the same ratio has been seen in major increments numbered 5, 6, and even 7. Such a regularity of finer increments per annual band may in some way have resulted from the influence of a subannual periodicity in the environment. For *I. vulgaris* this periodicity may have been fortnightly, there being about twenty-five fortnights to the year. If this species also formed finer increments with a diurnal periodicity, one would expect to find evidence of fourteen or fifteen finer increments within a given ridge. Despite poor internal preservation, one thin section of a shell of *I. vulgaris* has revealed that the ridges are related to cyclic thickening and thinning of growth laminae (Plate 14:5). The semi-opaque layers have a drusy appearance

and the translucent layers are only partly preserved. These sequences of relict growth laminae are not sufficiently complete for a lamina by lamina count through a complete ridge and interspace unit; however, their thicknesses in relation to the ridges (as viewed in the same section along the same growth radius) are on the order of magnitude of a periodicity of fifteen. Thus, based solely on the apparent groupings of growth layers in relation to the band-groove units considered to be annual, the concentric ridges are interpreted as fortnightly clusters of diurnal growth laminae. These apparently fortnightly increments have been counted through the major increments considered as complete annual layers on thirty-eight shells. The resulting mean weighted according to the number of major increments, is considered to indicate that there were 12.49 ± 0.07 months per year.

Upper Pennsylvanian

The *Myalina subquadrata* specimens bear low, foliar concentric ridges grouped within larger growth bands delimited by shallow grooves. These major increments number from three to six per shell. Due to loss of internal structure, they are interpreted as records of annual growth solely on the basis of their external features. The number of ridges per major increment is usually twelve or thirteen, but may decrease in the extreme old age increments located near the ventral margin. Increase of individual age is also related to a decrease in the sizes of the successive major increments and deepening of the concentric grooves. The regular tendency for there to be thirteen ridges per major increment is suggestive of a monthly cycle of ridge formation. In all cases, the concentric groove that follows the first-formed growth band is so wide and weakly marked that the drawing of a boundary seems impractical. The second-formed groove has been used to begin the traverses, since in each specimen it is sufficiently distinct. The traverses were terminated adjacent to old-age growth bands comprising obviously less than the usual number of ridges. The resulting average of 12.82 ± 0.07 provides an approximation of the months per year in the late Pennsylvanian.

Significance of fossil data

The preceding estimates of the number of days per synodic month are plotted with geologic age determinations (see Kulp, 1961) in Fig. 13.

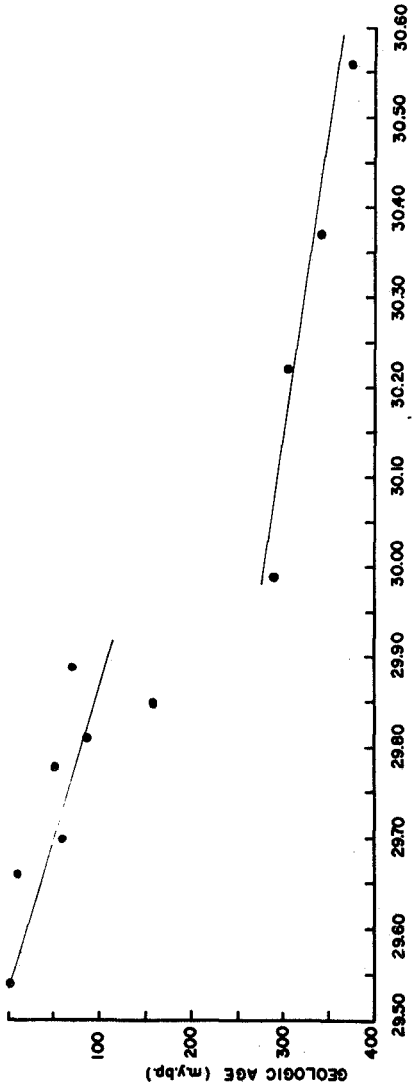


Fig. 13. Scattergram showing the days-per-month measurements in relation to geologic time: Middle Devonian to Late Pennsylvanian (lower right) and Mid-Jurassic to Recent (upper left).

estimates of synodical month are plotted with geologic age determination (see Kulp, 1961) in Fig. 13. Estimates of synodical month periodicities in exoskeletons of Paleozoic mollusks and corals (Pannella, MacClintock, and Thompson, 1968; and Scrutton, 1964) have also been averaged and plotted on this scattergram. No attempt is made to draw a detailed pattern of change in the days per month, because the standard errors of the few data are rather large. What can be shown without extreme curvings of the regression lines are two clusters of the plotted points. Differences in the slopes of the straight lines showing these trends indicate that the rate of change since the late Cretaceous had been only one-third as great as the change apparent for the Devonian-to-Pennsylvanian interval.

The months-per-year measurements seem to indicate that these decreases in the number of days per synodic month may have resulted from deccelera-tion of both the earth and the moon. Multiplying the synodic month measures by the months-per-year estimates, it is calculated that there would have been 373.3 days per year at the end of the Cretaceous and 384.5 days per year in the late Pennsylvanian. Wells (1963) reported an average of 399 days per yearly increment in tetracorals of Middle Devonian age. This figure is in close agreement with the estimate of 398.5 obtained by multiplication of the synodic month average of 30.56 times Scrutton's estimate of 13.04 months per year.

These data suggest that the days in the year decreased at the rate of 0.16 or 0.17 per m.y. during the late Paleozoic, as compared with averages of 0.10 and 0.11 in the Mesozoic and Cenozoic. The months per year appear to have decreased at rates of 0.0026 per m.y. and 0.0028 per m.y. in the Middle to Late Paleozoic and Mesozoic intervals, as compared with a rate of 0.0017 since the end of the Cretaceous. Thus, the detected changes in the synodic month may be attributed to actual lengthening of the month as well as to increases in the length of day.

If the two trends shown in Fig. 13 were combined, the data would appear to show a minimal rate of change for the early Mesozoic. Pannella, MacClintock, and Thompson (1968) cast doubt on the significance of their rather low estimates obtained from some Triassic specimens bearing dis-turbance rings. Also, the Jurassic datum provided by the present study is based on one sample. A meaningful number of samples would be required

before such a pattern can be substantially shown. Ideally, the critical sampling would be in Permo-Triassic and Jurassic time.

VII. SUMMARY

Research commenced with thin section study of the shells of eleven species of pelecypods known from field studies to have annual cycles of growth. Internal microstructural features of the annual layers in these shells provided criteria for recognition of similar, apparently annual shell increments in 86 of 87 other species.

The concentric bands related to rapid growth consist of relatively opaque additions to the palliostracum. The concentric rings or grooves marking seasons of slow growth are associated with relatively thin, translucent palliostracum deposits, or with a brown, optically isotropic substance similar to periostracum. The annual slow-growth layer, when viewed between crossed nicols, has a more regular extinction pattern than the adjacent rapid-growth band deposits.

In shells of some species, especially *Mercenaria mercenaria* and *Venus striatula*, the earlier annual growth layers may be characterized by a cyclic variation of the thicknesses of finer increments. The shells of most other species that were sampled do not show this clearly, if at all, the finer increments being almost equally spaced or of successively greater thicknesses. As the thicknesses of the finer increments indicate the rate of shell growth, most of the annual cycles apparent in the study material show an abrupt transition between the seasons of rapid and slow growth, and many of these cycles suggest an ontogenetic increase of growth rate.

Subannual Growth Layers

Based on observations of the number of finer increments per annual growth layer, it was hypothesised that the finer increments may be related to daily and fortnightly (and in some cases monthly) cycles in the environment. Two types of palliostracum increments, ranging from a few microns to half a millimeter in thickness, may be deposited at the rate of one per day, these are:

1. Complex growth laminae. In shells with the crossed-lamellar structure, the laminae consist of a gray or bluish-gray layer that is translucent in sections less than 30 microns thick,

and a series of much finer semiopaque layers that are usually quite opaque in sections more than 20 microns thick.

2. Simple growth lamina defined by a parting of the mesectostracum:

   a. Pteriidae. Growth laminae composed of segments of nonfoliated, prismatic CaC03

   b. Pectinidae. Growth lamina with foliated structure, the folia being twisted adjacent to the parting.

In the shells of 72 of the 98 species represented, the growth laminae are clustered in relation to concentric ridges or minor growth bands of the external shell surface. These clusters of growth laminae may have fortnightly and monthly periodicities, for there are commonly fourteen to fifteen or twenty-eight to thirty growth laminae per cluster. The number of clusters observed in an annual layer is usually less than the twenty-five (fortnightly) or twelve and a half (monthly) that would accumulate if the pelecypod grew its shell continuously throughout the year. Since all of the workers cited in Table 1 reported that shell growth may come to a complete halt during the slow-growth season, one may expect omissions of subannual cycles from the growth record, and therefore a tendency for less than twenty-five fortnightly (or twelve and a half monthly) smaller increments per annual layer. Likewise, it seems probable that minor hiatuses of a few days result in the omission of a few growth laminae from some of the clusters. In Chapter II it is argued that unless micro-hiatuses are detected in the growth-layering of the shell, counts of growth laminae per cluster may yield apparent periodicities either greater or smaller than the actual periodicity of cluster formation. This accounts for the fact that not each and every cluster in a shell has exactly the same number of growth laminae.

The author attributes the preceding subannual growth layers to processes similar to those known to be involved in the formation of annual growth layers. Alternations of light and dark layers or of shell and partings seem analogous to the larger scale annual growth layers, in that the apparent daily cycle may involve a phase of secretion alternating with a phase of slower or no secretion. Concentric ridges comprised of clusters of growth laminae are related to changes in the relationship between mantle and shell, as is the case for the formation of annual

growth bands. However the three orders of growth rhythms may be synchronized with daily, lunar, and annual environmental cycles, there seems to be an innate basis for the growth-layering phenomena.

Thus, the shell growth layer hierarchy is regarded as a record of geophysical phenomena. Critical to the substantiation of this hypothesis are the following: (1) microhiatuses, their manner of occurrence and whether or not they are expressed in the growth layers of the shell, (2) actual rates of formation of the supposed daily and fortnightly growth layers, and whether or not they are synchronized with cycles in the environment, and (3) relationships between concentric ridges and environments.

Observations on Recent Shells

Growth experiments

Through experiments with pelecypods living in natural and laboratory environments, it was demonstrated that lack of food organisms and various physical and chemical disturbances may induce the individual to suspend shell growth for weeks or as long as 8 months. Thus a major portion of any of the three orders of growth cycles may be omitted from the succession of growth layers deposited. Following a disturbance, a fine translucent growth layer is deposited on the endostracum and on inner part of the palliostracum. This slow-growth layer is considerably thinner than the annual slow-growth layer and forms a concentric microgroove on the shell surface. Experiments with sea mussels over a period of 3 months revealed that adequate food supply combined with a stagnation or calcium depletion of the seawater only permits the growth of periostracum. It is suggested that microgrooves capped by masses of periostracum record similar failures of the calcification process.

Although the preceding types of disturbances were recorded in the shells, minor hiatuses induced by exposing pelecypods to tetracycline were not associated with the formation of disturbance rings. The fact that minor hiatuses may be induced to occur under laboratory conditions tends to support the postulate that they occur in nature.

Attempts were made to raise pelecypods in aquaria where shell growth could be simply observed without repeated disturbance. Several intertidal species survived for long periods in the recirculating seawater aquaria maintained in the university warehouse at Richmond and in the aquaria supplied with seawater pumped in from the ocean at Bodega Head. None of these pelecypods grew under these laboratory conditions. Specimens that lived in the closed system either lacked adequate food or failed to feed normally due to some unknown inhibitory factors. Seawater pumped from the rocky shore of Bodega Head was laden with organic silt. As this seawater passed through a series of pipes and into a reservoir tank, anaerobic decomposition of organic matter charged the seawater with hyrogen sulphide. The resulting acidity of this seawater was an important factor inhibiting growth of pelecypods adapted for life in unrestricted marine environments.

One pelecypod species, *Kellia suborbicularis*, thrived within the seawater pipes and aquaria of the Bodega laboratory. This species is found in natural environments that are stagnant and acidic. Its shell is constructed by growth laminae that are not clustered in rhythmic patterns. Observations on the growth of individuals with tetracycline marks in their shells revealed that the growth laminae are formed with a circadian periodicity. This periodicity persisted both in constant darkness and constant light. Marked specimens were raised for a period of 4 months under various combinations of different illumination cycles and simulated tides. These variations of light and water flow were not expressed in the patterns of spacing of the growth laminae formed by the clams in the experimental aquaria, nor was there any indication of change in the apparent circadian periodicity of growth. Among individuals of the same age group, shell growth was most rapid in the specimens living in aquaria through which seawater passed at the greatest rate. The growth laminae were, on the average, thickest in the shells of these individuals. As in the 1- to 2-day lag time in the turnover of tetracycline, the utilization of food material needed for shell growth may be budgeted so that short-term variations of flow rate are not expressed in the thicknesses of growth laminae. The same time lag would explain the lack of an exogenous fortnightly rhythm of shell growth in this species under natural conditions.

Observations of the rate of formation of concentric ridges and minor growth bands in specimens living under natural conditions support the hypothesis that these increments are formed with fortnightly and monthly periodicities. In *Protothaca staminea* living in Bodega Bay harbor, a complete fifteen lamina cluster was observed to have formed 35 days after the shell margin was notched. Specimens that were left to grow for a total of 72 days formed three and one-half of these clusters of growth laminae, giving an apparent periodicity of 21 days, and so on, with the discrepancy due to an initial 20-day hiatus decreasing toward the expected period of 14.76. A similar rate of ridge formation indicating a 15-day growth periodicity was observed in the growth of marked specimens of *Chione undatella* in Cholla Bay, Mexico. Marked specimens of *Mytilus edulis* attached to a pier in the harbor of Bodega Bay formed minor growth bands with an apparent periodicity of 14 days. Individuals of this species raised on posts in San Francisco Bay seem to have formed their minor growth bands with a monthly periodicity. However, as these minor growth bands are often divisible into two finer growth bands, the underlying periodicity of growth may be fortnightly.

Despite these periodicities of growth, no obvious relationships were observed between phases of the lunar cycles and the formation of concentric ridges and troughs or of minor growth bands and grooves. To test for a statistical relationship, a population of *Chione undatella* was selected for intensive study at Cholla Bay, Sonora, Mexico, for a period of 1-1/4 lunar months. About twenty-five specimens were collected in the same area each 34 days. Comparison of margins of the specimens collected on different days revealed that ridge formation is most common during the new and full moons. There were no correlations between percentages of specimens forming ridges when collected and age group or sample position. Individual genetic variation and the presence of dormant specimens were seen as the most likely factors contributing to the observed asynchrony of ridge formation.

Adaptive significance of fortnightly rhythm

On the basis of mechanical principles, several functions were inferred for concentric ridges and minor growth bands as they occur on the shell as a whole and as they influence the configuration of the ventral margin.

Of these functions, retention of moisture, protection against predators, and stability in the substrate were considered to be the most important in shallow marine environments. This is supported by available ecological data giving evidence that pelecypods with well-developed ridges are adapted to passive burrowing in the intertidal zone, whereas forms with smooth shells or with very weak minor growth bands have life habits that reduce exposure to the effects of oceanic tides. The author's observations on intertidal pelecypods provided at least some indication that their survivoral during spring tide is greater if the concentric ridges are constructed at that time or shortly before. While this impression is the basis for interpretation of the synchronization of ridge building with the fortnightly cycle, the persistent monthly cycles apparent in seventeen percent of the species with clusters of growth laminae sampled in this study invite some other explanation. Whatever the means of synchronization may prove to be in further study, the suggested relationships between the features of concentric shell elements and intertidal environments are compatible with the endogenous properties of the rhythms revealed in the growth experiments.

Conclusions — The observations that were made of Recent shells substantially support the hypothesized relationships between shell growth and environment. In light of the experimental data provided by this investigation, it seems plausible to decipher records of growth related to daily, lunar, and annual rhythms in fossil shells. However, it is important that an unbroken sequence of growth layers be selected for the measurement of a periodicity. Sequences in which there are disturbance rings and anomalous variations in the number of finer increments should be avoided if an exact averaging of the periodicity is sought. Moreover, since it is evident that the rhythms are endogenous, the mere presence of a cyclic clustering of growth laminae does not necessarily carry accurate information about regular cycles in the environment. Species that are adapted to tidal flat dwelling may also be represented in the neritic zone where tidal phenomena are comparatively weak (if at all detectable by a mollusk), and it is a generally known feature of biorhythmicity that the periodicity may decrease or increase unless regulated by an external

stimulus. Study is better confined, therefore, to species known from independent geologic evidence to have grown their shells under littoral or near-littoral conditions.

Shell Growth and Paleontology

In addition to the measurement of periodicities, time-significant shell increments may serve as a basis for determining longevity and rate of shell growth in extinct species. The present investigation revealed several complications that are summarized below.

Population structure

Through study of *Chione undatella*, it was shown that a life span of 1 to 2 years and a recruitment pattern with an annual peak are related to a bell-shaped size-frequency distribution. A large number of shells (e.g., 1000) would be required for a statistical distinction between a sorted death assemblage and a biocoenosis of a community with life processes similar to those of *Chione undatella*. The computerized ecological predictions of Craig and Oertal (1967) pertaining to a size-frequency distributions were thus substantiated. This agreement between theory and the occurrences of growth layers in the shells of a living species tends to validate the paleogrowth method of determining population structures, although it is applicable only in the case of large numbers of specimens with adequately preserved growth layers. With regard to the possibility of using growth layers to determine seasonal distribution of mortality, the growth experiments revealed that the lack of a slow-growth deposit on the ventral margin of a shell is not a reliable indication that the organism expired during a season of active growth, nor is a marginal slow-growth layer of an empty shell necessarily indicative of fatality in a slow-growth season.

Paleoclimatology — Comparison of annual growth layers in species with wide geographic ranges yielded various contrary results: (1) a positive correlation between annual rate of shell growth and annual mean of water temperature, (2) positive correlation between growth rate and temperature in the northern part of the species range and negative correlation near the southern limit, and (3) lack of any obvious relationship between growth rate and temperature means.

Shell repair marks and sand grain inclusions occur in Recent shells, thus suggesting the possibility of compiling annual records of storms. However, the weaker disturbance rings have an uncertain meaning, because they are formed by pelecypods exposed to various locally occurring disturbances.

Although variation of subannual growth layer thickness is related to growth in a seasonal climate, interactions between seasonality of environment and internal ontogenetic factors of the species preclude evidence of a nonseasonal climate.

Paleogrowth studies, however useful in conjunction with other lines of evidence, do not seem to be a short-cut to the understanding of paleoclimates.

Observations on fossil shells and detection of change in rate of earth rotation

The author examined many pelecypod shells from shallow marine deposits of Pleistocene, Tertiary, Mesozoic, and Pennsylvanian ages. A few of these shells, especially those of the late Cretaceous and later ages, were sufficiently well-preserved for study of growth layers in thin section. In these specimens, annual and subannual growth layers were recognized as identical to the annual, fortnightly (or monthly), and daily increments of Recent pelecypod shells. Dealing with apparently uninterrupted sequences of growth layers, the number of apparent daily increments per cluster was averaged for different species, and in the shells of species having apparently complete records of annual growth, the number of clusters per year was averaged. The resulting data which were interpreted as estimates of days per month and of months per year agree with those of Pannella, MacClintock, and Thompson (1968), Scrutton (1964), and Wells (1963), in that there seems to have been a considerable increase in the length of day and month during the past 375 million years or more of geologic time. It is emphasised that differences between the data provided by this investigation and those of other workers are so small in proportion to the numbers of shell samples examined that further study is necessary before exact patterns of geophysical changes can be drawn from paleogrowth evidence.

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APPENDIX A

Growth Experiments: Richmond

Apparatus

Materials used in construction of the apparatus consisted of mass-produced articles. Four steel drums, each with a capacity of 55 gals., were lined with doubled, heavy-duty PVC (polyvinyl chloride) bags. These containers held the bulk seawater used in this experiment. Covered with sheets of polystyrene foam, these reservoir tanks were connected in series by PVC siphon hoses (I.D., or internal diameter, 1+1/2 in.). To promote the growth of algal flagellates as food for the pelecypods, an asbestos light bulb fixture was installed in each lid. Ordinary 75-watt light bulbs were used to illuminate the reservoir tanks for an interval of 12 hours every day.

Seven aquaria with stainless steel rims were obtained. Six of the aquaria had a capacity of 15 gals., one of them held 30 gals. These aquaria were sealed at the seams with an epoxy resin to prevent contamina tion of the seawater. The epoxy resin used in this experiment is known as "Resinbond Adhesive 907" (Resin Formulators Co., Culver City, California). A straight-through overflow pipe with an I.D. of 3/4 in. was epoxyed into a hole positioned near the top of each aquarium. I found it was simpler to install the overflow pipes in this manner than to bend the rather large glass tubes into tight "S" shapes. The overflow pipes were connected to the reservoir tanks by flexible PVC tubing. The aquaria were put on racks elevated 2 feet above the tops of the reservoir tanks, so that the overflow would fall downward through the flexible tubes. Each aquarium was equipped with a wooden cover and a 40-watt light bulb housed in a stainless steel reflector. To prevent interference with external lighting, the aquaria were painted black and covered with several thicknesses of paper.

A flexiliner pump circulated the seawater at a rate of 3 gallons per minute from the reservoir tanks to the aquarium tanks. This type of pump is essentially a large (O.D. 2 in.) PVC tube curved around an eccentric cam. The tube is squeezed in the direction of flow by the rotating cam, so that the water is pumped without coming into contact with any metallic part of the pump.

The system contained about 340 gallons of seawater taken from the shore of San Francisco Bay at Fort Mason near the Golden Gate and transported to the laboratory in polyethylene containers. On Aug. 16, 200 gallons of this weawater was discarded and the reservoir tanks were filled with an

equal volume of seawater obtained from the Steinbardt Aquarium, California Academy of Sciences. In the system the seawater was pumped from one of the drums through a 1-inch PVC tube to a group of smaller (I.D. 1/2 in.) "Y" shaped plastic connecting tubes located a few inches above the aquaria. PVC tubing attached to these "Y" tubes conveyed the water to glass tubes leading to the bottoms of the aquaria. Seawater returning from the overflow tubes passed through an 18-inch-diameter polyethylene cylinder containing a 6-inch deep layer of pebble-sized fragments of oyster shell supported by nylon window screening. It was presumed that spreading the seawater over many $CaCO_3$ surfaces would tend to replenish calcium taken up by the organisms. This layer of shell fragments filtered out coarser debris and allowed for some aeration of the water. The seawater was further aerated on raining down into the reservoir tank beneath the filter.

Five of the 15-gallon aquaria were equipped with an automatic fill-and-empty device. Flexible PVC tubing attached to the "L" shaped glass tube passed through a pinch-valve and on to a reservoir tank. Activated by solenoid magnets, the pinch-valves were powered by compressed air (18 psi). When the solenoid was not activated, the compressed air drove a piston down onto the PVC tubing and the flow of water was cut off. There resulted a filling of the aquarium. When the solenoid was turned on, the air flow was cut off and the resilient PVC tubing expanded to permit flow of water from aquarium to reservoir tank. One hour was required for emptying of a 15-gallon aquarium following activation of the solenoid on the pinch-valve. During this low tide period, the water level was maintained at the top of the "L" tube, as water coming from the inflow tube passed without obstruction to the reservoir. This device facilitated a reliable control of the simulated tide.

Light cycles and simulated tides operative in the aquaria were controlled by time switches having periods of 30, 24, 16, and 8 hours. The timers were adjusted so that the on and off phases of the cycles were equal. Thus, the 24-hour cycle consisted of 12 hours of light alternating with 12 hours of darkness, or of 12 hours of full flow (simulated high tide) alternating with 12 hours of the drained condition (simulated low tide). The illumination and tidal cycles simulated in the seven aquaria are shown in Table 8.

A 2-inch-deep substratum of medium-sized sand was lain on the floor of each aquarium. Since the surface of this substratum was situated 1/2 inch beneath the outlet pipe in each of the five simulated tide aquaria, the simulated low tides in this experiment were associated with quiet, shallow (<1/4 in.) pools of seawater. Similar pools are common on tidal flats inhabited by shallow burrowing pelecypods.

Temperature measurements

Air and water temperatures were measured to the nearest 1/2 °C with an all glass covered mercuric thermometer. On all occasions of temperature measurement, it was observed that the temperature of water stored in the reservoir tanks was the same as the temperature of water being circulated through the aquaria. The simulated low tide conditions were usually associated with temperatures that were 2 to 4 degrees higher or lower, depending on whether or not the drained aquarium was being heated by its incandescent lamp. Ideally, this experiment would have been free from external variations of temperature, but such was not the case. A series of measurements taken during July 13-14 showed that water temperature varied with diurnal changes of air temperature. This variation was smaller, ranging from 22°C in the morning to 24°C in the afternoon and evening, but was nevertheless present to influence shell growth. Temperature measurements taken in the afternoon show an increase during August and cooling during October and November. Finally, the anomalously high temperatures recorded on October 25 resulted from a temporary overheating of the building in which the apparatus was located. Thus, the experiment was less than ideal with respect to temperature, since the artificial periodicities were combined with externally controlled rhythms and accidental variations of temperature. Despite this, the artificial rhythms of temperature change were dominant in the simulated tidal tanks.

Hydrogen ion concentration (pH)

Dye indicators were used to measure the pH of the seawater on a weekly basis. On all occasions, the dye test was straw yellow and matched pH=7.0 in a standard color chart. The same result was obtained when the seawater was tested within a few hours after having been drawn from the shore at Fort Mason or from the tap at the Steinhardt Aquarium. Although absolute accuracy cannot be claimed for measurements of pH based on indicator dyes, the pH of the seawater appears to have been very close to the value of 7 (considered normal for seawater).

Salinity

Salinity was measured on three occasions by a hydrometer. On July 14, a reading of 1.021 was taken at a temperature of 20°C. On August 19 and November 16, the readings were 1.021 at 21°C. These three hydrometer readings indicate a salinity of 29 parts per thousand. This salinity measurement is considerably lower than the world average given by Sverdrup *et al.* (1942) as 35, and is closer to the annual mean for the Golden Gate (29.5).

Culture of food organisms

Algal flagellates are the principal constituents of the pelecypod's food. Over a period of several months, as in this experiment, nitrates, nitrites, and phosphates contained in a closed body of seawater would diminish towards the minimum required for the survival and growth of an algal flagellate population. For this reason, the author attempted to raise a rich algal flagellate culture for regular addition to the system.

Two 5-gallon enameled metal basins were lined with polyethylene and installed several feet above the aquaria. A culture medium was prepared from a powdered "Rosefood" fertilizer mixed with seawater in the proportion of 1 tablespoon per gallon. This mixture was heated to boiling, cooled to room temperature, and filtered through cheesecloth. On July 17, the algal tanks were filled with the filtrate and given equal portions of a 250-ml innoculate of encysted *Chlamydomonas*. These tanks were illuminated from above by four tubular 60-watt incandescent lamps. A small amount of the original *Chlamydomonas* innoculate was used to establish reserve cultures in three 4-liter flasks. These flasks were filled with the same culture medium and situated on a window sill where they were illuminated by sunlight.

On August 8, the flask cultures were deep green in color and excysted individuals of *Chlamydomonas* were observed through the microscope. The algal tank cultures were less densely populated, though all of the organisms observed microscopically were free-moving. Presuming that constant illumination might have been retarding these cultures, the four overhead lamps were connected to the 24-hour time switch so that the algal tanks were illuminated for only 12 hours each day. On August 20, the algal tank cultures were still poor. Nevertheless, it was decided to administer these cultures to the bulk seawater. The two algal tanks were interconnected with a 1/8 in. (I.D.) siphon. A siphon of 1/16 in. I.D. was installed to

connect the algal tanks with the principal reservoir tank. Controlled by a D-ring clamp attached to the siphon hose, the initial drip rate was set at 0.35-0.36 drops per second, equivalent to 0.71 gallons per day. Owing to loss of head pressure, this rate of flow decreased gradually, and there were about 2 gallons of algal culture remaining in the algal tanks on September 11, at which time this attempt to raise large quantities of algal flagellates was terminated.

APPENDIX B

Growth Experiments: Bodega Bay

Apparatus for the study of growth rhythms

Rhythmic variations of light and simulated tides were maintained in aquaria consisting of the seven stainless steel tanks used in the experiment at Richmond and twenty-one disposable polystyrene boxes with lids. The polystyrene tanks were opaqued with two exterior coats of spray enamel. Light fixtures mounted on asbestos pads were inserted through holes cut into the lids of these tanks. Silicon rubber was used to cement the overflow and L-shaped glass drainage tubes were inserted into the sides of these aquaria. The twenty-eight aquaria, with a total capacity of about 172 gallons, were situated on a specially constructed rack that had four drainage troughs leading to a seawater drain. Incoming seawater was supplied by a large (I.D. 1-1/2 in.) permanent pipe lined with PVC. This pipe was connected to a pair of smaller (I.D. 1/2 in.) seawater pipes situated above the aquaria on the rack. Along the lengths of these two pipes there were twenty-eight jets with fittings for fine plastic tubing. Flexible PVC tubing with an I.D. of 1/8 inch conveyed seawater from the jets to glass inflow pipes inserted through the lids of the aquaria. Overflow from the aquaria poured into the drainage troughs and out through the drain.

Time switches were used to control the illumination cycles and simulated tides that are listed in Table 8. The smaller 2-1/2 gallon aquaria were illuminated by 7-watt incandescent light bulbs. Four of these aquaria were equipped with red, yellow, green, and blue bulbs; the others, with white bulbs. Tides were simulated in the aquaria using devices of the previous experiment. However, as there were only a few pinch-valves and a greater number of simulated tidal aquaria, each pinch-valve was used to effect the cyclic draining and filling of more than one aquarium. This was done by connecting the drainage tubes of tidal aquaria having the same cycles through a series of Y-shaped connectors. The principal tube of each drainage system was inserted through the pinch-valve connected to the time switch having the desired periodicity. As a result of this arrangement, the amount of time required for draining the aquaria was increased to 3 hours.

The environment

Incoming seawater was usually laden with silt and sometimes

carried fragments of algae and driftwood. Detritus accumulated on the floors of the aquaria as a gelatinous ooze. This ooze appeared under the polarizing microscope as a mucoid suspension of algal fragments, silt, and fine sand. It was necessary to unclog the inflow tubes of the aquaria several times per week. This was accomplished simply,either by turning the seawater supply on and off several times in rapid succession or by removing detritus from individual tubes with a syringe. Pinch-clamps were attached to the inflow tubes in order to equalize the flow rates of twenty-seven of the aquaria. When the inflow tubes of these aquaria were completely free of detritus, the rate of seawater flow into a single aquarium was about 25 liters per hour. The 30-gallon aquarium had approximately twice this rate of flow.

Many invertebrate larvae and a few tiny fishes were deposited in the aquaria by the running seawater. Most of these were serpulid worms, a pelecypod species (*Kellia suborbicularis*), gastropods, and a few crustaceans. All of these organisms could have originated in the open rocky shore environment. Only the serpulids and pelecypods survived to maturity in the aquaria. In some parts of the laboratory, large seawater pipes became clogged and were disassembled for cleaning by workmen. Small balanoid barnacles and marine mussels had attached themselves to the insides of these pipes, but the most abundant organism was *Kellia suborbicularis*.

Temperature and salinity followed the variations in the nearby ocean. Due to the insulated quality of the room in which the aquaria were located, its air temperature was almost always within a degree of the water temperature. Consequently, the low tides simulated in the aquaria were associated with a lesser amount of heating than in the experiment at Richmond. Although there occurred some interruptions of the seawater supply, which resulted in overheating of aquaria located in the more open parts of the laboratory, temperature changes were less extreme, if felt at all, in the closed-off insulated room.

The seawater flowing into the aquaria often contained enough hydrogen sulphide to have an obvious "rotten egg" odor. As indicated by the presence of black sulphides and a strong odor of hydrogen sulphide in the seawater pipes of the laboratory, there must have been rapid decomposition of organic matter lodged within these pipes. Additional fouling of the seawater eventually occurred in the aquaria wherever organic detritus accumulated in piles. Chemically, the seawater must have been acidic and

depleted in oxygen as compared with seawater entering the pumping house on the open rocky shore.

Experiment with concentrated food media

Chlamydomonas has been used to raise the larvae of many different species of pelecypods to the prodissoconch and early dissoconch juvenile stages (Loosanoff and Davis, 1963). The author produced a large culture of this food organism in an attempt to induce adult pelecypods to form shell in the Bodega Marine Laboratory. A 5-gallon glass jug was filled with 18 liters of seawater that had been heated to boiling, cooled to room temperature, and filtered through cheesecloth. Two nutrient solutions were prepared:

Solution A - 100 ml. of distilled water containing:

NH_4CL:
$NaNO_2$: 15
EDTA: 1

Solution B - 100 ml. of distilled water containing:

Na_3PO_4 $12H_2O$: 2.00 g
Thiamine HCL: 0.02
Pyridoxine-5-phosphate: 0.01
$Ca(H_2PO_4)_2$ H_2O: 0.02

These solutions were added to the seawater in the concentrations of 1 ml. (A) and 1 ml. (B) per liter of seawater. With a few deletions of chemicals, this formula at least approximates the one given by Loosanoff and Davis (1963). The 18 liters of seawater in the jug were innoculated with a 300-ml. culture of encysted *Chlamydomonas* left over from the experiment in Richmond. The mouth of the jug was stopped with a wad of cotton through which two small (I.D. 1/16 in.) glass tubes were inserted. Attached to an airstone, one of these tubes was used to aerate the culture. To avoid possible contamination of the culture with oil, the air was filtered through cotton contained in a flask. The other tube provided a connection for a siphon hose through which the culture was administered to an aquarium. After a month of continuous aeration and illumination by ultraviolet light, the culture had become dark green in color. Through the microscope it was observed that the algal flagellates were extremely abundant.

Pelecypods were contained in a 1-1/2 gal. all-glass aquarium that had a plexiglass lid. The seawater contained in this aquarium was warmed by a thermastatically controlled heater and aerated. An "S"-shaped glass siphon tube was epoxyed to one end of the aquarium to maintain a constant water level. The algal culture was administered to the aquarium

through a neoprene siphon hose at the other end of the aquarium. Evaporation was made negligible since the preceding tubes were inserted through cotton-stopped holes in the plexiglass lid.

Minimal rates of flow of algal culture obtained by applying a clamp to the siphon hose ranged from 150 to 160 ml. per hour. This rate of administration of culture was too rapid, as more than 3-1/2 liters would have passed through the aquarium per day. The flow was rationed through use of a spare pinch-valve controlled by a 24-hour time switch. The time switch was adjusted so that a liter of algal culture flowed into the aquarium during a period of 7 hours once a day. A liter of treated seawater was added to the algal culture for every liter withdrawn. The productivity of this culture was high enough to sustain these daily harvests.