SHELL CHARACTERISTICS OF THE FAMILY PECTINIDAE AS ENVIRONMENTAL INDICATORS

Thesis by

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In Partial Fulfillment of the Requirements

For the Degree of

Doctor of Philosophy

California Institute of Technology

Pasadena, California

1969

(Submitted May 19, 1969)

ACKNOWLEDGEMENTS

To adequately acknowledge the assistance I have received on this project is impossible. I would like to mention a few of the many people to whom I am indebted.

Three people have been especially important to this work. Heinz A. Lowenstam has been a continual and most valuable source of advice and inspiration from the conception of the project to the reading of the final manuscript. Lynton Land gave generously of his time and energy to help establish the laboratory and collection phases of the study. My wife Patricia has been a source of perseverence without which this project might never have been completed.

For valuable discussion on various aspects of this work, I thank the following individuals: Edwin C. Allison, Gilbert Grau, Franz Halberg, Ralph G. Johnson, Valmore C. LaMarche, Jr., Wheeler J. North, J. A. Posgay, Colin T. Scrutton, Robert P. Sharp, Norman Shields, John W. Wells, and A. M. Ziegler.

For technical assistance I thank Mark E. Boule, Arthur A. Chodos, Asser Goudsmid, Stephen M. Horner, Victor E. Nenow, Ruth Z. Talovich, and Jurrie J. van der Woude, all of Caltech, Charles J. Brokaw, Bruce R. Benedict and Joe R. Deem, all of the Kerckhoff Marine Laboratory, John R. Devaney of the Jet Propulsion Laboratory, Donn S. Gorsline and Fred C. Ziesenhenne of the University of Southern California, Bruce Coull at the Bermuda Biological Station, Charles J. Wheeler and George Souza, both at Woods Hole, Massachusetts, and Robert L. Fernald and Cleave Vandersluys at Friday Harbor Laboratories.

I thank the Departamento de Estudios Biologicos Pesqueros for permission to collect pectinids in the Gulf of California, and thank Lederle Laboratories for a generous supply of tetracycline.

This research was supported by National Science Foundation Grant GB-6275, The Alfred P. Sloan Foundation, and The Division of Geological Sciences at Caltech.

ABSTRACT

Many characteristics of bivalve shells are related to environmental rather than hereditary conditions. If these acquired characteristics could be recognized and interpreted in fossil shells they would be of considerable significance in paleoecology. In this study a number of growth experiments were conducted on living representatives of the Family Pectinidae, a group of bivalves with an important fossil record. These experiments established the presence of several kinds of acquired characteristics in pectinids.

The fine concentric ridges present on many pectinid shells are shown to be daily growth lines, formed in response to a biological rhythm regulated by the cycle of light and darkness. Daily growth increments are also seen in radial sections through pectinid shells. These lines can be used as time markers to greatly increase the amount of information which can be derived from other acquired characteristics. For example, variations in growth rate are known to result from variations in environmental conditions, and these can be observed and measured by means of the daily growth lines. Moreover, they can be correlated between animals grown under the same conditions; this offers a technique for determining the temporal relationships between specimens in a fossil assemblage, a problem of some concern in paleoecology.

Daily growth lines were used to relate variations in shell chemistry (magnesium concentration) to time of growth, and thereby to variations in growth temperature. There appears to be a great potential for applications of this kind.

Experiments on *Leptopecten latiauratus latiauratus* and *Leptopecten latiauratus monotimeris*, two very different pectinid subspecies, strongly suggest that the morphological differences between the two are principally due to environmental differences. This has important applications for the paleoecology of these forms, and suggests that such strong environmental effects might not be uncommon in the fossil record.

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All characteristics of a living organism can be subdivided into two broad categories: the inherited and the acquired. It is through consideration of the inherited characteristics that the paleontologist distinguishes species and establishes the patterns of evolution so necessary to his work. His consideration of acquired characteristics extends only to their identification and separation from his main interests. Acquired characteristics, however, can be of great interest to the paleoecologist. As they are quite literally a reflection of the environment, they promise to be of considerable value in the reconstruction of past environmental conditions.

While any fossil possessing acquired characteristics could serve as an environmental indicator, the most useful fossils are those which represent accretionary skeletons. In these the characteristics of one portion will differ from the characteristics of another if environmental conditions have changed during the lifetime of the organism. Accretionary skeletons are formed by a wide variety of organisms, including foraminifera, corals, bryozoa, brachiopods, mollusks, and some other groups. In theory, these skeletons contain a record of the environment in which they formed. The problem lies in the interpretation.

One of the better studied of these groups is the bivalved mollusk. A wide variety of environmental parameters has been shown to affect their growth and shell characteristics.

Perhaps the most widely studied effect is the dependence of rate of growth on temperature. This seems to be a widespread, if not universal characteristic of bivalves (see, for example, Weymouth, McMillan and Rich, 1931; Coe, 1948; Loosanoff and Nomejko, 1949; Mason, 1957; Hallam, 1965). Variations in shell mineralogy with various environmental factors, principally temperature, have been demonstrated by Lowenstam (1954) and Dodd (1963, 1964). Epstein and Lowenstam (1953) showed that the oxygen isotope ratio in the carbonate shell can be used to derive the mean water temperature during the growth of the shell. Strontium and magnesium concentrations in the carbonate have been shown to vary with environmental factors by Dodd (1965) and Malone (1968). Morphological variations, especially with respect to ratios of dimensions, are known to be caused by a number of factors, including light intensity (Huntsman, 1921) and sediment composition (Swan, 1952). Eisma (1965) summarizes his and previous workers evidence for a dependence on salinity of the number of ribs in _Cardium_ _edule_.

Unfortunately, most of the effects discussed above have not yet realized their full potential as paleoecologic indicators. The most quantitative effect, the relation between oxygen isotope ratio and temperature, can be applied only to unaltered fossils. The relative dependence on temperature and salinity has not yet been thoroughly worked out for the strontium and magnesium effects, and they appear even more susceptible to alteration by mild diagenesis (see Dodd, 1966). Most of the other effects have not received sufficient study to be of quantitative value.

One potentially important effect is the dependence of growth rate on environmental conditions. This effect cannot be directly observed in an accretionary skeleton, but other effects which place time markers in the skeleton permit its measurement and interpretation. Thus Epstein and Lowenstam (1953) demonstrated two and a half years of growth in an increment of a gastropod shell by plotting the growth temperatures derived from oxygen isotope analysis of successive slices of the increment. In more subtle fashion Lowenstam (1954) demonstrated a two year maximum age in a growth series of *Mytilus californianus* by plotting the variation in mineralogic composition due to seasonal temperature changes. More important time markers for paleoecologic purposes are the annual rings, or check marks, formed in the shells of many bivalves. These appear to represent cessation of growth at extreme environmental conditions, such as low winter temperatures (see especially Belding, 1910; Coker, 1921; Orton, 1923; Chamberlain, 1930; Moore, 1934; Newcombe, 1936; Stevenson and Dickie, 1954; Mason, 1957; Merrill, Posgay and Nichy, 1966). These check marks permit comparison of annual growth rates, but they are of limited application since their presence implies that the record of growth preserved in such shells is not continuous. For this reason, and because the growth rate is likely to vary considerably during other parts of the year, there is no obvious way to relate small shell increments to particular environmental conditions. Time markers indicating changes rather than cessations of growth, and indicating shorter time intervals, would be required.

Such time markers would be of considerable value in study of other shell characteristics. Epstein and Lowenstam (1953) also found average temperatures varied between species, but remained within the range of recorded environmental temperatures at their collecting sites. These differences were interpreted as indicating variation in growth rate dependence on temperature, with some species growing uniformly throughout the year and other species growing most rapidly during specific seasons. Short term time markers in the skeletal material could help interpret such data in fossil assemblages.

In 1963 Wells published a brief note in Nature pointing out that if fossils could be found with both daily and annual markings, a count of daily marks between annual marks would give the number of days in the year for the time that the fossil lived. Since current geophysical theory states that the earth's rotation is slowing, counts of more than 365 days per year in the geologic past would confirm this theory. Furthermore, once the relationships were well established such fossils could be used as independent indicators of their absolute age. As an example, Wells presented some Devonian corals on which he counted about 400 fine growth lines per annual increment. This figure agreed with geophysical estimates (Munk and Davies, 1964; MacDonald, 1964).

Other workers extended this approach to other cycles and other invertebrates. Scrutton (1964) found bands, apparently representing lunar months, of from 27 to 35 presumably daily ridges on Devonian corals. His average of 30.59 days in a Devonian lunation was also compatible with geophysical estimates (Runcorn, 1964; McKenzie, 1966). Other workers have found patterns of growth lines within the shell material of intertidal bivalves; these appear to reflect daily, tidal, and other periodicities (Barker, 1964, 1966; Pannella and MacClintock, 1967,1968; Berry and Barker, 1968; House and Farrow, 1968). In a recent paper, Pannella, MacClintock and Thompson (1968) present data from bivalves, a cephalopod, and a stromatolite to construct a curve for the variations in rotation rate since the late Cambrian.

Although the experimental evidence for daily growth lines is scant, the remarkable agreement between internal growth line patterns and external events demonstrated by Pannella and MacClintock (1968) and House and Farrow (1968) leaves little doubt that these lines are daily. However, evidence of this sort is still limited to so few examples that no assumptions about the nature of fine growth lines in other organisms should be made without careful examination.

There is also some evidence for external daily growth lines in bivalves. Davenport (1938) made the observation that the fine concentric lamellae on the shell surface of Pecten irradians are formed daily. His evidence is limited but highly suggestive. A large number of bivalves have fine concentric sculpture patterns on their shells, and if these should prove to be daily growth lines their presence would be a major contribution to their potential value as paleoecological indicators.

A great deal of information remains to be gathered about acquired characteristics, including periodic time markers, before their full potential can begin to be realized. Since in some cases the most basic information is in shortest supply, it appeared that a few carefully monitored growth experiments might be of the greatest value. Accordingly I conducted a series of such experiments to study the relation of skeletal characteristics to changing environmental conditions.

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II. THE FAMILY PECTINIDAE

a. Suitability for Study

In selecting a suitable subject for experimentation, the experimenter must bear in mind not just the experiment but the potential application of the results. In this case it was not difficult to find a subject which seemed to have good possibilities for experiments as well as a vast potential for application of results. This subject is the scallop - the Family Pectinidae.

Since the purpose of this work is to develop new ways to obtain ecological information from fossil shells, a prime consideration in the choice of a subject is representation in the fossil record. Since the Pectinidae are probably the single most important group in the marine Cenozoic they are certainly to be considered. They have earned this importance on several counts; fossil pectinids occur in nearly every marine Cenozoic formation; they usually occur in large numbers, often forming the largest single element in the macrofauna; and there are a large number of species, usually restricted to single epochs of time (see Arnold, 1906; MacNeil, 1967).

Pectinids are also present in marine formations of Mesozoic age, and although they decline in importance below beds of Cretaceous age they include many useful guide fossils in the Jurassic and Triassic (Shimer and Shrock, 1944). Probable ancestral forms, such as <u>Aviculopecten</u>, extend back to the mid-Paleozoic (see Newell, 1937).

One reason for the abundance of pectinids in the fossil record is shell mineralogy. Scallops, like oysters, have shells composed principally of calcite. Since most mollusks have shells composed of the less stable polymorph of $CaCO_3$, aragonite, exposure of a fossiliferous formation to mild diagenesis will often leave nothing but scallops and oysters. In other situations, aragonite shells may be replaced by calcite, commonly with loss of internal structure. If this study is to include internal features, there is a clear advantage in selecting a subject with a calcite shell.

Since the method of approach is basically experimental, the animals used should be available as living specimens. The Pectinidae are again a good choice, for many genera have worldwide distribution, and several species occur in numbers sufficient for commercial fishing. Most coastal waters are populated by at least two common species. In addition, there are living representatives of all the major groups of pectinids, so there is little problem in applying the experimental results to the fossil forms.

Furthermore, as the study is aimed at finding differences between shells formed under different environmental conditions, the experimental subjects should have sufficient complexity for small changes to be noted. The pectinids are especially rich in complexity of surface morphology. The combination of essentially unchanging gross morphology and highly variable minor features is a major reason for the recognition of several hundreds of species of fossil and reent pectinids. More important, these features are quite variable within species. Some of this variability seems to be genetic and a part of the evolutionary process. However, some may be in response to changing environmental conditions, and may provide the group of acquired characteristics essential to this study (see Grant and Gale, 1931, pp. 155-156).

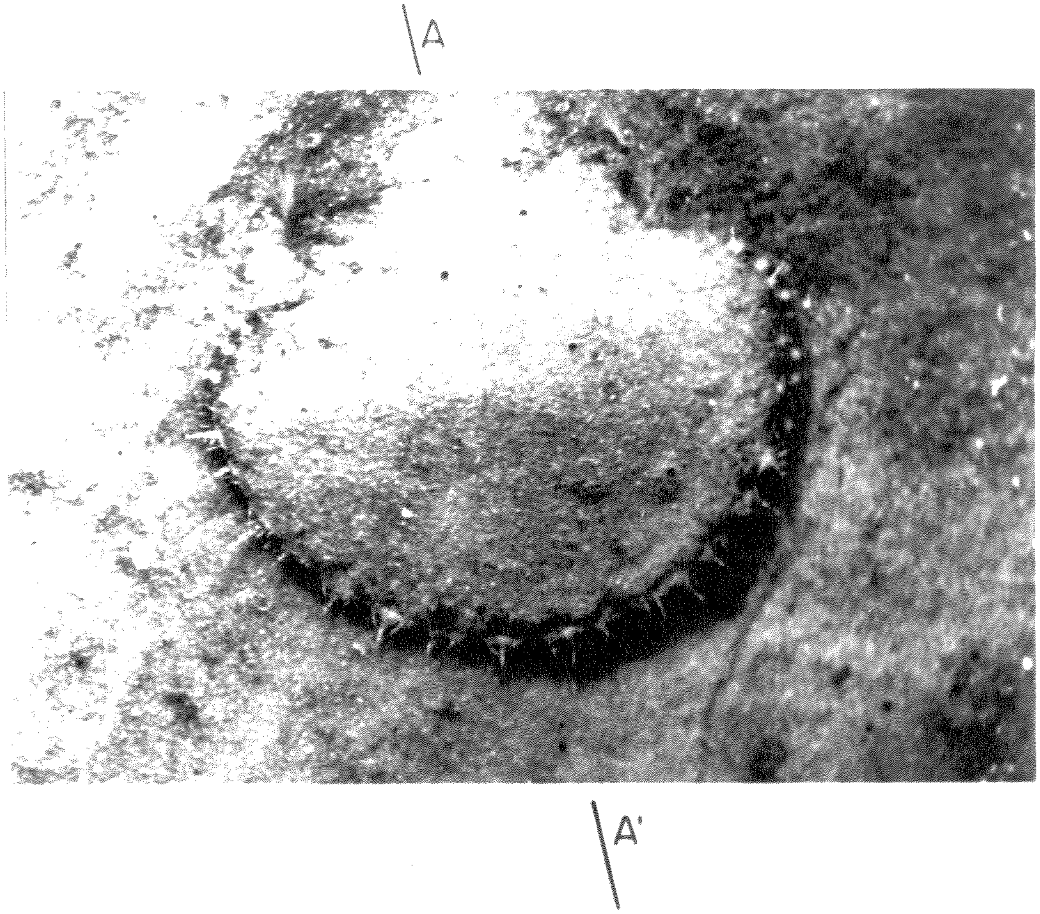
b. Ecological Aspects.

Pectinid species are known to live in a wide variety of marine environments, including tidal mudflats and abyssal depths, tropical lagoons and arctic seas, and are found on a wide range of substrates. Many species lie free on bottom sediments composed of mud, sand, or shell, but others live attached by a byssus or cementation to rocks, corals, or algae (including kelp). Most of the free-living forms excavate shallow basins in the sand, and some species (usually those with one flat valve) may be found partially buried in the substrate. These are oriented with the flat valve on top and level with the bottom, usually covered with a thin layer of sediment so that only the shell margin can be seen. I have observed this for two local species and one Caribbean species (see figure 1); for other descriptions see Belding (1910), Olsen (1955), Baird and Gibson (1956) and Baird (1958). The advantage of this behavior may be less in concealment than in an increased food supply. Like most bivalves, scallops are filter feeders, deriving their nourishment from the particulate matter they strain from the seawater passing through their gills. Water currents just above the substrate carry much more organic detritus than those elsewhere in the water column. For further discussion see Baird (1958) and Davis and Marshall (1961).

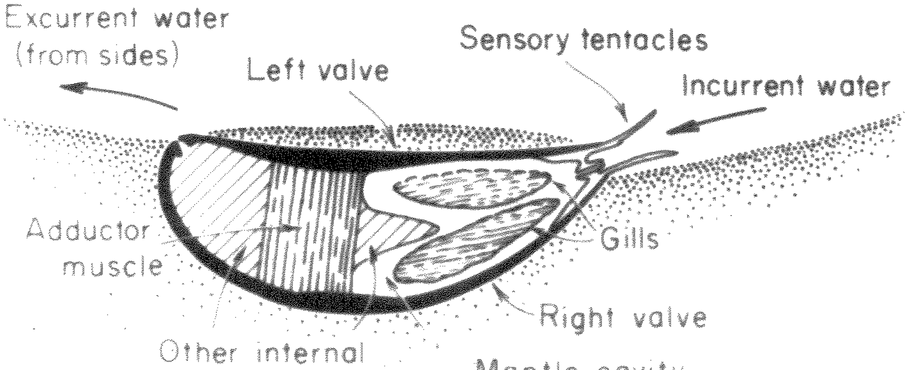
One of the most fascinating characteristics of scallops is their swimming ability. They swim by rapidly closing their valves while their muscular mantle forces the contained water to leave the

Figure 1

PHOTOGRAPHED FROM ABOVE



SECTION A-A'



Living Position of *Pecten vogdesi*

mantle cavity in selected directions. Using these jets of water for propulsion, the scallop can escape from an enemy or move out from under a newly deposited layer of sediment. The same process is used by the animal to excavate the bottom sediments and to dig into a semiburied position. Detailed descriptions and observations of this ability are provided by Dakin (1909), Belding (1910), Gutsell (1930), Yonge (1936), Olsen (1955) and Baird (1958).

Another interesting pectinid feature is their possession of well developed eyes. Unlike most bivalves, scallops have large numbers of light-sensitive organs located along the margin of the mantle. These organs are complex enough to be termed eyes, as they include cornea, lens, retina, and visual pigment. Although they have been shown capable of forming an image (Land, 1965), experiments designed to investigate the scallop's "eyesight" indicate that the animal is not very sensitive to most visual information (Wenrich, 1916; Dakin, 1928). The animal does exhibit a characteristic response to change in light intensity; when a light source is turned off or a shadow cast across the mantle edge, the animal closes its valves; there is no comparable response to a sudden increase in light intensity. A recent experiment by Cronly-Dillon (1966) indicates that the scallop possesses two distinct visual pigments; he notes, however, that some of the light sensitivity may be elsewhere than in the eye.

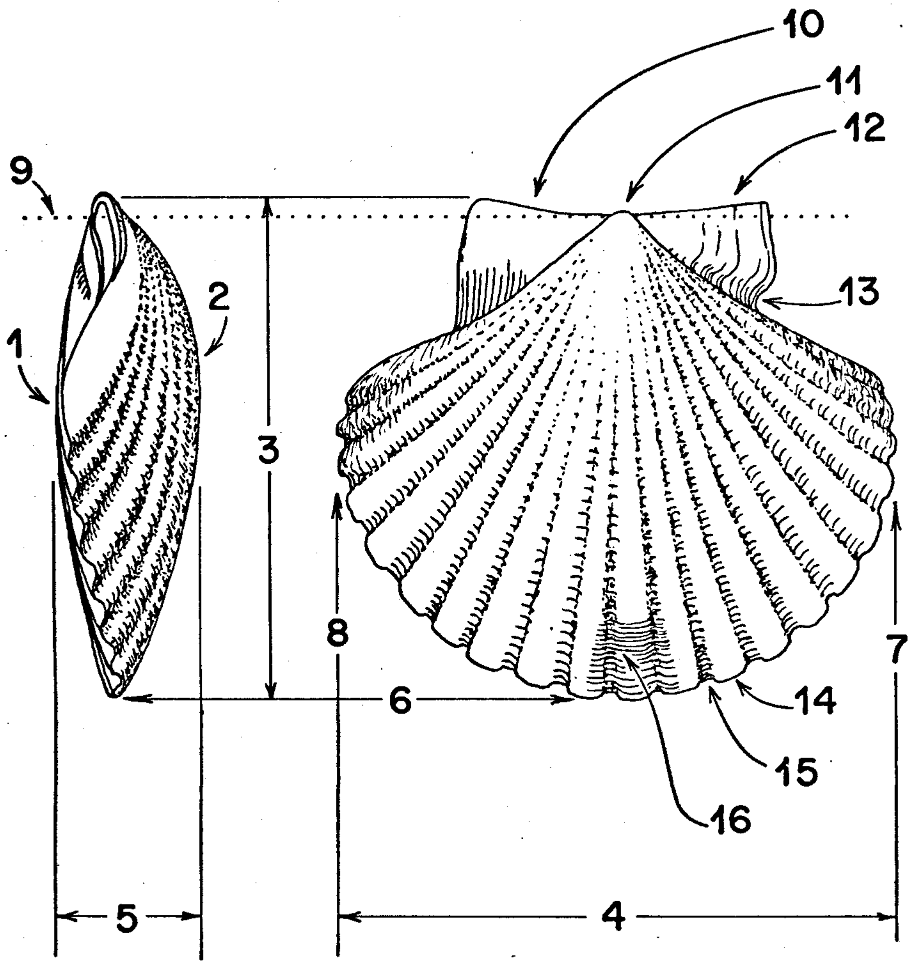
Different species of scallops have markedly different lifespans, although few species have been well studied in this regard. Normal lifespans which have been established seem to range from about two to fifteen years (see Belding, 1910; Gutsell, 1930; Tang, 1941; Mason, 1957; Merrill, Posgay and Nichy, 1966).

c. Shell Morphology

The form of the scallop shell is highly distinctive. There is a marked degree of symmetry between the halves of each valve, and often a lack of symmetry between the valves, both of which are in direct contrast to the symmetry usually associated with bivalves. There is commonly a stronger radial sculpture (ribs) than concentric sculpture (growth lines), but both may be absent. The two valves are joined by an elastic ligament which acts as a hinge. The shell lacks dentition, but relative movement other than opening and closing is minimized by an elongated hinge line supported by the "wings" or "ears" of the valves. Figure 2 illustrates the major external morphological features of a pectinid shell.

FIG. 2

PECTINID MORPHOLOGICAL FEATURES



1 Left valve
2 Right valve
3 Height
4 Length
5 Width
6 Ventral margin
7 Anterior margin
8 Posterior margin
9 Hinge line
10 Posterior
11 Beak
12 Anterior ear
13 Byssal notch
14 Rib
15 Interspace
16 Growth lines

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III. THE TETRACYCLINE APPROACH

Tetracycline and its derivitives, oxytetracycline and chlorotetracycline, are antibiotic drugs. It has recently been shown that tetracycline is readily incorporated into the growing calcareous tissues of various invertebrates (Bevelander, Goldberg and Nakahara, 1960; Nakahara, 1961; Bevelander, 1963). The presence of the drug in the carbonate is detected by its strong yellow fluorescence in the near ultraviolet. Although these investigators noted that it inhibited crystal formation and even growth of the animal at excessive dosages, it seemed ideal for use as a marker dye in growth studies, and Nakahara (1961) used it as such.

The first experiments of this study were conducted at the Bermuda Biological Station (St. George's West, Bermuda) in the summer of 1965. I had been curious about daily growth lines since reading Wells' (1963) article and had noticed fine growth lines on numerous elements of the Bermuda marine fauna. Other workers at the station, notably Bevelander, were using tetracycline as a marker dye, so it seemed a simple and obvious technique. I performed several experiments with the limited time and materials available.

I found that a variety of corals readily accepted the drug, but most retained it in their tissues (for as much as ten days) without incorporating any significant amount into their skeletons. Apparently this failure was due to a lack of growth during the experimental period, inasmuch as most of the corals had a faint fluorescence over their surfaces but none within their skeleton (as exposed by chipping or scraping). One coral had repaired a few marginal areas apparently damaged by handling, and the repaired areas exhibited vivid fluorescence. This limitation of growth was characteristic even of corals exposed to seemingly low dosages, so it is difficult to conclude whether it was due to the side effects of the drug or to other factors, such as physical disturbance.

Similar experiments with mollusks also presented problems. Limpets, chitons, and bivalves were subjected to various exposures of tetracycline, and results suggested that the dosage required to mark the shell was very close to lethal. The limpets and chitons appeared to be the poorer subjects, so further experimentation was confined to bivalves, notably Aequipecten gibbus. More refined exposures to tetracycline managed to establish a marking line on nearly all subjects, but some of these suffered from retardation of growth following exposure. In the last experiment in the series, six Aequipecten gibbus were successfully exposed to tetracycline and returned to their natural environment for seven days. Upon their retrieval, three showed no growth, but each of the other three showed six new growth lines!

After this encouraging beginning it was especially unfortunate that I had no time for further experiments for more than a year. Eventually, in the fall of 1966 I obtained space in the Kerckhoff Marine Laboratory at Corona del Mar, California. Setting aside for a time the problem of growth lines, I decided to grow specimens in aquaria with monitored temperature, and compare aspects of the new growth with the temperature. Tetracycline seemed an ideal technique for this experiment, since I could mark the beginning of the new growth on a large number of specimens by means of a short exposure to the drug, and then leave them all in the same tank without worry of confusion between specimens. After short periods, perhaps seven to ten days, I could again expose them and return them to their tank. After several months I should have numerous increments of growth, each partitioned between fluorescent lines.

Unfortunately, it was not this simple. It was nearly two months before I found satisfactory exposure conditions, and even then not all exposures were successful. In addition, specimens which incorporated the drug in their initial exposure did not necessarily do so in successive exposures. It appeared unlikely that any sort of incremental record, based on repeated tetracycline exposures at set intervals, could be established on more than a small fraction of an initial group of specimens. In addition, the drug appeared to retard the growth processes as it did in the Bermuda experiments. It was not unlikely that the growth between successive ten-day marker lines would actually represent only the last few days of the interval. Furthermore, it was found that the intensity of the fluorescence decreased rapidly with time. Lines which fluoresced vividly the day after exposure were very faint a month later, and were often imperceptible on pigmented shells.

Despite these problems I did initiate several experiments with tetracycline exposures, but before their completion I found a more satisfactory technique. I had earlier considered tagging and measuring as a method for monitoring growth, but had rejected tagging due to the very small size of many specimens. Then I found an alternative to tagging: a numbered plastic cage for each specimen. Thus, by keeping all the cages in one tank I could monitor the temperature, and by taking periodic measurements I could monitor the growth. Such a system would provide the same data as the one based on tetracycline, and although it lacked elegance it was much more dependable.

The last tetracycline exposure I conducted was on 12 June 1967, but many specimens discussed in this work, some involved in experiments long after that time, have been exposed to the drug. Most have a distinct mark on their shells which corresponds to that exposure, and this sometimes proves useful in the interpretation of their histories.

I should mention that I do not reject the use of tetracycline as an experimental technique. There are problems involved, but with experiments designed around these factors the drug should prove of great value in growth studies.

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IV: DAILY GROWTH LINES IN PECTEN DIEGENSIS

Data from this experiment provided compelling evidence for the daily periodicity of the fine ridges forming the concentric sculpture of Pecten diegensis. A method was developed for correcting for the absence of a few ridges in some specimens. This method was based on the discovery that the variation in spacing between ridges could be correlated among the different specimens grown at the same time. This discovery promises to have considerable paleoecologic application.

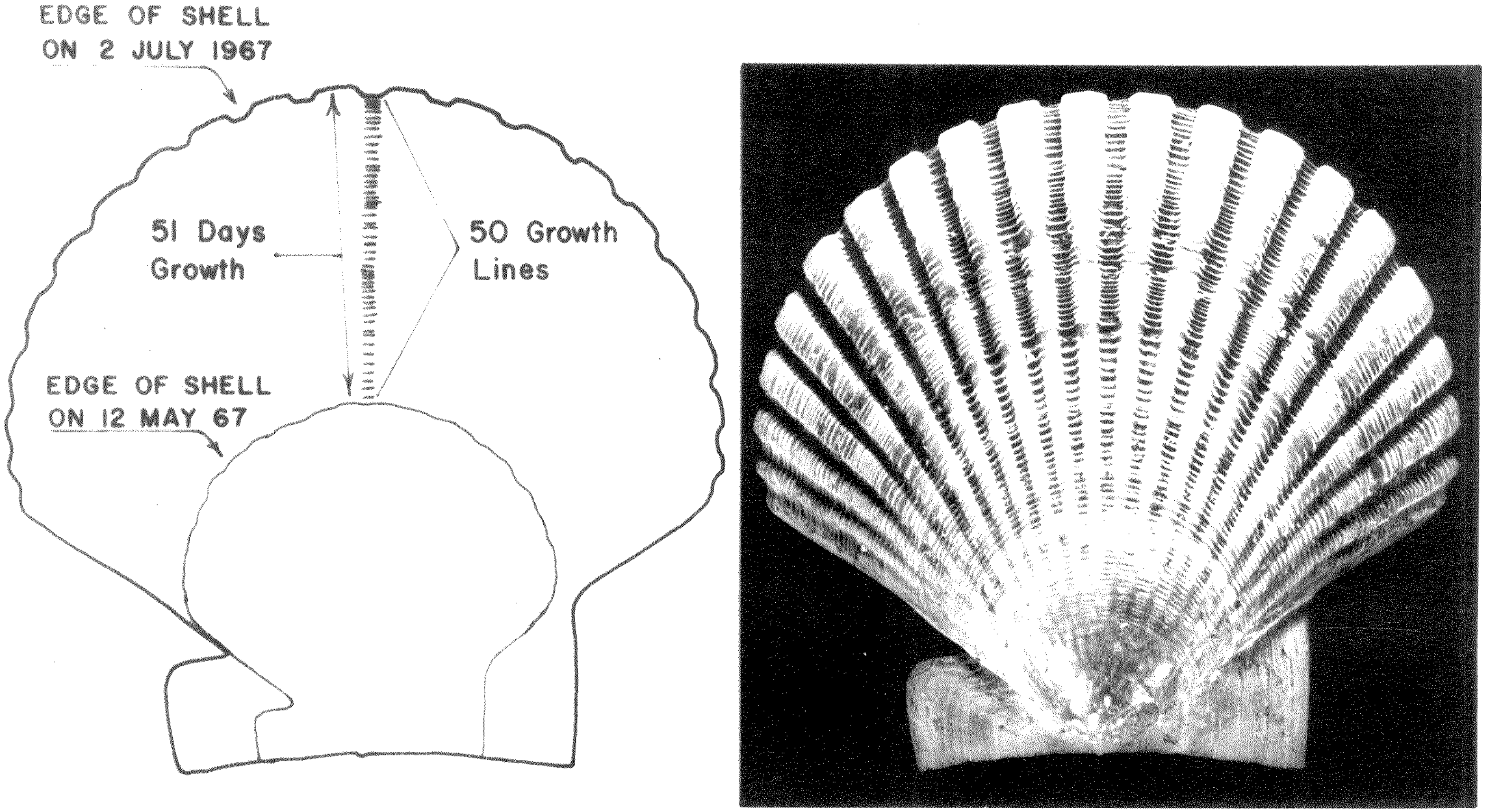
Twelve juvenile specimens of Pecten diegensis were kept in running seawater from 12 May to 2 July 1967, a period of 51 days. The height of each specimen was measured on 12 May, 1 June, 10 June, 20 June and 2 July. Specimen identity was preserved by the use of individual plastic cages.

Since each ridge, or growth line, represents the position of the shell margin at the time of formation of that growth line, the perpendicular distance from the hinge line to any growth line represents the height of the shell at the time that growth line was being formed (in Pecten diegensis, as in most scallops, the position of the hinge line does not significantly change during growth). Thus, if the height of the shell 10 days before the death of the animal is the same as the height of the tenth growth line from the margin, then for that period of time it is likely that one growth line formed each day. This concept is illustrated in figure 3.

The height of individual growth lines was determined from measurements on enlarged photographs of the specimens (the techniques

FIG. 3

SPECIMEN 0249 of *Pecten diegensis*

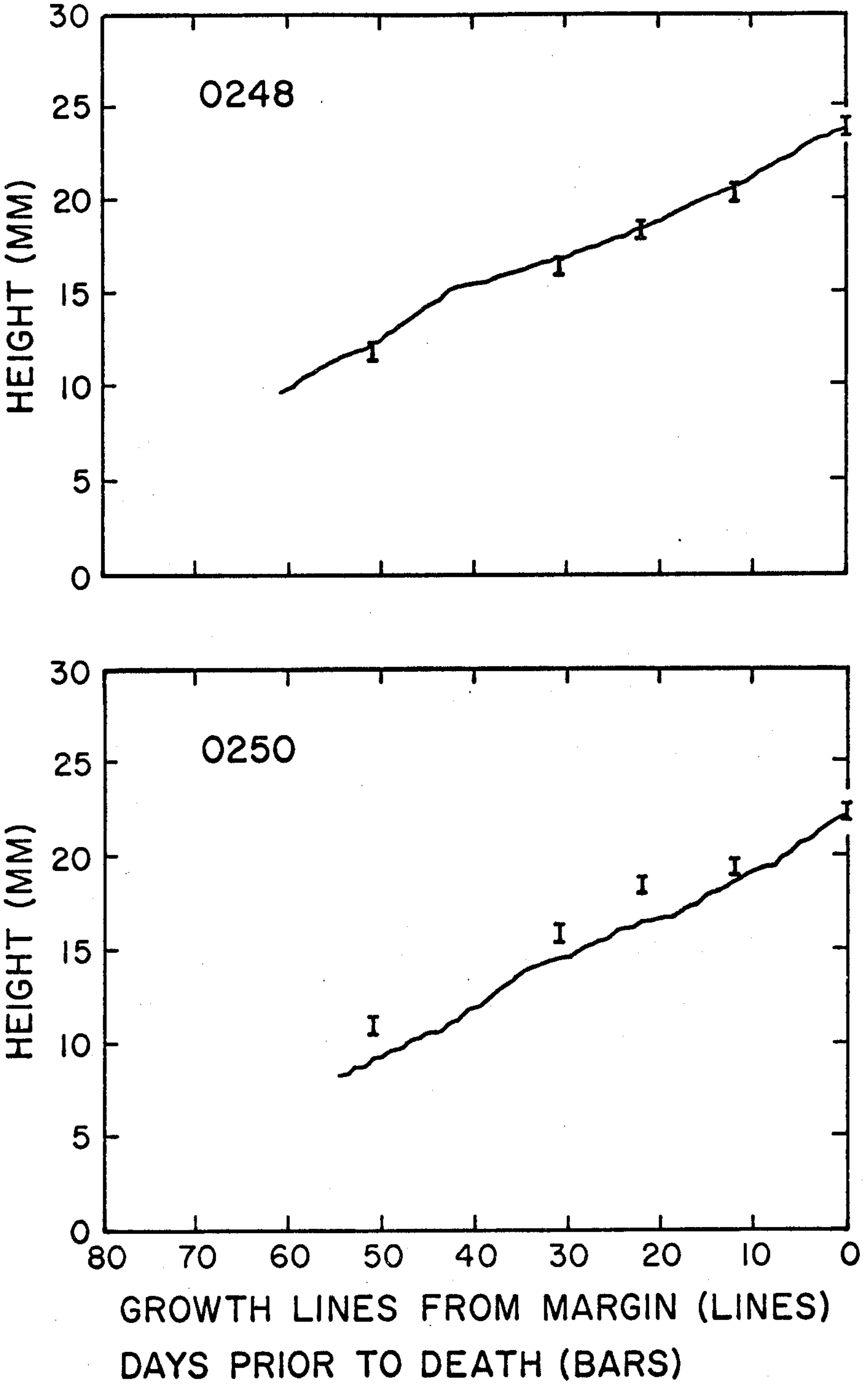


used reduced errors due to photographic distortion to insignificant levels). In figure 4 the cumulative growth derived from these measurements, plotted against growth line number, is compared with cumulative growth derived from the measurements made during the growth of the animals, plotted against calendar days. Six of the 12 specimens, like 0248, have formed growth lines in numbers compatible with daily formation. The other six, like 0250, have formed too few lines for this interpretation. This ambiguity might be resolved if the growth lines were assumed to be daily in both cases, but were too few in number in some specimens due to discontinuous growth.

Many bivalves stop growing at times of environmental or biological stress (see chapter I, and references cited therein on annual growth lines). Such a pause usually leaves a distinct line of disturbance on the shell, and is often accompanied by very close spacing of the growth lines. All of the specimens in this experiment show zones of closely spaced growth lines, and many appear to have one or more disturbance lines. This argues for further consideration of missing growth lines.

If the fine ridges are daily growth lines, then they can be used as time markers in the growth of the shell. The interval between adjacent lines would represent the growth during a particular day, and a change in the intervals between lines would indicate a change in the rate of growth. Since the rate of growth is known to vary with the environmental conditions (again, see chapter I), and all the specimens in this experiment were grown in the same environment, then any variation in growth rate should be present in all the specimens. The

FIG. 4

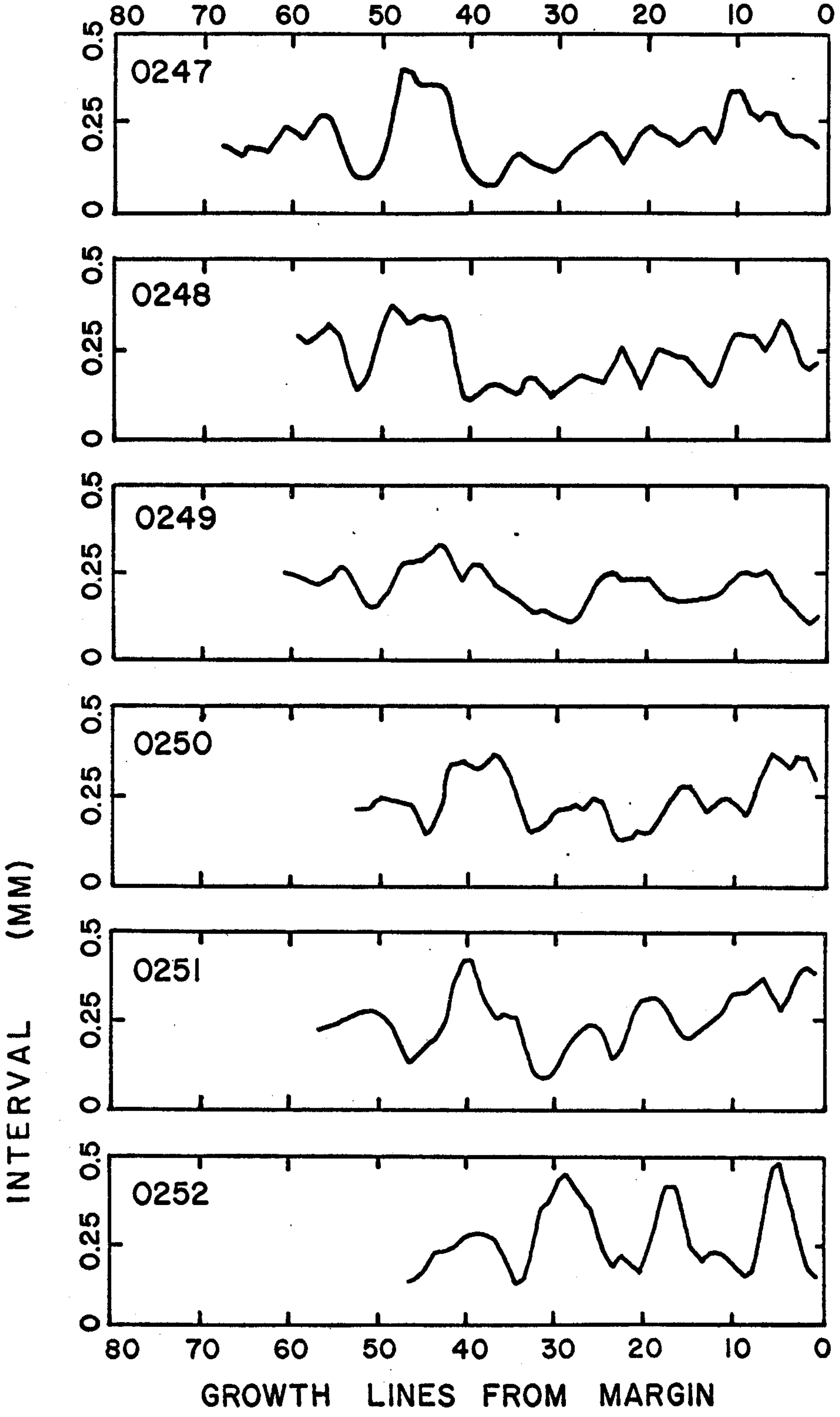

0248
0250
30
25
20
15
10
5
0
HEIGHT (MM)
80
70
60
50
40
30
20
10
0
GROWTH LINES FROM MARGIN (LINES)
DAYS PRIOR TO DEATH (BARS)

presence of daily growth lines would permit the measurement of daily growth increments, which in turn would permit the observation and comparison of short-term growth rate variations. By extension, a correlation between growth rate curves of different specimens prepared from intervals between growth lines would argue for the periodicity of those growth lines.

Growth rate curves prepared in this manner for the twelve specimens are illustrated in figures 5a and 5b. The first three curves in each group are quite similar, and if horizontal offset is discounted, all the curves have features in common. The correction for this offset would be in the direction of more growth lines; since the specimens requiring this offset are the same as those having too few growth lines to match cumulative growth curves (as specimen 0250, figure 4), there is a high probability that some growth lines are missing.

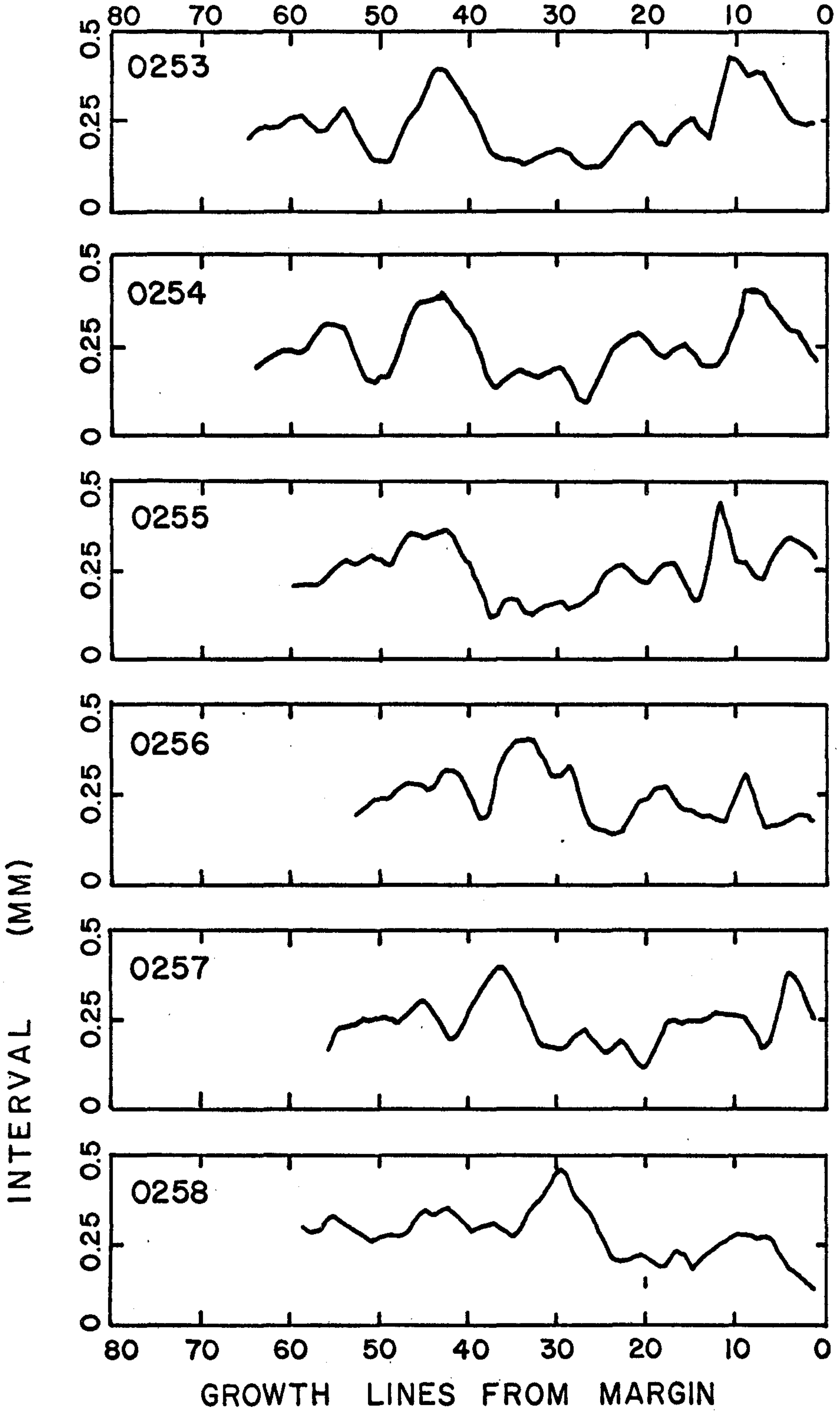
To test the validity of this interpretation, the horizontal axis (in units of growth lines) of both the cumulative growth curve and the growth rate curve was divided into segments at points corresponding to disturbance lines on the specimen. If each segment represents a portion of the shell where a growth line formed each day, then segments of the cumulative growth curve should fit the measurements at the same offset that corresponding segments of the growth rate curve most closely match the growth rate curves of specimens lacking no growth lines. This offset should represent the number of missing growth lines. This technique was applied (see figure 6) and confirmed offsets for the six specimens with too few growth lines.

FIG. 5a



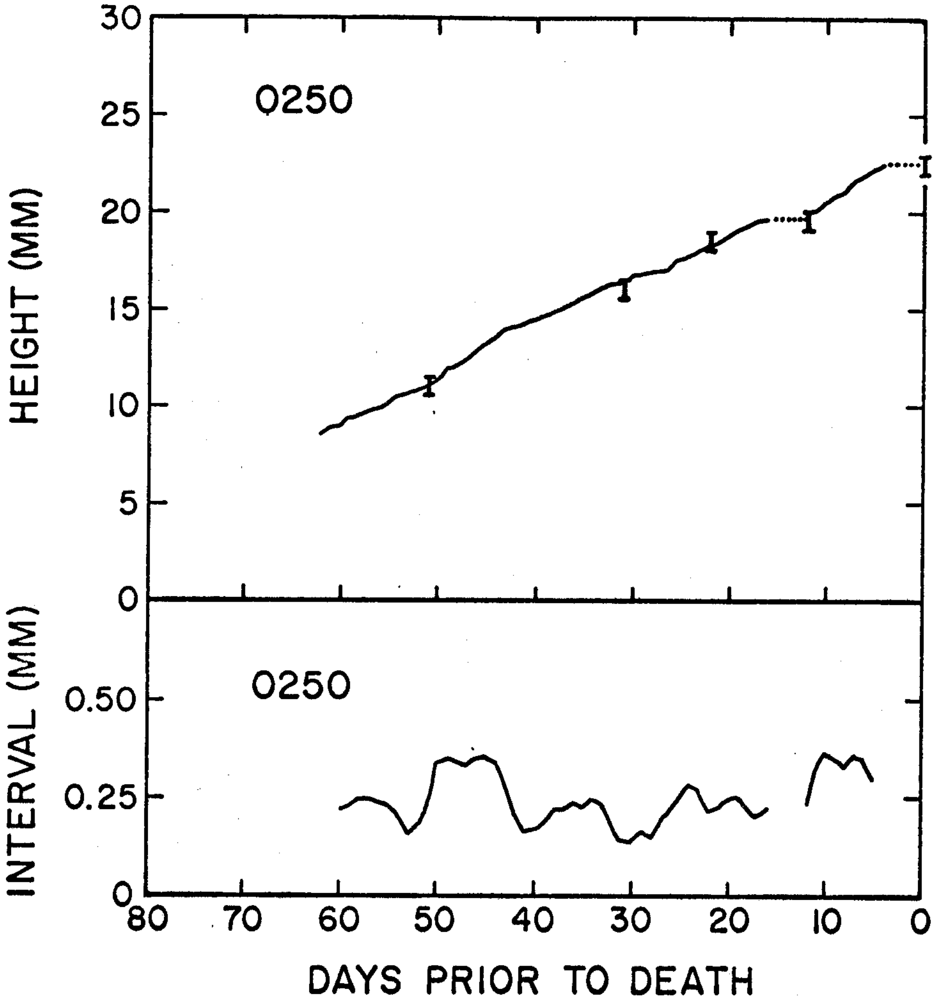
Growth Rate Curves Relative to Growth Lines

FIG. 5b



Growth Rate Curves Relative to Growth Lines

FIG. 6


0250
HEIGHT (MM)
30
25
20
15
10
5
0
0250
INTERVAL (MM)
0.50
0.25
0
80
70
60
50
40
30
20
10
0
DAYS PRIOR TO DEATH

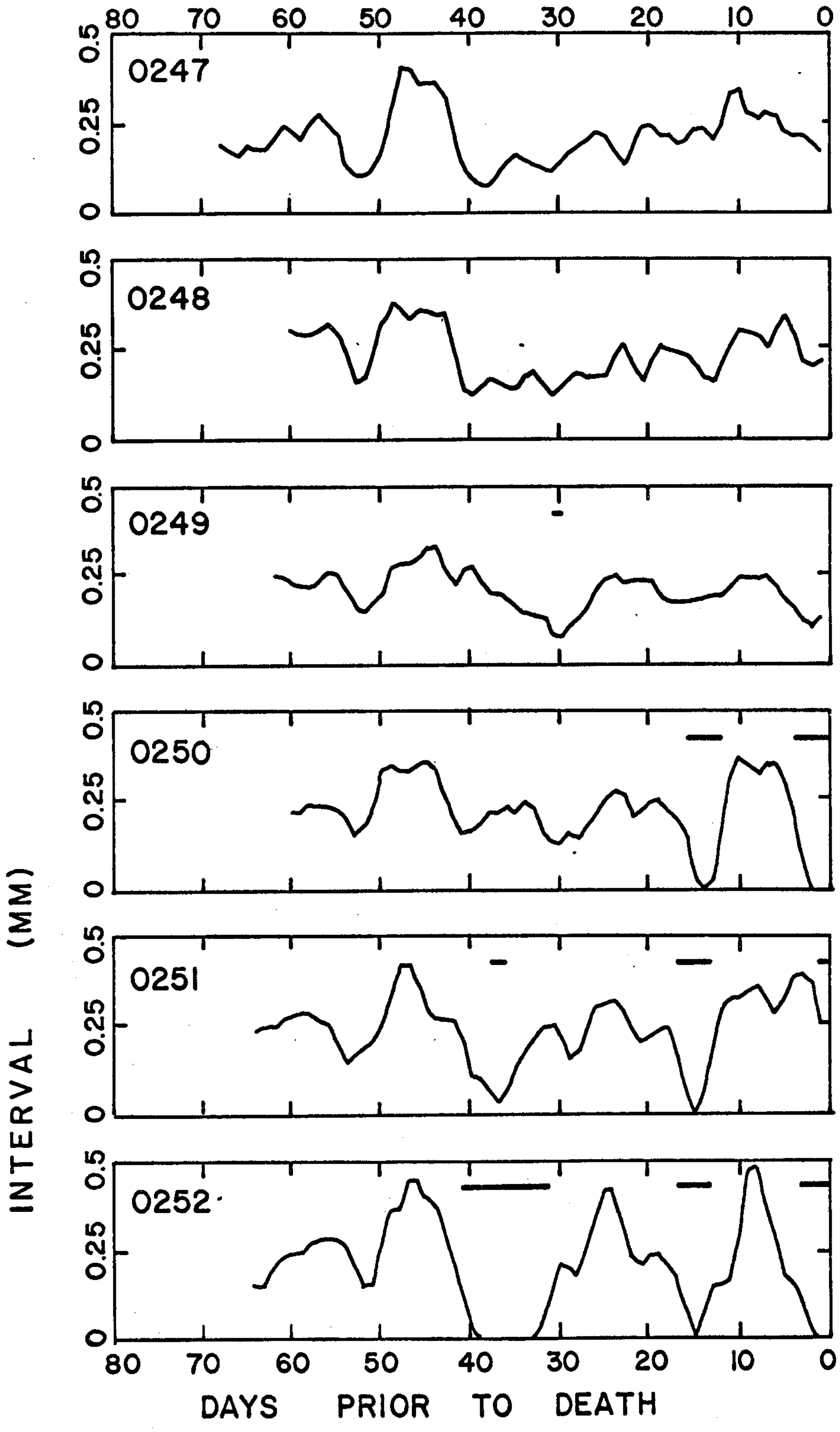
Moreover, the growth curves of four of the remaining six specimens showed improved relations through the introduction of minor offsets, and thereby demonstrated the sensitivity of this method. Figures 7a and 7b show the corrected growth rate curves for the twelve specimens. The horizontal lines above the curves indicate the location and extent of missing growth lines. Figure 8 is an overlay of all twelve curves on a single axis.

Although no single portion of the evidence presented here is conclusive proof, the combination presents a very strong argument for the daily periodicity of these growth lines. This has important implications for paleoecology and geochronometry.

In geochronometry (see chapter I) the accepted method of obtaining a figure for the number of days in a month or year is to count as many cycles as possible in a group of fossils and average the results. If the deviation from the mean is due to factors such as counting errors or variation in the position of the monthly or yearly mark, it is appropriate and correct to take the average value as representative. However, if the deviation is due to missing or extra growth lines the average value might be of little significance, for the factors responsible for missing growth lines might be totally unrelated to those responsible for extra growth lines. Thus the two effects would be unlikely to occur with equal frequency.

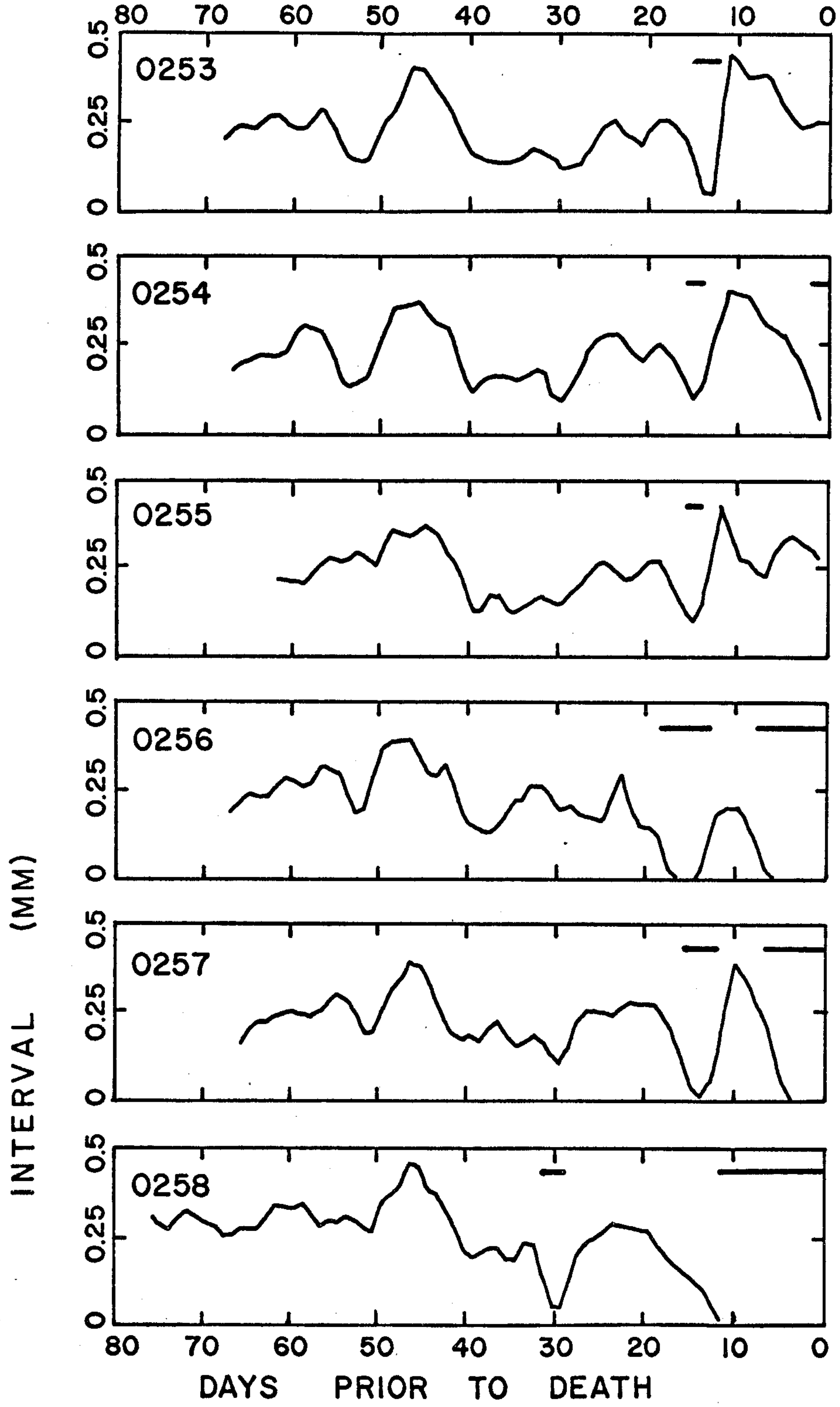
If the specimens grown in this experiment were to be examined in this manner, the interpretation would have been different. Counts made on the 12 shells range from 34 to 51 lines, with an average of 44.2. A frequency distribution of the data shows a strong

FIG. 7a



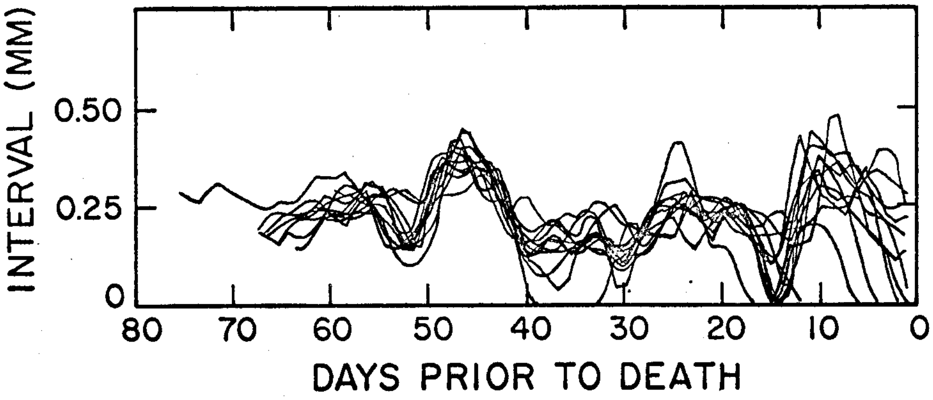
Growth Rate Curves Corrected for Missing Lines

FIG. 7b



Growth Rate Curves Corrected for Missing Lines

FIG. 8


INTERVAL (MM)
0.50
0.25
0
80
70
60
50
40
30
20
10
0
DAYS PRIOR TO DEATH

skew to the lower values, which might be attributed to the small size of the sample. With no better reason for believing the proper distribution to be other than normal, the average value would probably be accepted as representative. In fact, the distribution is far from normal, since 10 of the 12 specimens have missing lines, and apparently none have extra lines. The true number of days represented here is 51, the maximum value counted.

As mentioned before (chapter I), Scrutton (1964) took the average of his growth line counts to represent the number of days in the Devonian lunar month. The data he presents, unfortunately not in raw form, indicate a frequency distribution with a strong skew to the lower values. Moreover, he mentions that similar bands on modern corals have been observed to have "approximately" 28 increments. This figure, presumably an average, is lower than the 29.5 days in a present day lunation. These factors suggest, but do not prove, that missing lines are more important here than extra ones. If reevaluation of Scrutton's data gave a slightly higher value, these figures would still be compatible with geophysical theory (Lamar and Merifield, 1967).

In paleoecology, the short-term environmental control of growth rates implied by the correlation between growth rate curves would mean that each specimen in a fossil assemblage could carry an environmental record on the surface of its shell.

Even before we learn to interpret the environmental information in such a record, the growth rate curves of the different specimens in such an assemblage could be examined for correlations. In cases where the growth rate curves correlate for most of the specimens and terminate at the same point, the assemblage was most likely a fossil community which suffered a catastrophic death. Where the growth rate curves correlate but exhibit considerable overlap between specimens, the assemblage was probably a fossil community whose members lived their usual lifespans. Lack of correlation between growth rate curves probably indicates that the assemblage was not a community. This type of information is of prime importance in paleoecologic investigations (see Fagerstrom, 1964).

Of potentially greater significance is the possibility of using the growth line record to determine absolute environmental conditions in the past. Tree-ring studies, based on very similar measurements, have provided information on terrestrial paleoclimates for periods extending far beyond the lifetime of any single tree (see, for example, Ferguson, 1968).

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V: DAILY GROWTH LINES IN PECTEN VOGDESI

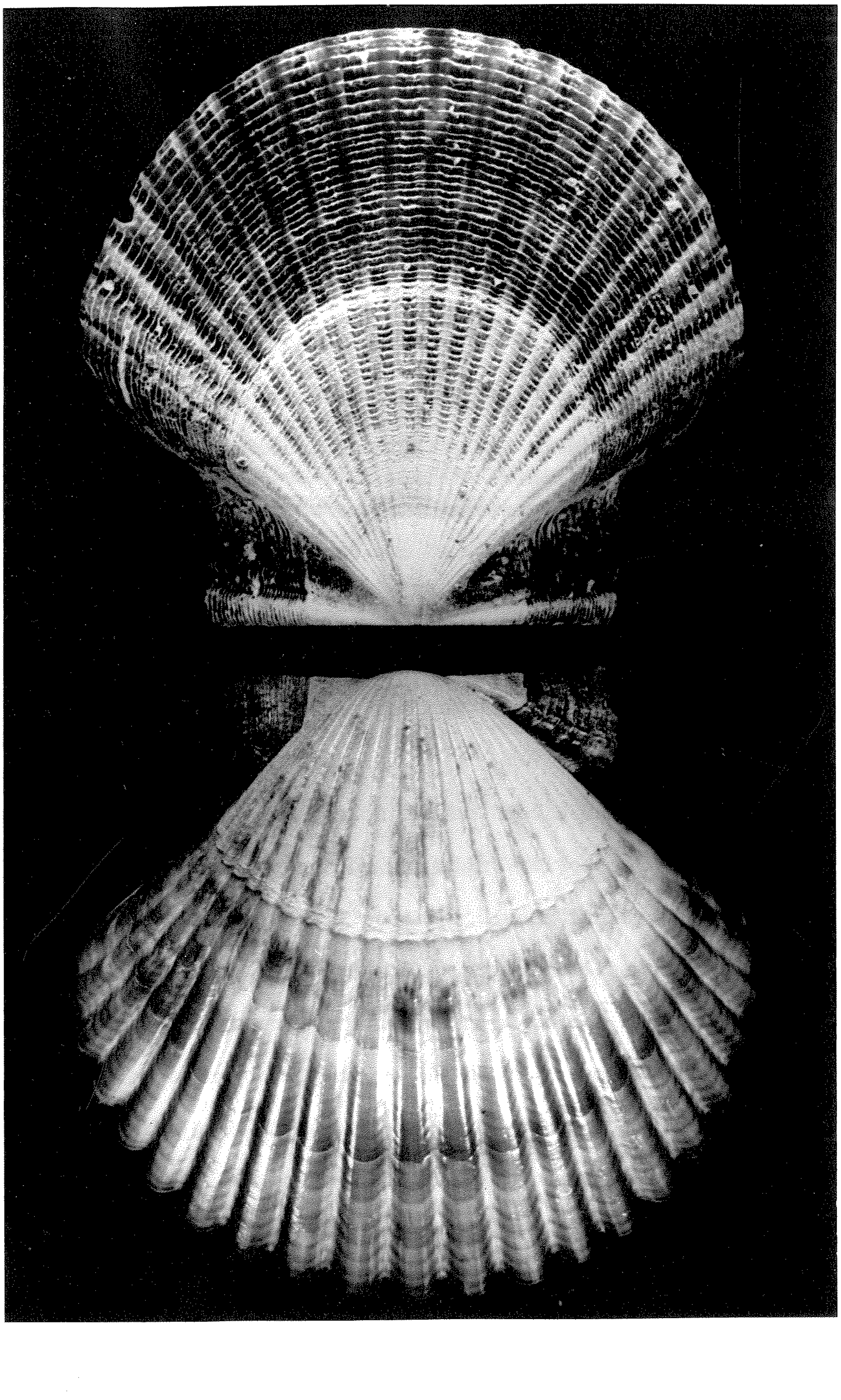
Data from this experiment showed that Pecten vogdesi forms two distinct varieties of daily growth line, one similar to that of Pecten diegensis and one very different. Growth rate curves derived from the two varieties correlate within single individuals, and also correlate well between the different specimens grown under the same conditions. Growth rate curves based on measurements made on the ears of the shells are essentially the same as those based on measurements made in the usual manner. These observations are of considerable significance for paleoecological applications of daily growth lines.

The two valves of Pecten vogdesi are very different. The right valve is deeply convex, the left flat or slightly concave. The right valve is light in color, the left richly pigmented. The right valve has smooth rounded ribs and no apparent concentric sculpture. The left valve has flattened ribs with fine concentric ridges, very similar to those found on Pecten diegensis (see chapter IV). Photographs of both valves of Pecten vogdesi are shown in figure 9.

Eight juvenile specimens of Pecten vogdesi were exposed to a tetracycline solution to form a fluorescent band at the margin of their shells (see chapter III). This would permit the identification of subsequent growth. The specimens were put in a small sand-bottom aquarium, supplied with running seawater, for 31 days. Twice during this period they were removed briefly from the water for measurement. They grew very rapidly, nearly doubling in size with an average increase in height of 15 millimeters.

At the termination of the growth period the subjects were

Figure 9



Specimen 0262 of *Pecten vogdesi*

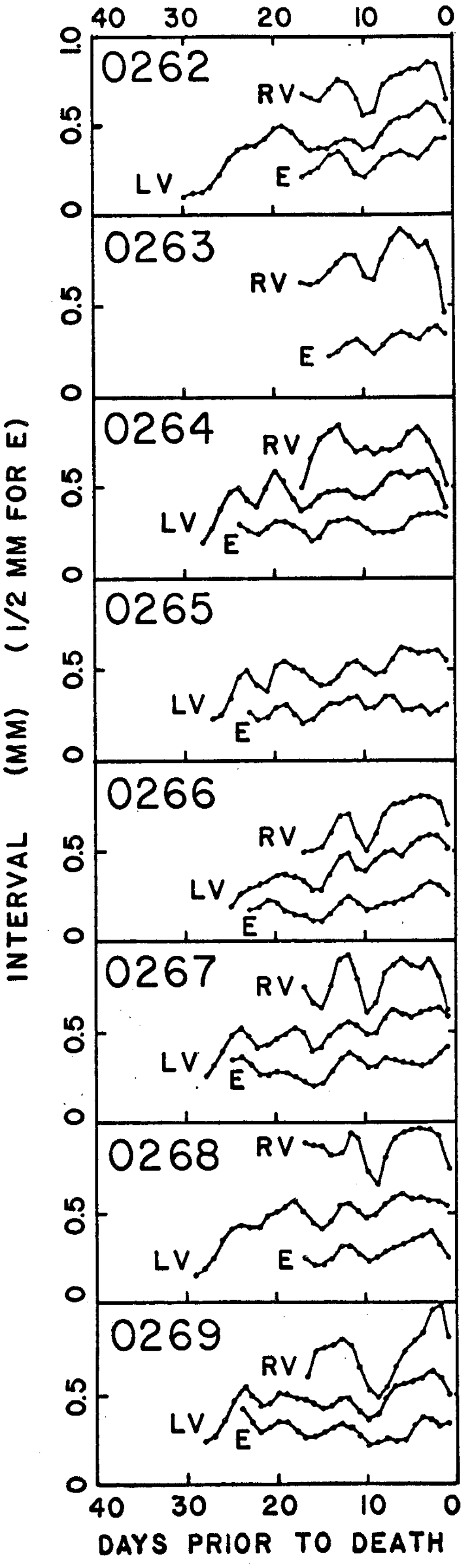
examined for fluouescence. None could be seen through the pigmentation on the left valves, but there was a distinctive line on seven of the eight right valves. Using a correlation curve prepared from a series of paired <u>Pecten</u> <u>vogdesi</u> valves, the positions of the fluorescent lines were extrapolated to the left valves. Ridges could be counted on six of the eight specimens, as one lacked distinct ridges and another, as mentioned, lacked a fluorescent reference point. The counts closely approximated the number of days of experimental growth. An exact correspondence, 31 ridges, was within the limits of error on five of the six specimens, but a count of 30 ridges fit the data on all six. The average count was 29.75, and the lowest reasonable interpretation for any specimen was 27 ridges. Tetracycline exposure has been shown to inhibit growth (see chapter III), so a number of ridges one or two less than the number of days does not argue against the case for daily periodicity.

Further examination of the shells yielded additional information. A common feature on the right valves of <u>Pecten</u> <u>vogdesi</u> is the disturbance check, a small steplike discontinuity in the shell surface apparently marking a former shell margin at a temporary interruption of growth. Such checks are not noticed on the left valves, possibly due to the strong sculpture. All the right valves had disturbance checks in the area of new growth; in most cases the two most prominent checks divided the new growth into three subequal zones. In addition, most of the new growth was marked with fine concentric lines of dark pigment, particularily prominent near the margin. These lines could not be counted across the entire area of new growth, but were counted within the outer two zones delineated by the disturbance checks. There were ten lines in the outer zone in all eight specimens, and nine lines in the middle zone in the seven specimens which could be counted. Although these lines were too faint to be counted in the inner zone, extrapolation from the outer two zones suggests that there would be about 30 pigmented lines in all three zones. As this implies daily periodicity, there was a distinct possibility that the two disturbance checks could be related to environmental stresses on the tenth and nineteenth days before the death of the animals. These dates were found to be those on which the animals were removed from the aquarium for measurement. In addition, the heights measured on those occasions agree with the heights of the disturbance checks. This is compelling evidence for the daily periodicity of the pigmented growth lines.

As a further test of the daily nature of both types of growth lines, they were compared by means of growth rate curves. If the lines on each valve delineate equivalent time periods, then periods of faster growth would be represented by widely spaced lines, and periods of slower growth would be represented by narrowly spaced lines, with the same sequence being followed on each valve. Figure 10 compares the growth rate curves of right and left valves for the eight specimens. This high degree of similarity supports the suggested equivalence of the pigmented lines of the right valve to the sculptured lines of the left valve, and thereby strengthens the independent evidence for the daily periodicity of each.

Figure 10 displays another interesting relationship. The

FIG. 10



GROWTH RATE CURVES FOR RIGHT VALVE (RV), LEFT VALVE (LV), AND ONE EAR (E) OF EIGHT SPECIMENS OF *PECTEN VOGDESI* similarities in growth rate curves between specimens are as strong as those between the valves of individual specimens. This, like the results of the Pecten diegensis experiment, suggests that the short-term variations in growth rate of different individuals are environmentally controlled. The paleoecological implications of this are discussed in chapter IV.

Growth rate curves were also constructed from measurements made on the ears of the right valve. These curves (anterior ear only) are included in figure 10. They show a good correlation with the growth rate curves derived from the main body of the shells. This implies that essentially the same curve can be constructed from any part of the shell, so long as measurements are made in the direction of growth. This has considerable application to paleoecology, because most fossil assemblages contain a large proportion of fragmental material.

VI: DAILY GROWTH LINES AS BIOLOGICAL RHYTHMS

Although the existence and validity of daily growth lines appear well established, it would be desirable to know something about the factors responsible for their periodicity. If there is any possibility that these lines are formed in response to environmental changes which are not exclusively daily, the paleoecologist should be fully aware of the exceptions.

In this investigation I considered several environmental parameters which fluctuate with approximately diurnal periodicity. Two groups of effects possess this periodicity; tidal effects, with a period of not quite 25 hours, and solar effects, with a theoretical period of 24 hours.

Although tidal effects have approximately diurnal periodicity, they also have approximately semidiurnal periodicity. In most places the semidiurnal periodicity is the dominant rhythm for most of the lunar month. For this reason it is unlikely that tidal effects could cause the formation of diurnal growth lines, although it is not impossible under exceptional conditions.

One important solar effect is variation in light intensity. This is certainly very important in the upper fifty meters or so, as this is the zone of primary productivity through photosynthesis. It seems to be an important factor at much greater depths, however, as vertical migration has been demonstrated in plankton as deep as 300 meters, in direct response to light intensity levels of about 10^{-7} of surface illumination (Clarke and Backus, 1956). Pectinids have been shown to be sensitive to light intensity variations (see chapter

II), but I know of no experiments to establish their range of sensitivity in low illumination levels.

Another solar effect is variation in water temperature. This is unlikely to exhibit significant daily variations under any conditions except very shallow water, but many species of pectinids occupy just such environments.

A third solar effect is variation in food supply. Pectinids are filter feeders and presumably derive much of their nourishment from the plankton. As mentioned above the plankton migrate up and down in the water column in response to changes in light intensity (see also Cushing, 1951). Since pectinids are essentially fixed in position (normal tidal variations are of insignificant magnitude compared to the vertical migrations of plankton), they would experience a daily variation in food supply.

Other solar effects are more subtle. One such is variation in oxygen concentration. Verwey (1929) demonstrated that this varies considerably from day to night on a coral reef. Ramsey (1962) found smaller but still significant variations in oxygen concentration in surface waters off the California coast. Other variations in seawater chemistry have been shown to occur with daily periodicity (Ryther, Menzel and Vaccaro, 1961).

Which of these factors can be related to my experiments? By a singular set of circumstances, it appears that most of them can be eliminated from consideration as possible causitive agents.

Kerckhoff Laboratory, where these experiments were conducted, is located on the inlet to Newport Bay, a sizeable estuary.

When the tide is falling, the water in the inlet is coming from the estuary; when the tide is rising, the water is coming from the open ocean; and the seawater in the laboratory passes through the system rapidly enough to closely approximate the seawater in the inlet at all times. Thus the characteristics of the seawater in the laboratory vary with the tides. Figure 11 illustrates this point for the water temperature. Other characteristics, such as food content and chemistry, are likely to be as different between ocean and estuary as the temperature.

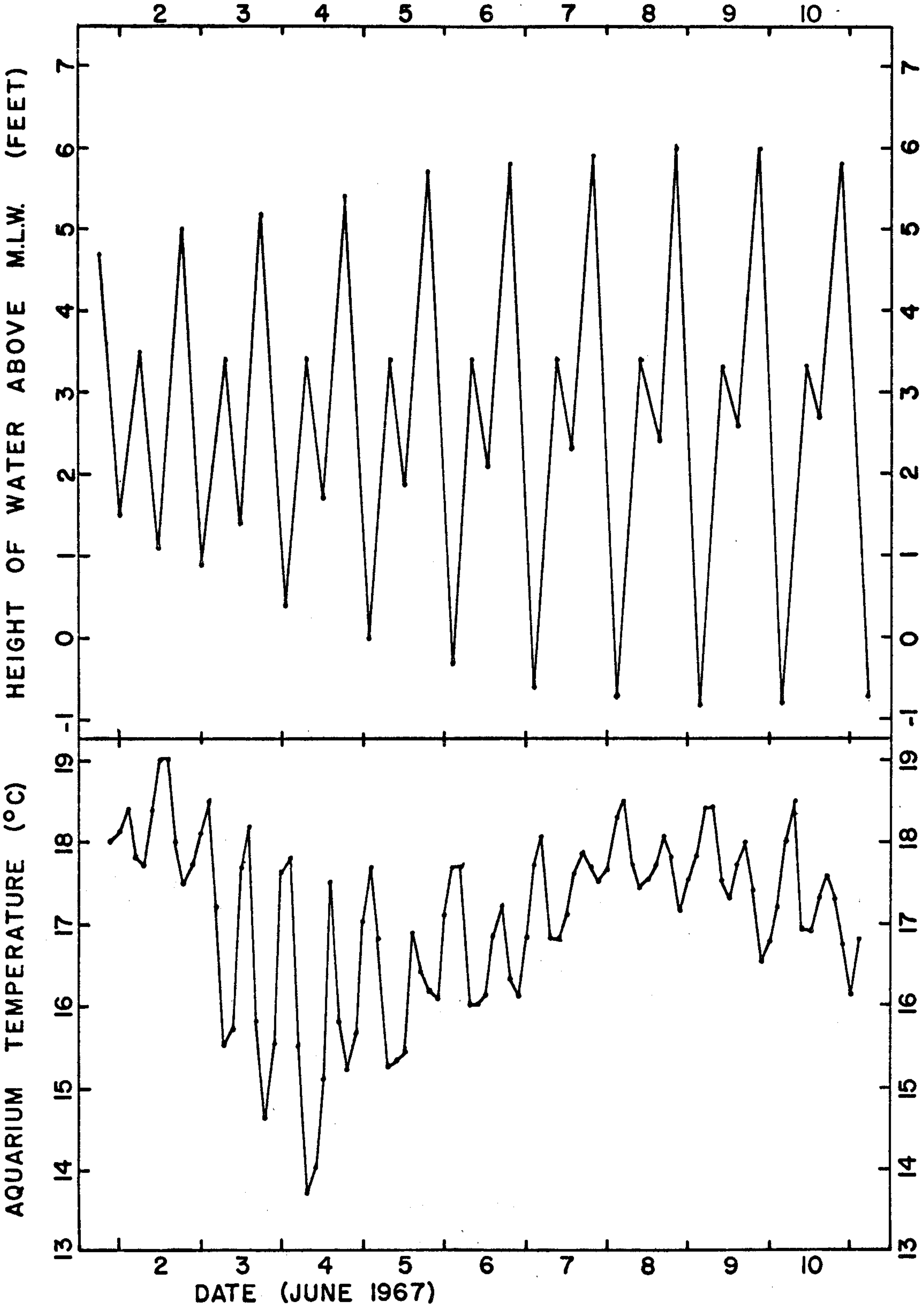
The only environmental variable experienced by the experimental animals which would not appear to be influenced strongly by the tidal period was light intensity. The animals were kept in transparent aquaria near a large window, but the rest of their environment was in the seawater that flowed through their tanks. To investigate this further, some experiments were conducted with artificial illumination.

In the initial experiment scallops of several species, including *Pecten diegensis*, *Pecten vogdesi*, and *Aequipecten circularis*, were put into four tanks and subjected to the following light regimes:

Tank One:	continuous light
Tank Two:	12 hours light, 12 hours dark
Tank Three:	8 hours light, 8 hours dark
Tank Four:	continuous dark

These tanks developed particularily severe problems with their flow of seawater, and several times the flow stopped completely for several hours at a time in one or more tanks. It was no particular surprise

FIG. 11



COMPARISON OF TEMPERATURE AND TIDAL VARIATIONS AT KERCKHOFF MARINE LABORATORY, CORONA DEL MAR, CALIF.

to find that most of the animals in tank three were dead when the experiment was terminated after 16 days. It was also no surprise to find that growth had been poor in the other tanks, but it was a surprise to find that there had been little difference in either growth or growth line formation between animals grown in the different tanks. Part a of figure 12 lists the counts of new growth lines for this experiment. Since the seawater had been heated slightly for the benefit of the warm water species, a second experiment was conducted with Pecten diegensis using unheated water. The results of this experiment are shown in part b of figure 12.

These data suggest that the direct influence of light-dark cycles is not important in the formation of growth lines, since for three different species the animals grown under constant conditions of illumination formed as many lines as those grown under a 24-hour cycle of light and darkness. This argument would be more convincing if the animals exposed to 16-hour cycles of light and darkness had lived and added the same number of growth lines. To resolve this point a third experiment, using a constant flow regulator, was run for 22 days with six specimens of Pecten diegensis. The experiment was interrupted on the tenth day for measurments, and the technique was further refined by notching the shells on the first and tenth days to permit an exact count of new lines. The data from this experiment are shown in figure 13.

Unlike the results of the previous experiments, these results demonstrate that the light-dark cycle has a direct effect on the formation of growth lines, since every animal formed more growth

SPECIES	TANK ONE (continuous light) Specimen	 No. of Lines	TANK TWO (12 hr light, 12 hr dark) Specimen	 No. of Lines	TANK FOUR (continuous dark) Specimen	 No. of Lines
a. Number of Lines Formed by Three Species over a 16-day Period in Three Different Lighting Regimes						
Pecten diegensis	0362	13 ± 2	0357	10 ± 2	0343	6 ± 3
Pecten vogdesi	0576	13 ± 1	0577	14 ± 1	0579	13 ± 1
Aequipecten circularis	0580	13 ± 2	0581	15 ± 2	0583	15 ± 2
b. Number of Lines Formed by *Pecten diegensis* over an 18-day period in Three different Lighting Regimes.						
Pecten diegensis	0349 0367	10 ± 3 14 ± 3	0350	11 ± 3	0358	12 ± 3

Figure 12

SPECIMEN NUMBER	FIRST PERIOD 10 days / 15 cycles	SECOND PERIOD 12 days / 18 cycles	BOTH PERIODS 22 days / 33 cycles
0631	15	17	32
0632	13	18	31
0633	11	16	27
0634	12	15	27
0635	11	15	26
0636	13	17	30

Number of Growth Lines Formed by Six Specimens of *Pecten diegensis* Grown for 22 Days under Conditions of Alternating 8-hour Periods of Light and Darkness

Figure 13

lines than it should have if such formation were regulated by diurnal variations in the environment. Growth line formation in half of the animals closely approximated the number of light-dark cycles in the experiment. Inasmuch as no previous examples of extra growth lines had been identified, while examples of missing growth lines are frequently encountered, it seems most likely that the growth lines were formed in direct response to the light-dark cycles. Yet how can these results be reconciled with those of the first two experiments?

In recent years biologists of widely differing interests have compared their experiences and found that 24-hour periodicity is a common phenomenon in all living things. Although the subject of biological rhythms is becoming exceedingly complex, a few points are pertinent to interpretation of my experiments.

Most rhythmic behavior was once thought to be exogenous, that is, in direct response to environmental stimuli. Thus it was believed that a flower opens its petals in the morning and closes them in the evening in direct response to the appearance and disappearance of the sun. However, experiments indicated that the flower will continue to open and close its petals for several days even when placed in total darkness. This phenomenon is called an endogenous rhythm, or biological clock. Such rhythms are widely encountered throughout the plant and animal kingdoms. Various workers have reported on rhythms in the movements of leaves in plants, the discharge of sporangia in fungi, the migration of pigments in arthropods, the emergence of insects from pupae, the variations in oxygen consumption in both plants and animals, the activity patterns of snails, bees, crabs, lizards, squirrels, and numerous other animals, the temperature in mammals, the production of innumerable metabolic products in mammals, the mitoses in cells of various plant and animal tissues, and even susceptibility of mice to various toxins (see Bunning, 1964; Halberg, 1960; Sollberger, 1965).

All these rhythms appear to obey a few simple rules. If the organism is in normal surroundings with a 24-hour periodic variation in the environment, the rhythms will continue indefinitely with a precise 24-hour periodicity. If the organism is then placed in constant surroundings the rhythm will continue for many days, but may shift from a 24-hour periodicity to a longer or shorter period and may eventually fade out. If the animal is raised under constant conditions it may show no rhythms at all, but any sudden change in the environment such as a flash of light in dark conditions may initiate a rhythm. The phase of the rhythm may be shifted by altering the environmental conditions, such as gradually inverting the light-dark regime. The period of the rhythm may also be shifted, so that under conditions of 10 hours of light and 10 hours of darkness the rhythm may adjust to a 20-hour period. However, most rhythms will revert to the sort of behavior exhibited under constant conditions if the artificial cycles differ by more than 6 to 8 hours from the normal 24-hour cycle.

My results indicate that the formation of daily growth lines follows the same rules as biological rhythm phenomena. The growth lines are normally formed daily, indicating a 24-hour periodicity. They continue to be formed, approximately one per day, under conditions of either constant illumination or constant darkness. In addition, they can be shifted to a shorter period by a shortened cycle in an artificial environment. The identification of a biological rhythm in the formation of daily growth lines permits the resolution of the apparently conflicting evidence in these experiments, and demonstrates that the cycle of light and darkness is a major stimulus in the formation of growth lines in these species.

If further experiments support this interpretation, daily growth lines will have many advantages in the study of biological rhythms. Experiments in most rhythmic phenomena require continual sampling or monitoring, either by the investigator or by special apparatus. In the mollusk shell the growth lines form their own record, with no need for external monitors. Moreover, experiments would not be limited to highly artificial laboratory situations, for these animals record the periodicity in their natural environment, free from disturbance by the investigator.

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VII: DAILY GROWTH LINES IN OTHER SPECIES

Experiments involving over 650 specimens of 14 different pectinid species and subspecies were conducted during this study. Although evidence is scant in several groups, it appears that when fine concentric growth ridges are present, as in species of Pecten and Aequipecten, they represent daily growth increments. When the surface sculpture is characterized by rows of spines or nodes, as in species of Chlamys and Hinnites, it does not appear to reflect daily growth increments. The following is a summary of data and interpretation for individual species.

Aequipecten circularis. Three specimens with well-defined growth added about one line per day. Others with discontinuous growth added fewer lines during the same periods. Growth line counts are presented in figure 14. These lines will probably be established as daily increments by further experimentation.

Aequipecten gibbus. This species appears to form growth lines by daily accretion. In figure 14, specimens 0008 to 0012 were grown in their natural environment in Harrington Sound, Bermuda. The others were grown at Kerckhoff Laboratory.

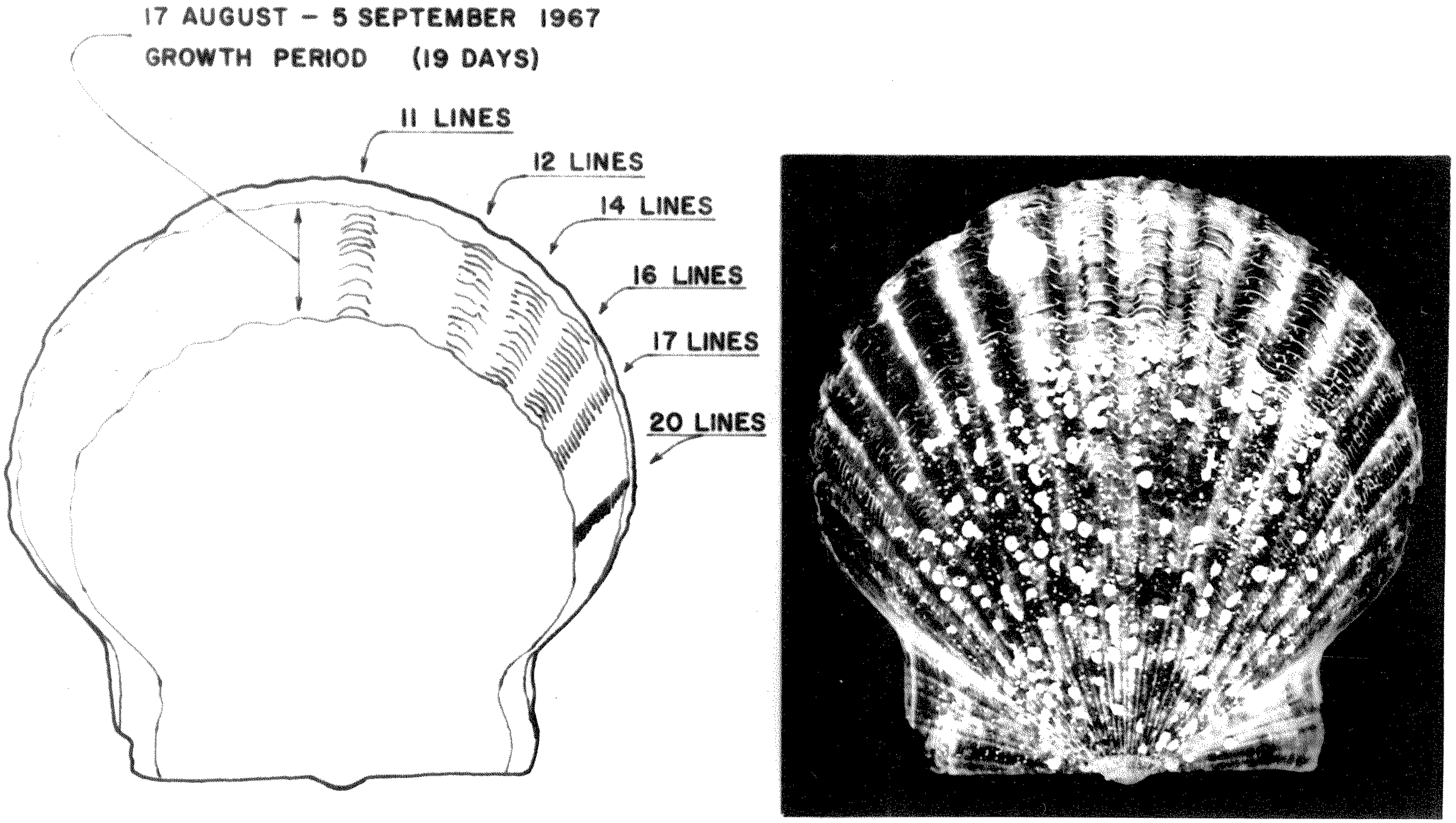
Aequipecten irradians. This species differs from the others studied from this genus in that the complete series of growth lines commonly appears only at the anterior and posterior margins and on the ears. The ventral margin usually shows only about 70% or less of the full number present. Photographs in figure 15 illustrate this effect. Counts of lines at the points where they are best developed agree closely with the number of days of growth. Figure 16 shows the data

SPECIMEN	DAYS GROWN	LINES FORMED	DAYS GROWN	LINES FORMED	DAYS GROWN	LINES FORMED
Aequipecten circularis						
0271	20	20 ± 2	20	20 ± 2	10	10 ± 2
0281	20	21 ± 2				
0306	20	22 ± 2	20	22 ± 2		
0566	32	15 +				
0569	32	20 +				
0570	32	27 ± 4				
Aequipecten gibbus						
0008	7	6 ± 1				
0009	7	6 ± 1				
0010	7	0				
0011	7	0				
0012	7	6 ± 1				
0477	14	16 ± 4				
0478	14	16 ± 4				
0479	14	19 ± 4				
0480	14	13 ± 4				
0481	14	18 ± 4				
0482	14	15 ± 4				

Figure 14. Relation between Days of Growth and Numbers of Growth Lines for Two *Aequipecten* Species.

FIG. 15

SPECIMEN 0413 of *Aequipecten irradians*



SPECIMEN	DAYS GROWN	LINES FORMED	NOTE
0413	19	20 ± 2	
0415	19	20 ± 2	
0416	19	19 ± 2	
0419	19	13 ± 3	
0420	19	16	edge abraded
0421	19	11	edge abraded
0423	19	16 ± 2	
0432	29	27 ± 4	
0434	29	24 ± 4	
0435	29	27 ± 4	
0436	29	23 ± 4	
0437	29	25 ± 4	
0438	29	20 ± 4	
0439	29	17 ± 4	
0440	29	27 ± 4	
0441	29	23 ± 4	
0442	29	23 ± 4	
0443	29	29 ± 4	
0444	29	22 ± 4	

Relation between Days of Growth and Growth Line Numbers for Specimens of *Aequipecten irradians*.

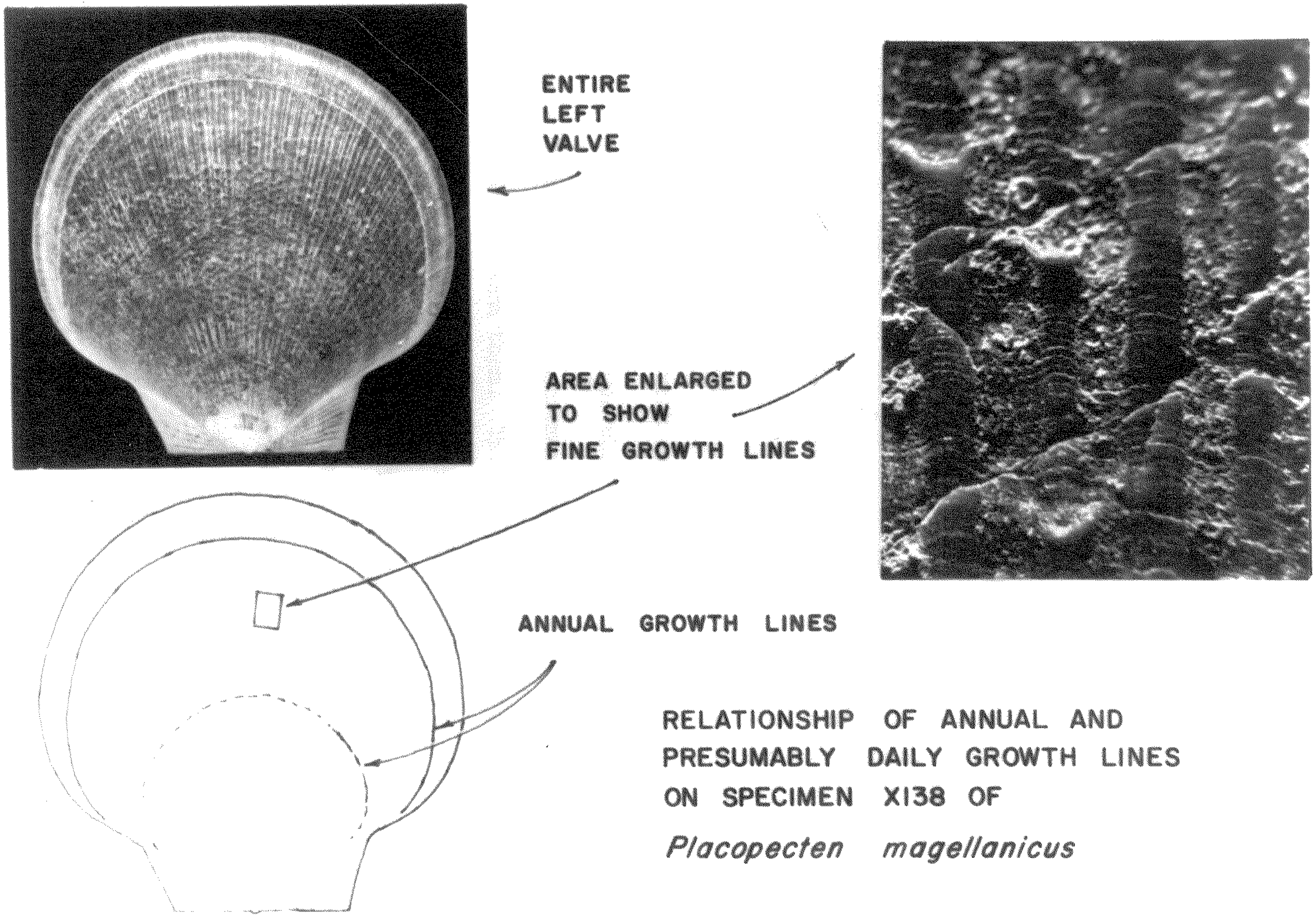
Figure 16

for seven specimens grown in their natural environment in the harbor at Woods Hole, Massachusetts, for 19 days, and for 12 specimens grown at Kerckhoff Laboratory for 29 days. Missing lines due to growth stoppages may account for the low counts on some specimens in the second group.

Placopecten magellanicus. Although this species does not form the high, narrow, concentric ridges typical of forms discussed so far, a fine concentric sculpture is present, as illustrated in figure 17. Specimens kept in the laboratory did not grow appreciably, but some line counts were made on specimens with well-defined annual rings. Counts ranged from 345 to 370 fine lines between annual rings, but probable errors introduced by interpolation (bypassing surface blemishes), interpretation (deciding whether a slight depression makes two lines of one), and uncertainty in the position of the annual ring (these are sometimes many lines broad, and are probably not formed on the same day each year) increase the realistic limits to perhaps 315 to 400 lines per annual increment. Still, this suggests that further investigation might find them to be daily increments.

Three species, *Hinnites multirugosus*, *Chlamys hastata herica* and *Chlamys hastata hastata*, form predominately spinose sculpture. Specimens of these species were grown in the laboratory but no relation was found between the numbers of rows of spines formed and the number of days grown. Some specimens appeared to have concentric ridges in early growth stages, but none formed these ridges on increments grown in the laboratory.

Leptopecten latiauratus monotimeris, a predominately smooth-



RELATIONSHIP OF ANNUAL AND
PRESUMABLY DAILY GROWTH LINES
ON SPECIMEN X138 OF
Placopecten magellanicus

FIG. 17

shelled form, did not appear to mark growth increments by either sculpture or pigmentation; thus no conclusions about its growth could be made. A few specimens of *Leptopecten latiauratus latiauratus*, which does form concentric ridges, were grown in the laboratory but results were not conclusive (see chapter X).

One specimen each of *Leptopecten palmeri* and *Aequipecten circularis aequisulcatus* grew poorly during the experiments. Counts of their growth lines indicate fewer lines formed than days passed, but this may be due to interruptions in growth.

Specimens of *Chlamys rubida* did not grow during the experiments at Kerckhoff Laboratory, probably due to the much higher seawater temperatures there than occur in their normal environment.

Although further work is suggested in some cases, the data presented here and in previous chapters strongly suggest that concentric ridges mark daily increments of shell growth in those species of pectinids which form them. This is an important point, for the concept of daily growth lines must be shown to be valid on a generic or higher taxonomic level before it can be widely applied to paleoecology. Without this confirmation, only those fossils with living representatives known to form daily growth lines could be used.

VIII: INTERNAL GROWTH LINES

Next to surface morphology, the shell characteristic most likely to be preserved in a fossil pectinid is the shell structure. If features within the shell can be used to define growth increments, thin sections and peels might be of considerable value in the interpretation of the history of growth.

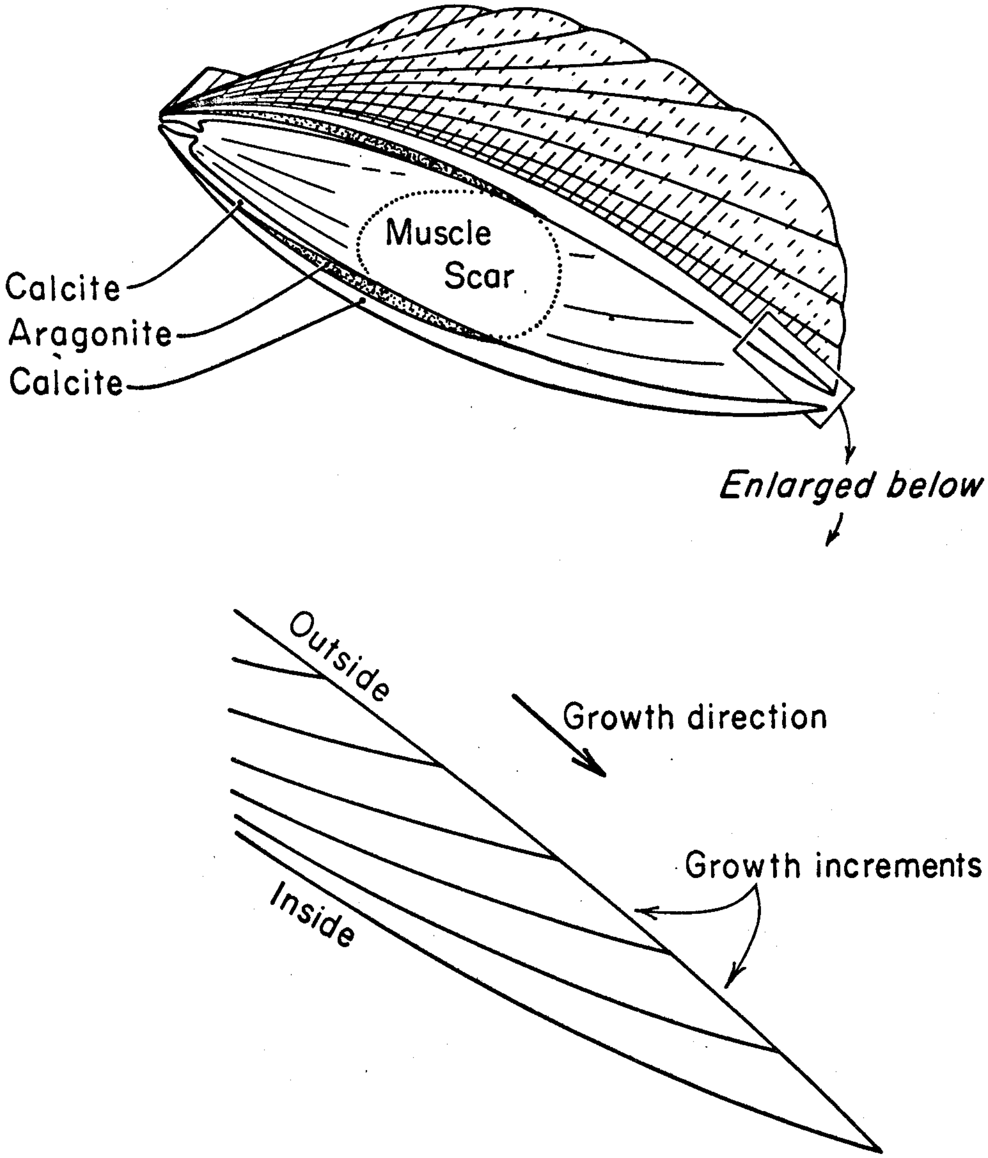
Barker (1964) reported periodic growth lines within species of bivalves, and Pannella and MacClintock (1968) and House and Farrow (1968) demonstrated the relationships of such lines to environmental factors, including the diurnal cycle. These investigations were conducted on bivalves composed of aragonite, and thus are not directly applicable to predominately calcitic shells such as pectinids (for discussion of shell mineralogy, see Bøggild, 1930, and Lowenstam, 1964).

Figure 18 illustrates the principal structural features of a sectioned pectinid shell. Note that aragonite is confined to the present and former position of attachment of the adductor muscle (in at least some species there is also a thin film of aragonite marking the present and former position of the pallial line). Sections not intersecting these zones are wholly calcite. A portion of the section near the margin has been enlarged to illustrate the idealized geometry of growth increments (see also Carter, 1967). All sections used in this study are radial, i.e., in a plane extending from the beak to a portion of the margin, approximately parallel to the direction of growth and perpendicular to the shell surface.

Sections were mounted in epoxy (Epoxylite 3101, Epoxylite

FIG. 18

Radial Section Through Both Valves of *Chlamys hastata herica*



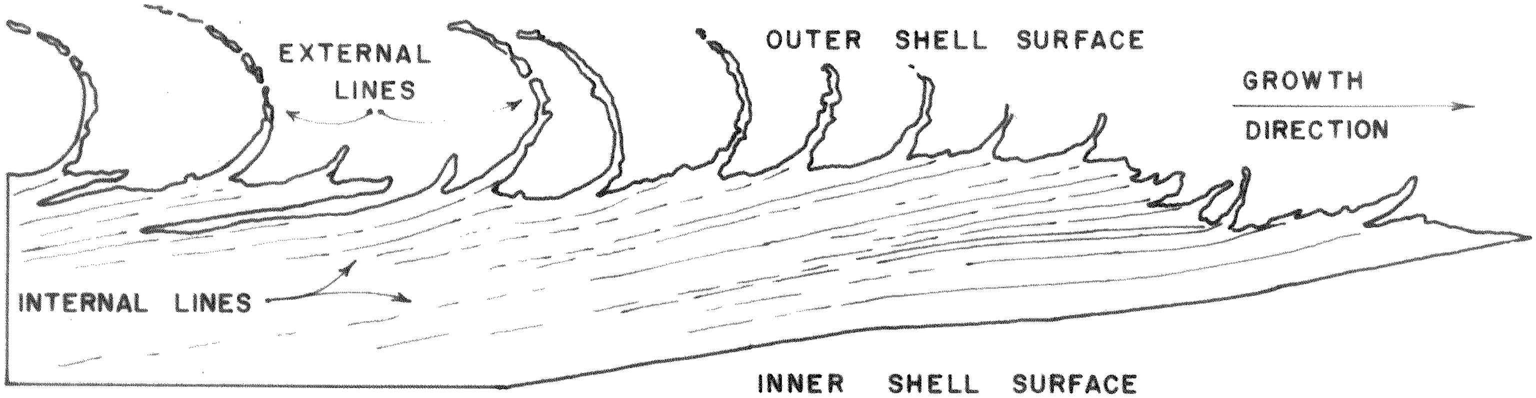
Corp., South El Monte, Calif.) to prevent splitting, ground flat and polished. Surfaces were etched for 10 minutes in 5% Disodium EDTA. After drying, peels were made with 10 mil acetate sheets applied after one surface was softened in acetone for about 15 seconds. Pressure was applied for long enough to remove bubbles and the peel allowed to dry for several hours. After removal from the section, the peel was trimmed and mounted on a slide with cover glass using either high viscosity immersion oil or a synthetic resin mounting medium. Examination and photography was under phase contrast illumination at magnifications from 100x to 1000x. In addition, a limited number of investigations were made at higher magnifications using a Cambridge "Stereoscan" Scanning Electron Microscope.

About 30 sections were examined, representing 22 specimens of 9 different species of pectinids. Figure 19 includes a section of *Pecten diegensis* and a graphical illustration of its orientation and major features. The diagram does not include the set of lines which is oriented about 35° from the internal growth lines, and which obscures the position of the growth lines in much of the photograph. These lines appear to be the boundaries between crystals or crystal aggregates, and are usually much more prominent than the growth lines.

The detailed relationships between these two sets of lines were investigated at higher magnifications with the scanning electron microscope. Figures 20 and 21 illustrate this for a portion of the shell of a specimen of *Pecten vogdesi*. As can be seen, the growth lines appear to be due to the terminations of individual crystals, while the other lines appear to be the boundaries of crystal aggre-

Figure 19

DIAGRAM ILLUSTRATING INTERNAL AND EXTERNAL GROWTH LINES



SECTION THROUGH MARGIN OF PECTINID SHELL

PHOTOGRAPH OF ACETATE PEEL

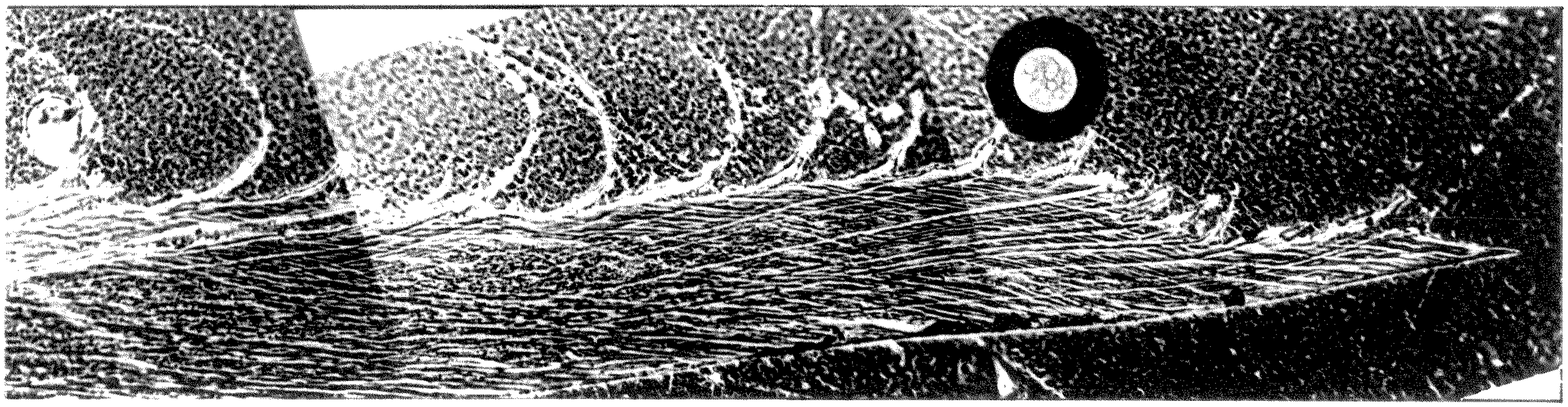
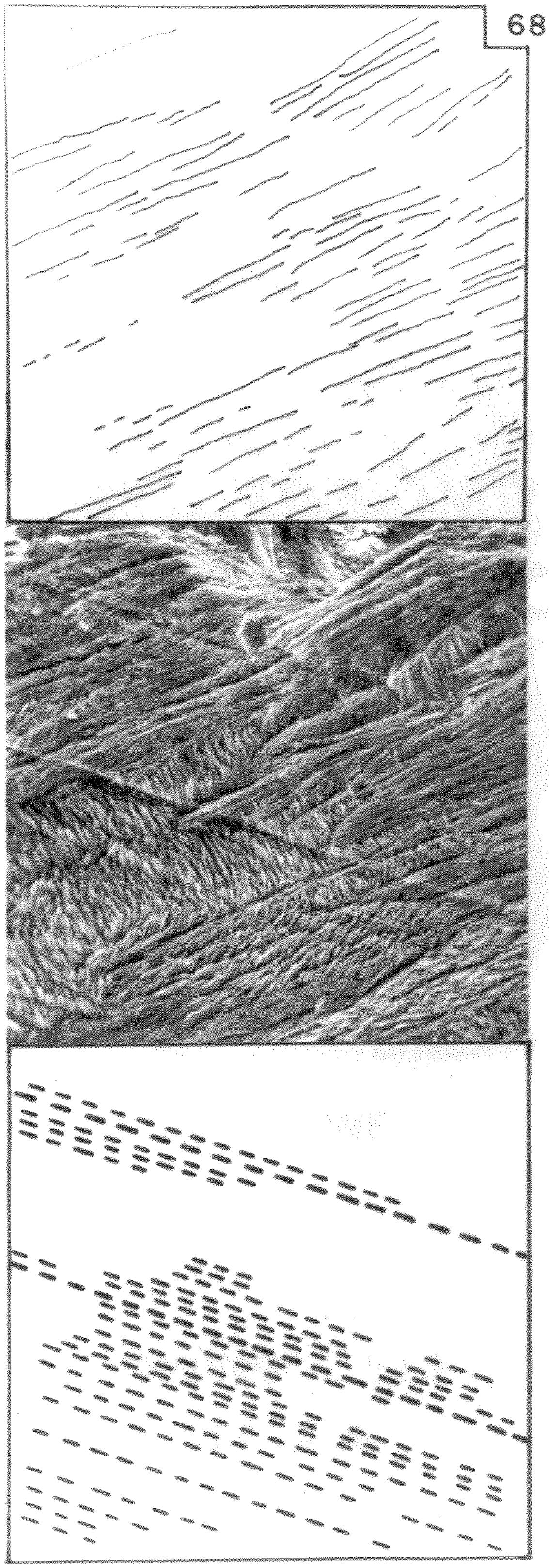


FIG. 20



CRYSTALLOGRAPHIC LINEATION

SCANNING ELECTRON MICROGRAPH

OF A PORTION OF THE SHELL (RADIAL SECTION) OF

Pecten vogdesi

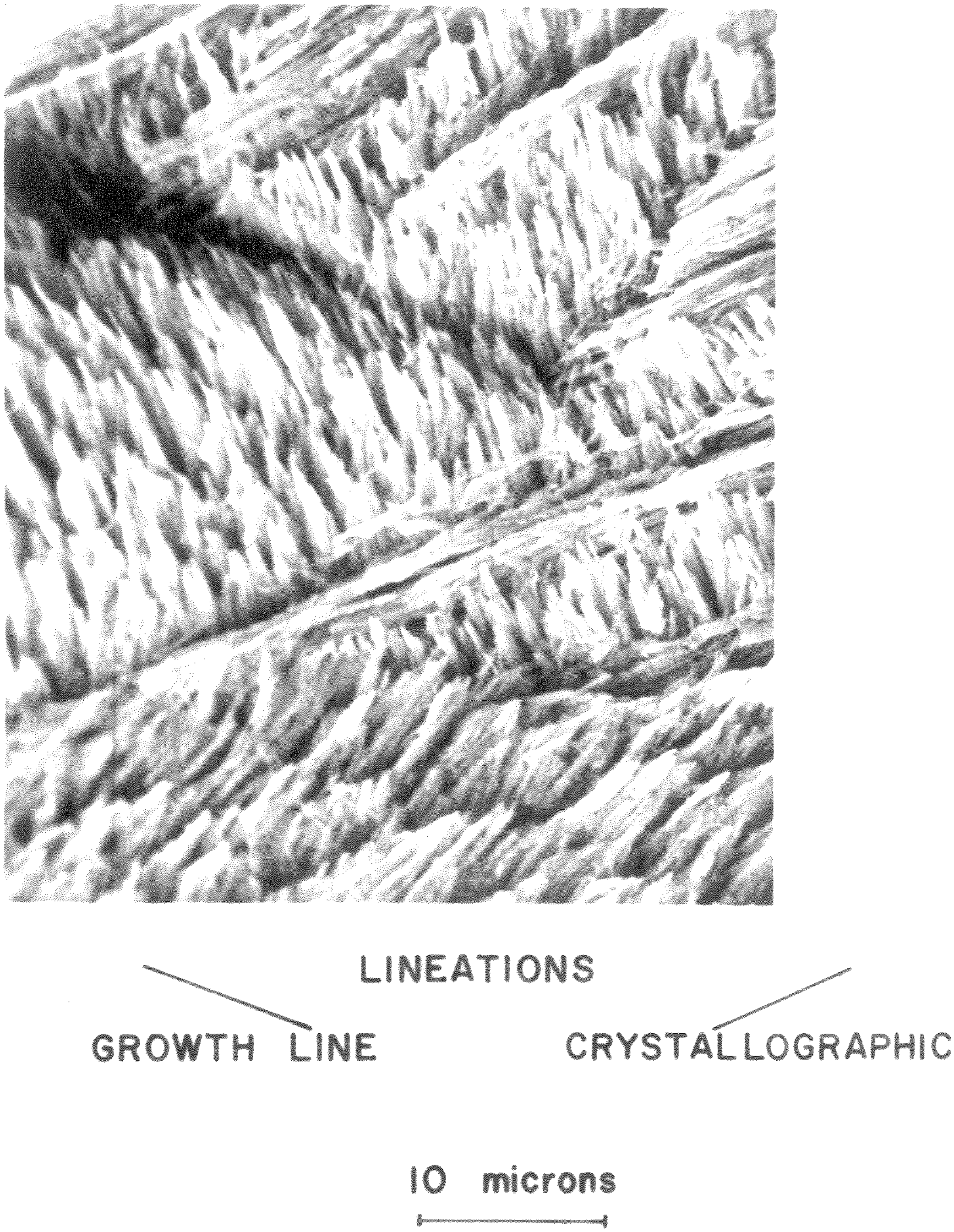
SCALE: ⊢⊣ 10 microns

GROWTH DIRECTION ←

OUTER SURFACE OF SHELL ↑

GROWTH LINE LINEATION

FIG. 21

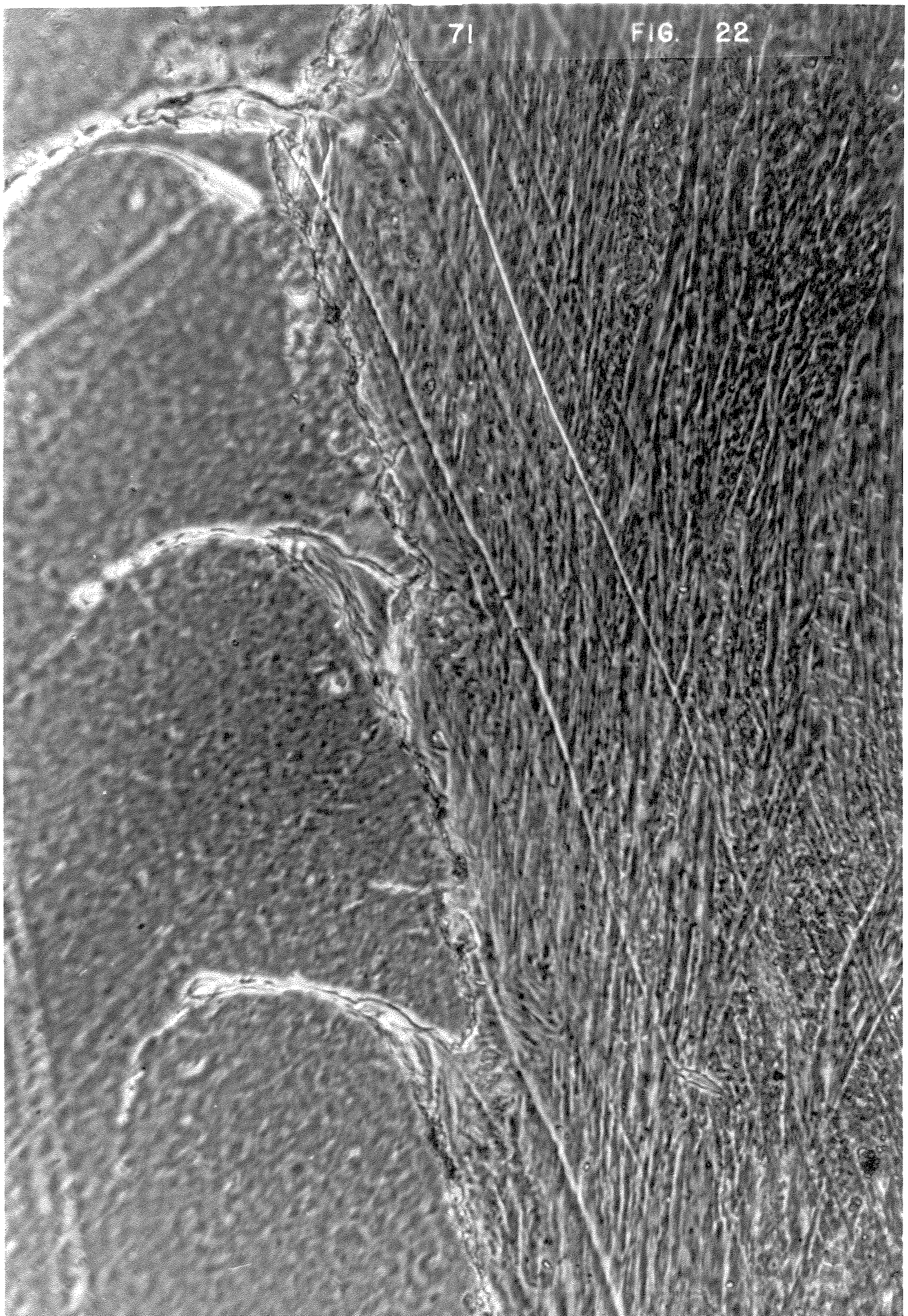


SCANNING ELECTRON MICROGRAPH OF A SECTION THROUGH THE SHELL OF *Pecten vogdesi* gates. The presence of a growth line appears to have no effect on the boundaries or the orientation of the crystal aggregates.

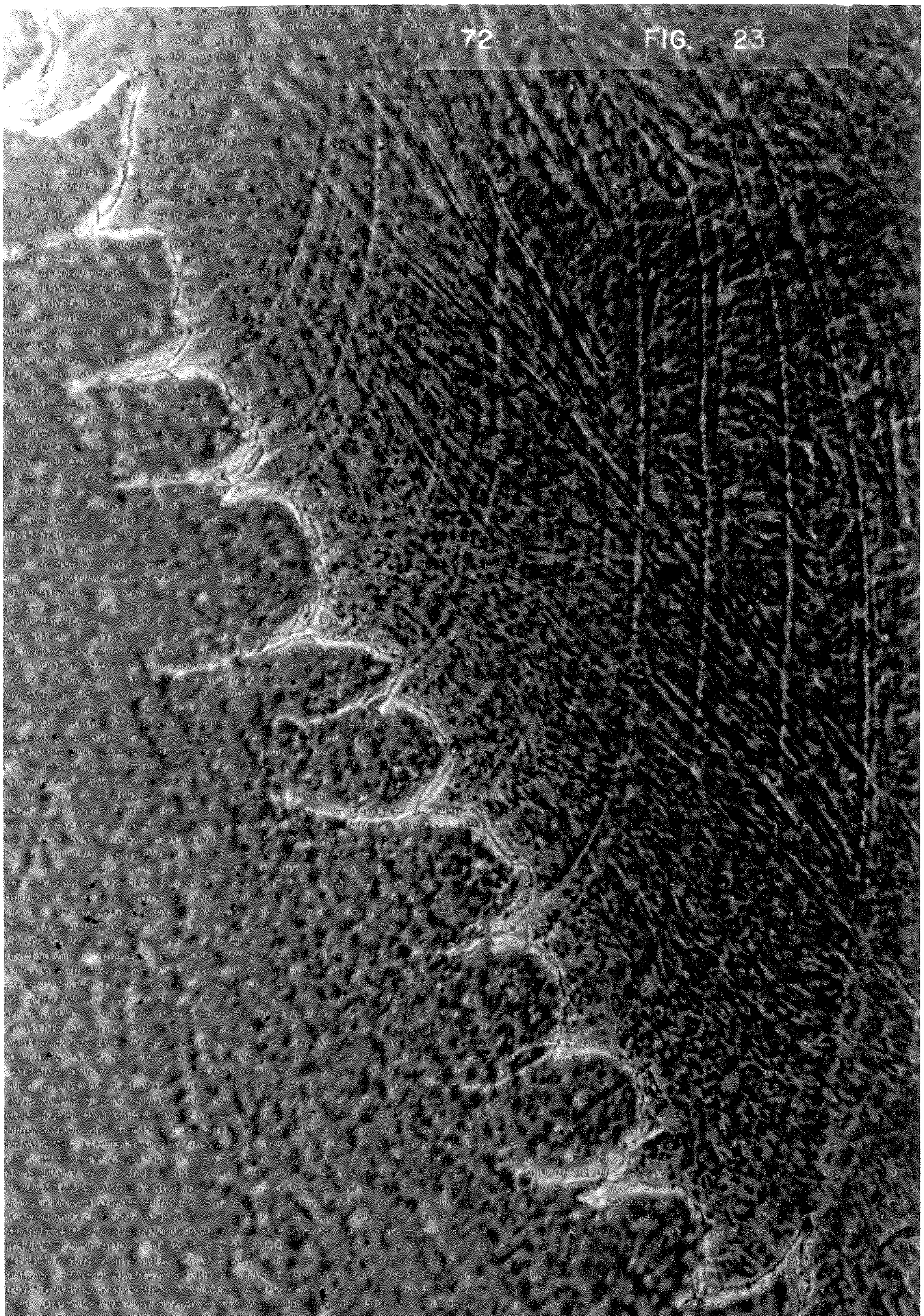
Growth lines were seen in at least some sections for every species studied. In five species they were prominent enough to be examined for periodicity, and seemed to be daily in each case. One of these species, *Chlamys hastata herica*, does not exhibit daily periodicity in its surface sculpture so daily growth lines in its shell structure would be of particular interest.

In those specimens which exhibit well developed internal and external growth lines, such as *Pecten vogdesi* (figure 22), *Aequipecten gibbus* (figure 23), and to a lesser degree *Pecten diegensis* (figure 19), it appears that the internal lines correspond directly to the external lines. Since the external lines have been shown (although not rigorously for *Aequipecten gibbus*) to be daily, it follows that the internal lines are also daily. However, in *Pecten vogdesi* and *Aequipecten gibbus* these internal lines appear to have subdivisions, consisting of perhaps two major and six to ten minor subunits in each daily increment (see also figures 20 and 21). This is a potential cause for confusion in the interpretation of such lines, especially in cases where external lines are absent or are not daily. See, for example, the section of *Placopecten magellanicus* (figure 24).

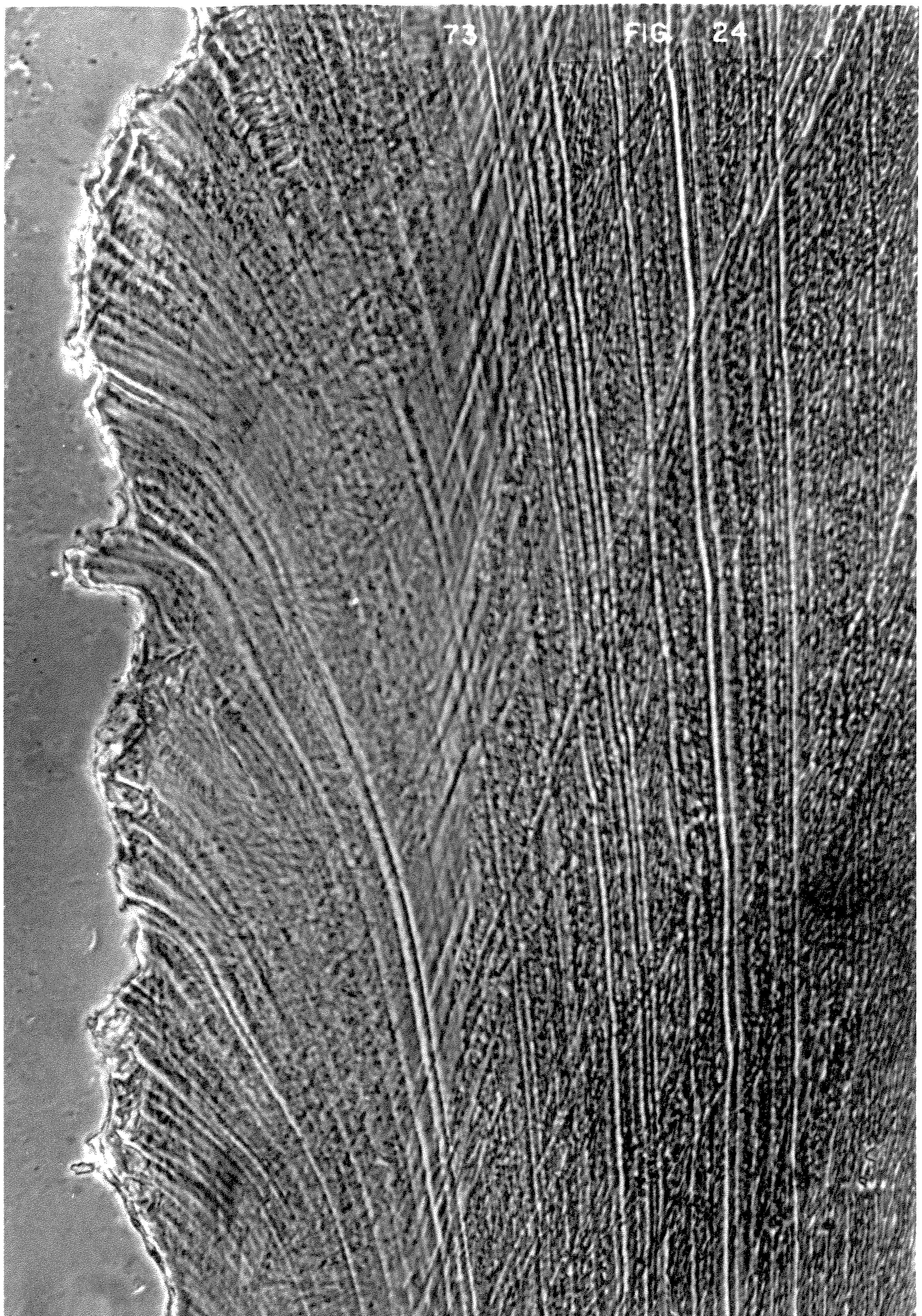
Many sections have good internal lines only at random intervals. This is the case for at least some sections in nearly every species studied. Good lines are especially rare in juvenile shells, although this may be a fortuitous observation. Only a few species, notably *Pecten vogdesi* (left valves), Chlamys hastata herica (figure



71 FIG. 22



72 FIG. 23



73

FIG. 24

25), and Placopecten magellanicus, have extensive series of well-developed internal growth lines.

In two instances, specimen 0415 of Aequipecten irradians and specimen 0515 of Chlamys hastata herica, these internal lines were sufficiently distinct and complete to be counted across a known portion of the shell. In each case the number of lines counted agreed with the number of days of growth, although the surface sculpture did not reflect this number. (Although Aequipecten irradians forms daily ridges, this section was made through the ventral margin, where, as discussed in chapter VII, only a part of the total ridges formed are found.)

Another situation where internal growth lines may be of considerable value is the disturbance line. It is often impossible by surface inspection to estimate the duration of growth stoppage or the extent of loss of former shell margins by abrasion. Yet, as can be seen in figure 26, a part of this information might be recovered by inspection of internal structure.

This study has demonstrated the presence of growth lines within the shell structure of every pectinid species examined. Where these lines are sufficiently prominent for investigation, they appear to be daily, although subunits are also present and may lead to the wrong conclusions if not recognized. These lines are often present only in some specimens of a species and in some portions of a section. For these and other reasons, internal growth lines do not appear as useful in paleoecologic investigations as the external growth lines

Figure 25

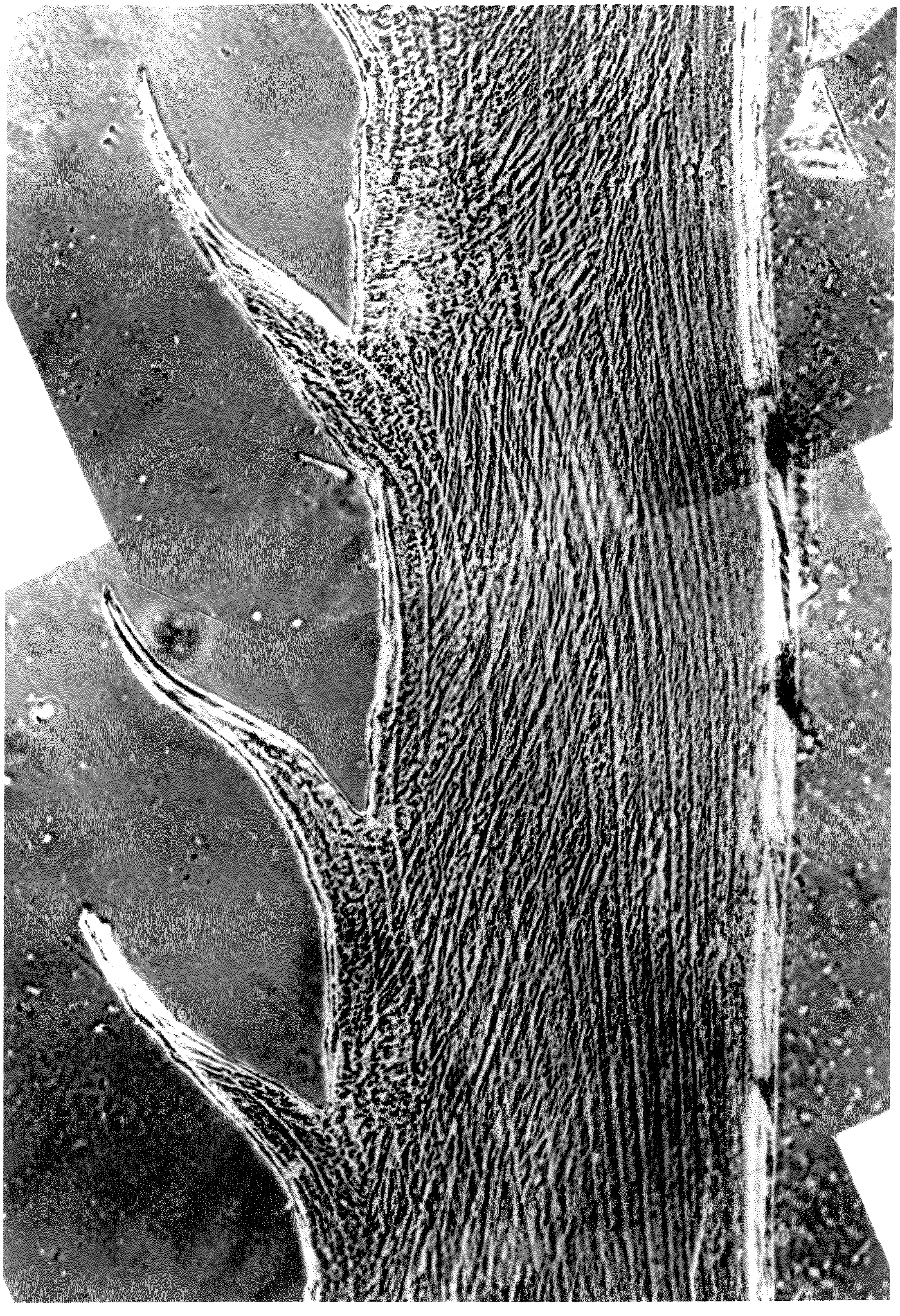
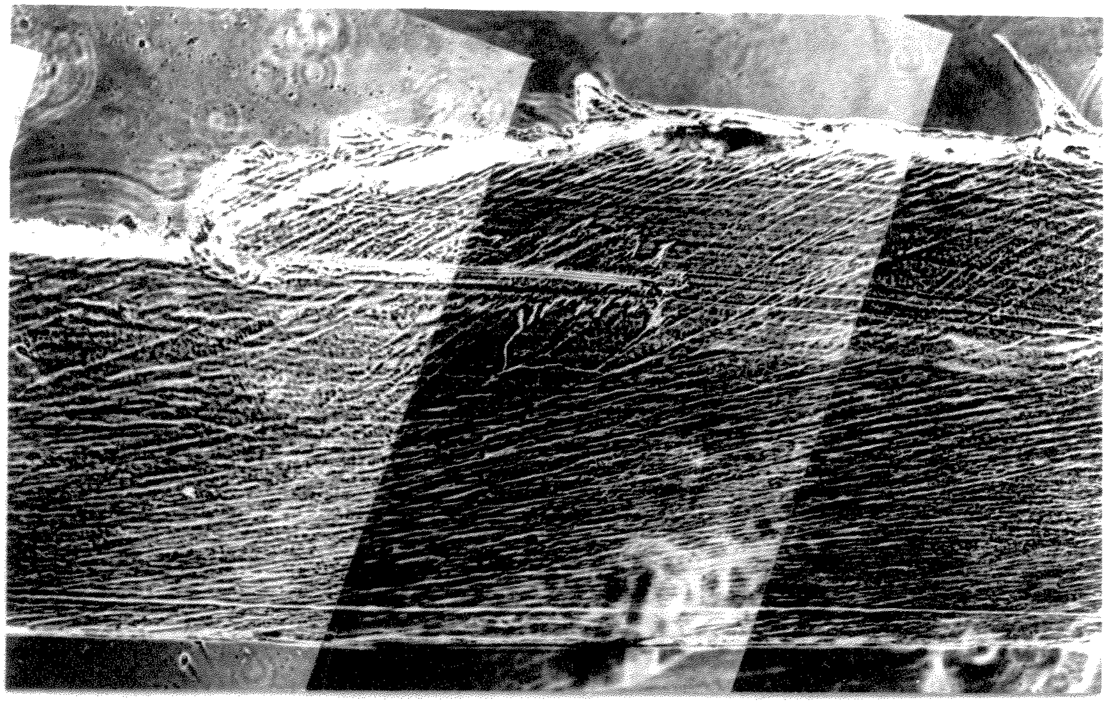
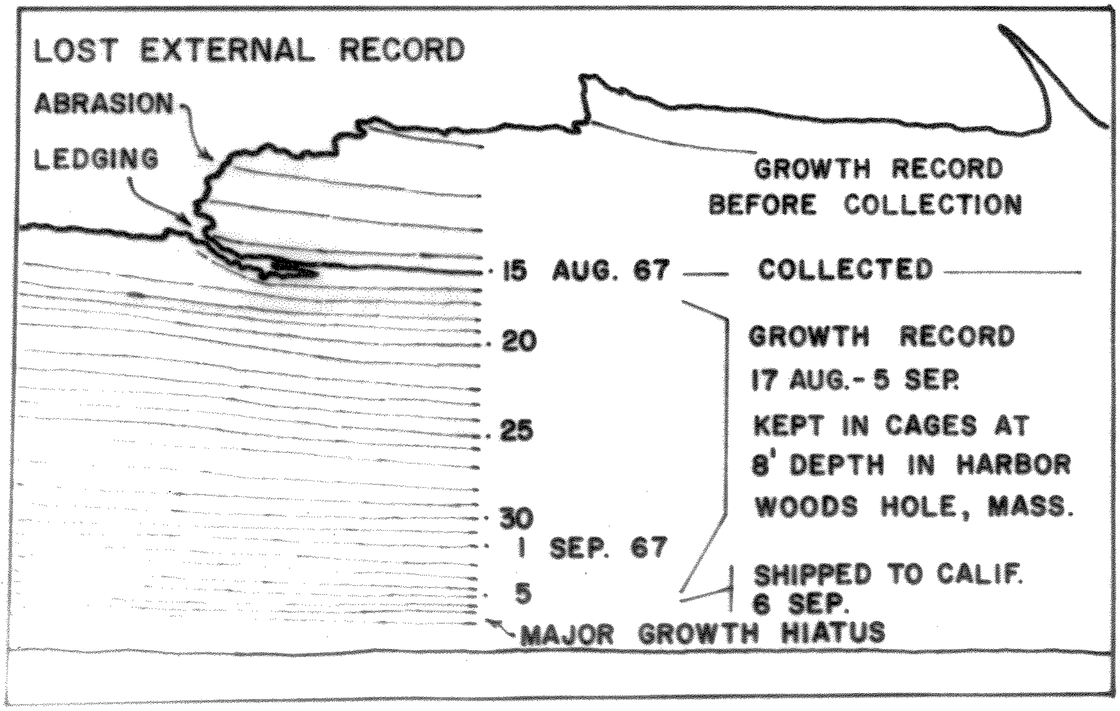


FIG. 26



SPECIMEN 0415 of *Aequipecten irradians*

PHOTOGRAPH AND OVERLAY
OF ACETATE PEEL



discussed in previous chapters, although they may be of considerable value in certain situations.

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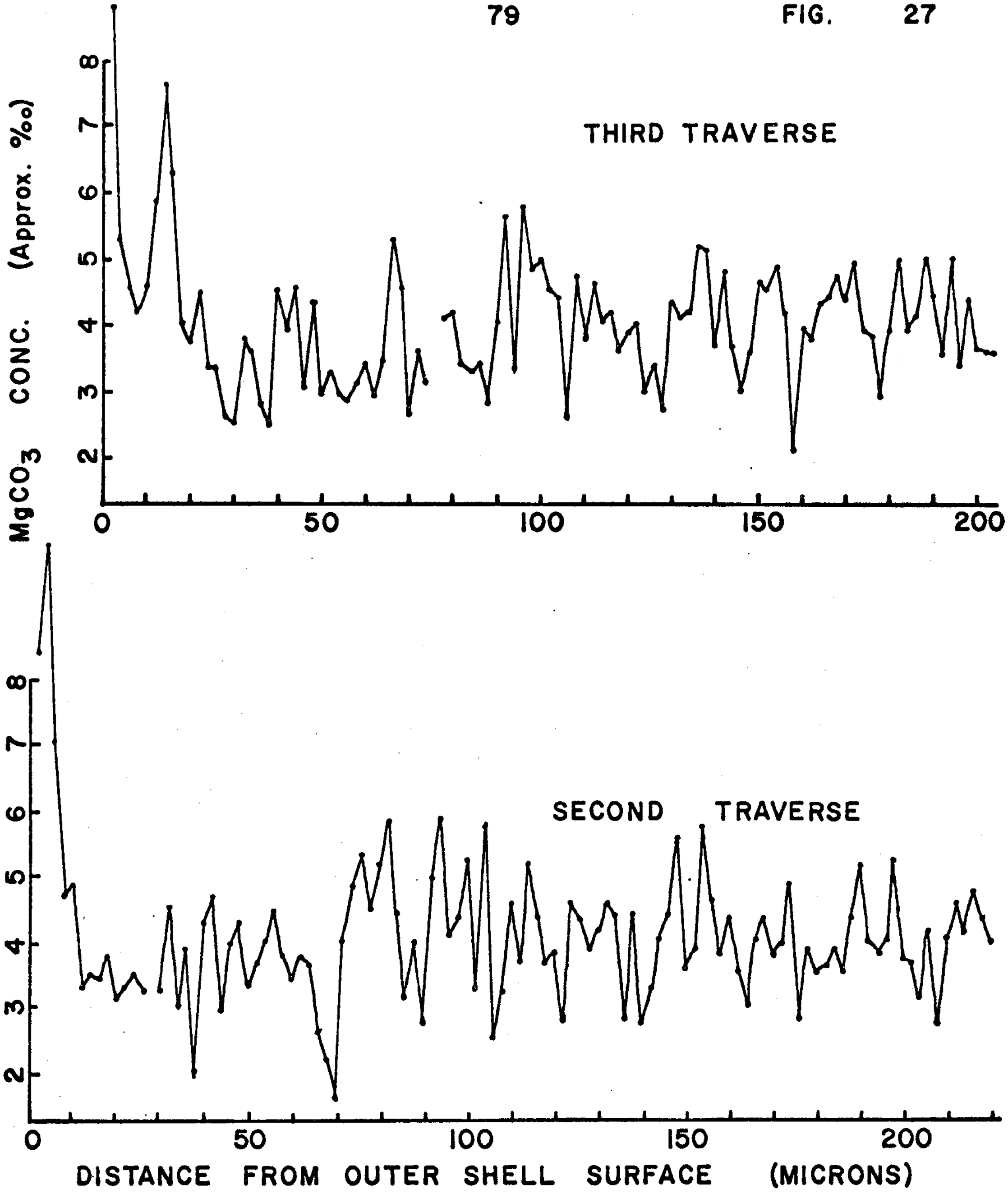
IX: DAILY VARIATIONS IN SHELL CHEMISTRY

Since concentrations in magnesium carbonate in calcite have been shown to vary directly with temperature (Chave, 1954; Dodd, 1961, 1965), and since the seawater temperatures at Kerckhoff Laboratory undergo considerable variation during a 24-hour period (see chapter VI, figure 11), it seemed possible that daily growth increments within the shell could contain variations in magnesium concentration.

Despite their small size, these increments are large enough to be analyzed with the electron microprobe. As a test of the feasibility of such a study, I took a shell section from which a peel had been made (see chapter VIII for details of preparation) and ran three traverses across a portion of the section where internal growth lines had been found. The traverses were made on an ARL instrument, using the smallest possible spot size (about one micron) at 15 KV and 0.01 microamperes. The traverses were about 200 microns long and 200 microns apart, approximately perpendicular to the outer shell surface. The first traverse was made using 4 micron intervals between points, but the second and third were made at 2 micron intervals for better resolution. Each point was counted for approximately 50 seconds. The data were reduced by subtracting background counts and dividing magnesium counts by calcium counts; data points were plotted in this form and later related to absolute concentration. Figure 27 shows the data from the second and third traverses.

After the run, another peel was made from the specimen. This showed the position of the traverses by the lines burned into the

FIG. 27

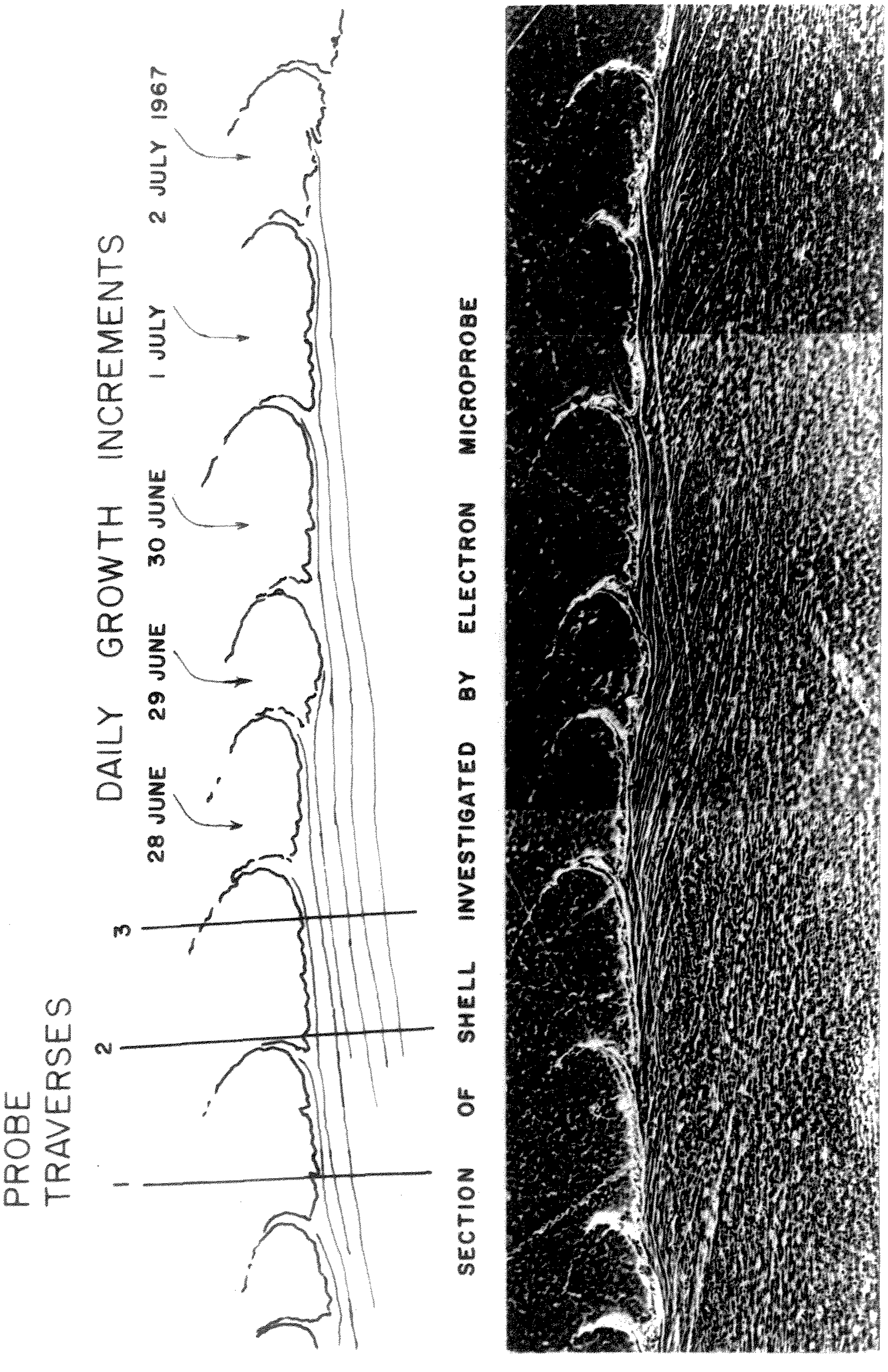


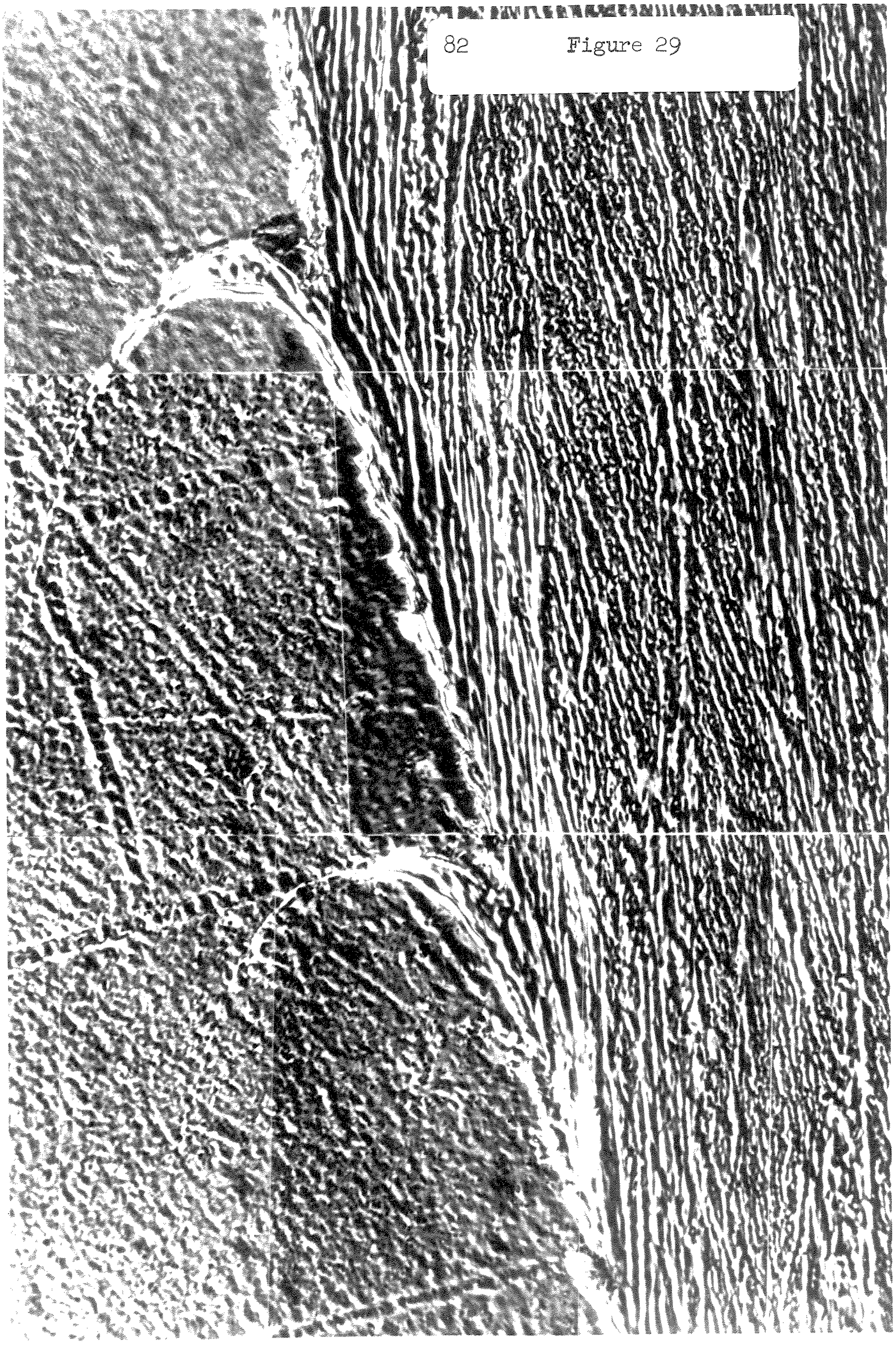
ELECTRON MICROPROBE TRAVERSES ACROSS DAILY GROWTH INCREMENTS WITHIN SHELL OF *PECTEN DIEGENSIS* epoxy by the electron beam, although no marks could be seen on the peel of the carbonate (black lines left by the probe on the section are believed to be carbon deposits from the diffusion pump oil). Figure 28 shows a photograph of the general region of the traverses, and illustrates the relationship of daily growth increments to the traverses. From external features the growth increments can be assigned specific dates, although the exact time of day of growth line formation is not known.

Figures 29 and 30 are a photograph and overlay of the immediate area of the second and third traverses, illustrating the detailed relationships of the traverses to five daily growth increments (A to E on figure 30). The positions of the less well defined growth lines were estimated from these and other photographs; they are more readily seen when the photographs are viewed from a low angle along the line of the growth increments. Inasmuch as the distance between traverses is known, the scale of the photograph and overlay can be calculated and the distances along the traverses to the positions of the individual growth lines can be measured. This permits the data gathered during the traverses to be directly related to the individual increments.

In figure 31 the top and bottom plots are portions of the second and third traverses shown in figure 27, but have been subdivided into daily increments corresponding to those in figure 30. Because these increments represent equal time intervals, the data can be adjusted along the horizontal axis to form five equal groups. The result of this adjustment is shown in the center of figure 31, where

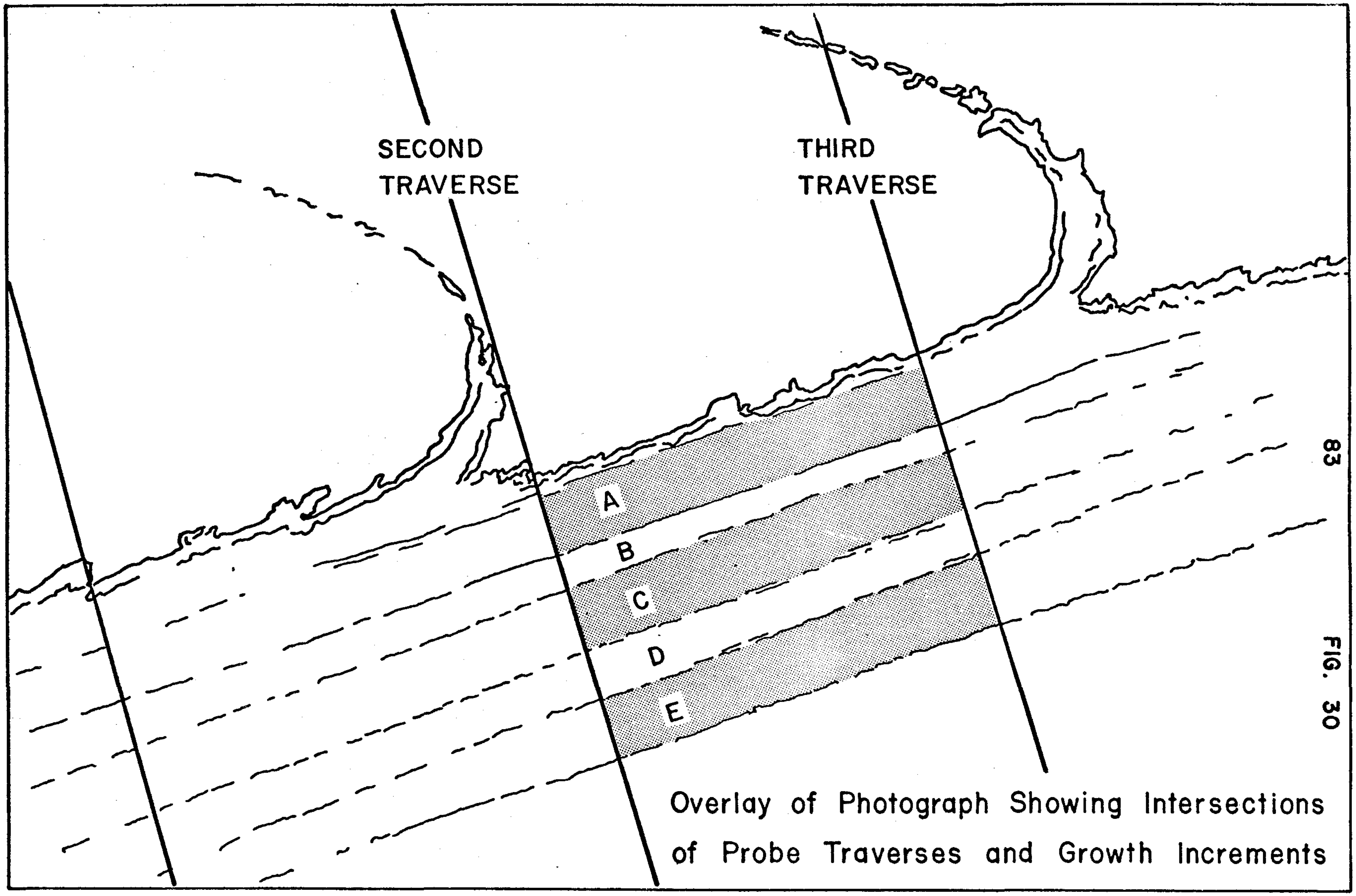
Figure 28


PROBE TRAVERSES
1
2
3
DAILY GROWTH INCREMENTS
28 JUNE
29 JUNE
30 JUNE
1 JULY
2 JULY 1967
SECTION OF SHELL INVESTIGATED BY ELECTRON MICROPROBE



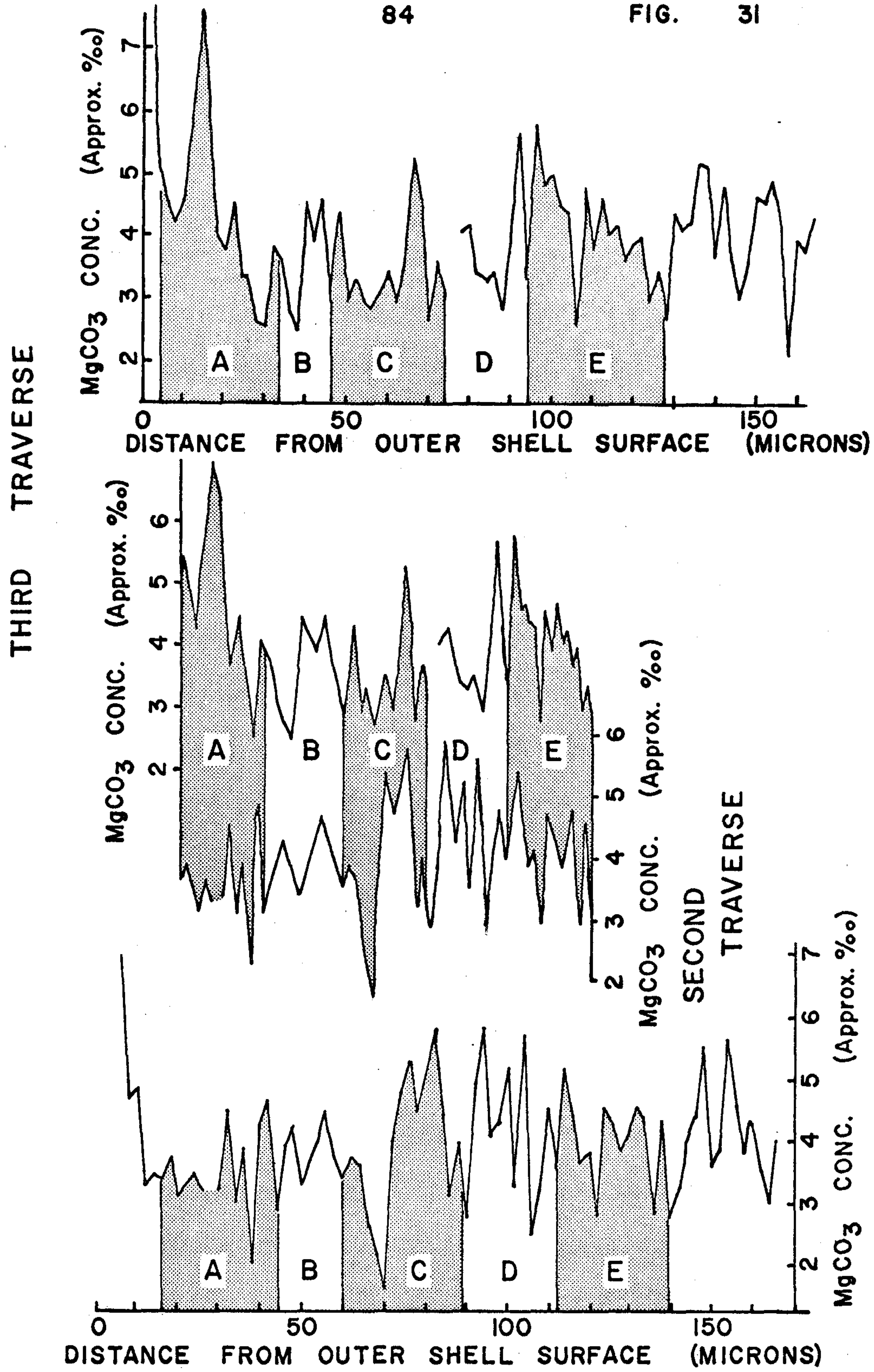
82 Figure 29

FIG. 30



Overlay of Photograph Showing Intersections of Probe Traverses and Growth Increments

FIG. 31

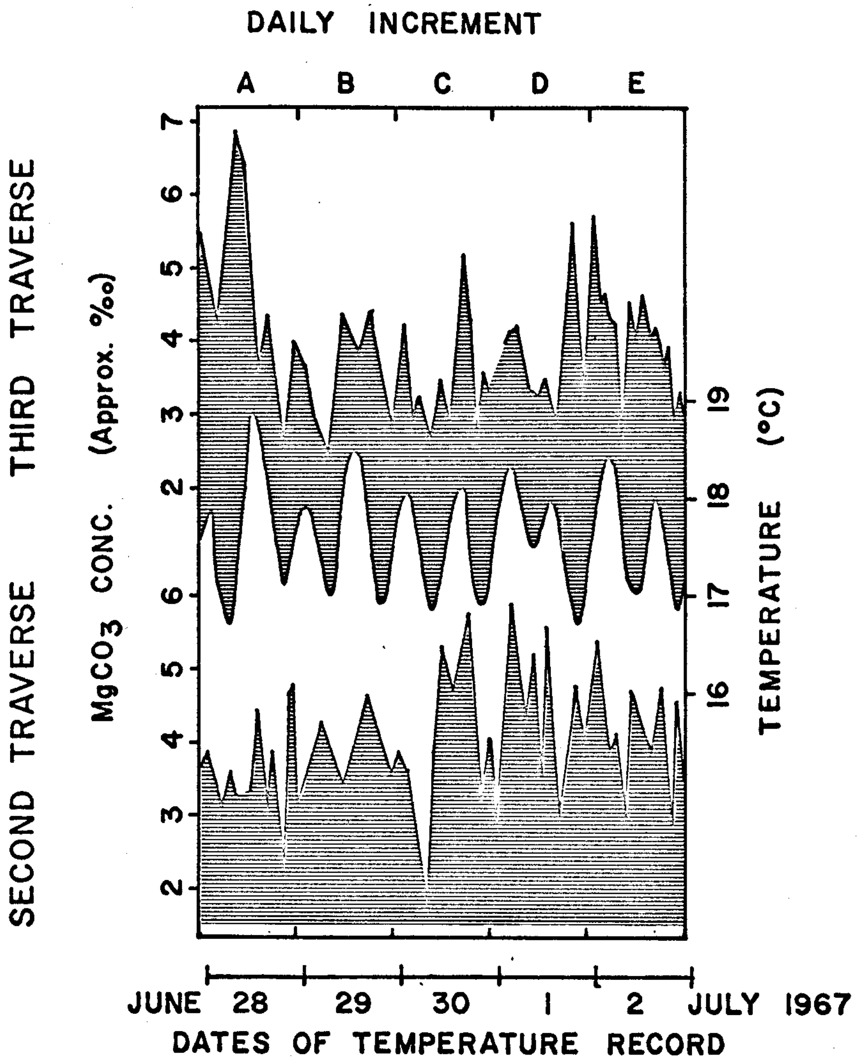


Conversion of Data from Variation with Distance to Variation with Time the upper plot is the adjusted third traverse (scale on left) and the lower plot is the adjusted second traverse (scale on right).

Now the data are in a form suitable for comparison with the temperature variations recorded in the aquarium the animal grew in. Inasmuch as we do not know the time of day that the growth lines form (although it seems to be afternoon or evening), there is a certain degree of freedom in comparing the two curves. Figure 32 illustrates one interpretation. The temperature curve (scale on right) is shown between the two adjusted probe traverses (scales on left). To visualize the relations between the magnesium concentration and temperature for the third traverse, compare the upper and lower boundaries of the upper shaded area; to visualize these relationships for the second traverse, do the same for the lower white area.

Although the general form of the magnesium and temperature curves agree, there is less than an ideal correlation. One contributing factor is that the specimen was not polished, but etched to produce the relief essential to making a peel. Inasmuch as the detectors for calcium and magnesium are in different directions, they will not always receive their proper share of the excited radiation. A second factor is that the daily growth lines may not form at exactly 24-hour intervals. If, for example, the line formation is stimulated by onset of darkness, different weather conditions might vary the time of formation by one or two hours. Thus the adjustment of the differing thicknesses of daily increments to a uniform size may introduce an error. Finally, since there are differences in increment thickness there may well be differences in thickness of subunits of increments.

FIG. 32



Comparison of Variations in $MgCO_3$ Concentration over Five Daily Growth Increments with Water Temperature for the Corresponding Times

If this is the case the uniform adjustment of entire daily increments will introduce error.

Despite these considerations, this study demonstrates the existence of variations in magnesium concentration within daily increments, and shows that the electron probe can be used to detect them. Further investigations on specimens with well-developed growth lines and uniform growth would minimize most of the sources of error discussed above. If the ecological factors involved can be more closely related to the chemistry variations, this effect could be of considerable value in paleoecology. Data on daily variations in temperature would be of considerable utility in interpreting the environment of a fossil shell.

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X: MORPHOLOGICAL FEATURES AS ENVIRONMENTAL INDICATORS

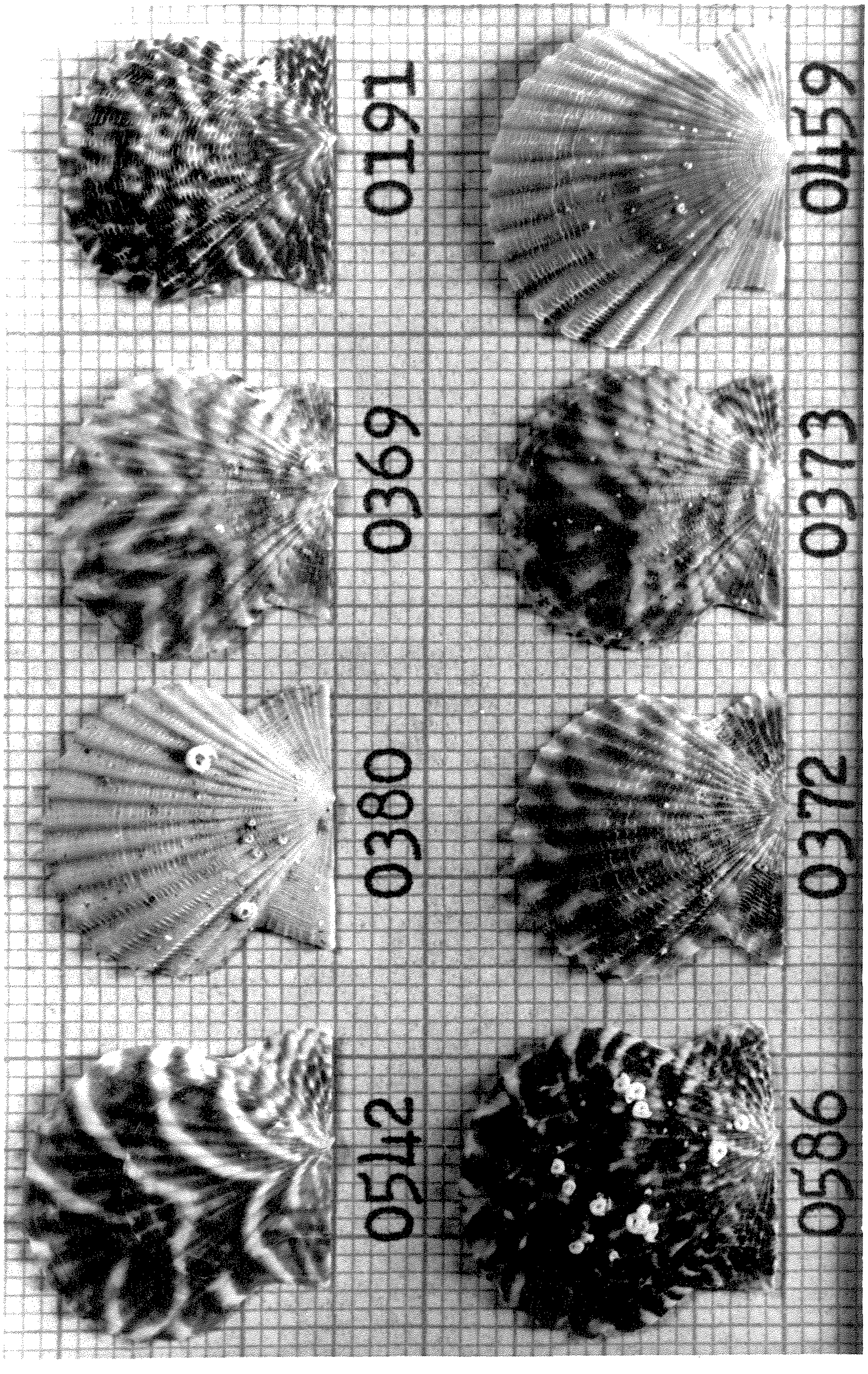
Two subspecies of Leptopecten latiauratus, L. l. latiauratus and L. l. monotimeris, are found in the Southern California area. These two forms are quite different in both morphology and ecology.

The basic morphologic differences are in prominence of ribs, number of ribs, presence of concentric ridges (growth lines), obliquity of shell, ratio of length of hinge line to length of shell, and shell thickness. Most of these differences can be seen between specimen 0380 (L. l. latiauratus) and specimen 0542 (L. l. monotimeris) in figure 33.

The ecological differnces are equally striking. Grau notes of L. l. latiauratus: "Bathymetric range: Recorded in 1 foot (minus tide) to 125 fathoms. Ecological data: Found attached to rocks or pilings in shallow water; in deeper water on rock, shale, gravel or sand bottoms, often attached to calcareous algae." (1959, p. 110) and of L. l. monotimeris: "Bathymetric range: Apparently (from available data) never more than a few feet below the surface. Ecological data: Usually attached by byssus to seaweed or eel grass, less frequently to pilings, bottoms of boats, calcareous algae or rocks." (1959, p. 113).

Leptopecten latiauratus monotimeris is the most abundant pectinid in the Corona del Mar area. During certain seasons of the year these small animals enter the laboratory seawater system as larvae and appear by the hundreds in the aquaria. Despite their abundance they are of little use for periodicity studies for they form no growth ridges.

Figure 33



Leptopecten latiauratus latiauratus, which does form growth ridges, is not so readily available. However, on 22 July 1967 I obtained 15 specimens of this form from a depth of about 60 meters in waters off Santa Catalina Island. I established these in an aquarium at Kerckhoff Laboratory to test the periodicity of their growth lines.

Twelve of the fifteen specimens had approximately doubled in size by 1 September; the other three did not grow. However, the new growth was unsuitable for growth line counts because in most specimens it lacked growth lines. Moreover, this new growth appeared to have changed in other aspects from a morphology characteristic of L. l. latiauratus to one more characteristic of L. l. monotimeris. In figure 33, specimens 0542 and 0586 are normal L. l. monotimeris. Specimen 0380 is the only specimen of L. l. latiauratus which retained its characteristic features during the experiment. Three specimens, like 0372, gradually changed character, and eight specimens, like 0369 and 0373, changed abruptly from a morphology characteristic of L. l. latiauratus to a morphology characteristic of L. l. monotimeris.

This strongly suggests that much of the morphological difference between the two subspecies is due to environmental factors. But which environmental factors might be involved? Several possibilities are suggested by the conditions of this experiment, as the environments at the collection site and at the laboratory differ in several important ways.

One obvious difference in environment is pressure. There is approximately six atmospheres more pressure at the 60 meter depth of the collection site than in the aquarium at the laboratory. It is not known whether pressure differences can cause such morphological changes, although Bé (1965) notes that structural changes in the tests of certain planktonic foraminifera correlate with depth. It has also been shown that a number of organisms, notably among the plankton, are sensitive to small pressure changes and use them to regulate their behavior (Knight-Jones and Morgan, 1966; Digby, 1967).

The amount of illumination present at the collecting site is not known, but I have noted that the water is unusually clear and the bottom is well illuminated while diving nearby in 25 meters. I would estimate that the differences in illumination between the collecting site and the laboratory are slight, although the duration of daylight would be less at depth.

The temperature is much lower at the collecting point than in the laboratory. In July, the bottom temperature at 60 meters is about 10° C. and the surface temperature is about 17° C. at the collecting site. The seawater temperature in the laboratory varied from 18° to 22° C. during this period.

Many other parameters, such as plankton concentration, turbidity levels, oxygen concentration, current velocities, etc., probably differ between the two environments but cannot be easily evaluated.

In an attempt to evaluate the pressure effect, I maintained 6 specimens of L. l. monotimeris at about 18 psi for 39 days. None appeared to have grown during this period, probably due to the limited circulation of water, food and oxygen in the system. No conclusions were possible.

Several specimens of L. l. monotimeris had been included in the light-dark experiments discussed in chapter VI. No differences in morphology were noted between specimens grown in continuous light, continuous dark, and alternate periods of light and darkness. In addition, many hundreds of specimens settled in the sea table in the dark laboratory during this period, and except for a very few hours, spent their entire lives in an environment of absolute darkness. These appeared in no way morphologically different from specimens from the same spatfall which settled in other locations in the laboratory near exterior windows.

I attempted to grow specimens of L. l. monotimeris in water at 9° C., using a refrigerated aquarium in Pasadena. No new growth was noted during the experimental period, again probably due to the limited circulation of water. Specimens grown at Kerckhoff Laboratory in running seawater at temperatures ranging from 17° to 25° C. show no obvious morphological differences. However, in examining some 200 specimens of L. l. monotimeris which I had collected at various times at the laboratory, I found 15 specimens with some features (notably growth lines) of L. l. latiauratus. Usually these features were restricted to juvenile portions of the shells. My records showed that all these had been collected in the winter months, when seawater temperatures ranged from 14° to 16° C. Specimen 0191 in figure 33 is one of these specimens. Other specimens collected at the same time were normal L. l. monotimeris.

A single specimen of L. l. latiauratus (specimen 0459 in figure 33) collected in 30 feet of water at Corona del Mar in September 1967 added growth without ridges until mid-October, then stopped growing until about mid-January, when it began growing again with typical *L. l. latiauratus* features. Temperatures in the laboratory in September and October were about 19° to 22° C.; in January they were about 14° to 16° C.

Another clue to the cause of morphological differences may come from the geographic ranges of the two subspecies. Grau notes that the northern limit of *L. l. monotimeris* is Monterey Bay, while *L. l. latiauratus* extends further north to Point Reyes (1959, pp. 110 and 113). Too much significance should not be attached to this, however, for the difference in surface temperatures, winter or summer, is less than one degree C. (Ricketts and Calvin, 1952, pp. 348-349). The southern limit for both forms is Cape San Lucas, Baja California (although *L. l. latiauratus* extends northward again in the Gulf of California, while *L. l. monotimeris* does not)(Grau, 1959, pp. 110 and 113).

Although far from definitive, such observations do strongly suggest that the difference in temperature is the major cause of the differences in morphology. This effect would not be unique; Ericson (1959) noted that the coiling direction in a species of planktonic foraminifera depends on the temperature. Also, it is possible that the effect noted by Bé is due to the temperature rather than the pressure changes involved. If further experiments with more advanced apparatus confirm and more precisely define the effect of temperature on the morphology of these subspecies, the presence of one or both of these forms in a fossil assemblage would give us valuable information about the temperature conditions present in their environment.

In addition to the environmental implications just discussed, these observations have some implications for the taxonomy of the group. Recent workers (Abbott, 1954; Grau, 1959) consider *latiauratus* and *monotimeris* to be subspecies, but some of the early taxonomists felt that the two forms were environmental varieties. For example, Dall, in speaking of the variety *fucicolus* (now *monotimeris*) says: "This form lives attached by the byssus to the giant kelp of the Californian coast, and the absence of shock, due to the floating situs, is probably correlated with the obsolescence of the ribs and posterior sinus. Intergradations with the type are not at all rare." (1898, p.710). Grant and Gale say of the variety *monotimeris*: "This variety lives in great abundance attached by its byssus to kelp. Its situs accounts for its special characters. Mrs. I. S. Oldroyd has informed the writers that the normal variety, although not so common, is found attached to worm tubes at low tide level near San Pedro." (1931, p. 205).

From my own observations I can add that *L. l. monotimeris* has a strong inclination to move upward. The animal climbs with surprising agility with its foot, which attaches to a smooth surface, pulls up the shell to the point of attachment, spins a byssal thread as a temporary anchor, and extends again upward to a new point of attachment. This procedure is repeated until the animal reaches the top of the object it is climbing, the surface of the water, or a major obstruction. If several hundred animals are put in the bottom of a small aquarium, the majority move to the uppermost portion of the walls of the aquarium within a few hours. They live there crowded together so closely that many form misshapen shells. Moreover, in some circumstances they seem unable to move downward; in several instances where stoppages in the drain temporarily raised the water level, the animals which moved up in response to this were stranded and died when the stoppage was cleared and the water level returned to normal.

This behavior pattern might be the reason for the environmental distribution of the two subspecies. In the absence of any evidence to the contrary (such as different breeding periods), let us assume that the two forms are genetically identical. At breeding times the larvae of both groups are widely distributed in the coastal waters of Southern California. Upon settling, the young L. latiauratus find themselves in a wide variety of environments. Following their instincts, they climb upward on any surface available. Those animals which reach the surface will often die from exposure when tidal fluctuations leave them stranded; the exceptions are those on kelp or other floating objects. These develop the morphologic characteristics of L. l. monotimeris. The rest, unable to reach the surface, develop the morphologic characteristics of L. l. latiauratus. Although highly speculative, this model may be worthy of further consideration.

Irrespective of the eventual solution of the taxonomic questions, this study has demonstrated that environmental factors can have a profound influence on the morphological characteristics of a pectinid shell.

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XI. SUMMARY AND CONCLUSIONS

This study was initiated to investigate the relationships between environmental variations and skeletal characteristics in a group of organisms suitable for paleoecologic applications. The Family Pectinidae was selected as a subject and a number of experiments were conducted on living representatives. The results of these experiments permit the following major conclusions.

1. The growth lines in two pectinid species occur with daily periodicity (chapters IV and V). Although many calcifying organisms are believed to form daily growth lines, few investigators have verified this periodicity by sound experimental methods. Most published studies depend for credibility on the internal consistency of numbers of presumed daily lines between presumed lunar or annual cycles. Although such evidence is significant, there is a decided need for verification of daily periodicity by carefully controlled growth experiments. My experiments are significant contributions toward this end.

2. By using the daily growth lines as time markers, short term variations in growth rate were demonstrated on the experimentally grown shells. These variations can be correlated between the shells of the different animals grown during the same experiments, implying that they occur in response to the changes in environmental conditions experienced simultaneously by the same animals (chapters IV and V).

3. The light-dark cycle provides the periodicity in the occurrence of daily growth lines. Moreover, the process is a biological

rhythm, perhaps the first such rhythm noted which forms a record in an accreting skeleton (chapter VI). A worker using data involving normally daily growth lines should know why they are formed, so that he can recognize the situations in which abnormal periodicities might be present. This information has not hitherto been available.

4. The concentric ridges present in most pectinid species appear to be daily growth lines in all cases where data are sufficient to permit conclusions. This suggests that such ridges are daily growth lines throughout the family, permitting their widespread application to paleoecologic problems (chapter VII).

5. Growth increments are commonly seen in radial sections through pectinid shells, and the most prominent of these appear to be formed with daily periodicity. However, these sections cannot always be readily interpreted due to the presence of increments representing subdaily periods and due to a crystallographic texture which commonly obscures the growth lines. Still, in some situations such sections can provide data not readily obtainable from the study of surface morphology, so this approach should not be disregarded (chapter VIII).

6. Daily growth increments in a shell section can be used to relate geochemical data to growth periods, as was done for magnesium concentrations within a pectinid shell in an electron microprobe study. This study also supported the premise that the magnesium concentration varies directly with the seawater temperature during growth (chapter IX).

7. Differences in environmental conditions can exert a profound influence on the shell morphology of a pectinid species, as demonstrated for Leptopecten latiauratus (chapter X). This effect was not recognized in the current taxonomy of this common living form; similar situations are likely to be unrecognized in paleontology. Once detected, such effects can be of considerable value in paleoecology. Both forms of Leptopecten latiauratus, for example, are common in the Pleistocene of California.

These conclusions promise to have application in several different areas of geological research.

In geophysics, the validity of the periodicity of daily growth lines is of considerable importance in current studies investigating the change in the earth's rotation rate during geologic time (chapters I and IV). My experiments not only make significant contributions toward the understanding of growth lines, but also demonstrate that in some cases specimens with lines missing can be detected and compensated for (chapter IV).

These studies can be applied to two aspects of taxonomy. First, they have demonstrated that growth experiments can in some cases distinguish between inherited and acquired characteristics (chapter X). Second, through the use of the daily growth line, the taxonomist can add data such as length of life, season and frequency of breeding periods, and similarities in growth rates to his list of data for determination of evolutionary sequences. The same techniques can help him identify dwarfed faunas.

The geochemist can use daily growth lines, both in surface morphology and internal structure, as time markers in studies of chemical variations within an accretionary skeleton. He can also use these lines to determine the age and seasonal growth rates for specimens used in whole-shell analyses (chapter IX).

Investigators of the calcification process should be able to make good use of the presence of daily and subdaily growth increments within the shell of a calcifying animal.

Several important applications are envisioned in paleoecology. First, as discussed in chapter IV, a fossil assemblage could be analyzed to determine what temporal relationships, if any, existed between the various individuals. Then, using the daily growth lines as time markers, the variations in growth rate and variations in shell chemistry and mineralogy could be used to obtain data on the seasonal and daily variability of the environment. Finally, in some cases environmental information can be determined from gross morphological characteristics, as in the case of Leptopecten latiauratus (chapter X).

The results of this study have not only added several new techniques to paleoecology, but have also greatly extended the potential applications of existing techniques in this field. I would like to hope that an even more important contribution will be the stimulation of further work in this important area.