

PERIODICITY STRUCTURES IN THE BIVALVE
SHELL: EXPERIMENTS TO ESTABLISH GROWTH
CONTROLS IN *CERASTODERMA EDULE* FROM
THE THAMES ESTUARY

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ABSTRACT. Growth patterns of living cockles from one year-group were analysed from a wide range of substrates occurring at different heights on the tidal flats. At similar population densities and tidal heights cockles from well-sorted sand grow larger and show more disturbance rings than examples from mud. Degree of tidal cover affects size only in the first year, but internally, erratically fluctuating microbanding characterizes high shore shells. In dense populations daily increment patterns suggest a much shorter growing season, growth diminution being greater on the higher parts of the flats. In any one population of cockles in their third year microstructural banding reveals 'hardy' and 'sensitive' groups whose total number of growing days varied from 795 to 650.

Mean monthly sea temperature does not correlate well with mean monthly shell growth, though internal patterns of growth may be related to air temperature variations. In susceptible individuals winter rings coincide with frosts over the cockle-banks: cockles are apparently more susceptible in their first winter, and may stop growing for several periods of up to a fortnight.

A warning is given against the casual use of growth banding in fossils for providing geophysical data on the history of the Earth's rotation rate.

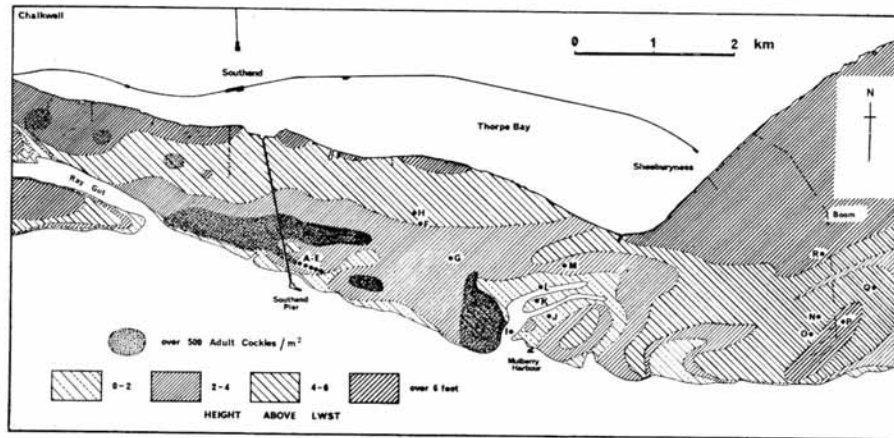
THE current interest in fossil growth lines shown by geologists and geophysicists stems from the demonstration by Wells (1963) of daily increments in the epithecae of corals. However, the recognition of daily increments in corals is governed by exceptional preservation of the epitheca, and since corals are abundant at only a limited number of horizons in the geological column, other organisms of more widespread occurrence whose internal banding is not seriously affected by abrasion were sought.

Barker (1964) sliced several Recent bivalve shells and suggested that some periodic markings were probably of daily origin, although experimental data were not presented to support the hypothesis. The suggestion had in fact already been made as a result of observations under natural conditions by Davenport (1938, p. 514) for scallops kept in a tide box, and by Høpner Petersen (1958, p. 14) for *Cerastoderma lamarcki* (Reeve). Ten years later, almost simultaneously, three works appeared which provided proof of the daily origin of bivalve microbanding and demonstrated its widespread occurrence in the group as a whole. Clark (1968) kept twelve juvenile *Pecten diegensis* for 51 days in tanks at the Kerckhoff Marine Laboratory, California, and stressed the importance in a population of noting the maximum not the average line count. House and Farrow (1968) showed that plots of growth increments in *C. edule* from South Wales indicated a correlation between tidal phases and bunching of the microbands such that a daily origin was beyond question. Pannella and MacClintock (1968) planted notched *Venus (Mercenaria) mercenaria* Linnaeus in Barnstable Harbour, Massachusetts, both intertidally and subtidally, killing selected specimens after one and two years. Shells showed the same number of growth bands as there were days between notching and killing, and also showed tidally controlled variation in the type and thickness of growth bands.

[Palaeontology, Vol. 14, Part 4, 1971, pp. 571-588, pl. 108.]

Similar banding, also thought to be diurnal in origin, was illustrated for *Glycymeris* and *Tridacna* (*Chametrachea*) *squamosa* Lamarck.

Daily growth lines in present-day bivalves have since been recognized in many other groups. The Veneracea and Cardiacea, because of favourable shell structure, have very well preserved banding, but preservation is not favoured by the shell structure of some groups, such as the Tellinacea, and the identification of banding in such common intertidal forms as *Scrobicularia plana* (da Costa) and *Macoma balthica* (Linnaeus) is extremely difficult. In the Pectinidae, periodicity structures are extremely well shown on the surface but cannot be studied by preparing thin section or peels as the foliated shell structure prevents their recognition. Likewise the larval stages of the oysters *Ostrea edulis* Linnaeus, *O. lutraria* Hutton, and *O. chilensis* Philippi show well-developed exterior diurnal growth layers (Millar 1968) though these become difficult to analyse either on the highly irregular surfaces of adult oysters or internally, owing to the foliated and vacuolar shell structure.



TEXT-FIG. 1. Distribution map showing sampling localities along the north bank of the Thames Estuary. Data on cockle population density (for flats west of Mulberry Harbour only) from Mr. G. Pickett, Fisheries Laboratory, Burnham-on-Crouch.

Extinct groups of fossils also show banding homologous to the daily structures present in Recent groups. Among fossil forms, Pannella, MacClintock, and Thompson (1968) have used Eocene *Crassatella* and *Cardita*, Cretaceous *Limopsis*, *Cucullaea* and *Tancredia*, Triassic *Cardita* and Carboniferous *Conocardium*. Among the Bivalvia, perhaps the most outstanding are the radiolitic rudists whose banding indicates very rapid growth, and at some reef horizons extremely severe tidal control.

TECHNIQUES AND DATA PROVIDED

Eighteen samples were taken from intertidal mud- and sand-flats exposed between Southend Pier and the Maplin Sands, a distance of seven kilometres. One group of samples was collected on 24 July 1965, other groups at intervals throughout August

1967. All specimens belong to the 1963 year-group which dominated the flats until the widespread spatfall of 1967. For each sample the nature of the substrate, cockle population density, presence and abundance of other organisms, and position with respect to low water springs were noted. Approximately thirty-five specimens were collected per sample, and these were killed by boiling for twenty minutes on the evening of collection; paired valves were retained and numbered. Daily records of sea temperature, air maximum and minimum temperature, sunshine and tidal range were obtained for the period 1963–1967 for comparison with the growth records preserved in the micro-structural banding of the cockles.

External growth-ring analysis. A summary of the macroscopic growth increments of all shells studied in the Southend and Shoebury populations (text-fig. 1) is shown in Table 1. Measurements were made with dividers, using height along the maximum radius from the umbo as the index of growth rather than length, since this is the direction along which peels were prepared; observations were made to the nearest half millimetre below.

TABLE 1. Macroscopic annual increments of *Cerastoderma edule* population (1963 year-group) from the Southend Flats and Shoebury Sands, Thames Estuary: measurements in millimetres expressed as $\bar{x} \pm \alpha$, where $\alpha = \sigma/\sqrt{n}$ (Hancock 1965). * Populations with densities of more than 500 cockles/m² B and D = 1800; J = 500 (1963 year-group), 1000 (1967 spatfall); Q = 1000. Localities shown on text-fig. 1.

Popula- tion	n	Substrate	Height above L.W.S.T. (feet)					Total (1963– 1966)
				1963	1964	1965	1966	
A	32	Dry sand	+4	9.6±0.29	16.7±0.48	—	—	—
B*	55	Wet, muddy sand	+3	8.0±0.15	9.5±0.16	—	—	—
C	64	Fine sand	+3	8.5±0.14	14.2±0.24	—	—	—
D*	89	Wet mud	+3	8.3±0.11	9.6±0.14	—	—	—
F	30	Fetid mud	+5	7.3±0.21	12.3±0.22	4.9±0.16	5.8±0.25	30.3
G	34	Rippled sandy mud with <i>Arenicola</i>	+3	7.4±0.22	12.9±0.26	5.2±0.18	5.9±0.23	31.4
H	35	Mud	+5	7.7±0.16	12.2±0.34	4.8±0.13	5.3±0.21	30.0
J*	40	Muddy sand	0	8.2±0.19	11.8±0.27	5.5±0.15	5.4±0.18	30.9
L	14	Soft mud	+1	7.7±0.18	13.9±0.35	6.5±0.33	6.0±0.32	34.1
M	30	Dry hard mud	+4	7.6±0.17	13.5±0.21	6.4±0.18	6.1±0.16	33.6
N	28	Soft mud	+6	7.5±0.23	13.4±0.25	6.0±0.20	5.6±0.23	32.5
O	35	Fine sand, edge of channel	+6	7.5±0.17	13.5±0.21	6.2±0.16	6.1±0.15	33.3
P	29	Thixotropic sandy mud	+6	7.3±0.24	12.9±0.22	5.8±0.26	6.1±0.24	32.1
Q*	27	Soft mud with algal plastering	+6	7.3±0.16	11.3±0.20	4.2±0.12	5.1±0.20	27.9
R	16	Soft mud	+7	6.9±0.25	14.4±0.30	5.4±0.13	5.6±0.25	32.3

Internal growth-ring analysis. Acetate peels of shell surfaces were prepared by the following method.

After cleaning the shells by boiling in hydrogen peroxide, cockles were sliced radially from umbo to ventral margin along the longest rib using a rubber bonded 240 grade carborundum cutting wheel 0.010" in thickness and 6" in diameter. Care was necessary at this stage to prevent slicing obliquely to the direction of growth and so crossing ribs, as this exaggerated the reflexed growth banding and rendered daily increments difficult to measure (Pl. 108, fig. 2). The sliced valve was then polished with

successively finer carborundum powders up to 1200 grade, and finished on a polishing wheel, using 5/20 fast-cutting alumina at 700 revs/min. Etching with 10% HCl for 10 seconds was sufficient to enhance the details of the growth banding without over-strengthening the crossed lamellar structure, which with over-etching tends to obliterate tangential growth increments. Once the etched shell was dry its surface was wetted with acetone and pressed on to 1/1500 acetate paper. The resulting peel was mounted between glass slides and examined under a Zeiss Ultraphot microscope. Photographic traverses with a final magnification in the region of $\times 160$ were prepared for the whole length of each peel. The increments shown on the traverses were measured along the surface of maximum growth (Pannella and MacClintock 1968, fig. 1) and plotted on calendar graph paper for comparison with instrumental records.

Viewed by transmitted light, individual daily increments of growth in *Cerastoderma edule* are represented by a doublet consisting of a thin white band of strong relief bordered by dark Becke lines, and a broad grey band relatively depressed (Pl. 108, fig. 1). Examination of the ventral extremities of peels prepared from shells killed on a summer evening clearly shows that the broad grey band is that most recently formed, and that the thin band therefore corresponds to the nocturnal element in the shell secreting cycle. Staining of etched shell slices with Rose Bengal demonstrates that the thin night band is rich in organic matter, and also that there is appreciable organic matrix in the day band. At ultrastructure level transmission electron micrographs reveal the presence of projections of organic material stemming from the nocturnal band.

Examination of acetate peels prepared from selected cockles serves to pinpoint those seasons of the year when high density exerts the greatest influence on growth, and also enables the shell secretion pattern of cockles from sandy and muddy substrates to be compared. However, it is first necessary to note the degree of variation in microstructural elements revealed by one supposedly homogeneous population.

There are two ways in which variation in growth rate between shells either in the same population or in different populations can be assessed microscopically. The first is somewhat generalized; the spacing in millimetres of units of thirty daily bands is plotted as a monthly total. Much detail is lost with this method, although it is rapid and can be carried out using a precision slide carrier with vernier X and Y scales. The second method, adopted by House and Farrow (1968), involves plotting each diurnal increment on calendar graph paper. This ultrasensitive growth trace makes possible the correlation of small-scale fluctuations in growth with other diurnally recorded environmental phenomena.

ENVIRONMENTAL SUSCEPTIBILITY OF INDIVIDUAL COCKLES

Since the yearly increments of cockles from sample A show the greatest standard deviation (Table 1) peels were prepared of all shells to ascertain the variation shown in the daily banding pattern: Table 2 gives the number of daily bands counted between annual rings on each specimen. For the number of days' growth during 1965 up to the collection date in midsummer the values quoted are probably accurate to within ± 2 or

EXPLANATION OF PLATE 108

Figs. 1, 2. Periodicity structures in *Cerastoderma edule*. 1. Rapidly secreted shell during the autumn following settlement, indicated by large daily increments; note the thin outer shell layer. $\times 120$. 2. Slower daily growth pattern during the second autumn, producing marked thickening of outer shell layer; note the effect of oblique slicing. $\times 120$.

3 days. In shells with pronounced black winter rings crossing the peel, estimates of the total age of the animal would be in error due to a stoppage in growth. It is possible, however, to obtain an indication of absolute age from those shells which do not show such black rings. In the sample of 33 there were five such shells which indicate spat originating in 1963 at intervals between 21 May (795 days) and 4 August (720 days). Shells with indications of slight stoppage approach these dates by a matter of a few days or fall within the range, though a group of six highly sensitive individuals falls well outside this range, their total number of growth days amounting to only 650. Even if

TABLE 2. Variation in number of days growth per year in *Cerastoderma edule* (population A) from sandbank east of Southend Pier, as measured by daily growth bands. Specimens collected 24 July 1965 (1963 year-group). Figures in brackets are external height in mm.

Specimen Number	1965	1964	1963	TOTAL
1	205 (4½)	—	—	—
2	213 (8)	—	—	—
3	235 (8)‡	360 (16)	—	—
4	235 (4)‡	360 (22)	—	—
5	210 (6)‡	300 (14½)‡	135 (10)	645 (30½)
6	165 (4)‡	315 (15½)‡	—	—
7	107* (4)‡	354 (18)	—	—
8	205 (7)	310 (15)‡	—	—
9	198 (5)‡	405 (17)‡	185 (14)	788 (36)
10	210 (5½)†	382 (18½)‡	163 (14)	755 (38)
11	200 (6½)	—	—	—
12	226‡	363	—	—
13	210 (5½)†	425 (19)†	160 (11)	795 (35½)
14	195 (7)†	340 (19)	—	—
15	230 (6½)‡	405 (18)‡	142 (9)	777 (33½)
16	207 (6½)‡	363 (14)‡	—	—
18	200 (6)‡	370 (16½)‡	—	—
19	225 (7½)‡	360 (19½)	—	—
20	210 (8)†	363 (15)†	147 (9½)	720 (32½)
21	207 (8)‡	383 (13½)‡	165 (9½)	755 (31)
22	204 (5)‡	366 (19½)†	140 (9½)	710 (34)
23	205 (5½)†	360 (18½)‡	—	—
24	220 (8)‡	396 (15)‡	—	—
25	209 (5½)†	372 (16)†	145 (9½)	726 (31)
26	207 (4½)‡	307 (14)‡	134 (8½)	648 (27)
27	228 (6)†	385 (15½)†	—	—
28	220 (6)‡	283 (13)‡	152 (10)	655 (29)
29	213 (4½)†	407 (20½)†	140 (11)	760 (36)
30	185 (5½)‡	343 (14)‡	—	—
31	210 (5½)†	420 (18½)†	146 (10)	776 (34)
33	170 (7½)‡	300 (14½)‡	—	—
34	214 (6½)‡	375 (19)‡	139 (8½)	728 (34)
35	236 (5½)‡	370 (15)	167 (12½)	773 (33)

* Pathological specimen.

Sensitive individuals in italics.

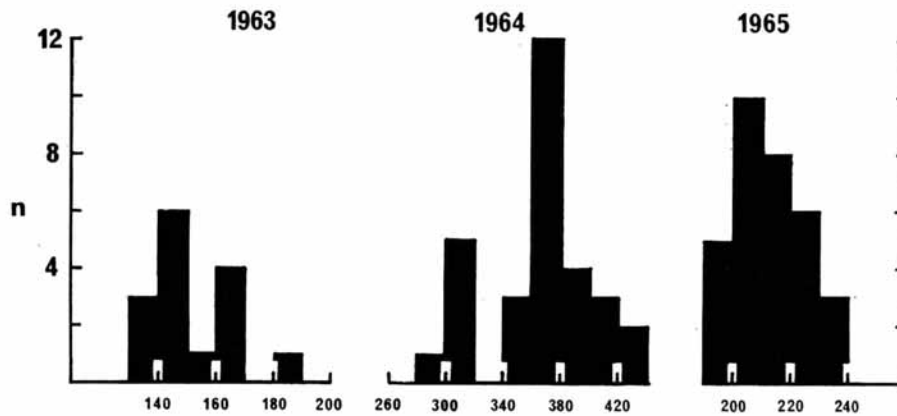
† No indication of growth cessation during winter.

Hardy individuals in bold type.

‡ Sharply defined winter ring.

these shells started life on the latest date indicated by continuously growing shells they must have stopped growing for at least one month in both winters, perhaps nearer two. It should scarcely require stressing that the facile analysis of fossil material by counting the number of supposedly daily growth bands between external annual rings is liable to extreme error; in population A estimates of the number of days in the year would vary from 283 to 425 days (Table 2). Since the palaeontologist is rarely able to select as large a sample as A, the use of this method on individual specimens must be avoided.

Daily growth patterns as an indication of 'hardy' and 'susceptible' individuals. Scrutiny of Table 2 will demonstrate that population A can be split nicely into two end members which represent extremes of susceptibility to external environmental pressures. The suggested grouping is indicated on Table 2, where it can be observed that correlation between individuals from year to year in the two groups is often very close. (There is striking comparison here with the statistical methods of dendrochronologists [e.g. Ferguson 1968, p. 843] who speak of 'complacent' and 'sensitive' growth traces.) The two groups are most easily separated by their second-year growth (text-fig. 2), where



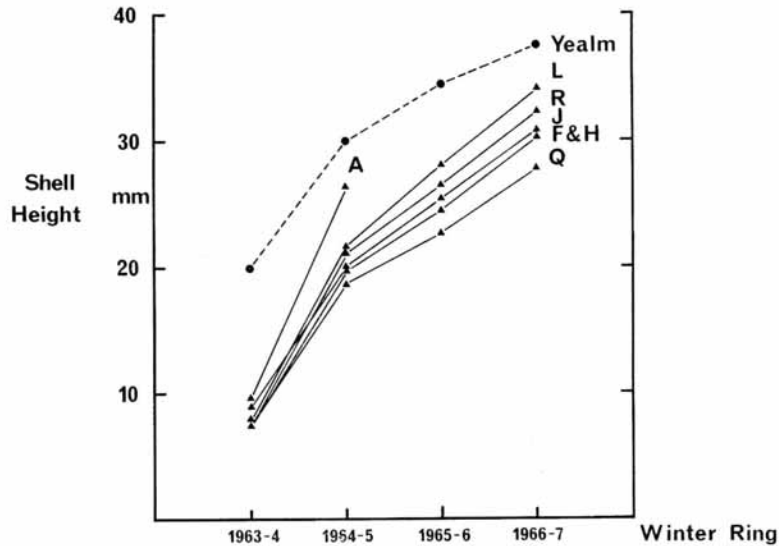
TEXT-FIG. 2. Histogram showing number of days growth per year in cockles from population A.
 1963, following summer spatfall (n = 15)
 1964, whole year (n = 30)
 1965, up to collection on July 24 (n = 32)

the sensitive individuals plot in isolation from the majority, which shows a sharp mode at 360 to 379 days growth and includes 40% of the population. For the first year of growth immediately following settlement data are scanty because of the difficulty of taking peels from the very thin shell, and also as a result of abrasion of the critical outer shell layer in the umbonal region. Daily banding in one shell, A35, could be counted throughout, but some others were so poorly preserved that no values could be obtained for 1963. In any specimen, however, where more than 100 bands were counted for the first-year growth estimates for the umbonal region were made using A35 as standard.

There is a suggestion in Table 2 that the sensitive individuals settled somewhat later in the year than the more hardy group. It is possible in this instance that because of their smaller size they were more prone to environmental fluctuations than the slightly older individuals, but this cannot be proved without additional material. A more likely explanation perhaps is that the factor of susceptibility is under genetic control, and hence independent of the degree of development attained in the initial months of growth. Nevertheless one feature is clear, that at the age of 2 years susceptible cockles are on average 6 mm smaller than hardy individuals from the same environment.

ENVIRONMENTAL INFLUENCES

Substrate. Fifteen of the eighteen samples contained a sufficient proportion of 1963 year-group to be suitable for statistical treatment. Most striking is the high growth rate of specimens from fine, well-sorted sand which dries at low water of ordinary tides. Comparing sample A from sand with samples F and H from fetid mud (text-fig. 3), all of which are situated at similar heights above low water spring tide and have relatively low population densities (30–100/m²), it will be seen that in both 1963 and 1964 growth was 25% greater in the sandbank population. Variation between specimens is also greatest in this population, where 30% of the cockles show pronounced disturbance rings in the autumn of their first year. Despite this, their growth is greater than that of



TEXT-FIG. 3. Cumulative growth curves for cockles from different habitats in the Thames compared with that from R. Yealm (Orton 1926). Localities shown on text-fig. 1.

A: sand, low density L: low density, near low water spring tide R: low density, high shore
 F and H: mud, low density J: high density, near low water spring tide Q: high density, high shore

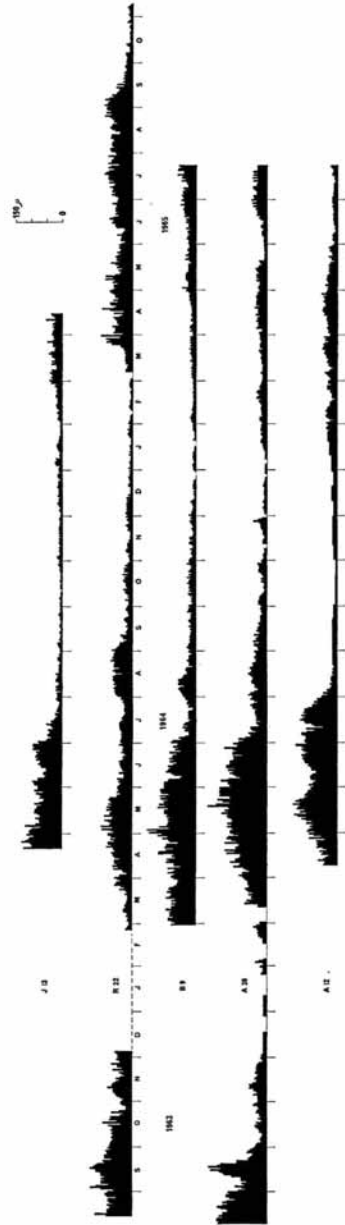
any other cockle population on the north bank of the middle estuary, and this higher growth rate cannot be ascribed to the earlier settling of spat on the sandbank than on the surrounding mudflats, for the daily growth line totals for 1963 are comparable.

Population density. To assess the importance of population density, two samples of different density from near low water springs L and J and two from the higher flats R and Q will be considered; these are plotted on text-fig. 3. Dense populations of cockles from near Low Water Spring Tides (J) are on average 3.2 mm smaller at their fourth winter ring than more scattered examples (L), this difference increasing to 4.4 mm in more elevated populations. The fact that the growth diminution caused by over-crowding is greater on the higher parts of the flats than near low water springs may be attributed to weaker currents and consequent poorer food supply further onshore. The supply is clearly sufficient for low density populations but not when densities of third-year cockles in excess of 1,000/m² occur. A gelatinous brown algal plastering at the site of sample Q may further have reduced the available food supply by trapping much of the plankton and detritus. In both examples differences in growth are greater between crowded and sparse populations at the same level on the flats than between high- and low-level populations. This, together with the demonstrably large effect of a sandy substratum, effectively swamps any controlling effect of tidal height on the macroscopic growth characteristics of the Thames cockles.

Examination of text-fig. 4 enables the effect of population density to be studied both in terms of the maximum daily increments achieved and with respect to the length of the growing season. Growth traces for B9 and J13 are from populations which occur at a density of adult cockles of more than 1,000/m²; A12, A26, R22 are from cockles occurring at about 30/m². The most prominent characteristic of the former profiles is their very low late summer and autumn growth in the second year. After maximum daily increments of around 125 μ m in early or mid-May (when all the Southend shells were growing most rapidly: cf. Burry Inlet, House and Farrow 1968, text-fig. 2) the amount of shell added per individual in dense populations gradually tails off to 12–15 μ m per day: this low level was reached by mid-August in population B, but was almost a month earlier in the low water springs population J. In the following (third)-year growth commenced earlier, and increments were higher than in less dense populations. In the case of the comparison with population A, it seems that substrate differences may be responsible for this, for with their rapid second-year growth shells inhabiting sand had already attained a height of 26.4 mm by their second winter, whereas population B from the mud nearby had only reached 17.5 mm. By early June 1965, however, the characteristic summer reduction in growth had set in, two months earlier than in the second year.

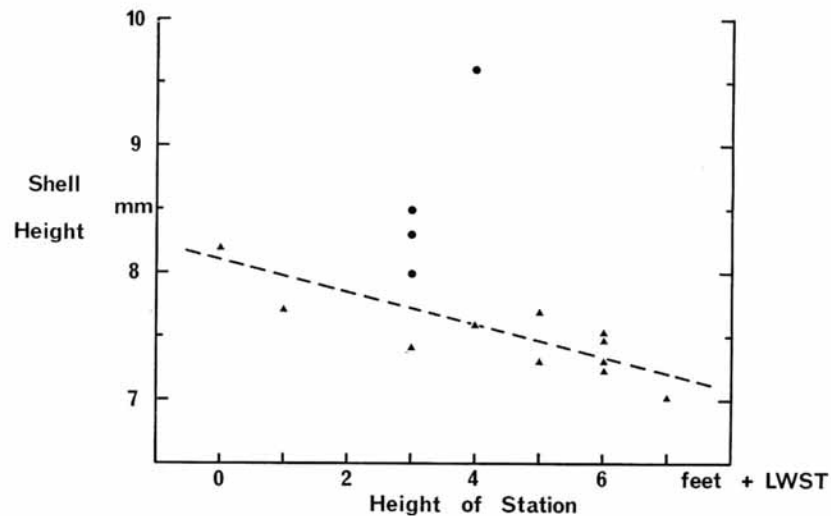
Summarizing, daily growth increment patterns suggest that dense populations of cockles have a much shorter growing season than sparse populations. The absolute daily maxima in first and second years are not, however, appreciably lower; here the effect of height above L.W.S.T. is more important.

Tidal cover. Comparison of the annual increments of shells from near low water springs with those from higher on the flats does not convincingly show a diminution of growth amongst inshore populations (cf. Hancock 1967, p. 141). Differences in growth are more conspicuous along the length of the Estuary (text-fig. 1, Table 1). Thus Thorpe Bay cockles (F, G, H) situated a little lower on the flats than those around the Boom at



TEXT-FIG. 4. Diurnal increment plots for five cockles from different habitats in the Thames Estuary. Localities shown on text-fig. 1. Placement on calendar scale of A12, A26, and B9 based on date of collection: J13 and R22 by temperature related growth disturbances (discussed in the text). Point of commencement of each curve determined by preservation of early part of shell: broken line denotes region where growth lines could not be counted.

comparable densities (N, O, P, R) are on average 2 mm smaller after their fourth winter. The salinity gradient along the Thames could possibly be of sufficient magnitude to effect such a difference in growth, but it might also be explained by the seaward location of the Boom beds in an area of more complex current activity and hence of richer food supply. The inverse relationship which seems to exist for the Shoebury populations J to R between growth in the first year and height above low water springs (text-fig. 5: cf. Cole 1956, p. 79) does not hold when the Southend Pierhead populations are also considered. This discrepancy may well be explained by differing settlement dates of spatfall in the two regions. No more than a week's separation of spat settlement is required to account for the difference, since Orton (1926, p. 261) has shown that small individuals may be growing shell at the rate of 1 to 1½ mm per week.



TEXT-FIG. 5. First-year growth (1963) compared with height of station above low water spring tide for Thames cockles. The linear relationship shown by Thorpe Bay and Shoebury populations (F to R: triangles) does not hold for the Southend communities (A to D: dots).

In the first year of growth, although the peaks of the diurnal increment profiles for A26 and R22 correspond (text-fig. 4), the more emergent specimen has a lower August and September maximum, but a greater October and November contribution. This extension of the growth season relative to lower shore cockles is seen again in the second year where the profile is strongly bimodal. After an early May maximum (substantially less than other shells) growth was sharply reduced in June and July, but recovered in August. There is evidence in the spring of both 1964 and 1965 that the higher shore cockle was later in starting growth, notably when compared with high density populations. By the time the third year of growth is reached diurnal increment totals are reversed, and the high shore example shows the greatest spring increase. Its extraordinary

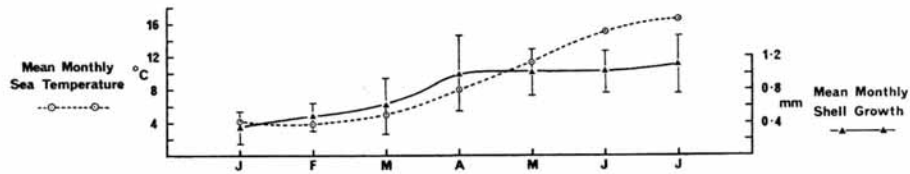
fluctuations make the curve quite different in character from all the others, and judging by similar amplitude variations amongst Burry cockles to be described in a second paper of this series this seems a particularly promising environmental indicator for fossil molluscs.

House and Farrow (1968, text-fig. 3) demonstrated a tidally controlled cyclicity in the growth of Burry cockles, especially in their first year. Southend cockles very rarely show this, though the sensitive low shore example A26 (text-fig. 10) may conceivably do so. Why the higher shore form R22 does not show lunar periodicity seems problematical: it might reasonably have been expected to show more evidence. However, it may be that the sandy substrate of A allows the water to drain completely at low water springs, whereas on the muddy banks interstitial water is retained.

TABLE 3. Monthly growth increments for early 1965 for 32 individuals of 1963 year-group *Cerastoderma edule* from sandbank population A, Southend, determined by spacing of units of 30 daily growth bands. Measurements in mm.

	Jan.	Feb.	March	April	May	June	July
A1R	0.2	0.4	0.2	0.6	0.7	0.8	1.0
A2R	0.6	0.7	1.3	1.5	0.9	1.3	1.9
A3R	0.3	0.7	1.0	1.3	1.2	1.8	1.1
A4R	0.5	0.4	0.4	0.5	0.8	0.7	1.3
A5R	0.3	0.3	0.4	1.0	1.3	0.9	1.3
A6R	0	0.2	0.5	0.5	0.5	0.6	0.5
A8R	0.3	0.5	1.0	1.1	1.2	1.1	1.4
A9R	0.1	0.3	0.5	0.8	0.9	0.8	0.9
A10R	0.2	0.3	0.7	0.7	0.9	0.7	0.6
A11R	0.7	0.3	0.3	0.8	1.1	1.0	0.6
A12R	0.1	0.2	0.3	0.3	0.7	0.7	0.9
A13R	0.2	0.3	0.5	0.7	0.7	0.8	0.7
A14R	0.2	0.8	0.7	1.1	1.3	1.3	1.1
A15R	0.3	0.4	0.8	1.1	1.1	1.1	1.1
A16R	0.2	0.6	0.5	1.0	1.0	1.1	1.5
A18R	0.3	0.3	0.7	0.9	1.1	0.9	0.9
A19R	0.5	0.8	1.1	1.3	1.1	0.9	1.1
A20R	0.7	0.7	1.0	1.1	1.3	1.1	1.1
A21R	0.3	0.5	0.9	1.7	1.4	1.3	1.3
A22R	0.3	0.7	0.3	0.3	0.5	1.0	1.1
A23R	0.5	0.3	0.3	0.8	1.1	1.1	1.1
A24R	0.5	0.7	1.3	1.3	1.6	1.5	1.4
A25R	0.6	0.4	0.7	1.1	0.8	0.7	0.6
A26R	0.5	0.6	0.5	0.7	0.7	0.5	1.0
A27R	0.3	0.7	0.5	1.1	1.1	0.9	0.7
A28R	0.6	0.6	0.6	0.9	1.1	0.9	1.1
A29R	0.3	0.9	0.3	0.5	0.9	0.7	0.8
A30R	0	0.4	0.6	0.5	0.8	0.9	1.3
A31R	0.2	0.3	0.6	0.9	1.1	1.1	1.1
A33R	0	0.4	0.4	2.7	1.7	1.3	2.3
A34R	0.3	0.3	0.7	1.1	1.4	1.3	1.1
A35R	0.3	0.3	0.6	0.9	0.9	0.6	0.8
Mean	0.33	0.49	0.63	0.97	1.03	0.98	1.09
Stand. Dev.	0.18	0.19	0.35	0.46	0.29	0.28	0.33

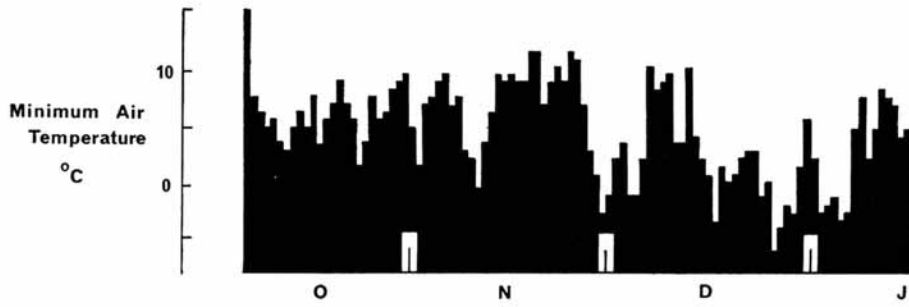
Temperature: the relationship between mean monthly shell growth and sea temperature. Table 3 gives for each member of population A the distance in millimetres separating units of 30 daily growth bands measured from the ventral tip back towards the umbo. Observations were confined to 1965 growth so that ambiguity resulting from possible winter stoppages would not affect the plots. Since the shells were killed on 24 July 1965 the increments do not exactly correspond with the calendar months on the table but overlap the previous month by six days. In January only three of the shells showed a complete absence of growth, while in the remainder increments varied from 0.15 to 0.7 mm. February's growth was within similar limits, but all shells had begun to grow. Standard deviations are greatest in March and April, and the much lower spread of



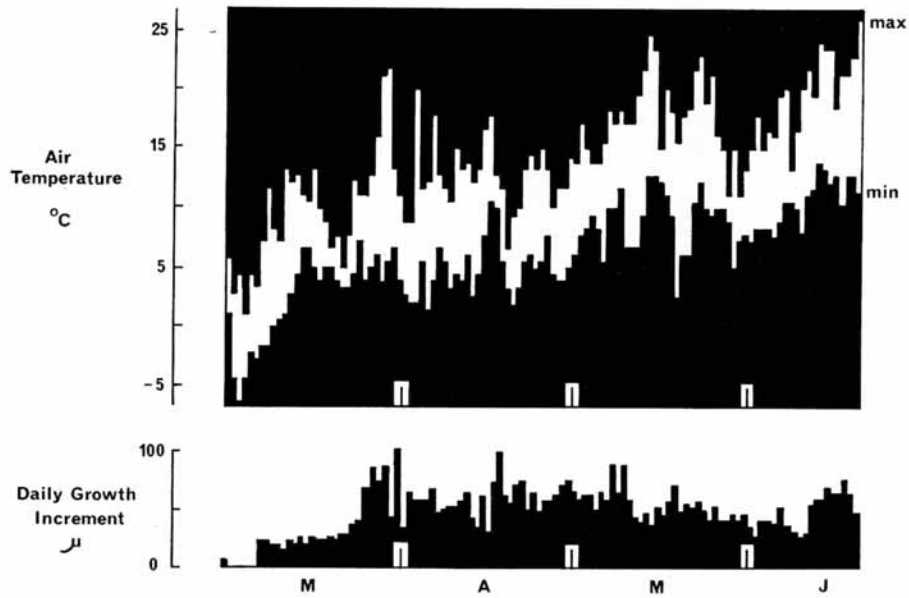
TEXT-FIG. 6. Mean monthly shell growth during early 1965 (determined by analysis of daily increments) for 1963 spat cockles from population A compared with mean monthly sea temperature (recorded daily from Southend Pierhead within $\frac{1}{4}$ mile of the living community). One standard deviation is shown on either side of each mean shell growth value. The high, easily discernible, April dispersion could be a useful palaeoclimatic indicator.

values for May is striking (text-fig. 6). This is to be expected in view of the extreme day-to-day variations in air temperature experienced in the spring, when mortality rates among cockles are also high (Kreger 1940, p. 191). Thus in April A22 put on only 0.25 mm of shell, while A33, making a late start, put on 2.7 mm. Thereafter the increment curve flattens off, with average monthly growth of 1 mm retained for four months regardless of a steep rise in the sea temperature curve. It is quite clear from text-fig. 6 that mean monthly shell growth does not parallel mean monthly sea temperature. Obviously some other major factor such as plankton supply must be exerting an overriding influence in early summer of the third year.

Winter rings and frosts. Text-fig. 4 shows diurnal increment plots for five shells: A12, A 26, B9 were collected on 24 July 1965; R22, J13 in August 1967. Placement on the calendar scale is based on the date of killing of the 1965 specimens, but difficulties arise with 1964 and 1963 increments since there are sharp black bands cutting across the shell structure during the winters of 1964/5 and 1963/4 which clearly indicate that cessation of growth had occurred. The problem is to decide for how long growth had ceased. A reasonable attempt can be made to estimate this by back-counting A26, for it is found that the first of the four 1964/5 winter rings coincides with a period of sub-zero temperatures. The number of growth lines which were counted between the next three rings is in close agreement with the number of days when air temperature rose above zero. The suggested correlation is indicated on text-fig. 7. The placement of R22 and J13 is based similarly on an assumed broad relationship to air temperature. The evidence for the

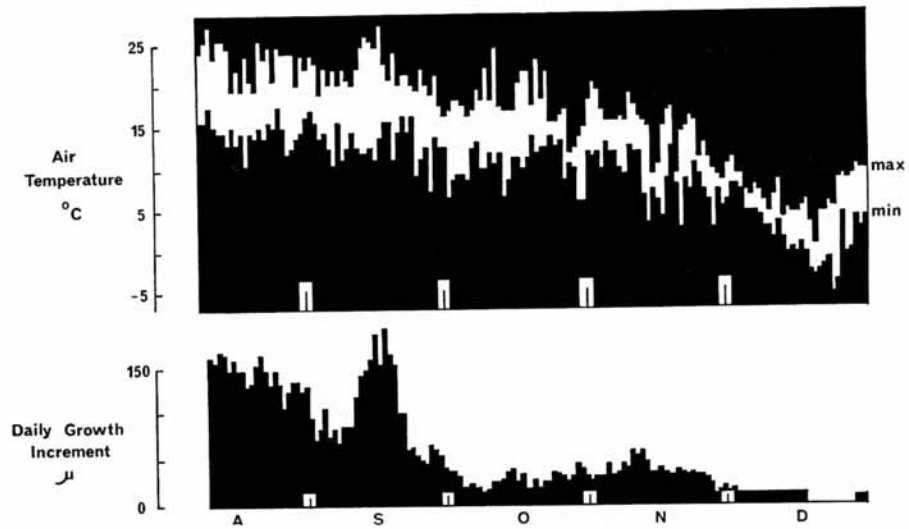


TEXT-FIG. 7. Suggested correlation of winter rings in A26, a sensitive individual (Table 2) with sub-zero air temperatures: 1964/5.



TEXT-FIG. 8. Possible correspondence of extreme growth fluctuations in R22 with air temperature variations in the spring of 1965.

correlation is presented in text-fig. 8, which shows the possible correspondence of extreme growth fluctuations in the high shore R22 with air temperature variations; the start of growth coincides with a period of rapid temperature rise after severe frost. The sudden increase in growth in mid-June may apparently be related to a similar trend in the sea temperature curve. Correspondence of disturbance rings and growth fluctuations in the summer of 1964 indicates that growth stoppages were not prolonged in the cockles' second winter, being of the order of two to five days, but if the same analytical techniques are applied to the growth curves for 1963, viz. that the first winter ring corresponds to the first winter frost (text-fig. 9), it is evident that growth stoppage was more prolonged during the first winter. Here, considering A26 (a sensitive individual, Table 3), growth ceased for a period of from ten days to a fortnight on four occasions.



TEXT-FIG. 9. First-year growth in A26 compared with air temperature: autumn 1963. Placement on calendar scale based on assumed correlation of first winter ring with first frost over the cockle banks (cf. text-fig. 7).

Even allowing for a slightly greater incidence of frost in 1963/4 than in 1964/5 the differences seem too large to be explained completely by temperature, and this tends to support the notion of House and Farrow (1968, p. 1386) that young cockles are more susceptible to environmental variables in their first winter than in their second (cf. Craig and Hallam 1963, p. 740). This is seemingly at variance with the evidence of external growth rings, which are usually more clearly marked in later life. The explanation for this discrepancy seems to be that in the first winter growth before and after the stoppage is rapid, and hence the ring is very narrow; whereas in the second and subsequent winters, although growth may never actually cease for more than two or three days at a time, the increments before and after the absolute minimum are low, and so a broader more easily seen ring is formed.

CONCLUSIONS

Practical contribution of the technique. Marine biologists currently involved in studies on shell growth will find certain critical problems in the interpretation of external growth rings alleviated by studying internal periodicity patterns in the manner indicated in this paper. One major difficulty concerns the recognition of the first winter ring, which may be badly abraded in certain specimens or ill defined externally in others from areas enjoying relatively high winter temperatures (Cole 1956, p. 78). In both instances internal examination by acetate peels should settle the question. Another outstanding problem, and one which has hampered the adoption of growth ring analysis by palaeontologists, is to separate disturbance rings from those of annual origin. Craig and Hallam (1963) achieved such a separation statistically, but this method requires large numbers of shells. If only small samples or isolated individuals are available analysis of micro-banding can readily distinguish a disturbance ring, with its sudden reduction in daily increment compared with relatively stable background values from the annual ring, where daily increments gradually diminish over a period of weeks.

In studies on population dynamics it is of considerable importance to know the degree to which the members of any one population react simultaneously to environmental changes. The contribution which analysis of daily growth banding can make to such studies may be assessed from the fact that it is possible by back-counting from midsummer collection dates to pinpoint exactly for each shell the date at which resumption of growth took place after the winter cessation. Using a vernier stage it is a relatively rapid process to count the banding of a statistically significant number of shells and calculate the date of the spring surge in growth rate, which may then be compared with diurnally recorded environmental variables and correlations sought. Thus in the Thames, even in the most variable cockle population, 75% started to grow within a period of one month at the beginning of their third year.

The diurnal growth plot for any shell provides moreover an absolute record of the animal's growth, which in many circumstances may be more useful than existing relative measures. This permits a true estimate of the actual length of the growing season, and one can demonstrate thereby that mature cockles living under crowded conditions have a much shorter growth season than more scattered examples. It would also be most instructive to compare the seasonal growth pattern of cockles living in conditions of reduced salinity with more normal examples: this could well be done in Poole Harbour (Cole 1956, pp. 82-83).

The validity of the technique of daily growth line analysis is demonstrated nicely by the close agreement of many of its results with those reached through shell length measurements on successive collections of a single population. Two examples will suffice. First, in the second-year growth rate as determined by daily banding increases rapidly in April to maximum daily values in May; this agrees with macroshell measurement (Orton 1926). Several shells showed midsummer reduction in growth which could not be correlated with temperature variations. It is possible that this phenomenon is associated with spawning activity, which is known to produce an external ring in *Pecten maximus* (Mason 1957), though to establish this firmly for *Cerastoderma edule* requires more specific collecting. Second, back-counting daily bands in continuously growing members of populations sampled in the summer of 1965 gave spatfall dates ranging

from late May to early September 1963, in very good agreement with observations in the Thames (D. A. Hancock, personal communication 1968) and generally accepted values for *C. edule* (Cole 1956, p. 84).

The particular value of the Thames experiments is that they were conducted on *in situ* specimens. Examination of periodicity structures in cockles removed to the laboratory showed that such tank-kept individuals were never normal after collection (cf. Rhoads and Pannella 1970, fig. 5), and caution is necessary when extrapolating results. Similarly, specimens which were drilled for the insertion of electrodes in connection with the work of Trueman *et al.* (1966) on burrowing activity also possessed abnormal shell growth patterns.

Not only can the date of origin of a population be determined from daily growth analysis but also, for dead shell accumulations, the season of death. This has relevance to both the ecologist and palaeoecologist concerned with mortality rates and the season of greatest mortality. On the potential significance of the method in these fields see also Hancock and Simpson (1962), Craig and Hallam (1963), Craig (1967) and Hallam (1967); already the technique has been used for seasonal dating in archaeology (Coutts 1970).

Palaeoecological significance of daily growth analysis. Rhoads and Pannella (1970) have recently reviewed the general field of periodicity structures in bivalves. One or two supplementary points of interest are, however, raised by the cockle work in the Thames. The first concerns the influence of substrate on growth rate. In his fascinating general study of cockle growth rates Cole (1956) noted considerable uniformity over a wide range of substrates, such factors as exposure to wave action being more important in limiting growth. Nevertheless it does seem that within a single area where exposure, temperature, and salinity values are closely similar in adjacent cockle beds the influence of substrate can be perceived. The observed higher growth rate in sand than in mud is paralleled in other infaunal bivalves such as *Mya arenaria* (Swan 1952), and it would be interesting palaeontologically to study molluscan growth rates in relation to biofacies variation, especially where widespread burrowing species are recorded from a range of sedimentary types.

The second point concerns the role of intertidal exposure in reducing shell growth. Elsewhere, particularly in the Burry Inlet, this is striking; but in the Thames its effect on periodicity structures is hard to detect. The large tidal range and abnormally high situation of the Burry beds (Hancock and Urquhart 1966, p. 16) must have a major bearing on this difference since certain cockles are completely emersed for several days during low amplitude neap tides. Not all cockles situated at the level of neap high water are necessarily of reduced size, however, as Cole (1956, p. 79) has pointed out in the case of the fascinating Furzey Island cockles from Poole Harbour, which are protected from desiccation by the roots of *Spartina townsendii* and are only marginally smaller than examples from mean tide level. In the Thames the effects of variations in population density and substrate effectively prevent the clear recognition of tidal control on shell growth.

One important palaeoecological point to emerge from this work is the demonstration of the very different response shown by various members of one supposedly homogeneous population to environmental factors such as sub-zero temperatures. Some

sensitive shells may stop growing on four separate occasions during the winter while others show no evidence of cessation. Variation in microtopography may conceivably be responsible, for Petersen (1958, p. 21) has already drawn attention to the importance of this in his ecological work on Danish cockles. Alternatively the shells may reflect genetic differences in growth pattern, and the possibility that the beds have been stocked from two distinct sources should be borne in mind; presumably a predominantly sublittoral population would provide more susceptible individuals. In a fossil population care should be taken to sample adequately in order subsequently to assess the range of susceptibility shown by each of its members; see Table 2 for the Recent model. This intrapopulation variability in growth increments, even when averaged over monthly periods, is so great that the use of periodicity structures in palaeotemperature investigations is likely to prove far from straightforward; currently it is certainly less promising than other aspects of the work. Correlation between mean monthly growth and mean sea temperature is low, but the sharp rise in growth rate between March and April of the third year, easily decipherable from internal daily microbanding, could be a useful seasonal indicator, especially as this is also very clearly the season of greatest increment variation between specimens (text-fig. 6). Cole (1956, p. 86) has noted anomalies in the relationship of cockle size to sea temperature, observing that although within Poole Harbour, the region with the highest summer temperatures, cockles are large, they are even larger off Barra (Walton 1919) where the summer temperatures are much lower. Availability of food and a relatively sheltered situation must be more important factors.

Acknowledgements. This work forms part of a project supported by N.E.R.C. which is being carried out at the University of Hull under the general direction of Professor M. R. House. The interest and collaboration of Dr. D. A. Hancock and Mr. A. C. Simpson of the Fisheries Laboratory, Burnham-on-Crouch, is a pleasure to record. They kindly made available population density data of cockles on the Southend Flats collected by Mr. G. Pickett. Messrs. J. Clapison and K. G. Walker were responsible for peel preparation and photography. Sea temperature and other daily records were supplied by Southend Pier and Foreshore Manager, Mr. G. S. Dawson.

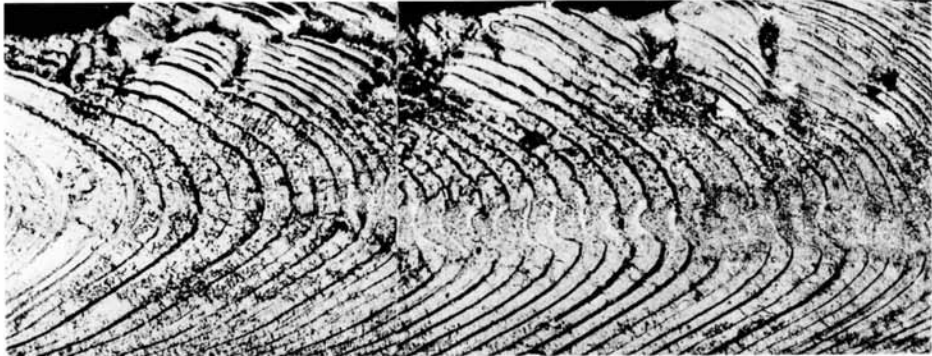
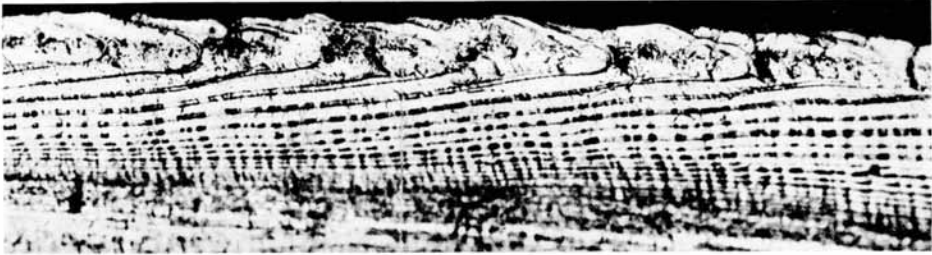
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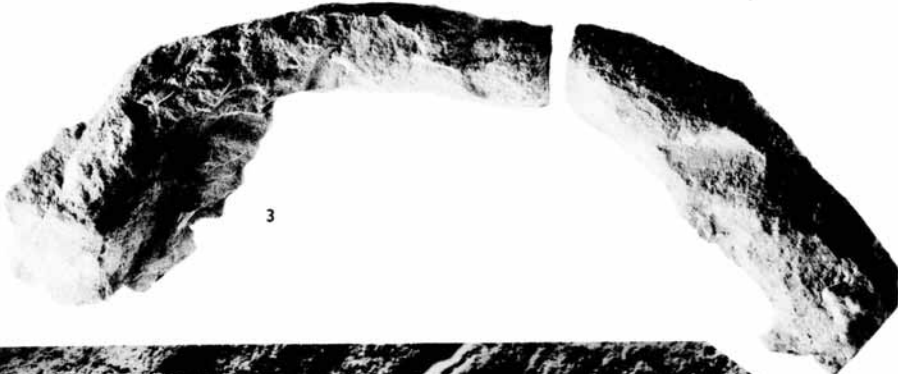
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Typescript received 28 November 1970



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FARROW, Growth banding in *Cerastoderma*
SELLWOOD, *Thalassinoides* with *Glyphaea*