PALAEOTIDAL CHARACTERISTICS DETERMINED BY MICRO-GROWTH PATTERNS IN BIVALVES

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ABSTRACT. SEM studies of growth patterns in the ligament groove of late Pleistocene oysters and in unidentified Miocene shell fragments have enabled the fossils' position within the intertidal zone and the tidal regime to be reconstructed. Whereas the present-day tidal regime in Osaka Bay has a strong diurnal inequality seen especially in the heights of low water, 70 000 years ago it possessed only weak diurnal inequality, as in the Miocene at another locality, where it was weakly discernible in the heights of high water. The late Pleistocene borehole material represents a mixed assemblage for it includes individuals that lived at various intertidal levels. The majority of the Miocene individuals lived at mean tide level. The arrangement of growth lines of alternating thickness inverts every 2 weeks. Sequences are plotted with successive days on the ordinate and the time of day on the abscissa. For the Recent this results in a vertical partition of thicker and thinner growth lines. If the partition is not vertical when fossil growth lines are plotted, a change in the number of days per month is indicated. The plots for the Miocene material indicate that the length of a synodic month in terms of the number of synodic days of that time was essentially the same as the present.

IN many invertebrate hard parts we can observe traces of macroscopic and microscopic growth (Neville 1967; Clark 1974; Termier and Termier 1975; Scrutton 1978; Chave and Erben 1979). These are commonly called growth lines, increments, bands, rings or ridges. Sequences of these features (referred to as 'growth patterns' in this paper) reflect the growth history of organisms as well as the environmental factors influencing it.

Wells (1963) called attention to the usefulness of analysis of fine growth features. He counted the number of the fine growth ridges between the major annulations on coral epithecas and assumed the latter formed annually and the former daily. His values were *c.* 400 per year for the Devonian Period and *c.* 390 for the Carboniferous Period. They were in good agreement with the estimates of days of the year obtained through present-day astronomical observations. Since then, various palaeontological studies of fine growth patterns have been made.

Molluscan shells, especially bivalves, have well defined and easily discernible growth patterns. They are also very abundant in aquatic environments, not only in present seas but also in the geologic past. Therefore they have been intensively studied as suitable material for growth pattern analysis.

In the early stage of growth pattern study, daily rhythm was thought to be ubiquitous and responsible for making growth patterns irrespective of the habitats of bivalves, but a few workers were conscious of the variability in shell growth rhythm. Le Gall (1970) suggested that tidal rhythm is responsible for the formation of fine striations on the shell surface of *Mytilus edulis* and called these striations *strie marée*. Evans (1972, 1975) demonstrated that individuals of the bivalve *Clinocardium nuttallii* (Conrad) living in the intertidal zone form their shell with tidal rhythm. In recent years data about the manner of the shell growth of intertidal bivalves have accumulated (Richardson, Crisp and Runham 1979, 1980*a*, *b*, 1981; Richardson, Crisp, Runham and Gruffydd 1980; Ohno 1983, 1985; Deith 1983). Extensive experiments on living animals in these studies clearly show that shells of intertidal bivalves grow with tidal rhythms and that the resulting patterns reflect features of the tides and related phenomena. Tidal growth rhythm is also known in gastropods (Antoine and Quemerais-Pencreac'h 1980; Ekarante and Crisp 1982; Ohno and Takenouchi 1984) as well as in barnacles (Bourget and Crisp 1975; Crisp and Richardson 1975; Bourget 1980).

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Apart from Deith's (1983) successful archaeological application of the tidal shell growth of *Cerastoderma edule* (Linné) in estimating the seasonal shellfish collecting activity of a Mesolithic site of southern Scotland, there are few works concerning tidal growth of prehistoric or fossil bivalve shells. Berry and Barker (1975) interpreted recurring clustering of growth increments on fossil bivalves as reflecting the change between neap and spring tides. Pannella (1976) showed a single growth pattern in a Late Cretaceous bivalve shell *Limopsis striatus-punctatus* Evans and Schumand, which he interpreted to be of tidal origin. Ohno (1984) made a short report on the tidal growth rhythm on late Pleistocene bivalve shell fragments.

In this paper I will introduce a method of recognizing tidal shell growth patterns based on recent experiments with living bivalves. Further I will demonstrate the existence of unequivocal tidal shell growth patterns in fossil bivalves based on this method. I will also try to reconstruct the features of tides of the biotopes in which fossil bivalves lived. Finally, an easy method of estimating the change of the number of lunar days per synodic month based on the tidal growth pattern of fossil bivalve shells will be proposed.

MATERIAL AND METHODS

Material examined

Fossil bivalve shells from two regions in Japan were examined in the present study.

One group were obtained from two boreholes from the basal part of a late Pleistocene marine clay layer in the western part of Osaka City. The clay is called the Ma12 Clay by local geologists. (The abbreviation Ma means marine.) Around Osaka more than ten cycles of marine clay beds and nonmarine clastic deposits of late Pleistocene age are known. The former represent the transgressive phases and the latter regressive phases of late Pleistocene eustatic sea-level changes. The basal part of the Ma12 Clay bed may have been deposited in the early phase of a transgression. This clay bed is correlated with a clay bed at the site of the off-shore international airport about 30 km south-south-west of the boreholes on the basis of pollen and Foraminifera (Chiji 1984; Furutani 1984; Nakaseko *et al.* 1984). The *Emiliania huxley acme*-zone is found in the Ma12 Clay bed at the airport site (Okamura and Yamauchi 1984), and its age is estimated to be 0·07 my (Gartner 1977).

Bivalve fossils were obtained from the Miocene Mizunami Group, exposed around Mizunami City, about 40 km north-east of Nagoya City. Itoigawa (1981) subdivided this group into four formations; the Toki Lignite-bearing, the Hongo, the Akeyo, and the Oidawara Formations in upward sequence. The first two are fresh water and the latter two marine deposits. The fossil shell samples examined in the present study were collected at a locality called Takenami (loc. 23 of Itoigawa 1974) from an outcrop of a shell bed considered to belong to the Akeyo Formation, assigned to N.8 of Blow's zonation (Itoigawa 1981). The molluscan assemblage of the bed indicates an embayment with a muddy bottom and an intertidal water depth (Itoigawa *et al.* 1974).

All the samples illustrated here are stored in the Department of Geology and Mineralogy, Kyoto University, Kyoto, Japan (registration no. JCTO-0001–JCTO-0013).

Methods of observation

Growth patterns of fossil bivalve shells were studied using a scanning electron microscope (SEM) mainly with BEI (back-scattered electron image) mode. This mode enhances surface topography of samples, and thus is suitable for observation of microgrowth patterns.

Growth patterns in oyster shells are observable on the surface of the ligament groove. Fragments with the grooves are mounted on the stage after cleaning with water in an ultrasonic bath for about 30 seconds and then coated with gold. In other samples the growth patterns are observed along the cut sections of the valves. If the samples are free of matrix they are embedded in plastic, then cut radially between the umbo and the ventral margin of the shell to obtain the longest growth sequence possible. If they are in a sedimentary matrix, the cut direction is not predeterminable. Thus rock samples containing shell fragments are cut in an arbitrary direction and shell fragments suitable for the observation of growth patterns are selected. The cut shell surfaces are ground with powders up to no. 3000, polished with diamond paste, and then etched with 0·1 mol HCl for about 10 to 30 seconds. Then they are coated with gold and examined by SEM.

TYPES OF TIDES

To understand tidal shell growth patterns, it is necessary to be familiar with the different types of tides.

Tide is a periodic rise and fall of water level of the sea caused by the gravitational forces of the moon and sun on the water mass of the earth. The most familiar 12·4 hourly rise and fall of the water is caused by the moon's gravitational force, which is strengthened and weakened by the sun's gravitational force causing a 2-week change resulting in spring and neap tides. Obliqueness of the moon's orbit to the earth's equator causes diurnal inequality of the tides. This is most clearly expressed as the difference between the heights of the two succeeding high tides or of the two low tides of a day. The periodicities of these oscillations, reflecting the celestial movements of the earth, moon, and sun, are constant, but their amplitudes and phases are variable from place to place, depending upon the depth of the ocean, shape of the shore line, etc. Thus the actual tides in the world oceans varies from place to place.

Tides can be classified into several types according to the intensity of diurnal inequality. In the present paper, they are divided into four types (text-fig. 1). If the diurnal inequality is weak, 12·4 hourly rise and fall of water occurs resulting in approximately two low tides and two high tides per day (semidiurnal tide; text-fig. 1A). The increase of the diurnal inequality of the tides is most clearly expressed in the increasing difference of the heights of two succeeding high tides as well as of two succeeding low tides (mixed tide). The difference is emphasized in the heights of low tides (text-fig. 1B), or that of high tides (text-fig. 1C). There are all possible intermediates between these two extremes and the inequality may appear in heights of both low and high tides in one tidal curve. Finally, when the diurnal inequality becomes sufficiently large, approximately only one high tide and one low tide appear per day, with a periodicity of 24·8 hours (diurnal tide; text-fig. 1D).

TIDAL GROWTH PATTERNS

Components of growth: growth line and growth increment

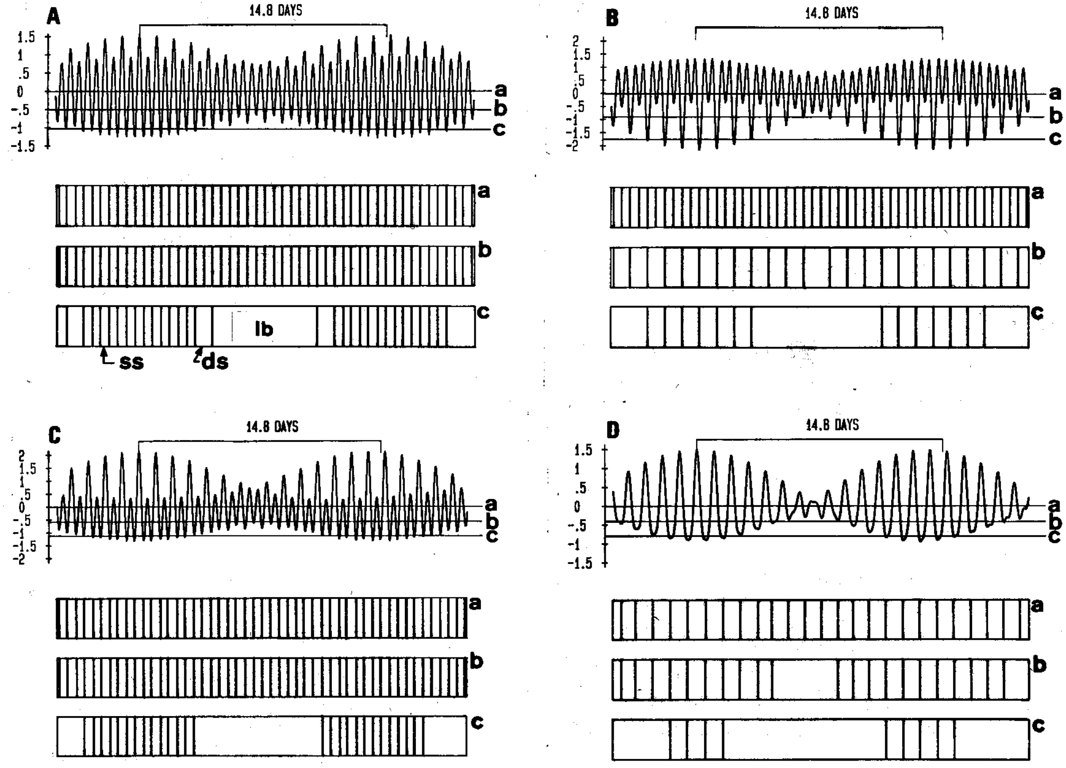
Growth of bivalve shells consists of two components, namely growth lines and growth increments. They are most easily observed in sections vertical to the shell surface. Growth lines are thinner shell layers, resistant against etching with diluted HCl or other etching agents. Growth increments are layers between growth lines. They are usually thicker than the growth lines and form the major part of the shell. Similar components are also visible on the bivalve shell surface as well as on the ligament area: the thinner ridges or grooves will be called growth lines and the thicker stripes between them, growth increments, by analogy with the components seen on the cut surfaces. Growth of bivalve shells results in the formation of a sequence of growth lines and growth increments one beside another, which will be called growth patterns.

Intertidal growth patterns: previous studies

Studies of the correlation between bivalve shell growth patterns, tides, and related phenomena, have been done with *Cerastoderma edule* (Linné) (Richardson, Crisp and Runham 1979, 1980*a*, *b*, 1981; Richardson, Crisp, Runham and Gruffydd 1980; Ohno 1983, 1985; Deith 1983), *Clinocardium nuttallii* (Conrad) (Evans 1972, 1975), and *Fragum unedo* (Linné) (Ohno 1985). The results of these studies are summarized here (see also Table 1).

Tidal exposure and growth line formation

Growth line formation in intertidal bivalve shells has been most intensively studied in *Cerastoderma edule*. This species lives along European coasts where tides are semidiurnal with weak diurnal inequality. Individuals near the MTL (mean tide level) are exposed every 12·4 hours at low tide. Richardson *et al.* (1979) and Ohno (1985) let their marked individuals grow in natural or simulated tidal cycles. These shells formed growth lines in almost precise correspondence with the number



TEXT-FIG. 1. Four typical tidal types and possible arrangement patterns of tidal growth lines corresponding to them. (The tidal height in arbitrary scale is shown on the left side of each diagram.) A, semidiurnal tide with faint diurnal inequality. B, mixed tide with diurnal inequality strongly expressed in the heights of the low tides. C, mixed tide with diurnal inequality strongly expressed in the heights of the high tides. D, diurnal tide. Hypothetical growth line arrangement patterns are shown at three different levels (a, mean tide level; b, between MTL and low water; c, near LW) for each tidal type. Three stripes represent parts of shell cut parallel to the shell growth direction. Patterns are produced assuming that one tidal growth line is formed at one low tide, but only when the bivalve shell is exposed above water. In the stripe for a specific water level, one vertical line representing a tidal growth line is drawn under the corresponding low tide, when the shell is exposed at low tide: ss, single spacing of tidal growth lines; ds, double spacing of tidal growth lines; lb, irregular bundle (see Table 1 for definitions). (Possible variation in growth line thickness and increment thickness as well as non-tidal growth lines in irregular bundles are not indicated in these hypothetical patterns, in order to show clearly the relationship between growth lines and tidal exposure.)

of tidal cycles which they experienced during their growth after the marking. Deith (1983) collected two sets of specimens of *C. edule* from a precise locality in an intertidal zone on two different dates. The number of growth lines from the last winter to the growing edges was counted. The difference of the means of growth lines between the two sets are well in correspondence with the number of tides during the interval between the dates of collecting. This study also suggests that one growth line is formed at each tidal cycle.

To determine when during each tidal cycle a growth line is formed, Richardson *et al.* (1981) collected individuals of the species at approximately 1 hour intervals at a fixed point near the MTL of an intertidal zone for two tidal cycles and compared the amount of shell growth beyond the last growth line with the phase of the tide at the time of collecting. Their work demonstrates that one growth line is formed at the end of each tidal exposure (growth line of tidal exposure origin will be called tidal growth line; Table 1). Consequently, a growth increment which separates two tidal growth lines is formed during the time between two tidal exposures, i.e. during inundation at high tide.

Growth lines are also formed subtidally (these will be called non-tidal growth lines), when bivalves are submerged continuously for more than one semidiurnal tidal cycle. Richardson *et al.* (1980*b*) claimed that these lines in *C. edule* are formed with endogenous tidal rhythms, although the number of such growth lines formed during each of a series of their experiments varied significantly from specimen to specimen. Ohno (1985) found that the number of the subtidally formed growth lines in his experimental samples of *C. edule* did not correspond to that of the tidal cycles during the duration of the experiment. He concluded that the subtidal growth line formation was not rhythmical.

Despite this debate, it is easy to distinguish non-tidal growth lines from tidal ones, because the former are more weakly defined and more irregularly spaced than the latter (Richardson *et al.* 1980*b*; Ohno 1983, 1985). The spacing of subtidal growth lines sometimes becomes abnormally

TABLE 1. Tidal growth patterns, their definitions and causes.

I. Growth lines

Tidal growth lines: growth lines formed during tidal exposure at low tides.
Non-tidal growth lines: growth lines formed subtidally.

II. Patterns in growth line arrangement

Regular bundles: bundles consisting of well defined and more or less regularly spaced tidal growth lines. Spacing of growth lines in regular bundles can be classified as follows:

(*a*) Single spacing of tidal growth lines: spacing of tidal growth lines formed during tidal exposure at low tides occurring approximately 12·4 hours apart. This spacing is very often accompanied by alternating thicker and thinner growth lines (see III of this Table).

(*b*) Double spacing of tidal growth lines: spacing of tidal growth lines formed during tidal exposure at low tides occurring approximately 24·8 hours apart.

If growth lines of 12·4 hourly tidal exposure origin and those of 24·8 hourly tidal exposure origin occur in one shell growth pattern, the spacing of the latter lines are about twice as wide as that of the former. Thus the latter ones are referred to as double spacing and the former as single spacing. Spacing of the tidal growth lines of 24·8 hourly exposure origin are also referred to as double spacing, even when they solely occur in a growth sequence.

Irregular bundles: bundles consisting of weak and irregularly spaced non-tidal growth lines formed subtidally.

Alternating regular and irregular bundles: sequence caused by the change of periodic tidal exposures during spring tides and continuous submergence during neap tides.

III. Pattern in the growth line thickness

Alternating thicker and thinner growth lines: caused by the interference of semidiurnal tidal exposure and 24 hour change of day and night; thicker growth lines formed at daytime low tide, thinner ones at night-time low tide. Thus the pattern is diagnostic to semidiurnal tidal exposure. Order of the arrangement of thicker and thinner growth lines inverts approximately every 28·5 growth lines, which corresponds to the number of 12·4 hour tidal cycles per one fortnight.

IV. Pattern in the growth increment thickness

Alternating thicker and thinner increment: caused by alternating shorter and longer duration of submergence at successive high tides because of the diurnal inequality of tides; thicker increment formed during the longer submergence and thinner one during the shorter submergence. The order of arrangement of thicker and thinner growth increments inverts approximately every 26·4 increments, which corresponds to the number of 12·4 hour tidal cycles per half a tropical month.

wide, more than twice or three times wider than that of the more or less uniformly spaced tidal growth lines (Ohno 1983, 1985), if they are present in the same individual. Wide spacing of growth lines documented in a sample of *C. edule* in plate 8*c* of Farrow (1972) was also probably caused by the same mechanism, as its location in the lower intertidal zone suggests.

Patterns in arrangement of growth lines

The arrangement of tidal growth lines alone, or together with non-tidal growth lines, in intertidal bivalve shells reflects the kind of tidal exposures determined by the type of tides in their habitat and the level at which the bivalves lived. For example, *C. edule* that live low in the intertidal zones are semidiurnally exposed only during spring tides, and continuously submerged during neap tides. This change is recorded as alternating bundles of more or less regularly spaced tidal growth lines (which will be called regular bundles) and of weak and irregularly spaced non-tidal growth lines (irregular bundles). The proportion of the regular bundles to the irregular bundles decreases in the lower intertidal zone (Ohno 1983).

Patterns in growth line arrangements are also found in *Fragum unedo* (Linné) and *Clinocardium nuttallii* (Conrad). Evans (1972, 1975) studied the growth patterns of *C. nuttallii* from California, USA. He did not make field experiments with living individuals, yet correlation between tidal exposure and growth line formation is fairly obvious. Because of the change of magnitude of the diurnal inequality of the local tide, his specimens were exposed semidiurnally during a specific period of half a tropical month, but only once a day during the rest of the time. The resulting growth pattern consisted of bundles of more or less constantly spaced growth lines alternating with those of regularly spaced growth lines in which spacing is about twice as wide as those of the former bundles. The former bundles were interpreted to be composed of growth lines of semidiurnal tidal exposures and the latter of those of diurnal tidal exposures (Evans 1972, 1975). In this case, the growth lines are all of tidal origin, but the frequency of their formation alternates periodically from semidiurnal to diurnal.

The spacing of tidal growth lines formed through semidiurnal tidal exposures will be referred to as single spacing and that of those formed during diurnal tidal exposures as double spacing.

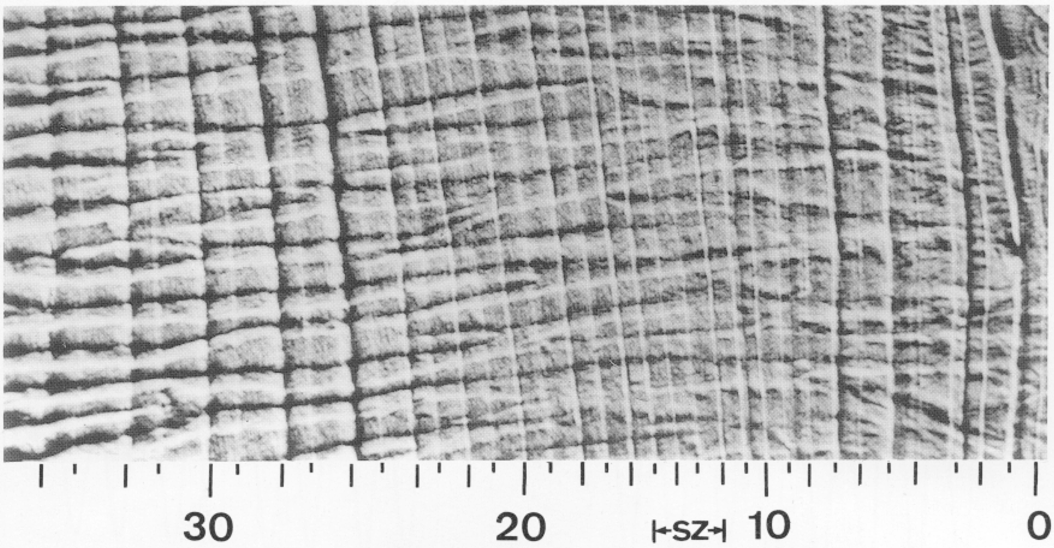
F. unedo (Ohno 1985) lives in the lower part of the intertidal zone of Ishigaki Island, Japan. Because of the strong difference in the height of the low tides, due to the strong diurnal inequality of the local tide, they were exposed once a day during spring tides, but continuously submerged for several days during neap tides. As a result, regular bundles with double spacing of tidal growth lines formed during spring tides alternate with those of irregular bundles formed during neap tides. This bundle alternation pattern is quite similar to that of lower intertidal individuals of *Cerastoderma edule*. The only difference is that the tidal growth lines were formed diurnally in *F. unedo* rather than semidiurnally.

These patterns of tidal growth lines together represent only those formed at a few levels in the intertidal zone with two of the four general tidal types. To complement the real arrangement patterns, hypothetical ones are shown in text-fig. 1.

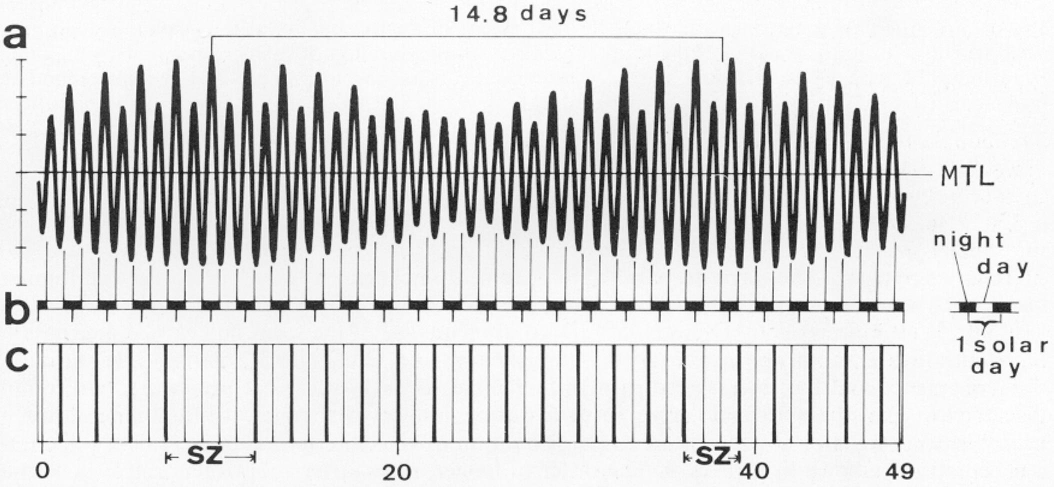
Alternating growth line thickness

Several growth patterns occur exclusively in the bivalves of intertidal zones. One of these, perhaps the most conspicuous one, is the alternation of thicker and thinner lines (text-fig. 2). It was first discussed by Dolman (1975) based on *C. edule*. Richardson *et al.* (1980*a*) experimentally found that this pattern was the result of the difference of air or substrate temperature between daytime and night-time tidal exposures: thicker lines are formed during daytime exposure and thinner ones during night-time exposure. Ohno (1985) came to the same conclusion and furthermore showed that, in the summer season at least, the formation of this alternation pattern near the MTL is not affected by the duration of exposure at low tides, which varies to a certain extent due to the weak diurnal inequality of the tides in the habitat of his samples.

Formation of the pattern of thicker and thinner growth lines is schematically shown in text-fig. 3. Because low tide occurs about 50 minutes later than on each preceding day, the 'daytime' low



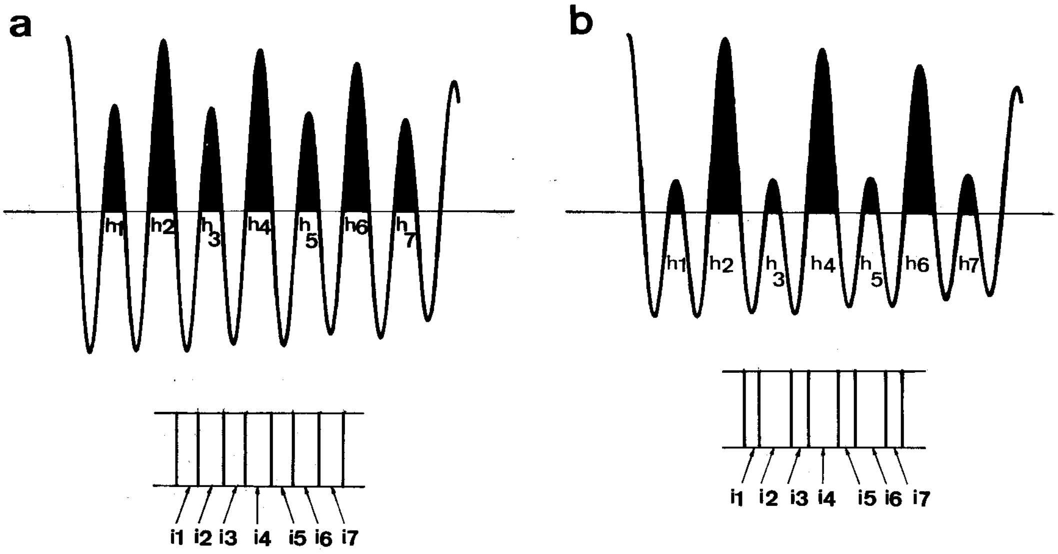
TEXT-FIG. 2. Alternating thicker and thinner growth lines. A, radial section of the shell of a recent intertidal specimen of *Cerastoderma edule* (Linné) collected near the MTL from Vogelkoje in the vicinity of List/Sylt, German North Sea. Sample no. P361, registration no. JCTO-13, ×315; growth from right to left. Note that the order of arrangement of thicker and thinner growth lines inverts from right to left, so that in arbitrary numbering the lines with odd numbers are thicker near the right corner, whereas lines with even numbers are thicker near the left corner. Where the inversion occurs, there is a zone of a few lines of similar thickness (SZ, switch zone).



TEXT-FIG. 3. Schematic explanation of the formation of the alternation of thicker and thinner growth lines. For simplicity, it is presumed that the thicker daytime growth lines are formed between 6 and 18 o'clock and the thinner night time ones between 18 and 6 o'clock. *a*, semidiurnal tide for fifty tidal cycles (tidal height in arbitrary scale); *b*, sequence of 12-hour day (white segments) and 12-hour night (black segments); *c*, schematic presentation of resulting alternation of growth line thickness in a bivalve living near the mean tide level (MTL). Note the inversion of the order of arrangement of thicker and thinner growth lines every fortnight. The inversion occurs in switch zones (SZ).

tide will change into the 'night-time' low tide after a fortnight. Consequently the order of appearance of thicker and thinner lines inverts after every 2 weeks (28·54 semidiurnal tidal cycles). This inversion is also seen in the middle of the growth sequence of the recent *C. edule* shown in text-fig. 2. Where the inversion of growth line thickness occurs, there is a zone with a few lines of more or less similar thickness. This zone is called 'switch zone' in this paper.

This pattern of line thickness alternation and inversion is also recognized in the gastropod *Monodonta labio* (Linné) (Ohno and Takenouchi 1984).



TEXT-FIG. 4. Alternating increment thickness through strong diurnal inequality in the heights of high tides (tidal height in arbitrary scale). *a*, if the inequality is not strong, duration of submergence at each high tide (here indicated with h1 to h7) does not vary significantly from one to another and the corresponding increments (i1 to i7) have more or less similar thickness. *b*, the inequality in the height of the high tides causes alternation in duration of submergence at each high tide (h1 to h7), which in turn results in the alternation of increment thickness (i1 to i7).

Alternation of increment thickness

The characteristics of tides are also reflected in increment thickness. Alternating thicker and thinner increments were found in *C. edule* which were experimentally grown near the mean sea level in List/Sylt, West Germany, by Ohno (1985). Diurnal inequality of the local tide caused alternation in the duration of submergence at every 12·4 hourly high tide. Ohno (1985) compared the duration of submergence and the thickness of growth increment formed during each high tide and found that thicker growth increments were formed during longer submergence and thinner growth increments during shorter submergence. The formation of such alternation in increment thickness is schematically shown in text-fig. 4. The order of longer and shorter submergence inverts with a periodicity of 26·4 tidal cycles (half a tropical month); the order of thicker and thinner increments inverts after every 26·4 tidal cycles.

Tidal vs. daily growth rhythms in intertidal bivalves

Claims have been made that intertidal bivalves form their growth patterns with 24-hour solar daily rhythm. If that is true, the tidal formation of growth patterns observed in the above three species would lose general applicability in interpreting growth patterns of fossil intertidal bivalves. These claims are examined below.

The claim of House and Farrow (1968) for daily growth rhythm in the intertidal *C. edule* was not accompanied by any field experiments. As stated above, a massive amount of experimental studies on this species (Richardson, Crisp and Runham 1979, 1980*a*, *b*; Richardson, Crisp, Runham and Gruffydd 1980; Ohno 1983, 1985) has shown clearly the tidal growth rhythm of intertidal specimens of *C. edule*.

The growth rhythm of intertidal individuals of *Mercenaria mercenaria* (Linné) has been variously interpreted as: a 24-hourly solar daily growth rhythm (Pannella and MacClintock 1968; Rhoads and Pannella 1970); a solar daily growth rhythm which is interrupted by tidal exposure at low tide (MacClintock and Pannella 1969; Pannella 1972, 1975); a purely tidal rhythm (Pannella 1976).

Ohno (1985) carried out experiments with intertidal individuals of *M. mercenaria* in tidal creeks in South Carolina. In one group (MC of Ohno 1985) the average of increments (55·7) was near that of the semidiurnal tidal cycles during the experiment (60). In another group, from a different tidal creek (MO of Ohno 1985), with occasional interruptions of growth caused by the severe environmental conditions of the marsh region, the number of increments formed was variable among individuals. The average number of increments (43·8) exceeded that of the days of experiment (33) significantly.

Further, Ohno's specimens formed alternating thicker and thinner growth lines. Examination of photomicrographs published by Pannella and MacClintock (1968) also show that the alternation of thicker and thinner growth lines is very common. Their 'complex increment' (e.g. their pl. 1, fig. 5) also reveals itself as nothing more than a pair of increments bounded by growth lines of alternating thickness. Such alternation of growth line thickness should be, as mentioned already, interpreted as the result of the interference of the semidiurnal tidal exposures and the 24-hour change between day and night. Thus the growth pattern is quite probably formed tidally, although the growth may be occasionally and locally disturbed by environmental stress. The agreement of the number of the increments formed with the number of days of the experiments in the work of Pannella *et al.* (1968) may be coincidental, as Pannella (1975) suggested.

Koike (1973) studied growth line formation in *Merterix lusoria* (Roeding) from the intertidal zone of Kyushu, Japan. She divided growth lines arbitrarily into five different types. Based on the correspondence of the sum of lines of her type A and type B with the number of days of the experiment, she concluded that the lines of these two types were formed diurnally. However, as stated by Ekarante and Crisp (1982) the single photograph provided to illustrate the supposed sixteen daily growth bands clearly contains many more. Koike's belief in daily growth line formation is not acceptable without further experimental evidence.

Hall *et al.* (1974) studied shell growth of intertidal *Tivela stultorum* (Mave) assuming daily shell growth rhythm, but they did not confirm their assumption.

As discussed above, there is no substantial evidence of daily growth rhythms among the intertidal bivalve species.

RECONSTRUCTING ANCIENT TIDAL TYPES

Recognizing fossil tidal growth patterns

All the tidal shell growth patterns observed among living intertidal bivalves discussed earlier in this paper are summarized in Table 1. The formation of several important growth patterns are schematically explained in text-figs. 3 and 4. The possible arrangement patterns of tidal growth lines at three different levels for each of four general tidal types are shown in text-fig. 1.

Referring to these figures and tables, we can begin to interpret tidally formed growth patterns among fossil bivalve shells. The first step is to find a fossil bivalve assemblage from one locality, where individuals show growth patterns which are similar or identical to the present-day tidal growth patterns. The frequent occurrence of tidal growth patterns cannot be attributed to chance and allows us to conclude that we are dealing with fossils from the intertidal zone.

Procedure for reconstructing ancient tidal types

Based on the peculiar combinations of tidal growth patterns characteristic of a specific tidal type, it is possible to reconstruct the tidal type and habitat of fossil bivalves.

There are several approaches to reconstructing tidal types and the habitat of the fossils based on their tidal growth. One approach is the flow chart in Table 2. Here, patterns which may appear in a wide variety of tidal types are considered first. Moving down the flow chart, characters more and more specific to particular tidal types are taken into consideration.

The growth line thickness alternation accompanied by the inversion of the order of arrangement of thicker and thinner growth lines is diagnostic of semidiurnal tidal exposure, although the inversion does not always occur if the preserved growth sequence is too short or if the bivalves are submerged continuously during the time of the 2 weeks favourable for its formation. Semidiurnal tidal exposure can be seen in semidiurnal tides and two types of mixed tides (text-fig. 1A–C). The common occurrence of double spacing of tidal growth lines together with the alternation and the inversion in growth line thickness is indicative of mixed tides with diurnal inequality expressed in the heights of low tides. The common occurrence of alternation of growth increment thickness accompanied with the alternation and the inversion of growth line thickness indicates mixed tides with diurnal inequality expressed in the heights of high tides. The common occurrence of the alternation and the inversion in growth line thickness without the diagnostic features of diurnal inequality described above is characteristic of semidiurnal tides with insignificant diurnal inequality.

Under the lack of growth line thickness alternation the existence of double spacing and alternation of regular and irregular bundles is characteristic of the diurnal type of tides. In practice, the recognition of double spacing as such is not possible, if it is not accompanied by the alternating regular and irregular bundles. Double spacing alone appears to be nothing more than regular spacing of growth lines and therefore may be confused with regularly spaced growth lines with a different periodicity. The co-occurrence of the alternating regular and irregular bundles, which is the reflection of spring and neap tides, ensures that the accompanying regular spacing of growth lines is formed through tidal exposures. To summarize, in the absence of alternating growth line thickness, these two growth patterns indicate the existence of diurnal tides.

Once the tidal type of the habitat of a fossil assemblage is reconstructed, the intertidal level for the fossil individuals can be easily deduced by comparing the arrangement patterns of tidal growth lines with possible arrangement patterns for reconstructed tidal curves (text-fig. 1). For example, in an intertidal zone with a semidiurnal tide with insignificant diurnal inequality of tide, the individuals with growth patterns consisting exclusively of single spacing live near the mean tide level (MTL), whereas those with the alternation of the regular and irregular bundles live in the lower part of the intertidal zone. The increasing proportion of irregular bundles in growth patterns indicates increasingly lower living levels of bivalves.

ESTIMATE OF THE CHANGE IN THE NUMBER OF SYNODIC DAYS PER SYNODIC MONTH IN THE GEOLOGICAL PAST: A GRAPHIC METHOD

It is inferred that tidal friction caused the change in the velocity of the earth's rotation and the moon's orbital motion throughout the geological past. This resulted in the change of the periods between two succeeding low tides and the length of the solar day, and consequently in the change of the length of the synodic month in terms of the number of synodic days.

As mentioned earlier, the order of the arrangement of growth lines of alternating thickness inverts every 2 weeks. The number of growth lines between two inversions (Ng) is equal to the number of semidiurnal tidal cycles per fortnight (Nf). Because the duration of a semidiurnal tidal cycle is half a synodic day and that of a fortnight half as long as a synodic month, the number Nf

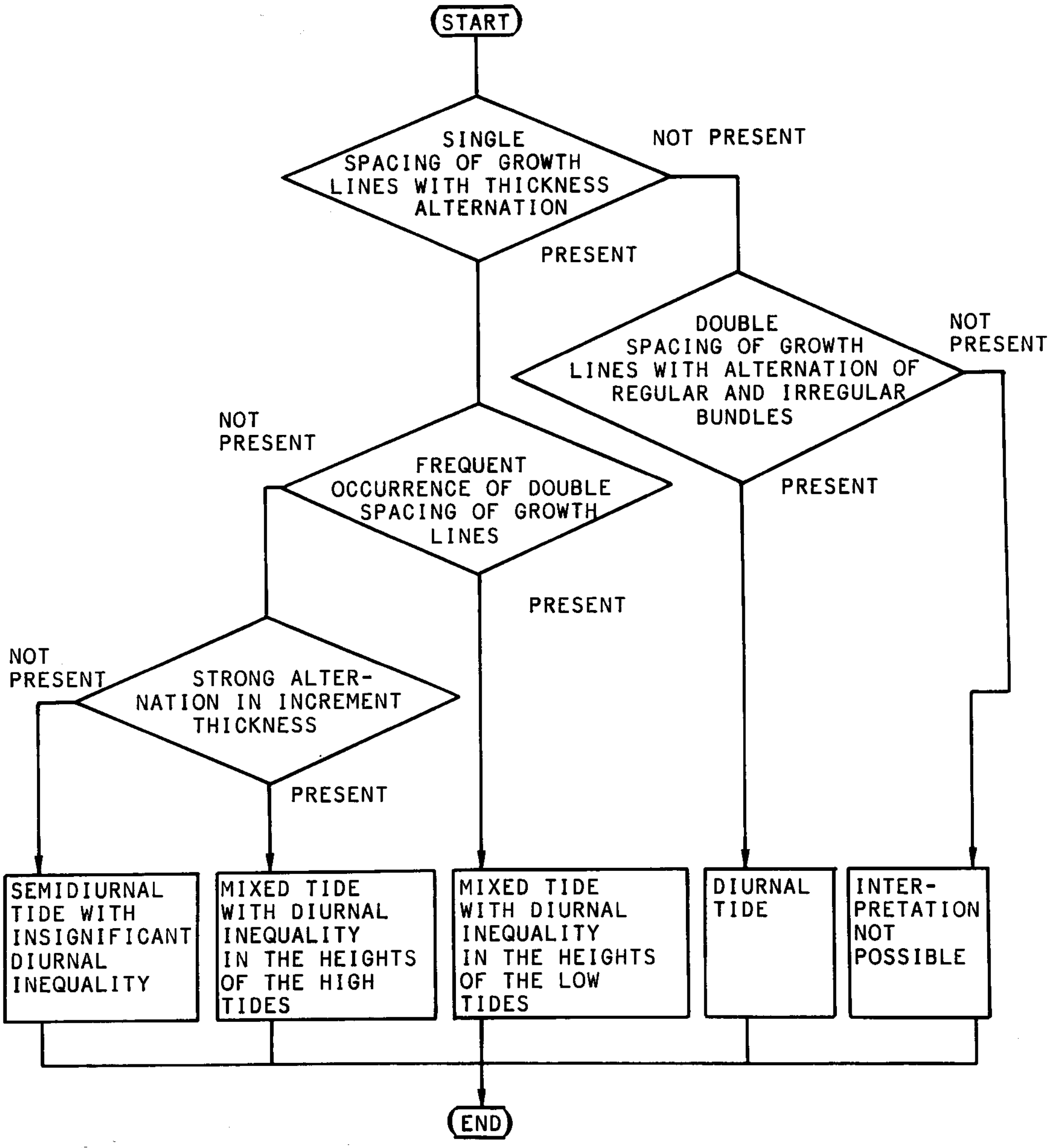


TABLE 2. Procedure for reconstructing tidal types from tidal shell growth patterns of bivalves.

equals the number of synodic days per a synodic month (Ns). Therefore the growth line thickness alternation, if found in fossil bivalves, will provide information on the number of synodic days per synodic month (Ns) in the past. The simplest method is to count the total number of growth lines between several switch zones, then divide it by the number of intervals between the switch zones. Because switch zones usually contain several lines of similar thickness, the resulting value is accompanied by a certain amount of ambiguity. If a long sequence can be obtained the ambiguity will become negligible. But in fossil bivalves, and even in living ones, it is very difficult to obtain long and undisturbed growth sequences. However, it is easy to tell qualitatively whether the Ns was larger or smaller than the present value with the help of a simple method described below.

The thickness of each growth line in a sequence of alternating growth line thickness is classified as follows:

thicker = a line thicker than the preceding and succeeding lines.
thinner = a line thinner than the preceding and succeeding lines.
undifferentiated = a line equal in thickness to the preceding and the succeeding lines.

This sequence is then plotted with successive days on the ordinate and the time of the day on the abscissa. Because tidal growth lines are formed at each low tide, the thickness of each growth line is plotted with the interval of semidiurnal low tides: a thicker growth line with a large solid rectangle; a thinner one with a small quadrate; a point for an undifferentiated line.

For the Recent sequence of alternating growth line thickness the result of such a plot is a vertical partition of the thicker and thinner growth lines. The thicker ones of daytime tidal exposures are distributed in a vertical zone in the middle of the co-ordinate, at both sides of this zone thinner ones of night-time tidal exposures are distributed (text-fig. 5*a*).

If the two parameters, the period of semidiurnal tides and the duration of the solar day, are different from the present ones, the number of the growth lines of alternating thickness between two succeeding inversions, which corresponds to the number of synodic days per one synodic month, may also vary. If the amount of change in both parameters is known, an appropriate co-ordinate with correct low tide intervals can be prepared and the sequence of growth line thickness alternation formed under the changed condition can be plotted on it. For example, text-fig. 5*b*1 is a plot of a hypothetical alternation sequence on the appropriate co-ordinate for the time when the period of the semidiurnal tides is slightly longer than the present-day value. Text-fig. 5*c*1 is another plot for the slightly shorter period of the semidiurnal tides on the appropriate co-ordinate. The result is the vertical partition of the thicker and thinner growth lines in both cases, although the number of tidal cycles per fortnight is different from the present-day value.

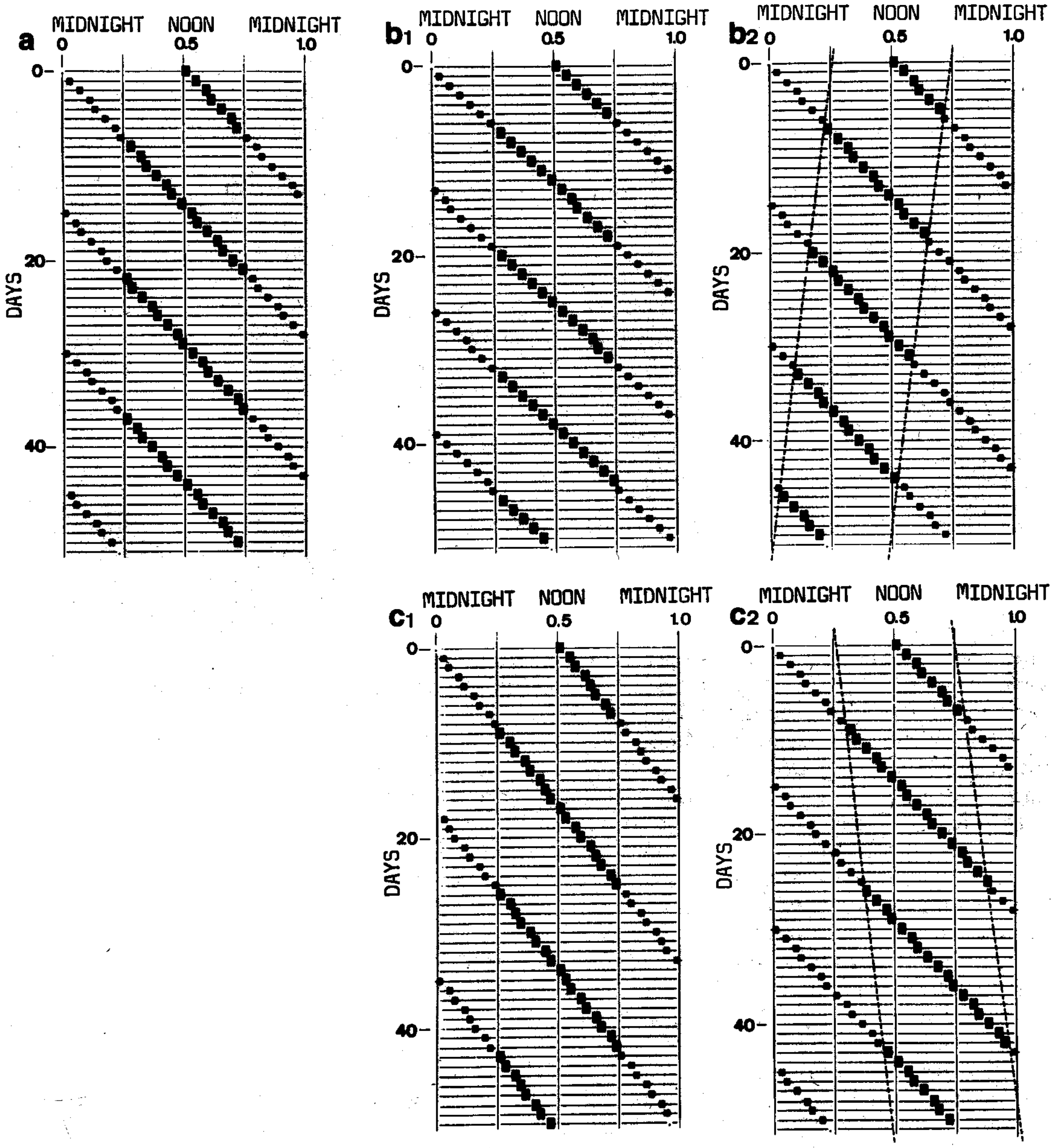
In practice, for fossil growth line thickness alternation patterns the amount of change in the earth's rotation or that of moon's orbital motion is not known. However, any fossil sequence can be plotted on the co-ordinate with the present-day intervals between succeeding low tides. If the zones with the same symbol on such a plot run parallel to the abscissa, it means that the number of synodic days per synodic month (Ns) of the period, when the fossils lived, is equal to the present-day one. If the zone with the same symbol shifts from the vertical row it indicates that the number of the synodic days per synodic month (Ns) is different from the present-day value. For example, the plot of hypothetical growth line alternation sequences for the time when the periods of two succeeding tides is slightly longer than the present-day value yields a shift of growth lines of different thickness from top right to bottom left (text-fig. 5*b*2) and for the time of slightly shorter semidiurnal tidal cycles a shift from top left to bottom right (text-fig. 5*c*2). The degree of the shift depends on the amount of change in the motions of the earth and moon compared to present-day conditions.

Thus the zonation pattern on the co-ordinate with the present-day low tide intervals will tell us whether or not the number of the synodic days per synodic month was different in the geological past.

FOSSIL TIDAL PATTERNS

Samples from the late Pleistocene Osaka Group

Twenty-nine shell fragments from two bore holes at the same horizon were examined. More than half (16) are oyster shells, on which growth patterns are most clearly visible on the surface of the ligament groove that is coated with a thin layer of acicular crystallites (Pl. 31, figs. 5 and 6). Shell material including this layer, which was examined by electron diffraction method using a



TEXT-FIG. 5. Plots of alternating growth line thickness (simulation). For simplicity, it is presumed that the growth lines formed between 6 and 18 o'clock are thicker than those formed between 18 and 6 o'clock. (Ordinate of the co-ordinates = successive days; abscissa = time of day expressed as a fraction of the period of day, so that 0, 0·5, and 1·0 mean 0 o'clock, 12 o'clock, and 24 o'clock, respectively.) *a*, plot of a sequence of the present-day growth line thickness alternation on the co-ordinate with the present-day low tide intervals (Ns = 28·5). *b*, pair of plots for the hypothetical slight lengthening of low tide intervals (0·5% decrease in angular velocity of the moon's rotation around the earth; rotation velocity of the earth unchanged; Ns = 24·8): *b*1, plot on the co-ordinate with changed low tide intervals; *b*2, plot on the co-ordinate with present-day low tide intervals. Distribution boundaries of thicker and thinner growth lines are marked with broken lines. *c*, pair of plots for the hypothetical slight shortening of low tide intervals in comparison with the length of the solar day (0·5% increase of the angular velocity of the moon's rotation around the earth; the rotation velocity of the earth unchanged; Ns = 33·4): *c*1, plot on the co-ordinate with changed low tide intervals; *c*2, plot on the coordinate with present-day low tide intervals. Distribution boundaries of thicker and thinner growth lines are marked with broken lines.

transmission electron microscope, consists of calcite with a very minute amount of aragonite. Aragonite might be a remnant of oyster resilium, as observed in several oyster species (Taylor *et al.* 1969). Therefore, the thin layer lining the ligament groove can be considered to be composed of calcite. On the floor of the ligament groove the broad and flat growth increments are bordered by growth lines as thin ridges (Pl. 31, figs. 1 and 5). On several specimens the thin layer of acicular crystallites is lacking, probably through dissolution or wear. In such cases the growth lines are narrow grooves (Pl. 31, fig. 7); yet the growth patterns are well developed as the negative impression of the original topography.

Occurrences of various growth patterns are summarized in Table 3. On all of the specimens, alternating thicker and thinner growth lines are visible (Pl. 31, figs. 1, 2, 4, 5). The ubiquitous occurrence of the alternating growth line thickness is diagnostic of the semidiurnal tidal exposure. On several of them the inversion of the order of arrangement of thicker and thinner growth lines also can be seen (Pl. 31, figs. 1 and 4), which strengthens the diagnosis. Consequently the specimens must have experienced frequent semidiurnal tidal exposure.

How strong was the diurnal inequality of the tides in the fossil habitat? The rare occurrence of both double spacing of growth lines and the alternation of increment thickness (Table 3) suggest the weakness of the diurnal inequality expressed in the heights of the low tides and of the high tides, respectively. It is therefore concluded that the tidal type of the habitat of the present specimens was a semidiurnal one with weak diurnal inequality. The schematically reconstructed tidal curve is shown in text-fig. 6*b*, and deviates strongly from the mixed type of tide with strong diurnal inequality expressed in the heights of low tides of the present-day Osaka Bay (text-fig. 6*a*).

The examined shells seem to contain individuals from various levels within the intertidal zone. Several specimens show a continuous sequence of growth line thickness alternation of more than 28·5 growth lines (Pl. 31, fig. 1), which is larger than the semidiurnal tidal cycles per 2 weeks at present. Therefore, they must have lived near the mean tide level, where they were exposed at each low tide, even during neap tides. The majority of specimens showing alternation of regular and irregular bundles (Pl. 31, figs. 2 and 3) must have lived lower in the intertidal zone, where they formed regular bundles during spring tides and irregular bundles during neap tides. The number of well-defined growth lines within a single regular bundle (nine to twenty-two) is well within the

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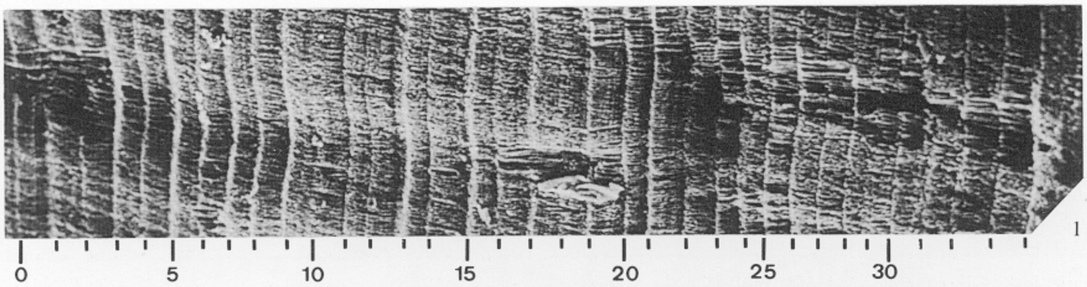
EXPLANATION OF PLATE 31

Figs. 1–7. SEMs of material from the late Pleistocene 'Ma12' Clay from Osaka: 1–4 in back scattering electron image (BEI) mode; 5–7 in secondary electron image (SEI) mode. 1, ligament surface of oyster shell with more than thirty growth lines (marked with bars and numbers). Growth from left to right. Alternation of growth line thickness is visible: near the left corner (between the lines numbered 0 to 19) lines with odd numbers are thicker, whereas near the right corner (between the lines with numbers 24 to 34) lines with even numbers are thicker. Sample no. pl. 1-1, registration no. JCTO-0012; from borehole B, × 270. 2, ligament surface of oyster shell with alternating regular bundles (marked with solid lines) and irregular bundles (marked with broken lines). Alphabets correspond to the occurrence of abnormally thick increments shown in text-fig. 7*d*. Growth from right to left. Sample no. P294, registration no. JCTO-0009; borehole A, × 44. 3, radial section of bivalve shell fragment showing alternating regular bundles (marked with solid lines) and an irregular bundle (marked with broken line). Growth from right to left. Sample no. P103, registration no. JCTO-0001; borehole A, × 125. 4, ligament surface of oyster, with alternating thicker and thinner growth lines as well as the inversion of the order of their arrangement. Lines with even numbers are thicker near the left corner, whereas those with odd numbers are thicker near the right corner. Growth from left to right. Sample no. P354, registration no. JCTO-0011; borehole A, × 250. 5, part of ligament surface of oyster with alternating thicker growth lines (indicated by thick downward arrows) and thinner ones (indicated by thin downward arrows). Growth from right to left. Sample no. P294, registration no. JCTO-0009; borehole A, × 260. 6, enlargement of the area marked with white frame in fig. 5, × 1600. 7, part of ligament surface of oyster with growth lines as grooves. Sample no. P293, registration no. JCTO-0008, × 280.



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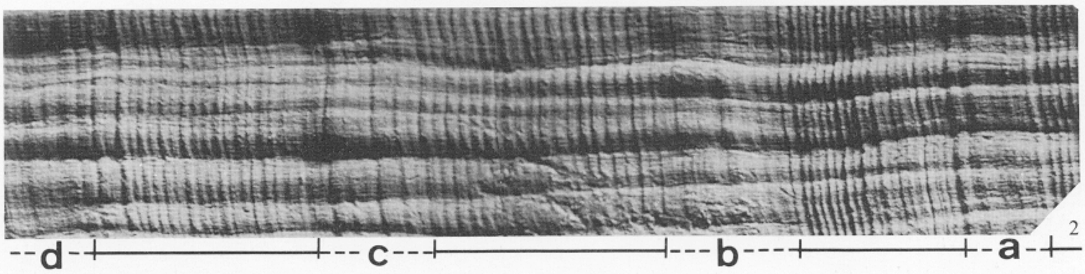

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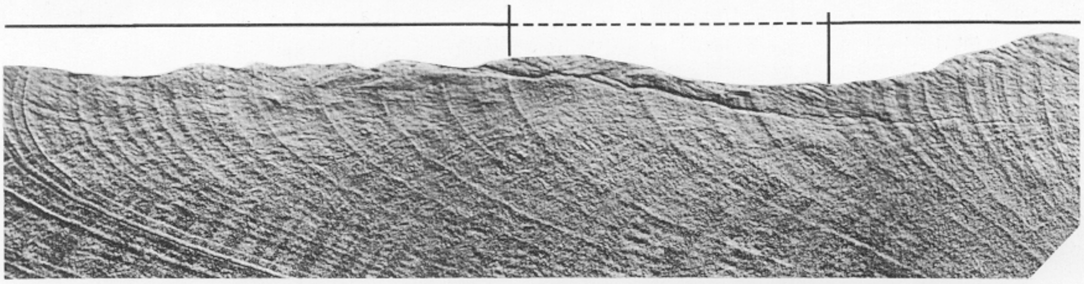

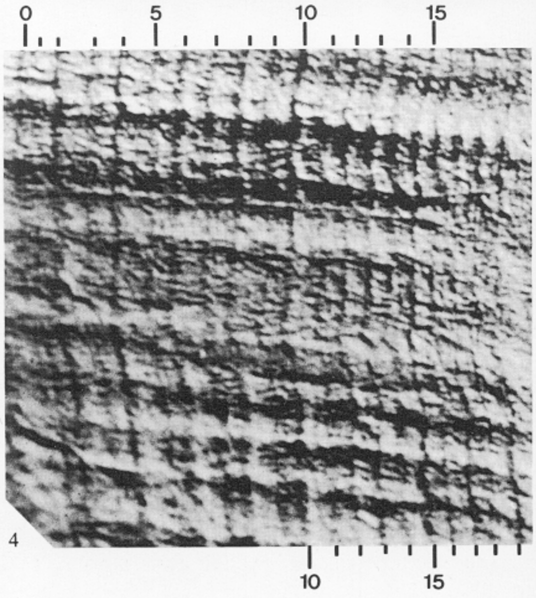

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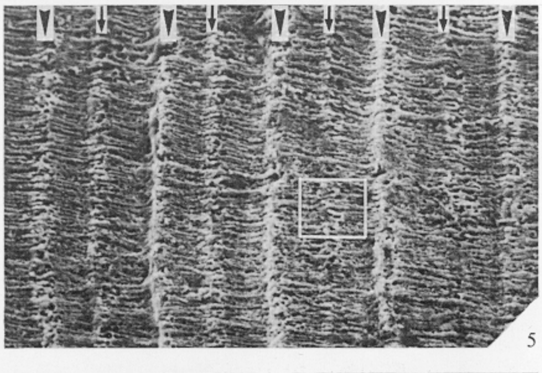

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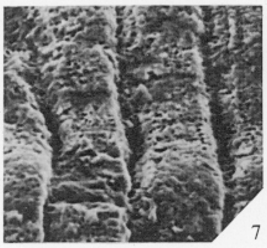

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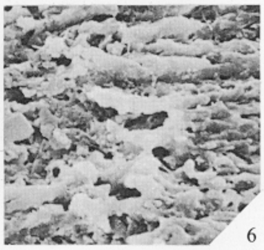

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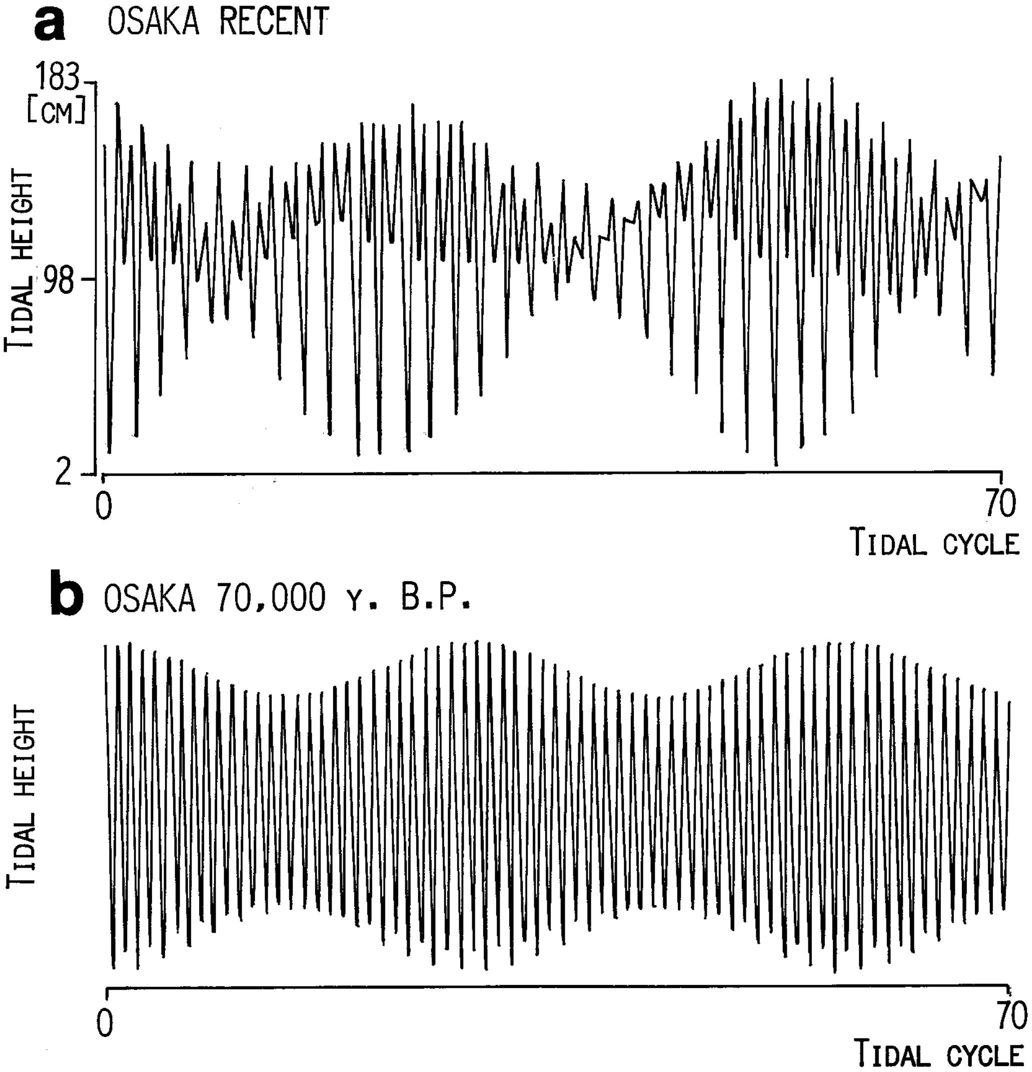
OHNO, Bivalve microgrowth patterns

TABLE 3. Tidal growth patterns in fossil shell fragments from the 'Ma12' Clay of the late Pleistocene Osaka Group, p = present; f = faintly expressed; . = not present; — = observation or counting not carried out. Shell structure: gr. = granular structure; cl. = crossed lamellar structure; ac. = acicular cristallites. Number of growth lines: if irregular bundles are prevalent in growth sequence, number of growth lines are not counted. Alternation of thicker and thinner growth lines: a. = line thickness alternation; i. = inversion of order of occurrence of thicker and thinner growth lines. Alternation of regular and irregular bundles: the number of pairs is given in parentheses if the alternation is well developed; if growth sequence is without irregular bundles the number is not given.

Sample no.	Shell structure	Growth line				Alternation of regular and irregular bundles	Alternation of growth increment thickness
		Number of growth lines	Thickness alternation		Double spacing		
			a.	i.			
Borehole A							
Ligaments of *Ostrea* sp.							
P293	ac.	95 >	.	.	.	p	.
P294	ac.	160 >	p	.	.	p	.
P295	ac.	—	p	.	.	p(5)	.
P296	ac.	—	p	.	.	p(3)	.
P297	ac.	85 >	p	.	.	p(2)	.
P298	ac.	75 >	p	.	p	p(3)	.
P299	ac.	55 >	p	.	.	p(3)	.
P330	ac.	66 >	p	p	.	.	.
P332	ac.	140 >	p	.	.	p	.
P334	ac.	—	p	.	p	p(2)	.
P350	ac.	100 >	p	p	.	p(4)	.
P351	ac.	50 >	p	.	p	p	.
P352	ac.	—	p	.	p	p(3)	.
P353	ac.	100 >	p	.	.	.	.
P354	ac.	70 >	p	p	.	p(4)	.
Other bivalve shell fragments							
P335	cl.	21	p	.	.	.	.
P339	—	220 >	p	.	.	.	.
P342	cl.	200 >	p	.	.	p	.
P343	cl.	—	p	.	.	p(5)	.
P344	cl.	21	p	.	.	p	.
P346	cl.	40 >	p	.	p	p(2)	.
Borehole B							
Ligament of *Ostrea* sp.							
P11-1	ac.	36	p	.	.	.	.
Other bivalve shell fragments							
P095	cl.	50 >	p	.	.	f	.
P097	cl.	30	p	.	p	p	.
P099	gr.	28	p	.	.	.	.
P102	cl.	100 >	p	.	.	p	.
P103	gr.	34	p	.	.	p	.
P12-1	cl.	—	.	.	p	p	.
P12-3	cl.	—	p	f	.	p	.



TEXT-FIG. 6. Tidal curves along the Osaka Bay in the present day and in late Pleistocene time (*c.* 70 000 years BP). *a*, the present-day tide along the Osaka Bay, drawn from the prediction for July and August, 1980, from the tide tables published by the Maritime Safety Agency, Japan (ordinate = tidal height; abscissa = semidiurnal tidal cycles). *b*, the reconstructed tidal curve for late Pleistocene time on the basis of the fossil tidal shell growth patterns (tidal height in ordinate is arbitrary; abscissa = semidiurnal tidal cycles). Note that the late Pleistocene curve has relatively weak diurnal inequality in comparison with the present-day curve.

maximum growth line number formed through semidiurnal tidal exposures per 2 weeks at present (28·5), and it decreases inversely with the increase of the relative width of the irregular bundles.

Many oyster specimens show extremely wide growth line spacings (text-fig. 7), which occur periodically and exclusively in irregular bundles (for example, compare text-fig. 7*d* and Pl. 31, fig. 2). This makes it easy to detect the change of spring and neap tides. However, the wide spacings must be the result of the break of an otherwise constant semidiurnal rhythm of growth line formation, as known in the recent intertidal *Cerastoderma edule* (Ohno 1983, 1985). Thus the estimate of the length of a fortnight in terms of semidiurnal tidal cycles on the basis of the periodically swinging curves in text-fig. 7 is inevitably accompanied with a large error and has not been carried out in the present work.

Samples from the Miocene Mizunami Group

Bivalve shell fragments from the Mizunami Group are all preserved in a consolidated sedimentary matrix. Therefore specific identification could not be made. Original shell microstructures such as granular structure (Pl. 32, fig. 3) or crossed lamellar structure are very well preserved in most specimens. Sometimes the outer surface of the shell (Pl. 32, fig. 5) or the growth lines (Pl. 32, fig. 4) are lacking because of post depositional dissolution. Only specimens with well-preserved growth patterns were studied.

Growth patterns are usually easily observed. Sometimes, depending on the shell microstructure and the amount of etching, the relief of the lines is fairly weak, but most such cases shell growth patterns are obvious, if photographs of the specimens are observed in oblique position (for example, Pl. 32, figs. 2 and 6).

Forty-six shell fragments were studied (Table 4) and on each shell fragment there are fifteen to 111 growth lines. All of the specimens show the alternation of growth line thickness (Pl. 32, figs. 1, 2, 6, 7; text-fig. 8). About half of them also show the inversion of the order of arrangement of thicker and thinner lines (Pl. 32, figs. 1, 2, 6; text-fig. 8). These observations show that samples were very frequently exposed at semidiurnal low tides.

The double spacing is seen only in five specimens and its proportion in the growth patterns is very small. This indicates that the diurnal inequality of tides expressed in the height of low tides was weak. The alternation of thicker and thinner growth increments occurs in eighteen samples. It is fairly obvious (Pl. 32, fig. 1) only in three of them and is weak or very faint in the others. Therefore, the diurnal inequality was expressed in the height of the high tides, but it was probably not strong. These observations together indicate that the type of the tide when and where the examined shells lived was semidiurnal with a moderate amount of diurnal inequality expressed in the height of high tides. This tidal type was intermediate between the tidal types shown in

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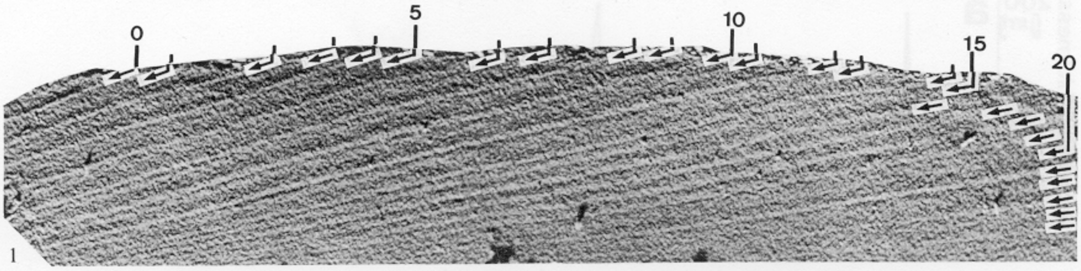
EXPLANATION OF PLATE 32

Figs. 1–7. All figures are SEMs of shells from the Miocene Mizunami Group: 3 and 4 in SEI mode; others in BEI mode. 1, radial section of shell fragment. Growth lines are seen as narrow white stripes indicated with arrows and numbers. Alternation of increment thickness is visible: increments between growth lines numbers 5 and 6, 7 and 8, 9 and 10, 11 and 12, 13 and 14 are thicker than adjoining increments. Alternating growth line thickness as well as inversion of its order are also observable; lines with even numbers are thicker near the left corner, whereas those with odd numbers are thicker near the right corner. Growth from left to right. Sample no. P270, registration no. JCTO-0005, × 185. 2, radial section of shell fragment. Growth lines are seen as narrow white stripes marked with arrows and numbers. Because of the coarse grain size of shell material the resolution of the lines is not good. Yet lines can be fairly well recognized if the pictures are observed obliquely from the side. Alternating growth line thickness as well as inversion of its order are visible: lines with even numbers are thicker near the left corner, whereas those with odd numbers are thicker near the right corner. Growth from left to right. Sample no. P277*a* registration no. JCTO-0006, × 250. 3, part of a shell showing very well-preserved crystallites. Sample no. P195, registration no. JCTO-0002, × 2850. 4, shell fragment in which growth line material (running horizontally) is dissolved away. Sample no. P201, registration no. JCTO-0003, × 760. 5, shell fragment in which a part of the outer layer is not preserved. Well-defined growth lines are still visible in the inner part of the shell. Sample no. P277*b*, registration no. JCTO-0007, × 108. 6, alternating thicker and thinner growth lines. Because of the coarse grain size the resolution of the lines is not good, yet lines can be fairly well recognized if the pictures are observed obliquely from the side. Growth from top to bottom. Sample no. P258, registration no. JCTO-0004, × 370. 7, alternating thicker and thinner growth lines. Each growth line is marked with an arrow. Growth from top to bottom. Sample no. P195, registration no. JCTO-0002 same as illustrated in Plate 32, fig. 3, × 415.

PLATE 32



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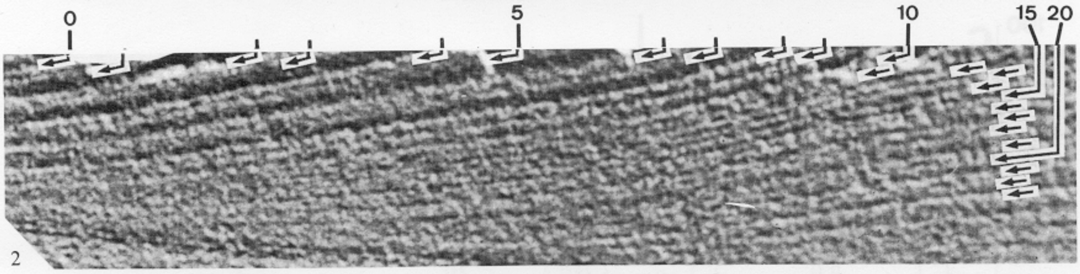

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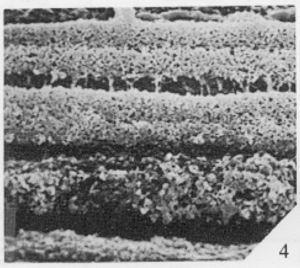

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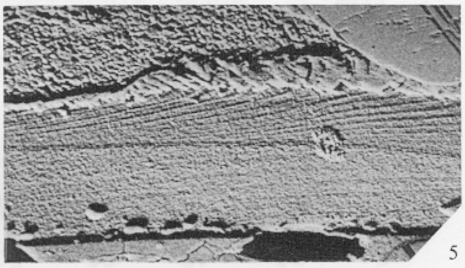

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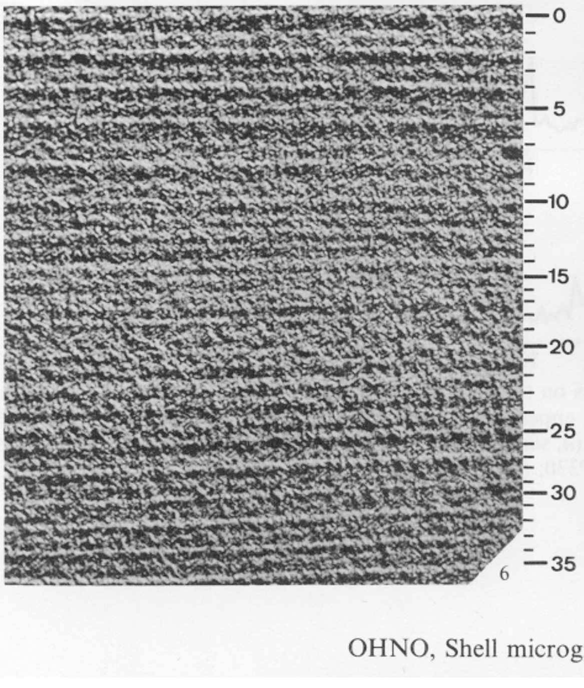

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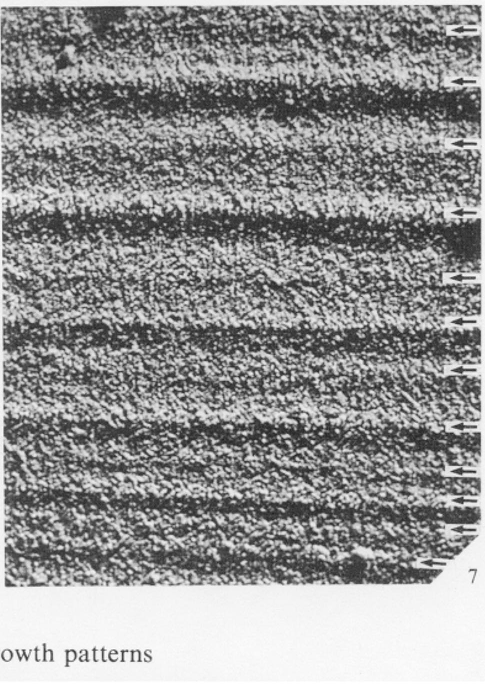

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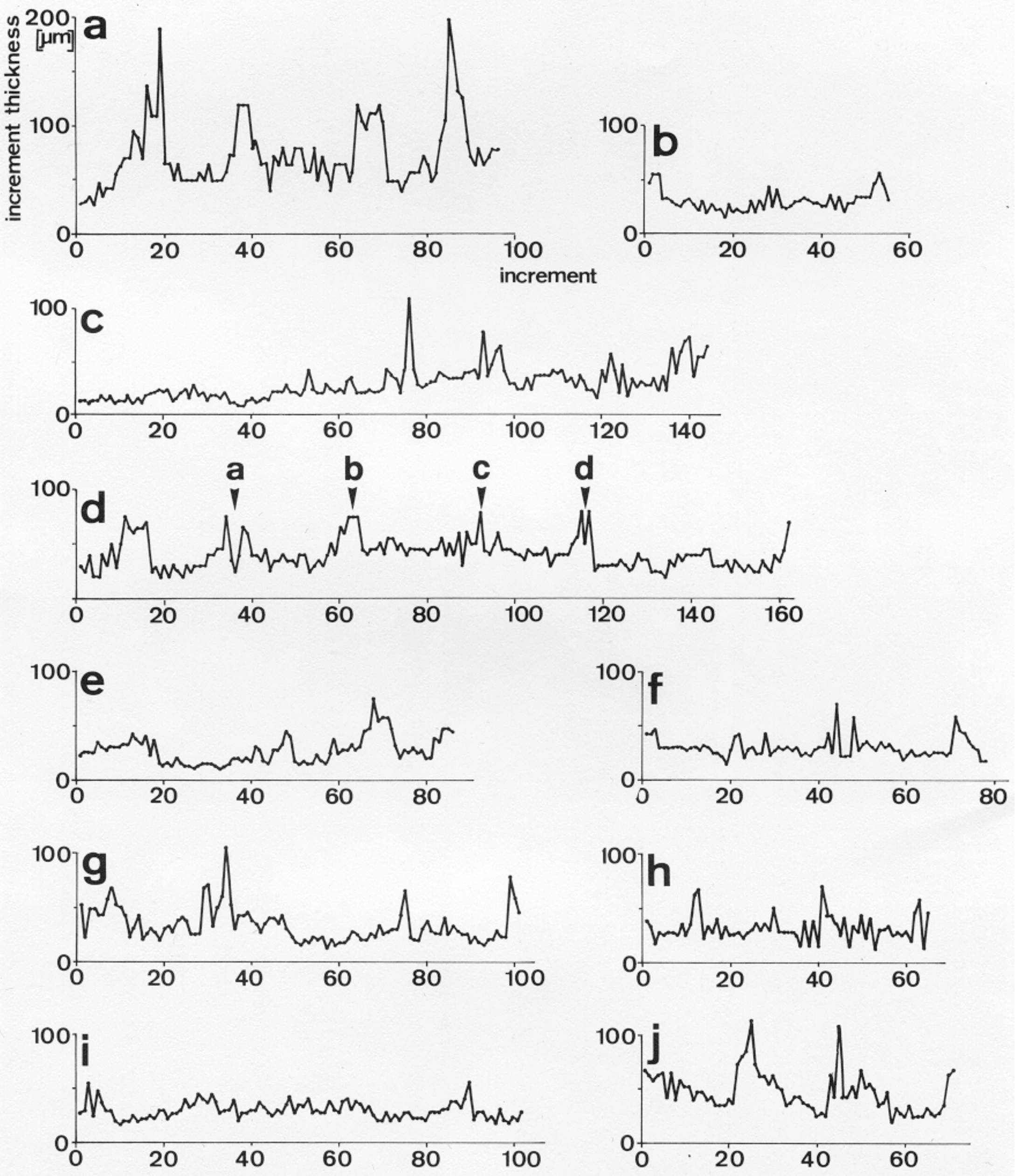
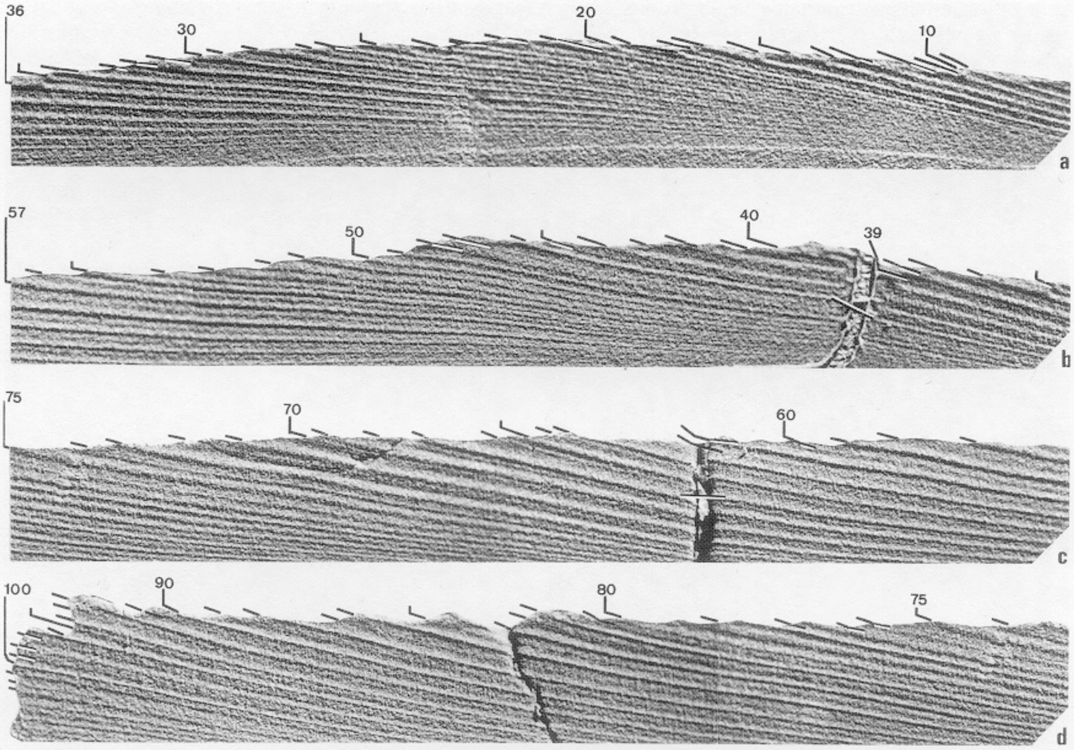
OHNO, Shell microgrowth patterns



TEXT-FIG. 7. Measurements of increment thickness on the surface of the oyster ligaments. Note the periodic change of the increment thickness with recurring appearance of extremely thick increments. Alphabets in *d* correspond to irregular bundles in Plate 31, fig. 2 (*a*, sample P293; *b*, P299; *c*, P332; *d*, P294; *e*, P297; *f*, P298; *g*, P350; *h*, P330; *i*, P353; *j*, P354).

TABLE 4. Tidal growth patterns in fossil bivalve shell fragments from the Miocene Mizunami Group, p = present; f = faintly expressed; s = strongly expressed; . = not present; — = observation or counting not carried out. Shell structure: gr. = granular structure; cl. = crossed lamellar structure. Alternation of thicker and thinner growth lines: a. = line thickness alternation; i. = inversion of order of occurrence of thicker and thinner growth lines.

		Growth line					
		Number of growth lines	Thickness alternation				
Sample no.	Shell structure		a.	i.	Double spacing	Alternation of regular and irregular bundles	Alternation of growth increment thickness
P195	gr.	43	p	p	.	.	p
P206*a*	cl.	42	p	p	.	.	.
P206*b*	cl.	58	p	p	.	.	p
P207	gr.	32	p	p	.	.	p
P208	gr.	47	p	p	.	.	p
P209	gr.	26	p	p	.	.	.
P253	gr.	69	p	.	.	p	.
P254	gr.	36	p	p	.	.	p
P256	gr.	75	p	p	.	.	.
P257	—	30	p	p	.	.	p
P258	gr.	40	p	p	.	.	.
P265	gr.	55	f	.	.	.	.
P265*b*	gr.	54	p	.	.	.	.
P266	gr.	43	p	p	.	.	s
P267*a*	gr.	17	p	.	.	.	.
P267*b*	gr.	20	p	.	f	.	.
P268	gr.	60	p	.	p	p	.
P269*a*	cl.	30	p	.	p	p	.
P269*b*	—	30	p	.	p	.	.
P270	gr.	30	p	p	.	.	s
P270*b*	gr.	16	p	.	.	.	.
P271	gr.	15	p	.	f	.	.
P276	gr.	59	p	p	.	.	.
P277*a*	gr.	48	p	p	.	.	s
P277*b*	gr.	60	p	.	.	.	.
P301	gr.	111	p	p	.	.	p
P304	gr.	26	p	f	.	.	.
P310*a*	gr.	43	p	p	.	.	p
P310*b*	gr.	35	p	p	.	.	.
P311	gr.	29	p	p	.	.	f
P313	gr.	46 >	p	p	.	.	p
P314	gr.	49	p	p	.	.	f
P315	cl.	30	p	p	.	.	.
P317	gr.	50	p	.	.	.	.
P318	gr.	34	p	f	.	.	.
P319	gr.	14	p	.	.	.	.
P320	gr.	64	p	.	.	.	p
P321	gr.	50	p	.	.	.	p
P322*a*	gr.	68	p	.	.	.	.
P322*c*	gr.	30	p	.	.	.	.
P323	cl.	49	p	p	.	.	.
P324	gr.	18	p	.	.	.	.
P325	gr.	58	p	p	.	.	f
P326	gr.	23	p	.	.	.	.
P327	gr.	32	p	p	.	.	.
P328	gr.	17	p	p	.	.	p



TEXT-FIG. 8*a–d*. Radial cross-section of a bivalve shell from the Miocene Mizunami Group with continuous sequence of growth lines of alternating thickness (SEM micrograph in BEI mode). The numbering corresponds to that of the growth lines plotted on the co-ordinate of text-fig. 9*d* (sample no. P301, registration no. JCTO-0010, × 138).

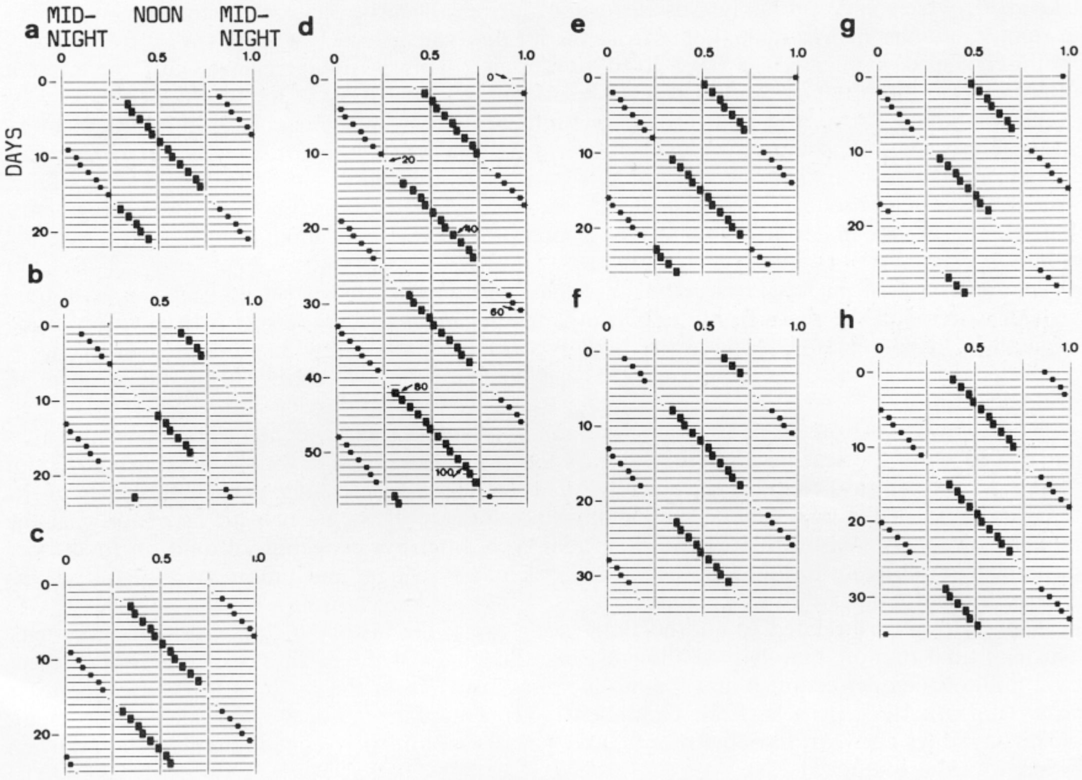
text-fig. 1A and C. With regard to the magnitude of the diurnal inequality, it is most similar to the one in text-fig. 1A. The less frequent occurrence of irregular bundles in only three specimens shows that few of the samples lived in the lower part of the intertidal zone. The majority of the specimens lived near the mean tide level, where they formed one growth line at each semidiurnal tidal exposure.

NUMBER OF SYNODIC DAYS PER SYNODIC MONTH IN THE MIOCENE EPOCH

Eight of the samples from the Miocene Mizunami Group have a relatively long and continuous sequence of alternating thinner and thicker growth lines without any sign of disturbance. For example, one sample (text-figs. 8 and 9*d*) has the longest growth sequence with 111 successive growth lines. The sequence of alternating growth line thickness of these eight samples is thus plotted on the co-ordinates with the present-day low tide intervals, in order to see whether the number of the synodic days per synodic month was different in the Miocene than it is today.

A clear partition of thicker and thinner growth lines is visible in all of the eight plots (text-fig. 9). In plots *b*, *d*, and *e* the left boundary of the thicker growth lines slightly shifts from right at the top to left at the bottom. But the distribution of the thinner growth lines, as well as the right boundary of thicker growth lines, is almost parallel to the ordinate. Thus there is no need to consider the partition of the zones with thicker and thinner lines inclined to the ordinate. In the other five samples the situation is similar. While certain boundaries of the zone are slightly inclined from the right to left, other boundaries are almost vertical to the ordinate.

Generally the partition of thicker and thinner growth lines can be regarded as parallel to the ordinate. Thus it is concluded that the number of the synodic days per a synodic month in the Miocene epoch was almost the same as that of today.



TEXT-FIG. 9. Sequence of alternating growth line thickness obtained from fossil bivalve shells of the Miocene Mizunami Group plotted on the co-ordinate with present-day low tide intervals: ordinate = successive days; abscissa = time of day expressed as a fraction of the period of day, so that 0, 0·5, 1·0 mean 0 o'clock, 12 o'clock, and 24 o'clock, respectively. The time of the first low tide of each plot is arbitrarily determined. *a*, sample P195; *b*, P208; *c*, P274; *d*, P301; *e*, P314; *f*, P322; *g*, P325; *h*, P353.

DISCUSSION AND CONCLUSIONS

The two examples described in this paper demonstrate that tidal growth patterns of fossils can be used to recognize habitats of the ancient intertidal zone, reconstruct tidal types of these habitats, and infer the living level of bivalves within the intertidal zone. In addition, information can be obtained on geophysical aspects related to tidal phenomena, e.g. the change of the earth–moon system through tidal dissipation.

Despite such potential applicability, there have been very few attempts to identify the fossil tidal growth patterns of bivalves. In addition, the photomicrographs of fortnightly clustering of growth increments in a Palaeocene venerid shell (Berry and Barker 1968, 1975) and tidal growth patterns of a Late Cretaceous *Limopsis striatus-punctatus* (Pannella 1976) do not show any of the tidal growth features summarized in Table 1. More material needs to be examined to verify these studies.

Because of the fragmentary nature of the shells and their preservation in hard matrix, specific identification of the bivalve fossil shells examined could not be carried out. However, the ubiquitous occurrence of the various growth patterns among them, which are identical to those seen in living intertidal bivalves, justifies the interpretation that the two fossil bivalve shell assemblages also grew intertidally with a tidal growth rhythm. The Osaka samples come from the lower part of the Ma12 Clay bed, which very probably was deposited during an early phase of a transgression. The examined samples of Mizunami come from the locality where Itoigawa *et al.* (1974) found many molluscan species inferred to have lived intertidally. This is in agreement with the present interpretation that the two examined bivalve assemblages once lived in the intertidal zone.

As mentioned above, the tidal growth patterns are clearly recognizable even in fragmentary shells. This makes almost any type of shell-bearing sediments suitable for growth pattern analysis. For example, a vast number of cores stored in various institutions might be examined successfully, because even in a borehole core of small volume, there is often a large number of shell fragments. Indeed, the Osaka material obtained from boreholes provided a good sample with successful results.

The tidal types of the late Pleistocene, as well as the Miocene, reconstructed from the fossil tidal growth patterns of the shells from the two Japanese localities, is semidiurnal with a weak diurnal inequality. In comparison to these the tidal type of the present-day Japanese Pacific coasts is characterized by strong diurnal inequality. This is the first proof of a change of tidal types through geological time.

Tidal type varies from place to place depending on factors such as configuration of shore lines and the depth of the sea. Because 70 000 years seems not long enough for the basic geography of the Osaka Bay to have changed tectonically, the eustatic sea-level change may be the cause of the drastic change of the tidal type in Osaka Bay since the late Pleistocene. Little can be said at the moment about the reason for the Miocene tidal type. Intensive collecting of data on fossil tidal patterns from different localities and geologic ages may provide a much more vivid picture of the change of tidal type as well as its causes.

Tidal patterns are related to another interesting topic: the history of the earth–moon system. Through tidal friction, mainly in shallow oceans, the length of the earth day increases (at present by 2 milliseconds per century) and the moon spirals away from the earth by a few centimetres a year (Runcorn 1967; Brosche 1971; Goldreich 1972). Thus astronomical cycles such as the length of the day, days per year, days per month, and synodic months per year are thought to have been different in the geological past.

Estimates of the length of 'fortnights' (2 weeks) or synodic months in the geological past have been carried out previously by several authors using fossil growth patterns (Berry and Barker 1968, 1975; Pannella and MacClintock 1968; Pannella *et al.* 1968; Pannella 1972). Clusters consisting of groups of thin increments with relatively thick ones were interpreted either as formed fortnightly or monthly and the increment numbers per cluster were estimated. The reasons for assigning such clustering to fortnightly or monthly periodicity, as well as whether the basic rhythm is semidiurnal, solar daily, or lunar daily, were not clearly given, as Scrutton (1978) pointed out. Further, as already mentioned in the observation of the fossil material from Osaka, such a periodic clustering could result from the break of rhythm of growth line formation in some part of the growth sequence.

In attempting to estimate astronomical values concerning earth–moon history, two points are critical for the accuracy of such estimates. One is whether the patterns concerned really reflect the inferred periodicity. The other is how precisely the periodicity is recorded in the growth pattern.

The alternation of thicker and thinner growth lines together with periodic inversion of their order of occurrence, described earlier in this paper, is so peculiar and complicated a pattern that it could not be formed by any other means than those which cause it to form in recent bivalve shells; namely, the interference of the semidiurnal tidal exposure and the 24-hourly change of temperature. This pattern, also very easily recognizable in fossil shells, can be used to estimate whether the number of synodic days per synodic month was shorter or longer in the past than it is in the present.

How exactly are growth lines formed at each low tide? Ohno (1985) experimentally showed that near the MTL (mean tide level) of a region with a semidiurnal type of tide with insignificant diurnal inequality, individual specimens of *Cerastoderma edule* formed exactly one growth line and increment at each tidal exposure and immersion respectively. Thus they faithfully recorded the tidal cycles.

Further, the alternation of thicker and thinner growth lines can be used to check the completeness of the growth record. Assume, for example, that one growth line fails to be formed at a certain low tide. In the plot of such a growth sequence on the co-ordinate used in text-figs. 5*a* and 9*a–h*, there will be a dislocation in the vertical partition of thicker and thinner growth lines at the point which corresponds to the missing growth line. With the increase of missing lines, dislocation occurs much more often and the resulting pattern may be something like that on a chequer-board. Thus we can exclude plots with dislocation and thus minimize misinterpretation.

Selected sequences of growth lines of alternating thickness from the Miocene Mizunami Group provide plots that show no detectable inclination in partition. This means that the number of the synodic days per synodic month about 15 ma ago was almost the same as the present value.

Efforts should be made in the future to determine the alternating pattern of growth line thickness in specimens from older geological epochs in order to obtain a clear picture of the change in the number of the synodic days per synodic month throughout earth's history. The present finding of tidal growth patterns in oyster shells is encouraging, because oyster shell material is composed of calcite and resistant against diagenetic change. Oysters also have a good fossil record which begins in the Late Triassic. Tidal growth patterns most likely exist in fossils other than bivalves, because tidal growth patterns or rhythms also can be seen in the Recent gastropods (Antoine and Quemerais-Pencreac'h 1980; Ekarante and Crisp 1982; Ohno and Takenouchi 1984) and barnacles (Bourget and Crisp 1975; Crisp and Richardson 1975; Bourget 1980).

Tidal growth patterns may also apply to a much wider range of problems than those treated in this paper. For example, estimates of fossil shell growth rate based on periods of semidiurnal or diurnal tidal cycles can be easily made and surely other astronomical periodicities can also be documented in shell growth patterns. For other patterns with periodicities, we have not yet as safe criteria as those for tidally formed patterns.

Further investigations with intensive experimental studies on recent organisms should be carried out in order to find out criteria for such periodicities. If we find such criteria in the future, we will be able to retrieve quite new and valuable information from growth patterns, which cover a spectrum of problems from the ontogeny of an individual fossil organism to the history of the earth–moon system.

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