

## Origin of Concentric Banding in the Spines of the Tropical Echinoid *Heterocentrotus*<sup>1</sup>

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THE CONCENTRIC BANDS or rings which are evident in transverse sections of echinoid spines have attracted the interest of biologists for more than a hundred years. First, the basic cause of ring formation remains obscure although at least two controversial hypotheses have been proposed, and elucidation of the ring-forming mechanism is important to a better understanding of the general processes involved in growth. Second, there is a practical aspect to the "growth-ring problem" because, if the number of rings in a spine is closely and directly related to the age of the animal, killing the urchin for age determination is obviated, thus facilitating ecological, population, and other practical studies in marine research.

According to one hypothesis (Carpenter, 1870; Swan, 1952; Deutler, 1926; G. P. Moore, 1966; and others), the prominent banding in echinoid spines is analogous to annual ring formation in trees caused by seasonal variation in growth, although the authors cited above might not necessarily agree that the period recorded by each successive band is actually one year. In some cases there is evidence for yearly banding since the number of rings is about the same as the number of years, or age of the animal, as determined by other means (H. B. Moore, 1935). McRae (1959), in reporting a study of *Evechinus chloroticus*, stated that it is very tempting to regard the rings as annual phenomena. For some urchins there is a positive correlation between the number of rings in the spines and other growth indicators, such as the volume, diameter, or weight of the test (e.g., Moore, 1966; Ebert, 1967). The correlation, however, is usually not as good as might be expected if the relationship between these two

variables were causal. Ebert (1967) proposed a different hypothesis for the origin of the radial rings, and argued that the correlation between ring number and age is indirect and fortuitous.

Ebert's theory was based on the results of a study of the growth and repair of spines of *Strongylocentrotus purpuratus* (Ebert, 1967), but he implied (p. 148) that the proposed mechanism holds for echinoids in general. According to this theory, a ring forms whenever the spine is broken and the damage is repaired by regeneration of the lost distal portion. As older animals are likely to have suffered more broken spines during their lifetime, their spines will contain proportionately more rings, hence the origin of the positive correlation between the size of the urchin and the number of growth rings. The idea that banding is directly due to regeneration of broken spines is quite different from conclusions drawn from earlier studies (e.g., Borig, 1933) that the rings were unrelated to regeneration. It was widely held that a broken spine would not regenerate a new tip until the next period of growth, at which time, a ring or band would be formed even if no break had occurred.

The conclusion reached by Ebert is difficult to accept, for the corollary to this hypothesis is that unless a spine is broken it cannot grow larger, and it seems unlikely that further enlargement of a spine should be dependent upon spine breakage. A study of the internal spine structure of *Heterocentrotus trigonarius* described in this paper clearly demonstrates that the growth ring mechanism proposed by Ebert is not valid, at least for *H. trigonarius*. It is important to emphasize, however, that Ebert studied *Strongylocentrotus purpuratus*, whereas the present investigation concerns only *H. trigonarius* and to a lesser extent *H. mammillatus*. Nevertheless, the Echinometridae and Strongylocentrotidae are closely related families,

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and it is likely that the results of this study can be extended to *Strongylocentrotus* and perhaps to regular echinoids in general.

#### REGENERATION AND GROWTH BANDING

The phenomenal regenerative abilities possessed by echinoderms have long been known. Echinoids, for example, can not only regrow the missing portion of a severed spine, but can replace the entire spine should it be removed from the test (Swan, 1952). At least some species can regenerate an entire set of spines (Chadwick, 1929). Hobson (1930) has reported a case where specimens of *Psammechinus* threw off all of their spines except those on the oral surface when they were placed in an aquarium. A new crop of spines began to appear within a week, and after two months, the majority of these individuals could scarcely be distinguished from those which had not lost their spines. The extent to which regenerated spines occur on echinoids appears to range widely (McRae, 1959; Cutress, 1965; Ebert, 1967), as would be expected considering variations in age, environment, shape and strength of spine, and type of predator.

In Ebert's theory for the origin of growth banding, spine damage and regeneration is essential for the formation of radiolar rings. This conclusion is based on his study of 500 spines in which he found (p. 146): "(a) Spines always had a cycle of crystals on the outside. If the cycles were formed only at certain periods during the year, then, at some time, the fine crystalline meshwork would have to appear on the outside; (b) in longitudinal section, the cycles were always distally terminated at a sharp discontinuity which suggested a break." In other words, spines which had never been broken or otherwise damaged, and spines without a coarsely crystalline growth band located on the surface were not observed in the set of *Strongylocentrotus* spines examined by Ebert. This is not the case, however, for spines of *H. trigonarius*.

#### METHODS OF STUDY

My interest in details of the morphology of echinoid spines arises from some of the unusual

mechanical properties found in echinoderm skeletal elements (Weber et al., 1969). For these studies, hundreds of specimens of *H. trigonarius* and *H. mammillatus* were collected by the author from both barrier and exposed fringing reefs at Tahiti, Fiji, New Caledonia, the Great Barrier Reef, Palau, Guam, and Saipan. The results reported here are based on an examination of 1,050 spine sections of specimens from Teahupoo, Tahiti, although a smaller number of samples from the above localities were also studied to show that the results for the Tahitian urchins apply also to *Heterocentrotus* living elsewhere. At Teahupoo, these echinoids form large communities on the fore-reef slope of the outer barrier reef, just below the algal ridge. This is a zone of heavy surf, but with experience and good timing, it is possible to collect individuals without damaging the spines in any way. These specimens were preserved in formaldehyde and were individually packed for shipment in such a way that the animals arrived in the laboratory with virtually no damage en route.

Organic matter was removed from the skeleton by immersion in a 5 percent solution of sodium hypochlorite, a treatment which does not affect the pigment contained within the skeletal calcite. After the tests were weighed, 15 specimens spanning the range from the smallest (dry weight of test = 1.5 grams) to the largest (105.5 grams) of the urchins collected, were selected for detailed examination. The range in maximum spine length and weight for these 15 animals is from 24 mm, 0.9 gram to 115 mm, 13.6 grams. The 70 largest primary spines of each were assigned an identification number, and were individually weighed and measured for size. Subsequently, each spine was sectioned transversely a fraction of a mm above (distally) the milled ring, and longitudinally along the axis. For several hundred of the spines, distances between growth bands in both transverse and longitudinal sections were measured with a traveling microscope, but ring counts were made for each of the 1,050 spines. To ensure that all of the rings were observed, it was necessary to section the proximal portion of the spine (which was first cut just above the milled ring) parallel to the long axis of the spine but not exactly at the axis. Then, under a binocular

microscope, the skeletal calcite of the core was gradually removed by gentle scraping with a sharp scalpel. In this way, the smallest and earliest formed growth bands appeared and then disappeared as the sectioning progressed from one side of the axis, through the axis, to the opposite side.

#### MORPHOLOGY OF THE SPINE

Although X-ray diffraction and optical methods indicate that each spine behaves as a single crystal of high-magnesium calcite, this skeletal material is secreted with a pronounced fenestrate structure. Photomicrographs obtained by scanning electron microscopy show this structure in three-dimensional perspective (see Weber et al., 1969). In transverse section, wedge-shaped calcite crystals in crystallographic or optical continuity appear to radiate from the core (Fig. 1). Prominent concentric banding arises from repeating cycles, each cycle beginning with small wedges which gradually increase in size peripherally. Although they are light colored in the photomicrograph (Fig. 1) of the thin-section (30 microns thick) viewed in transmitted light, the wedges are pigmented, resulting in prominent color banding which is readily evident even without magnification. The smaller rings (Fig. 3A, B) in the center of a spine are deep, brilliant purple, the exterior color of the spines of very young animals. Growth bands further from the core are dark green, the color of the spines of older urchins. When a new cycle begins, the number of wedges increases, by intercalation of a new radial series (Fig. 1B) or by bifurcation of a preceding radial series (Fig. 1A). In *H. trigonarius*, the rings are not truly circular, but curve outward on one side of the spine to produce a more or less triangular shape in transverse section (Fig. 2). There is, however, considerable variation from nearly circular to decidedly trigonal-shaped spines, often within the same individual. The finely crystalline meshwork between the radial wedge series is usually white, very light green, or light pinkish-orange.

#### RESULTS

1. In many longitudinal sections there is evidence of one or more breaks which have been completely repaired by regeneration of the lost distal portion of the spine (Fig. 3D, F). The percentage of the 70 largest primary spines which exhibit such damage ranges from zero in the two smallest specimens, to 80 in specimen 3 (Table 1). Broken spines whose tips had not yet been regenerated were exceedingly uncommon in hundreds of animals examined, suggesting that the process of repair must be fairly rapid. The pigmented growth bands terminate abruptly at the point of breakage. Distally from this point, the regenerated portion of the spine is light pinkish-orange, sometimes with barely perceptible variations in color density which suggest progressive stages of calcite deposition during regeneration.
2. As would be expected, larger spines are more likely to have been broken than the smaller spines of the same animal. For example, the percentages of broken-but-regenerated spines in the three length ranges, 10–50 mm, 51–80 mm, and 81–110 mm, are respectively 4, 46, and 78 for specimen 12; and 14, 58, and 78 for specimen 13.
3. The regular sequence of growth bands, more or less equally spaced, observed in other sections shows that these spines have never been broken (Fig. 4D–G).
4. Some spines have apparently replaced a predecessor which was pulled from its place on the test or else discarded by the urchin, possibly because damage was too extensive to repair. Such spines are characterized by large, light green or pinkish-orange cores lacking the small purple growth bands. Replacement spines of this sort can be fairly large (Figs. 3E, G; 4C). Most of these spines possessed one or more growth rings in the peripheral area of the cross section (Fig. 3A, B). One large spine had obviously regenerated but had not yet secreted a growth band of coarsely crystalline wedges. In this case the entire spine surface consisted of pinkish-orange, finely crystalline calcite which is quite soft; it can be scratched easily with a finger nail.
5. Some spines were found to be undergoing the process of growth band formation. In these spines, some of which had never been broken, the various stages are clearly evident. During a

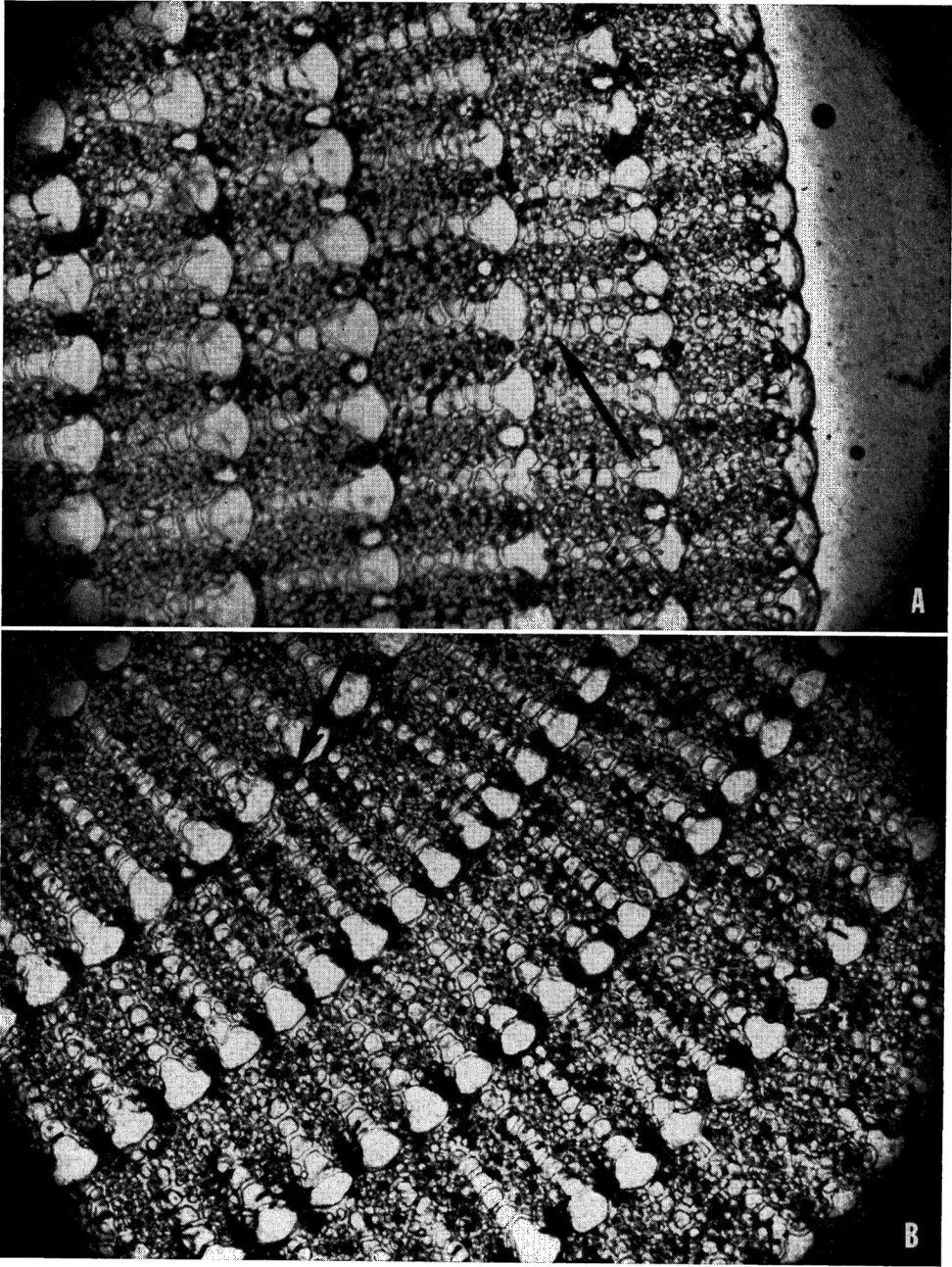


FIG. 1. Spine of *Heterocentrotus trigonavius*. *A*, Transverse section, 30 microns thick, viewed in transmitted light, showing banding produced by layers of large wedges which contain a green pigment, presumably spinochrome. The periphery of the spine is at right. Black circles at right are air bubbles trapped in plastic bonding medium. *Arrow* points to increase in the number of wedges with growth by bifurcation of a radial series.

*B*, Same as *A* except the surface of spine is out of the field of view to the lower right. *Arrow* points to increase in the number of wedges by intercalation of a radial series. The area shown in each photomicrograph is approximately 1.2 by 0.85 mm.

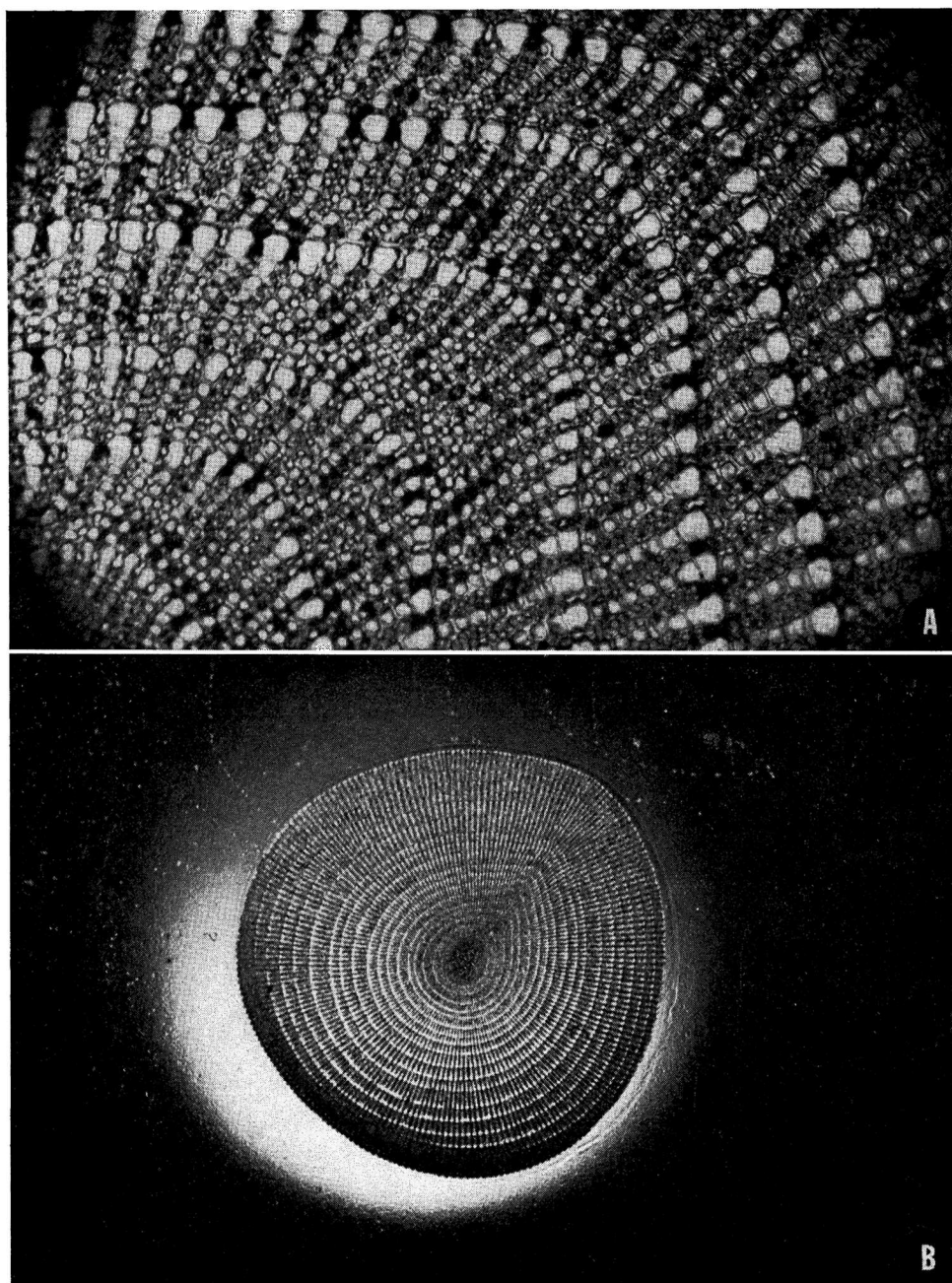


FIG. 2. Spine of *Heterocentrotus trigonarius*. *A*, Transverse thin-section, 30 microns thick, viewed in transmitted light showing curvature of growth bands which creates a more or less trigonal aspect to spine shape. Area about 1.2 by 0.85 mm. *B*, Transverse thin-section, approximately 10 mm in diameter, viewed in transmitted light, showing prominent concentric growth bands and the radial series of wedges.

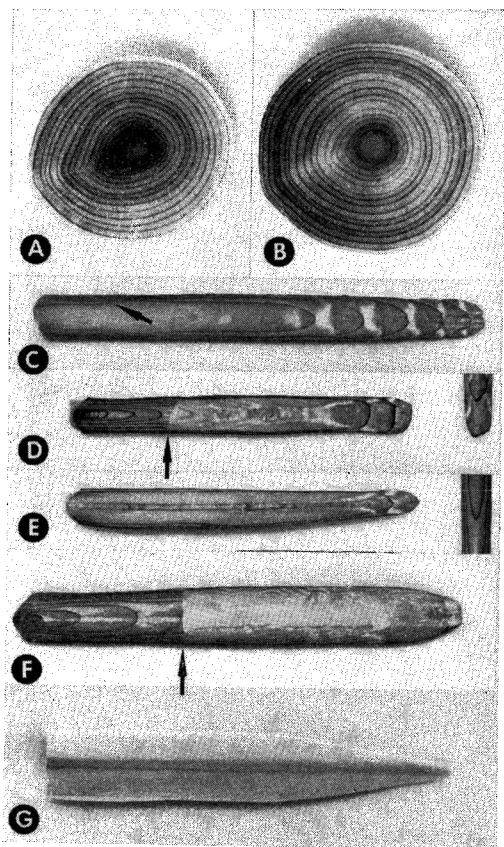


FIG. 3. Spines of *Heterocentrotus trigonarius*. *A* and *B*, Transverse cross sections cut at the milled ring, viewed in reflected light, showing numerous concentric rings, which are brilliant purple near the core and dark green near the periphery. The smallest bands in *A* are triangular. Additional bands are beneath the surface in the core area. *C*, Longitudinal section (98 mm) showing replacement spine with disappearing growth band indicated by arrow. After this spine regenerated to replace a predecessor removed from the test, 6 additional growth bands were formed. *D*, Abrupt termination of growth bands resulting from a break at the point indicated by the arrow; 74 mm long. *E*, Regenerated replacement spine, 76 mm long. *F*, 84-mm spine with regenerated distal portion to right of arrow. *G*, Spine, completely regenerated, with part of a single layer of large wedges forming at lower left, otherwise completely free of growth bands. Length from milled ring (cut off at left) to tip is 51 mm.

TABLE 1  
SIZE AND OTHER DATA FOR 15 SPECIMENS OF *Heterocentrotus trigonarius* FROM TEAHUPOO, TAHITI

SPECIMEN	WEIGHT OF TEST (g)	LENGTH OF TEST (mm)	WIDTH OF TEST (mm)	MAXIMUM NUMBER OF RADIOLAR RINGS	% OF 70 LARGEST PRIMARY SPINES BROKEN AND REGENERATED
1	50.7	80	68	23	6
2	36.4	71	63	21	38
3	65.5	86	75	24	80
4	61.5	80	70	23	19
5	49.5	75	65	21	54
6	46.6	75	65	23	18
7	16.0	50	42	18	10
8	6.6	38	32	15	0
9	1.5	23	19	10	0
10	7.7	41	36	15	29
11	98.5	91	80	25	22
12	85.1	89	58	25	33
13	105.5	98	84	26	44
14	24.5	62	52	21	2
15	19.6	57	45	19	3



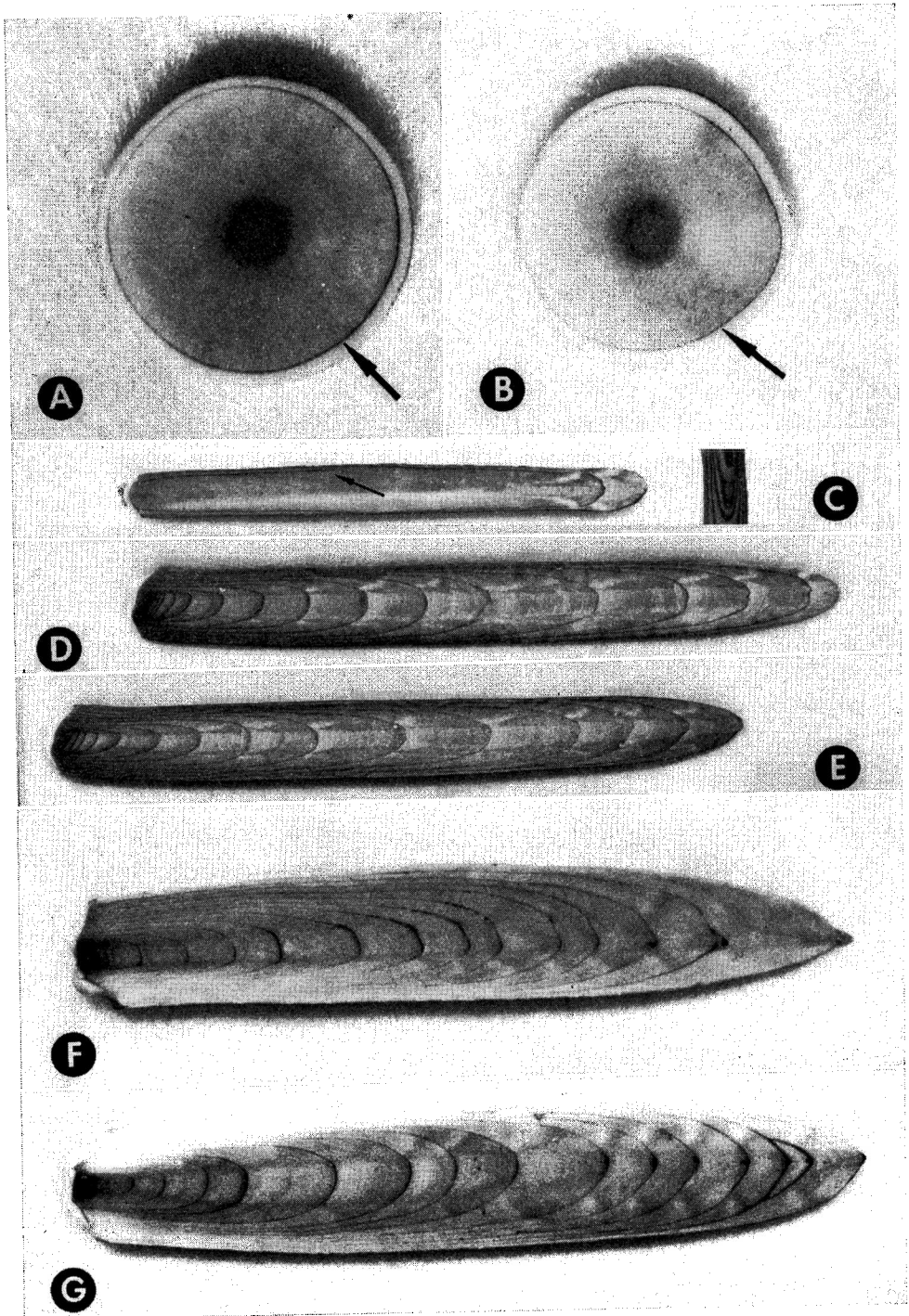


FIG. 4. Spines of *Heterocentrotus trigonarius*. A and B, Transverse sections at milled ring, viewed in reflected light, showing large, ring-free core and growth band (arrow) at periphery, characteristic of spines which have been completely regrown to replace a predecessor. The core is a deeper shade of orange-pink in the very center, but appears dark in these photographs reproduced from kodachromes. C, Spine 77 mm long.

new period of growth, skeletal carbonate is not deposited over the entire area of the spine at a uniform rate. A new layer of finely crystalline calcite meshwork begins at the base of the spine and gradually progresses toward the tip. The coarsely crystalline layer of pigmented wedges also begins to form near the milled ring and follows the secretion of the pale pinkish-orange to very light green meshwork up toward the tip of the spine. Spine S-10 from specimen 11, sketched in Figure 5, illustrates the sequence. In this case, a portion of the spine between the tip and the milled ring was covered with the finely crystalline meshwork (Fig. 6A) whereas the surface of the tip was covered by the large green wedges of the *previous* cycle, and the proximal portion of the spine was covered by the large green wedges of the *new* cycle, in progress. Furthermore, during the growth cycle, the pigmented layer forms faster on the aboral side of the spine than on the oral side. The transverse cross section in Figure 6B shows the gradation between the two types of skeletal calcite. The radial series of smaller wedges underlying the outer layer of largest wedges is often poorly developed in the outermost one or two growth bands (Fig. 6B). This suggests that after a layer of finely crystalline calcite is deposited and subsequently covered by a layer of large wedge-shaped crystals, recrystallization of the fine meshwork takes place and the layers of smaller wedges form.

5. Several fairly large spines were observed which appeared to be growing to replace a large predecessor which had been removed from the test. These spines were characterized by a very large core (Fig. 4A, B) with one or two growth bands near the periphery. Because a large quantity of new skeletal material is required to completely regenerate a large spine, the process was not completed before a new period of growth began. In these cases (e.g., spine S-7 of specimen 15, Fig. 5) the pigmented layer of large wedges which began to form at the base of the spine did not have time to cover the distal

portion of the spine before precipitation of the fine meshwork of the next cycle had started. As a result, the dark green growth band gradually disappears distally as shown in Figures 3C, 4C, and 5. This situation is distinctly different from that in which the abrupt termination of layers of large wedges is caused by a break.

6. One spine (S-17 from specimen 11, Fig. 5) was broken at the tip during the period when the finely crystalline meshwork was being deposited, that is, at a time when the tip of the spine was not covered by a layer of large wedges. This is shown by the sudden repetition of the faint, barely perceptible "ghost outlines" of minor growth stages recorded by subtle changes in the color density of the finely crystalline calcite. The markings are similar in shape to the outline of a sharpened pencil. Although care was taken to watch for this feature in other spines, it was found in only this one. The significance of the observation is that this particular break did not cause the formation of an additional growth band.

7. If growth rings in *Heterocentrotus* spines were specifically due to the regeneration of broken spines as Ebert proposes for *Strongylocentrotus*, the number of rings in broken-but-regenerated spines should be greater than for spines that have never been broken. Although the number of growth bands can be counted quite accurately, this test does not really provide conclusive evidence for either hypothesis because of the difficulty sometimes encountered in recognizing spines that were completely replaced early in the life of the animal. Such spines may still have small growth bands in the core, but if growth is regular and periodic, fewer rings would be found than in spines which had never been wholly replaced by regeneration. If replacement occurs much later, of course, this is readily evident from the large ring-free core and the difference in the color of the core. Nevertheless, the mean ring numbers for once-broken and never-broken spines, given

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with disappearing growth band as in Figure 3C. D to G, Longitudinal sections of spines which have not been broken. Lengths respectively are: 104, 102, 66, and 69 mm. (Except for 3G all of the spines used to illustrate the major structural features were taken from specimens of *H. trigonarius* not belonging to the group of 15 urchins described in the text, as the spines of the latter were sectioned as indicated under "methods of study.")



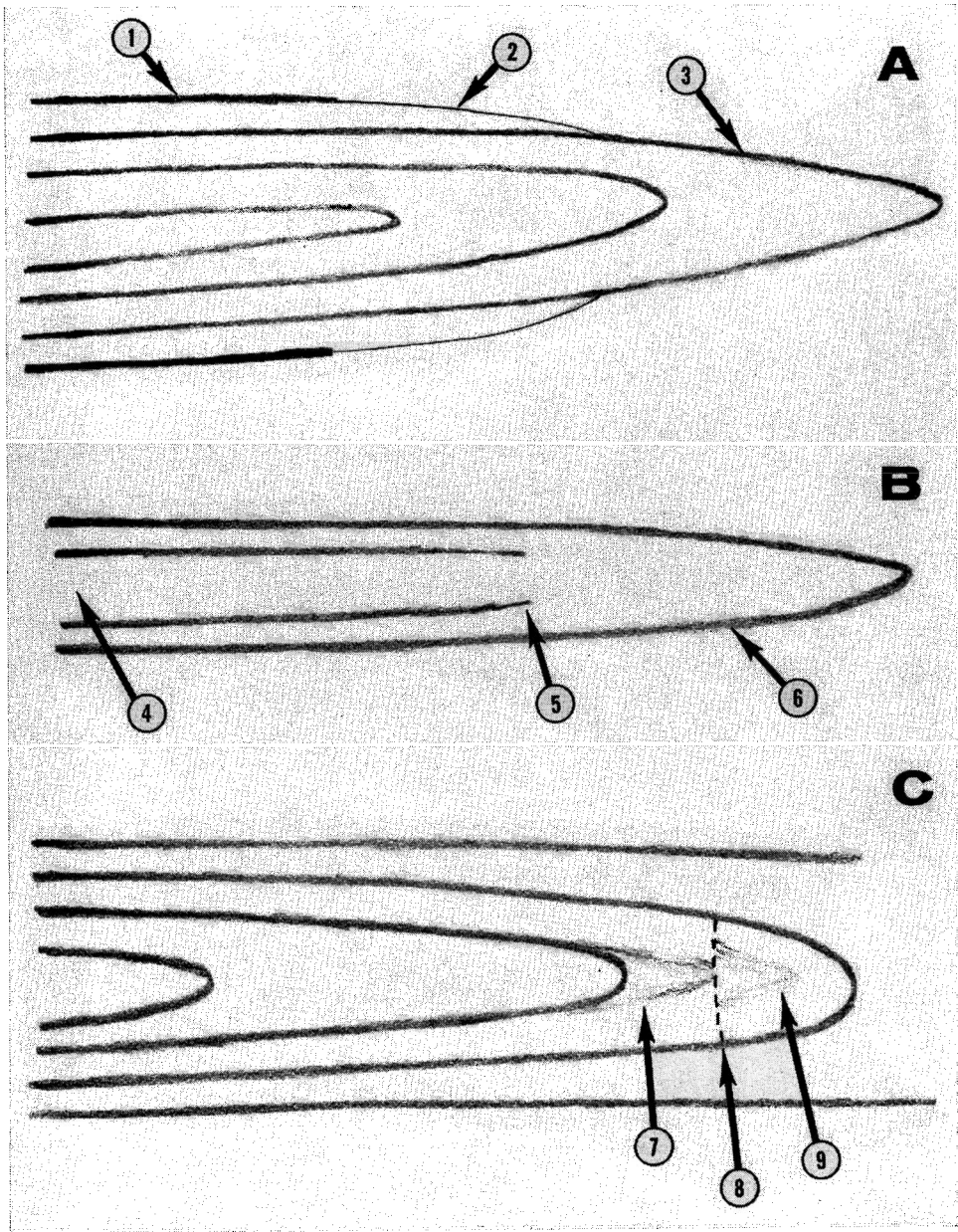


FIG. 5. Exaggerated sketches of longitudinal sections illustrating critical features described in text and shown in part by photomicrographs. *A*, Spine S-10 from specimen 11; total length prior to sectioning, 80 mm. 1, Layer of large wedges at exterior, dark green color, as is case in Fig. 1*A*. 2, Layer of fine meshwork at surface of spine, very light green to pinkish-orange in color, as is case in Fig. 6*A*. 3, Layer of large wedges at exterior like 1, but formed in previous growth cycle. *B*, Spine S-7 from specimen 15; total length prior to sectioning, 51 mm. 4, Large core indicates total regeneration to replace a predecessor. 5, Growth band of large wedges not completed before new growth cycle began. 6, Layer of large wedges of subsequent, completed cycle. *C*, Spine S-17 from specimen 11; total length prior to sectioning, 80 mm. 7, Barely perceptible "ghost" outlines in fine meshwork. 8, Break occurred along dotted line during time meshwork was being deposited but before being covered with layer of large wedges. 9, Tip regenerated before cycle was completed by formation of the large-wedge layer.

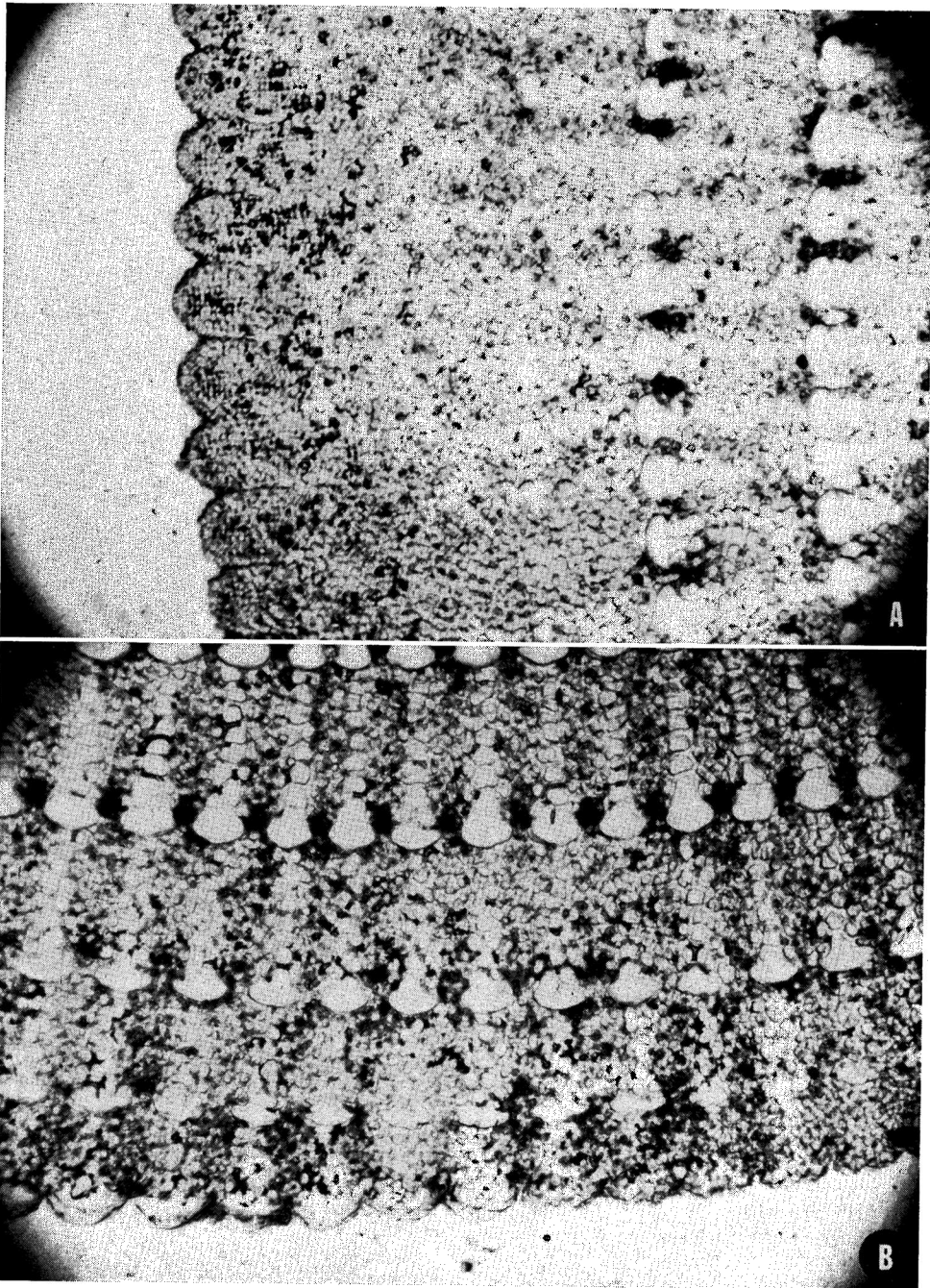


FIG. 6. Spine of *Heterocentrotus trigonarius*. Transverse thin-sections, 30 microns thick, viewed in transmitted light. Area approximately 0.85 by 1.2 mm. *A*, Fine, pinkish-orange meshwork appears on outer surface of spine which shows the characteristic external ribbing at right. *B*, The exterior surface of the spine is located at the top of the photomicrograph. This section, perpendicular to the axis, was made at a point where the coarse layer of green wedges is well developed on the aboral surface but just beginning to cover the oral surface. The wedges at the surface at upper right gradually disappear toward the upper left where the fine meshwork covers the surface.

TABLE 2  
COMPARISON OF MEAN RING NUMBER FOR BROKEN  
AND UNBROKEN SPINES

SPECIMEN	AVERAGE NUMBER OF RINGS IN SPINES	
	NEVER-BROKEN	BROKEN AND REGENERATED
2	12	12
3	16	14
4	15.5	15.5
5	12	13
6	14	14
10	7	7
11	15	16
12	13.5	13
13	13	16

in Table 2 for urchins which had enough spines in both categories to permit comparison, are not significantly different.

8. For many of the specimens, the ring numbers of the primary spines are more or less confined to a small range (discussed in paragraph 9) whose median is more or less positively correlated with the size of the animal. Spines with considerably fewer rings have large cores and are obviously wholly regenerated replacements. Specimen 4, however, appears to have lost an appreciable number of its primary spines "two growth rings ago," as 18 spines had but 2 growth bands, one spine had 6, and the remainder contained between 16 and 23.

9. The number of rings in the spines is positively correlated with other growth or age indicators such as the weight of the test or the length of the test, but as in earlier studies of other urchins (e.g., Moore, 1966) there is considerable scatter in the data. This is not the case, however, when the *maximum* number of growth bands for each specimen is plotted. Figures 7 and 8 demonstrate the excellent linear correlation between the maximum ring number and the logarithm of the weight of the test or of the length of the test. The maximum number of rings was always found in the spines characterized by the occurrence of small purple growth bands (which are prominently triangular with rounded edges, in contrast to later, more circular bands) in the core. The mean number of rings for each set of spines is a poor indicator

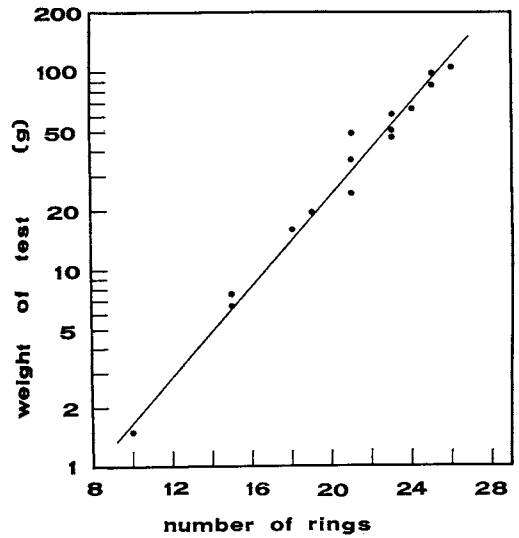


FIG. 7. Positive, linear correlation of the maximum number of growth rings found in the spines of *Heterocentrotus trigonarius* with the logarithm of the weight of skeletal calcite of the test.

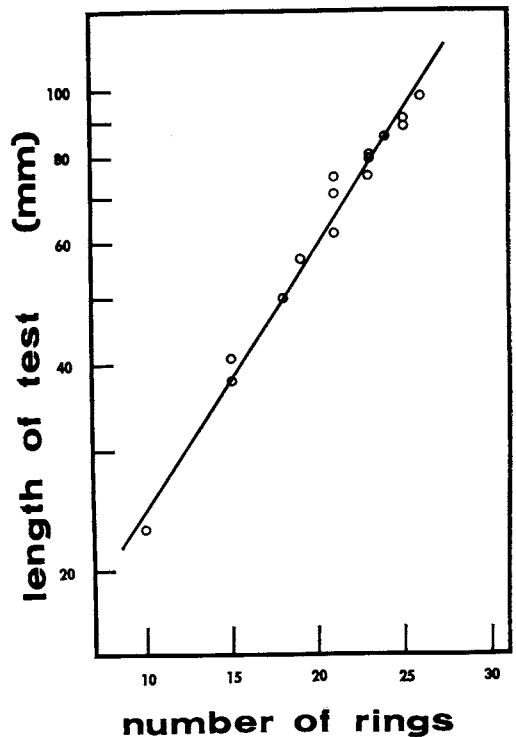


FIG. 8. Positive, linear correlation of the maximum number of radiolar rings of *Heterocentrotus trigonarius* with the logarithm of the length of the test at the ambitus.

of relative age as it would depend upon how many primary spines had been completely replaced during the animal's life and when such loss and regeneration had taken place.

#### DISCUSSION OF THE RESULTS

The evidence presented above is difficult to explain except by the concept of regular growth intervals. For *Heterocentrotus*, both of the critical observations were made which were lacking in the study of *Strongylocentrotus*, and upon which the theory of the regeneration origin of growth bands is founded. The fact that the pinkish-orange to light green layer of fine meshwork is rarely seen on the outside surface of the spines suggests that, once a period of accretion begins, the new layer is completed in a short period of time. Although there is no doubt that the bands represent periodic growth, there is little evidence to indicate whether the rings represent equal or regular periods of time, except perhaps, that the bands are more or less equally spaced as are the growth rings of perennial woody plants.

Growth banding is found in the skeletons of other marine invertebrates. For some molluscs, the growth lines recorded in the shells have been shown to result from daily increments of calcium carbonate (e.g., House and Farrow, 1968; Clark, 1968), and it is fairly certain that this is also true for fossil molluscs (Berry and Barker, 1968), and for some fossil corals (Wells, 1963; Scrutton, 1964). Superimposed on the sequence of daily growth increments in the molluscs *Tridacna* and *Mercenaria* are other periodicities (Pannella and MacClintock, 1968), for example, a 14-day cycle of deposition in *Tridacna* due to thin daily increments during neap tides and thicker daily increments during spring tides. The causal relationship between the rate of skeletal secretion and periodic changes in external conditions such as temperature for calcareous algae, or light intensity for hermatypic corals, is not difficult to understand. Solar and lunar frequencies of many different biochemical and biological processes are common among intertidal animals (Brown, 1960) as their activities, including feeding, reproduction, and habits protecting them from predation, are influenced by tidal cycles.

Thus, where external conditions vary, periodic growth might be expected. A daily origin for the growth bands of *Heterocentrotus*, however, is unacceptable. Despite the relatively rapid growth of echinoids (Swan, 1958, 1961; Lewis, 1958; Fuji, 1963; Moore et al., 1963, 1963a; Moore and McPherson, 1965; McPherson, 1965), it is difficult to conceive of an urchin secreting several hundred grams of calcium carbonate in as short a time as 26 days.

A yearly period for the rings, as has been suggested for some other urchins (e.g., McRae, 1959), is also unlikely for *Heterocentrotus*, as the spines of the largest specimen collected had a maximum number of 26 rings. It is commonly believed that most species live only a few years, with a maximum life span of about 10 years (Moore, 1966; Buchanan, 1967). Hyman (1955) concluded, after a review of published reports, that in nature, echinoids grow rather rapidly, may spawn at the end of their first year, and live from 4 to 8 years, depending on the size of the species. Nevertheless, as so many different cycles seem to reflect the cycle of sunspots (see Fairbridge, 1961), the possibility of correlating the distances between rings with known long-term periodic phenomena could not be overlooked. Such data were obtained, using a traveling microscope, from both transverse and longitudinal sections of many spines having large ring numbers. No recognizable patterns or trends were observed which might be correlated with external factors. Correlation of interring distances along various radii of one transverse section is fair despite imperfect concentric growth. There was, however, no significant correlation among spines from the same animal, even though cross-correlation techniques (Merriam and Sneath, 1967) were applied.

In accord with this information, a lunar periodicity is worthy of consideration, as, assuming a relationship to lunar cycles, the largest specimen would be two years and two months old. After all, *Heterocentrotus* lives in the intertidal zone, and the passage of the moon is responsible for the progression of spring and neap tides. The maximum tidal range at Teahupoo, however, is almost negligible, barely 34 cm. Furthermore, variation in water temperature is also slight, amounting to only a few degrees in the course of a year. Despite the

prominent growth banding in these spines, there appear to be no external factors to which they can be related.

I conclude, therefore, that the rhythm producing growth banding is likely endogenous, and possibly of lunar frequency. There is some evidence of lunar periodicity in egg or sperm production during the breeding season for some urchins (Harvey, 1956: 56-57) but no evidence of such periodicity in others. The answer will come only from careful field studies which are often difficult to make. These will involve tagging large numbers of individuals by methods developed by Ebert (1965) and permitting them to live in their natural environment, followed by frequent sampling and observation. For *Heterocentrotus*, at least, this task is enormous, as its normal habitat is in the zone of heavy surf. The chances of retrieving a given urchin from the labyrinth of crevices created by overturned tabular heads of *Acropora* cemented together on the fore-reef slope are probably very small, at least on all of the reefs where I have discovered substantial populations.

#### CONCLUSIONS

Growth banding in *Heterocentrotus* is due to periodic growth and not to the regeneration of broken spines as has been proposed for some other echinoids. Although the regularity and frequency of the cycle of ring formation are not known, there is an excellent positive, linear correlation between the maximum number of radiolar rings and the logarithm of such growth indicators as length and weight of the test. Presumably, therefore, the number of rings in a primary spine which has never replaced a predecessor on the test is closely related to the age of the animal. As a practical measure of age, however, even when the frequency of band formation is discovered, the use of ring counts will not be accurate unless there is some assurance that the spine has been associated with the animal throughout its entire life.

#### SUMMARY

Investigation of the nature of the prominent concentric banding in spines of *Heterocentrotus trigonarius* from Teahupoo, Tahiti, contradicts

an earlier model for ring formation based on a study of *Strongylocentrotus*. Rings in *H. trigonarius* and *H. mammillatus* are not caused by the regeneration of broken spines but are added to both damaged and undamaged spines alike at certain intervals. The addition of a new layer of skeletal material begins near the proximal portion of the spine with the deposition of a fine, soft, pinkish-orange to very light green meshwork which eventually covers the entire surface of the spine. A pigmented (dark green), hard layer consisting of large calcite wedges subsequently covers the meshwork and completes the cycle. There is an excellent positive, linear correlation between the maximum number of growth bands and the logarithm of both the weight of the test and the length of the test at the ambitus, both of which are presumably related to the age of the animal. The structure of 1,050 primary spines from 15 Tahitian specimens ranging from 1.5 grams (dry weight of test calcite) to 105.5 grams was examined in addition to that of a smaller number of spines from urchins of the genus *Heterocentrotus* taken from other Pacific localities. The maximum number of growth rings observed was 26. Possible causes of growth banding and its frequency are considered.

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