



Fig. 4. Same location as in Fig. 3 but in fourth-stage juvenile. Note absence of vacuolated spaces and the closer packing of cilia-like structures ( $\times 38,800$ ).

with a Siemens Elmiskop I electron microscope at 60 kv.

The results showed that the labial, cephalic, and cervical papillae and the amphids all contain dendritic structures, part of which resemble a cilium. However, the number of fibers is not consistent with that of true cilia, and it is probable that the dendritic processes have been greatly modified. Each labial papilla consists of a single dendritic structure having ten outer doublets with zero to four microtubules or vesicles in the center. Further evidence is needed to determine the exact structure of these central fibers. The four cephalic papillae have a pair of these structures surrounded by an electron-opaque layer of tissue. The structure at the base of all the papillae is difficult to determine in the third-stage juvenile. However, in the fourth stage several unmyelinated axons can be seen extending posteriorly towards the nerve ring. The cervical papillae are not noticeable in the third-stage juveniles, as they are folded under the external cuticle. The papillae contain a single "cilium" that has ten doublets and zero to four central fibers and in which the fibers extend inwards until they merge with lateral nerve axons (Fig. 1). It is difficult to determine the exact position of the "cilium" in relation to the papilla, and it will be necessary to look at later parasitic stages to obtain this information.

The amphids in the third-stage juve-

niles consist of a cuticular pit ending in a pouch-shaped structure with a total length of  $18 \mu$ . The dendritic processes extending forward from the nerve endings at the bottom of the pouch become very closely packed (Fig. 2) and end just before the amphid aperture, the internal structure being difficult to interpret. Toward the bottom of the pit the dendrites become more clearly defined as they spread apart, and ten outer doublets with zero to four inner microtubules or vesicles become evident (Fig. 3).

There is a striking resemblance between the structure of the amphids in the third-stage juveniles and the structure of some types of insect sensory organs (7). Roggen *et al.* (3) also commented on this. This resemblance is lost when the juvenile reaches the fourth stage. The dendrites become more closely packed, and the vacuoles and villi-like structures disappear as the buccal capsule enlarges (Fig. 4).

Further studies in earlier and later stages could yield clues to the specific

functions of these organs during the growth of the parasite from the free-living stage to the parasitic adult.

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## Planktonic Foraminifera: Field Experiment on Production Rate

**Abstract.** *In a study of the rate of production of four species of planktonic Foraminifera in the region of the California Current it was found that their life spans are of the order of 1 month. Reproduction seems to take place mainly in the upper hundred meters. Results are in contrast to previous evidence presented in favor of yearly life cycles and maturing at great depth in other species of planktonic Foraminifera.*

Planktonic Foraminifera are of interest and value in studies of marine zoogeography and paleoecology. Little is known, however, about their life cycles and productivity. The hypothesis that reproduction of some planktonic Foraminifera takes place at great depth, expressed by Walther in 1893 (1), has recently been considered proven (2) based on the occurrence of heavily encrusted living foraminifera at depths of more than 500 m in the Atlantic. It has been suggested that in the North Atlantic *Globorotalia truncatulinoides* reproduces below a depth of 500 m during November, which implies a yearly cycle of submergence and reproduction for this species (3).

However, if one assumes an annual overturn for planktonic foraminifera, their production of empty shells was found to be inadequate by a factor of 10, when the budget for river in-

flux and ocean sedimentation of calcium carbonate on a worldwide basis was examined (4). It therefore seemed problematic whether annual submergence and reproduction could be extrapolated to all or even most species.

We attempted to obtain evidence bearing directly on this problem by simultaneously ascertaining both the concentration of planktonic foraminifera in the water column by net hauls and the output of this population by collecting falling tests in a sediment trap. At the same time the physical characteristics of the water column were measured from the surface to the bottom (Fig. 1). The location of the experiment was in the center of the Santa Barbara Basin off Southern California. Here the bottom is shallow, and therefore the vertical distance traveled by the shells, as well as their lateral displacement during sedimentation, is minimized. The surface cir-

Table 1. Density profile of planktonic foraminifera in the open-closed net tows, expressed as the number of specimens per cubic meter, and the catch of empty tests in the sediment trap, expressed as the number per square meter per day. The total catch during 4 days was 73 specimens, 3 of which were smaller than 150  $\mu$ . Between 250 and 500 m<sup>3</sup> of water was filtered in each tow.

| Species                        | Number per cubic meter at depths (m) of |       |        |         |         | Number per square meter per day |
|--------------------------------|-----------------------------------------|-------|--------|---------|---------|---------------------------------|
|                                | 0-35                                    | 35-45 | 45-100 | 100-300 | 300-500 |                                 |
| <i>Globigerina bulloides</i>   | 9.7                                     | 4.0   | 2.2    | 0.3     | 0.3     | 8.6                             |
| <i>Globoquadrina eggeri</i>    | 5.5                                     | 1.3   | 2.2    | .9      | .6      | 10.0                            |
| <i>Globigerinoides ruber</i>   | 1.7                                     | 0.2   | 0.2    | .1      | <.1     | 1.0                             |
| <i>Globigerina quinqueloba</i> | 1.7                                     | .5    | 1.2    | .1      | .1      | 4.8                             |
| <i>Globigerinita glutinata</i> | 0.2                                     |       |        |         |         | 0.0                             |
| <i>Globorotalia hirsuta</i>    |                                         |       |        | .1      | .3      | 0.0                             |
| <i>Globigerina calida</i>      |                                         |       |        | <.1     | .2      | 0.0                             |
| <i>Hastigerina pelagica</i>    |                                         |       |        | <.1     | .1      | 0.0                             |

culcation appears to be rotational, so that the system may be regarded as semiclosed for time spans of a few days. Thus it seems likely that the empty tests falling to the bottom represent the production in the water column above.

We assumed a steady-state condition for the concentration of living foraminifera and their empty shells in the water column during the experiment. Under these conditions the output of empty shells measured on the ocean floor equals the input from perishing individuals above. In addition, the rate of reproduction must balance the rate of attrition in the living population in order to maintain the population at the given density. Thus the turnover time may be calculated by dividing the standing crop of living foraminifera above a given area of the bottom by the number of empty tests deposited on this area during a specified time. Basically, this is the same reasoning that Bramlette used (4).

In order to obtain valid results with this approach, the calculations would have to be made separately for each species and life stage. For a first approximation, the size of foraminifera may be taken as a measure of the life stage, so that life spans should be calculated for narrow ranges in size. We took 150  $\mu$  as a minimum adult size and treated all specimens larger than this on an equal basis, which results in turnover times that are longer than average life spans. Many foraminifera grow to a size somewhat larger than 150  $\mu$ , and their density in the water column is consequently smaller, since large specimens are rarer than small ones in the surface water. This leads to a smaller standing crop

from which to draw the output of empty shells, and hence a more rapid overturn is required. In view of the other uncertainties involved, a more detailed calculation on the basis of the distribution of sizes in the adult range seemed unjustified.

Eight plankton tows were taken with nets (150- $\mu$  mesh) during the nights of 29-30 and 30-31 August 1966, at the following depths: 15 to 0, 35 to 0, 45 to 35, 100 to 45, 300 to 100, 480 to 300, 500 to 300, and 450 to 0 m. Depths were controlled by an acoustic pinger attached to the nets, and the nets were closed by a tripping device operated by a propeller flowmeter. Between 250 and 500 m<sup>3</sup> of water was filtered in each tow, and

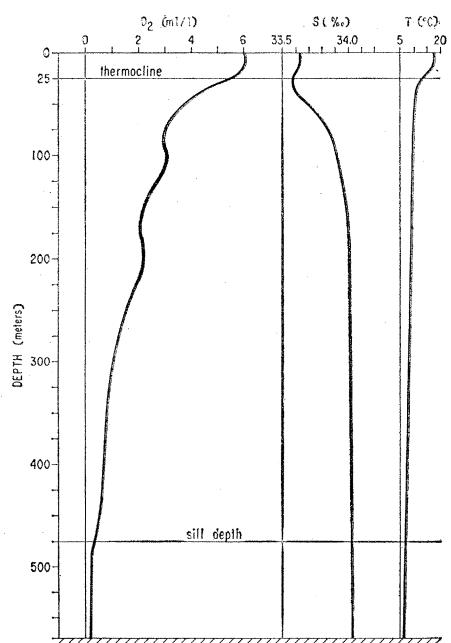


Fig. 1. Physical properties of the water column in Santa Barbara Basin during the last part of August 1966.

samples were preserved in buffered formalin. The foraminifera extracted by gravity separation from each sample were stained with methylene blue (5), which facilitated identification and recognition of live specimens. Half of the remaining part of each sample was washed and combusted (6), in order to obtain those shells that had not fallen out in the settling tube. Combustion at about 400°C preserves some carbon in living foraminifera. This is desirable because empty tests settle out preferentially in the gravity process, and thus falsify the ratios of live to dead foraminifera. Populations of living individuals that are larger than 150  $\mu$  are given in Table 1. From the multiple control afforded by the various overlapping tows, we conclude that the values are correct to within  $\pm$  50 percent.

The sediment trap is an umbrella-shaped free vehicle with an aperture of 0.7 m<sup>2</sup>. The folded trap was released on 25 August 1966, and it sank to 6 m above the bottom within 2 hours. Approximately 6 hours later a Schick bimetal release parted and opened the trap. The instrument remained open for 4 days and then slowly pursed shut. A short time after the closing was completed a weight was released, and the trap floated to the surface. The contents were removed by pumping and subsequent washing of the trap. Results of the count of foraminifera larger than 150  $\mu$  (in this case 96 percent of the total) are tabulated in Table 1 (7).

It is necessary to evaluate whether the data are representative before interpretations are possible. The concentrations of foraminifera are probably reliable, since a similar series of tows taken 10 weeks later yielded comparable results. This suggests that the assumption of a steady state is valid. It is not possible, however, to be as confident about the sediment yield, since an attempt to repeat the experiment with a modified trap failed.

Sediment traps tend to increase the turbulence at the place of collection and this affects the results. It seems likely that the trap would catch less than the normal amount of tests settling over the area, since local turbulence would retard the sinking speed of the particles passing over the trap and thus increase their density at that position. It follows that fewer tests are then caught in the instru-

ment. We believe, therefore, that the catch in the trap is a minimum amount. Bottom currents at the time of collection varied from 1 to 28 cm/sec, with an average current velocity of 6 cm/sec.

If the data are accepted with the reservations outlined, one can draw the following tentative conclusions:

(i) The main growth of the species *Globigerina bulloides*, *Globigerina quinqueloba*, *Globigerinoides ruber*, and *Globoquadrina eggeri* is likely to take place in the upper layers of water, as shown by the relatively dense populations there. Also, the oxygen deficiency of the water at greater depths may be expected to be detrimental to growth and reproduction. (ii) The individuals below 100 m seem to have been brought in with submerged southerly water, judging from the assemblage of species there. Species that were not represented in the upper waters at the time did not contribute to the sediment catch on the bottom. They do not seem to reproduce at a rate comparable to the other species, and their turnover time must be very long under these circumstances. (iii) If the entire population below 100 m can be considered inert on the basis of these arguments, the turnover times for the species found in the surface layers are obtained in the following way. The densities given in Table 1 are converted to standing crops for the upper 100 m of the water column. These productive standing crops for each species are divided by the appropriate fluxes of empty tests, which are also given in Table 1. The resulting turnover times for *Globigerina bulloides*, *Globoquadrina eggeri*, *Globigerinoides ruber*, and *Globigerina quinqueloba* are 58, 33, 73, and 27 days, respectively (8). For reasons given above, the average life spans of these species should be shorter than the turnover times by a factor of 1 to 2.

These conclusions do not preclude the existence of a longer cycle, including the submergence of mature individuals under adverse environmental conditions. Such cycles are described for copepods (9) and may well run parallel to the shorter cycles of high productivity proposed here.

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#### References and Notes

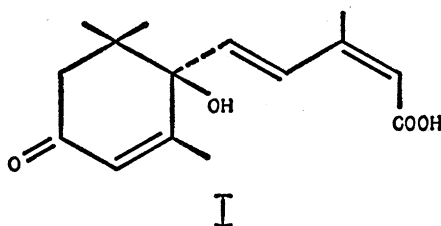
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## Dormin (Abscisin II), Inhibitor of Plant DNA Synthesis?

**Abstract.** *Dormin (abscisin II), inhibits growth of Lemna minor cultures. At 1 part per million ( $3.8 \times 10^{-6}\text{M}$ ), the culture appears nearly completely dormant but can be revived readily by transferring it to fresh medium free of dormin. The cytokinin benzyladenine, but not auxin or gibberellin, will counteract the dormin effect. Quantitative restoration of normal growth by cytokinin, however, can be achieved only if the dormin concentration does not exceed a critical level. Separation, after phenol-detergent extraction, of nucleic acids on methylated albumin kieselguhr columns showed suppression of nucleic acid synthesis by dormin in all fractions. Inhibition of the synthesis of the DNA fraction seems to precede that of RNA. Cytokinins reverse the process. They promote synthesis of all nucleic acid fractions, but again DNA seems to lead. Further work on the interaction of dormin with growth-promoting hormones might be facilitated by adopting the Monod model of allosteric transition, with, for example, DNA polymerase as the protein, dormin as the inhibitor, and cytokinin or other growth promoters as activators.*

Plant growth and development is regulated by a number of naturally occurring substances of hormonal nature. These chemically well-defined agents include gibberellins, cytokinins, auxins, ethylene, and, most recently, also dormin (1). Dormin, an appropriate and physiologically descriptive appellation given by Wareing to the dormancy regulator of sycamore (2), was identified and synthesized by Cornforth *et al.* (3). Its absolute stereochemical configuration (I) was also determined by



Cornforth and associates (4). Dormin turned out to be identical to abscisin II from cotton fruit, earlier described by Addicott *et al.* (5). Dormin is also identical to the lupin growth inhibitor (6) and the peach seed inhibitor (7), and seems to occur widely in buds, leaves, tubers, seed, and fruit (8). Be-

low we report studies concerned with the mode of action of dormin. This appears to be the inhibition of the synthesis of all nucleic acid fractions as analyzed in the methylated albumin kieselguhr (MAK) column, with the possibility that inhibition of DNA synthesis is an early effect of dormin.

In order to avoid any preconceived notions of its mode of action, part-per-million concentrations of synthetic ( $\pm$ )-dormin from Cornforth's laboratory were applied to all sorts of biological objects: bacteria, fungi, algae, higher plants, insects, and mammalian cell cultures. Only the higher plants responded, and among these, cultures of *Lemna minor* (duckweed) were the most sensitive. Therefore, sterile cultures of *L. minor*, grown under constant fluorescent light ( $27,500 \text{ lu/m}^2$ ) and constant temperature ( $22^\circ \pm 1^\circ\text{C}$ ) were used throughout our tests as experimental material. Growth is vegetative, by budding, and was determined as increase of fresh weight. A dormin concentration as low as 1 part per billion ( $10^9$ ) ( $3.8 \times 10^{-9}\text{M}$ ) causes detectable inhibition (Fig. 1). At 1 part per million (1 ppm) ( $3.8 \times 10^{-6}\text{M}$ ), growth inhi-