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Zoology

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AN ANALYSIS OF THE BURROWING BEHAVIOR OF TWO SEA ANEMONES FROM THE GULF OF CALIFORNIA

by

Dorothea Caskey Mangum

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ZOOLOGY
In Partial Fulfillment of the Requirements
For the Degree of
DOCTOR OF PHILOSOPHY
In the Graduate College
THE UNIVERSITY OF ARIZONA

1967
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be accepted as fulfilling the dissertation requirement of the degree of Doctor of Philosophy

Peter E. Pickens Dec. 12, 1966
Dissertation Director Date

After inspection of the dissertation, the following members of the Final Examination Committee concur in its approval and recommend its acceptance:*

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SIGNED: Dorothea Casley Mangum
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ABSTRACT

Two varieties of the tropical burrowing anemone *Phyllactis concinnata* were studied. The physiological and morphological properties of the nervous and muscular systems of *Phyllactis* were compared with those of well studied anemones such as *Metridium*, *Calliactis*, and *Stomphia*. The *Phyllactis* exhibited the facilitated response to a series of electrical stimuli that has been found characteristic of anemones, and the methylene blue stained nerve net of the retractor and column of the *Phyllactis* was similar to that described for *Metridium* and *Calliactis*, though no multipolar cells were seen. The general morphology of the *Phyllactis* is comparable to that described for other anemones except that *Phyllactis* possess a ruff around the oral disc and very powerful retractor muscles.

The burrowing behavior of these anemones was described on the basis of the properties of the nervous and muscular systems and compared with other purposeful and coordinated movements of anemones. It was found that burrowing in the *Phyllactis* that lived in the rocky intertidal zone was a modification of walking, and in this instance the pedal disc inflates and contracts as the column
alternately shortens and elongates. This results in the progressive attachment and loosening of the pedal disc. The variety of the *Phyllactis* that burrows in the sand flats is the more efficient and specialized burrower of the two. This anemone seldom walks on its pedal disc, but when it does, it appears that the same muscular and coordinating systems are used as in burrowing. Both walking and burrowing require the parietal and circular muscle sequence that is seen in many aspects of the anemone behavior such as feeding, and the slow inherent movements that have been studied in *Calliactis* and *Metridium*. The most unique feature of the burrowing behavior is the very consistent and predictable quality of the rhythmic contractions of the column which may be maintained over a long period of time.

The *Phyllactis* is representative of a tropical anemone fauna which, with the exception of *Bunodactis*, has not been examined. It was found that the most obvious adaptation to the water temperature was to remain active over a wide temperature range.
INTRODUCTION

Members of the phylum Coelenterata are regarded as the most simply organized animals to have a nervous system. Various representatives of this group: hydra, jellyfish, coral and sea anemones, have recently been studied in detail. This interest in the study of the morphology and physiology of the coelenterate nervous system dates back to the excellent anatomical research of the Hertwig brothers (1878-1879). Their description of a nerve net consisting of bipolar nerve cells that do not anastomose is more widely accepted today than it was forty years ago when it was believed to have been superceded by the syncytial nerve net described by G. H. Parker (1919). Careful investigation by Batham, Pantin, and Robson (1961), Batham (1965), and Robson (1961, 1963, 1965) on Metridium, Mimetridium, Calliactis, and Stomphia confirmed and further extended the Hertwigs' work and showed that many of Parker's conclusions were based on straining artifacts.

This actinian nervous system consists of a network of bipolar nerve cells which supply the column, mesenteries, and oral and pedal discs. The neuron may be as long as 8 mm in the mesenteries (Batham et al., 1960; Robson, 1961). Sense cells are small
and spindle-shaped with a distal flagellum and have one, two, or three neurites (long processes of a nerve cell). They are particularly abundant in the oral disc near the tentacles and line the areas where the mesenteries attach to the column and the pedal disc. The neurites of these sense cells connect with the processes of the bipolar neurons of the nerve net. The neurites of the nerve cells may pass from one region to another by going directly through the mesoglea or in association with muscles that penetrate mesoglea. Multipolar nerve cells are found in the column and retractor preparations of some species (Robson 1961, 1963, 1965).

The basis for the understanding of nerve function in sea anemones is a series of papers entitled "The Nerve Net of the Actinozoa" published by C. F. A. Pantin in 1935. From his investigations on Calliactis parasitica, Pantin described the most important physiological characteristics of the actinian nerve net. He found no response to a single electrical stimulus, but a definite reaction to a second stimulus if it occurred within a certain period of time after the first. Pantin called this "facilitation" and suggested that it occurs at neuromuscular sites in the column and mesenteries and between parts of the nerve net in the disc. Conduction is diffuse and may travel great distances, as in the mesenteries, or may be restricted, as in the oral disc. The greater spread in the
mesenteries is due to a "through-conduction" system with a velocity of conduction of over 1 meter per second. In the general, or slow system, conduction occurs at 10 to 20 centimeters per second. The through-system mediates a symmetrical response of the whole anemone and is usually associated with a rapid reflex.

Studies of Batham, Pantin, and Robson (1960) provide histological counterparts for the physiologically fast or through-conduction system and the slow or general conduction system. The muscles capable of a fast response, such as the retractor muscles which lie longitudinally on the mesenteries, are overlaid by a comparatively dense nerve net of bipolar cells that are also relatively stout (up to 13 microns in diameter) and that tend to run longitudinally; whereas the slow muscles of the column and the disc are covered with an apparently random scattering of more slender nerve fibers. The retractor muscles are capable of two kinds of contraction — fast and slow, but there is no evidence of double innervation of muscle fibers; therefore the two kinds of contraction must be determined by frequency and number of impulses (Batham et al., 1960).

It has been concluded that the impulses which traverse the nerve net of the actinians are of the same all-or-none character as those in higher animals (Bullock, 1965). To date it has not been
possible to record action potentials from sea anemones, but workers have been successful with other coelenterates. Horridge (1953) reported action potentials from the nerve net of *Aurelia*, and more recently Josephson (1965) and Passano (1965) have been successful in recording neuronal activity in hydroids and medusae respectively.

Recently the interest in anemones has centered on trying to explain various types of behavior, such as swimming (Sund 1958; Wilson 1959; Robson 1961, 1963) or attachment to mollusc shells (Ross, 1961; 1965), on the basis of what is known about the anatomical and functional properties of anemone nervous and muscular systems. For example, Robson (1963) has found relatively large multipolar cells around the column of *Stomphia* which she postulates may serve as a labile pacemaker system that controls the rhythmic bending of this animal that is described as "swimming".

The purpose of the study that follows is to describe burrowing behavior in anemones, to explain some aspects of this behavior on the basis of the properties of their nervous and muscular systems, and to compare their burrowing with various other purposeful coordinated movements. Prior to this, digging (Stephenson, 1935) and walking (Batham and Pantin 1950c) have been observed in anemones, but not analyzed, although Batham (1965) notes the apparent similarities in the two activities. The animal
chosen for this study, the sea anemone *Phyllactis concinnata*, is of particular interest, not only because it walks and burrows, but also because it is representative of a tropical anemone fauna which, with the exception of *Bunodactis* (Pantin and Vianna Dias 1952), has not been thoroughly examined.
MATERIALS AND METHODS

Collection and Maintenance of Anemones

Two varieties of *Phyllactis concinnata* were collected at localities near Puerto Peñasco, Sonora, Mexico: the sand *Phyllactis* from the intertidal sand flats in Cholla Bay and the rock *Phyllactis* from the rocky intertidal zones at Norse Beach and the Marine Research Station. The anemones collected ranged in size from 1/2 to 2 1/2 inches across the oral disc.

The anemones were maintained in the laboratory in 20 gallon salt water aquaria with sub-sand filters under 2 inches of sand and shell hash. *Phyllactis* usually dug into the sand within a few hours. They were fed living adult *Artemia* once a week and the sea water was changed periodically. This method of maintaining the animals proved satisfactory, and it was possible to keep individuals for 6 months to a year.

Morphological Studies

Methylene blue, an intra-vitam nerve stain, was used to map the distribution of the nerve fibers on retractor muscles and the column. Reduced methylene blue was prepared following Pantin's (1962) method. Five drops of 24% HCL are added to 100 cc
of a 0.5% methylene blue solution. This solution is filtered, 2 cc of 12% Rongalite is added to the filtrate, and the mixture is heated slowly in a 70°C bath until it takes on a green tinge. It is then removed from the bath and stirred constantly until it becomes clear. After 24 hours this reduced methylene blue is suitable for staining and can be used with good results for a week. The most important requirement in this procedure is that a new solution of Rongalite be used every time the stain is prepared.

Prior to staining, the anemones were placed in the dark for several hours and, when well expanded, were relaxed by adding three or four drops of chlorotone to the surface of the water. If an anemone was not responsive to touch after 4 or 5 hours, it was taken out, cut open, and pinned on a wax plate. The surfaces of the retractor muscles were cleared of gonadal material.

Methylene blue was diluted five times in salt water; then 3 or 4 drops of the diluted solution were added to the exposed surface. Column preparations were made by removing all mesenteries from the inside of the column before adding the dilute methylene blue.

Stained cross and longitudinal sections of both varieties of Phyllactis were prepared in order to compare muscle, column, and mesenteries of these anemones with those of the most frequently
studied forms. The anemones were relaxed as described above. Then they were fixed for 24 hours in Zenker's solution prepared according to Pantin's (1962) method. The fixed specimens were washed in running tap water for 24 hours, kept in Lugol's solutions overnight and then placed in a 5% sodium thiosulfate solution. This was followed by infiltration in a saturated toluene-paraffin solution at room temperature. The tissues were taken through three paraffin baths in the oven, embedded, and after hardening for 24 hours, were sliced into 8 to 10 micron sections and placed on slides.

The sections were stained with Mallory's triple stain. The wax was removed with toluene baths and sections rehydrated through a series of alcohols. The sections were taken through Lugol's iodine solution, through a 5% hypo solution and a distilled water washing. Finally, the slides were taken through Mallory's solutions I and II with 2% phosphomolybdic acid being used as the mordant, and then were dehydrated through a series of alcohols.

**Analysis of Behavior**

Three methods of recording data were employed to analyze the behavior of these anemones: physiograph recordings, direct observation, and photography. Three channels of the four channel Physiograph, manufactured by the E. & M. Instrument Company,
were used to record transducer potentials, while the fourth was used as a time base. The transducers were "A" myographs to which long lever arms were attached and counterbalanced. One end of a monofilament thread was tied to the end of the long arm of the lever and the other attached to a heavy thread sewn into the oral disc or column of the anemone. Extensive anemone muscle movements could be recorded without the digging performance of the anemone being appreciably affected by the change in tension of the myograph spring.

The majority of the physiograph recordings were made from anemones that had three thread loop attachments sewn to the sphincter muscles with threads coming up through the ruff directly over the column. The attachments were made at equal distances around the column by counting the mesentery insertions. The anemones were not anaesthetized prior to attachment because it was hard to be certain when the animal had recovered. This resulted in some variation in the position of the thread in the ruff, but the consistency of the records indicate this variation was not enough to influence the results.

Prior to every experiment amplifiers for each myograph were adjusted so that arbitrary, but equidistant, excursions of all the three lever arms produced equal excursions of the recording
pens in each channel. Further testing showed that natural and electrical stimuli which produced rapid and equal contractions of all the retractor muscles resulted in recordings of the same time course and amplitude on all three channels.

After an anemone had been attached to the levers, it was placed in a 1 gallon glass aquarium filled with sea water with a 2 inch layer of sand on the bottom. The water was aerated continuously and renewed with each new animal. The sea water temperature usually was maintained between 20.5°C to 22°C, but in some experiments it was lowered by circulating water from a refrigerated water bath through a submerged glass coil, or it was raised by using aquarium heaters.

The physiograph records were accompanied by direct observations over long periods of time in order to attribute the appropriate activity to recorded movements. Certainly the effect of tying anemones to levers cannot be discounted, but observations in the laboratory and in the field indicate that behavior such as digging is little changed by the attachments. Many other observations on the behavior of anemones not attached to levers were made in the laboratory and in the field to supplement those gained by an analysis of the recorded movements.
Substrate Composition and Digging Behavior

It was apparent upon cursory examination that the substrates in the two habitats were not composed of the same sized sand grains. To determine the effect of grain size on digging behavior, sand (primarily a shell hash) was sieved through a series of U.S. Standard sieves and divided into six different grades. The U.S. Standard number and the mesh size of the sieves were as follows:

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<th>U.S. Number</th>
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<tr>
<td>(Large shell fragments)</td>
<td>.5</td>
</tr>
<tr>
<td>4</td>
<td>.187</td>
</tr>
<tr>
<td>10</td>
<td>.079</td>
</tr>
<tr>
<td>20</td>
<td>.040</td>
</tr>
<tr>
<td>40</td>
<td>.0165</td>
</tr>
<tr>
<td>60</td>
<td>.0098</td>
</tr>
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In referring to grain size in the results, the U.S. Standard number of the sieve on which the sand and shell fragments were retained will be indicated, rather than the mesh size. The six different substrates were used for two types of experiments. In the first series, amplitudes and rates of muscle movements of the rock and sand Phyllactis were recorded as they dug into different substrates, ranging from coarse to very fine sand (U.S. numbers 4, 10, 20, 40), in order to determine what effect the type of substrate has on the different components of digging behavior. In the second type
of experiment, efforts were made to determine if there was a
tendency for anemones to creep along the surface of the sand until
they had selected a suitable habitat (i.e., grain size). Anemones
were placed in a 5 gallon tank with a 2 inch layer of sand on the
bottom. The sand layer was composed of four different grades of
sand (U.S. numbers 4, 10, 40, 60). Each grade was spread out on
the floor of the aquarium in the shape of an isosceles triangle, so
that the apexes of the four triangles met at the center of the aquar­
ium and their sides were contiguous. At the start of an experiment
the anemones were placed in the center of one triangle.

**Electrical Stimulation**

A Grass S.D. 5 stimulator with insulated platinum
electrodes was used to give electric shocks. Stimulus duration
was 2 milliseconds, the voltage was set at two times threshold,
and stimulus frequency was varied depending upon the purpose of the
experiment. In some cases electrical stimuli were applied during
the digging sequence; in others efforts were made to characterize
the response of buried anemones or those lying loose on the sub­
stratum to stimuli given at different frequencies. Movements re­
sulting from the stimuli were recorded on the physiograph.
RESULTS

Gross Morphology

Carlgren (1951) has given a description of two species of *Phyllactis* found in the Gulf of California. Gross dissections and examination of histological sections during this study confirm his findings and emphasize the following points (Figs. 1-3).

The pedal disc is well developed. The column is elongated in the relaxed anemone, and it can be strongly contracted upon appropriate stimulation. The tentacles number from 40 to 48 and are rather short. At the top of the column there are 40 to 48 longitudinal rows of verrucae to which sand grains and bits of shell adhere. Above the verrucae lies a ruff or a collar which may have a diameter of as much as 4 inches. The ruff is characteristic of the genus and is formed of fronds which bear a variable number of papillae. It is quite sensitive to tactile stimulation and may be of chemosensory value in alerting the anemone to food. It is absent in the other anemones (*Metridium, Calliactis* and *Stomphia*) that have been studied in detail, but in other respects the gross external appearance of *Phyllactis* is not very different. A well developed pedal disc is not often found in burrowing anemones; it is more
characteristic of intertidal anemones that are attached to rocks, pilings, or shells. Each of the two varieties of Phyllactis uses the pedal disc to attach to a substrate, but it is much better developed in the rock Phyllactis and the attachment is stronger.

Internally, there are usually two siphonoglyphs and 20 to 24 pairs of perfect mesenteries. A number of different muscles are associated with the mesenteries and most of these play a part in the digging behavior. The strong longitudinal retractors are located on the endocoelic surface of the mesenteries (except in the case of the directive mesenteries; there the muscles are exocoelic). On the opposite side of each mesentery there is a light sheet of transverse radial fibers (Figs. 2-3). Growing over these in the bottom half of the column are the well developed parieto-basilar muscles which originate at the base of the mesentery and form a triangular patch that tapers toward the upper part of the column. The parietals are strong and run longitudinally on each side of the mesenterial attachment of the column and form a continuous band with the parieto-basilars in the upper part of the column. Endodermal circular muscle lines the column and oral and pedal discs. There is a weak sphincter muscle below the ruff which may be derived from the circular muscle (Robson 1965).
In comparing the musculature of these burrowing anemones with that of the non-burrowing forms, there are noted some differences in the degree to which different muscle systems are developed. Batham (1950a) points out that compared with other types, the burrowing anemones have very powerful retractor muscles to execute a quick withdrawal. The environs of the burrow limit the possible distortion of the column and cause a greater increase in the internal pressure; this requires a stronger retractor muscle.

The sphincter muscle of these anemones is not well developed, and the only method by which one can produce a sphincter closure is by excess electrical stimulation. The sphincter muscle is part of a fast closure reflex in both Metridium and Calliactis (Robson, 1961), and is involved in the various "buttoned up" moods that Metridium assumes. The Phyllactis do not have protective closure of the oral disc. They withdraw rapidly into the burrow and only after much prodding will the Phyllactis fold the ruff up over the oral disc. Furthermore they do not show the "buttoned up" appearance of the other species. As in Stomphia (Sund, 1958), the parieto-basilar muscles of the two varieties of Phyllactis are well developed and serve an important function in the attachment and movement of the pedal disc.
The long column is characteristic of most burrowing anemones, and in the sand *Phyllactis* it may be as much as 30 cm long. When cross sections of the two varieties of *Phyllactis* are compared, there does not appear to be a difference in the thickness of the mesoglea or circular muscle in the column (Figs. 2-3); but the column of the rock *Phyllactis* does not rupture readily, while that of the sand *Phyllactis* does. The integrity of the column in the latter seems to depend on support from the sides of the burrow. It may be that differences in the ultrastructure of the mesoglea in the two varieties will be found. These two features, the longer column and the weaker body wall, added to certain components of its behavior (see below) make it appear that the sand *Phyllactis* is better adapted to burrowing and more dependent upon the protection of the burrow than is the rock *Phyllactis*.

**Nervous System**

**Histology**

The vital staining of the nerve net of an anemone with reduced methylene blue is a tedious process and does not always produce results. Enough success was attained in staining the two varieties of *Phyllactis* to compare the results with the description of the nerve nets of *Metridium* and *Calliactis* (Batham et al. 1960,
Fig. 1. The General Morphology of *Phyllactis*.

A cut-away view showing the exocoelic face of one mesentary and the endocoelic face of another. Part of the mesentarial arrangement is illustrated by their foreshortened insertions on the pedal disc.
Fig. 2. Cross Section Through the Column of the Rock Phyllactis.

Top: Column at mesentary insertion. Bottom: Retractor muscles on endocoelic surface of the mesentary. M, mesoglea; PB, parieto-basilar; C, circular muscle; R, retractor muscle; G, gastrovascular cavity; E, exocoelic face of the mesentary with transverse radial fibers.
Fig. 3. Cross Section Through the Column of the Sand Phyllactis.

Top: Column at the mesentary insertion. Bottom: Retractor muscles on endocoelic surface of the mesentary. M, mesogelea; PB, parieto-basilar; C, circular muscle; R, retractor muscle; G, gastrovascular cavity; E, exocoelic face of the mesentary with transverse radial fibers.
1961; Robson, 1961). There is a comparatively dense network of large bipolar cells that cross one another at intervals on the surface of the retractor muscle. They do not appear to be syncytial. The length of these bipolar cells depends upon the extent of relaxation of the anemone, but maximum lengths were 6 mm. The nerve net is sparse on the radial surface of the mesentery. There are no multipolar cells on the mesentery as there are in Calliactis (Robson, 1961). The column has few bipolar nerve cells and no multipolar cells in contrast to that of Calliactis or Stomphia. The sense cells are small but numerous; they are most numerous at the junctions of the mesenteries and column, in the oral disc, and in the tentacles. With the exceptions noted above, the nerve net in the Phyllactis does not appear to be basically different from that of Metridium, Calliactis, or Stomphia.

Functional Aspects

Both varieties of Phyllactis exhibit the characteristic facilitated response that has been described for other anemones (Pantin, 1935; Pantin and Vianna Dias, 1952). There is normally no response to a single electrical shock applied to any part of the column or ruff. However, if there is a series of shocks, there will be a symmetrical shortening of the column to each shock after the first, if the interval between shocks is shorter than 1.5 seconds.
at 21C. As the frequency increases there is a faster and stronger shortening. As in other anemones, this response is considered to be brought about primarily by the contractions of the retractor muscles. The extent of the retractor response (that is, how much the column shortens) is determined by the number of shocks. When the interval is lengthened, a retractor response will occur after the third or fourth shock, or not at all. The response in the Phyllactis is not always completely symmetrical; some records show a greater contraction of the column on the side nearest the stimulating electrode. After the termination of a series of shocks, there may be a greater contraction of the retractors, or an "after discharge" (Pantin 1935). Furthermore, there may be a parietal response around the column, or in one portion of it, usually within 30 seconds. This response is characteristically slower. Within a few minutes after the application of a series of shocks, the column elongates as a result of subtle peristaltic movements until the anemone is taller than it was before stimulation.

The intensity of the stimulus does not influence the size of the response unless it is many times threshold, and then it will increase the extent of the contraction. In some instances a single
shock of low intensity produces a retractor response, but this is usually true of anemones that have been stimulated electrically within the hour.

In both varieties of anemones the facilitating effect of a stimulus is influenced by temperature. At 21°C the longest interval between the first stimulus and a second which will produce 5% of the maximum response is 1.5 seconds. At 10°C the interval lengthens to 3 seconds, and at 32°C it is less than a second. These values are within the range of those recorded for Metridium and Bunodactis (Pantin and Vianna Dias, 1952).

As is true for Bunodactis, there was no obvious adaptation of the facilitation rate of Phyllactis to the tropical temperature range. As a consequence, at the normal or average environmental temperature, the greatest interval between facilitating stimuli is almost 3 seconds for Metridium and only 1 second for Phyllactis and Bunodactis. Like Bunodactis, Phyllactis does show some adaptation to the warmer waters in its rate of response and the range of temperature in which it remains active. That is, Phyllactis contracts at the same rate as Metridium when the water temperatures for the two anemones are those of the respective habitats. Metridium remains responsive to electrical stimuli at temperature of 5°C, whereas Phyllactis shows little response to
electrical stimuli at 10°C. *Metridium* will die before a temperature of 30°C is reached, and *Phyllactis* remain quite responsive at temperatures well above 30°C, as does *Bunodactis*.

*Phyllactis* also exhibit the typical slow responses to stimuli that are given at too low a frequency to elicit a retractor response. These responses are characterized by having a variable latent period; that is, they occur very shortly after a series of stimuli, applied once every 3 or 4 seconds, or several minutes later. The response itself varies. A series of ten or more shocks given to the rock *Phyllactis* at a low frequency causes the ruff to be raised until it sticks straight up and the column to elongate as a peristaltic wave of circular muscle passes downward. In the sand *Phyllactis* the low frequency shocks may cause some slight movements of the ruff and the column will usually elongate. In both varieties of anemones there are instances in which the low frequency stimuli will produce a slow shortening of the column. This is thought to be due to simultaneous contractions of the parietal muscles, but the activity then subsides. Parietal contractions have been studied quite extensively in *Metridium* (Batham and Pantin, 1950b), *Calliactis* (Needler and Ross, 1958), and *Bunodactis* (Pantin and Vianna Dias, 1952). Batham and Pantin (1950b) showed that facilitation of this slow response occurs under a different set of
conditions from those which result in the retractor response. The parietal musculature in Phyllactis is constantly active and gives varied responses to stimuli depending on the "mood" of the anemone. On some occasions only one or two parietal contractions will occur; at other times the same stimulus causes an elongation of the column as a peristaltic wave passes down the column.

There is another response that occurs frequently, and it is elicited by several stimuli at a low frequency, or by one shock. This is a sharp bending of the column, usually towards the stimulating electrodes. There may be as many as three quick contractions on one side in response to separate stimuli, but they are not additive as is the retractor response. This response is more rapid than that seen when the parietals contract and is limited to one side of the column, so it would appear that the bending is due to a contraction of the parieto-basilar muscles. The sharp parieto-basilar contractions of Phyllactis due to a single stimulus or to a series of stimuli is very similar to that which Hoyle (1960) reported for Stomphia. Ross (1965) states that the quick response of parieto-basilar muscles in Stomphia is rare in anemones and that it indicates these muscles are especially adapted physiologically for their role in detachment and swimming. However, a one-sided response of the column is seen in Metridium in response to a beam
of light and in *Bunodactis* when the column is stimulated mecha-
nically (Pantin and Vianna Dias, 1952). These movements are re-
ported as parietal responses. Pantin (1965) says, however, that
another assessment of these responses is necessary.

Analysis of Burrowing Behavior

The Buried Anemone

The buried sand *Phyllactis* in Cholla Bay has only the ruff,
oral disc and tentacles exposed. When the tide is out the ruff and
oral disc may be covered with sand, and the anemone is hardly
visible. During the tidal excursions in the summer when the sand
flats may be exposed to the sun for more than an hour, the anemones
pull back as much as two inches into their holes, leaving an im-
print of their ruff in the sand. When the tide starts to come in, the
anemones elongate until the oral disc is level with the top of the
burrow again. Strong mechanical stimuli will cause the animal to
withdraw. Apart from periodic elongations and withdrawals, there
does not appear to be much activity on the part of these anemones.
Nevertheless, they do not seem to be as readily found in the in-
tertidal areas in summer as they are in winter, when the lowest
tides occur at night, and there is a possibility that they migrate to
deeper waters. In an effort to test this hypothesis, twelve sand
Phyllactis were released in a marked location and allowed to dig into the sand. They remained in this location for two summer months and showed very little lateral movement, so that these anemones must be scarce for some other reason.

Rock Phyllactis buried in a tide pool have the ruff, oral disc, and tentacles exposed, but those located in crevices have just the ruff exposed. These anemones do not live in as definite a burrow as do the sand Phyllactis, but are firmly attached to the bottom or side of a rock and their column is surrounded by sand. They, too, will pull back into the sand if strongly stimulated.

Both varieties of the anemones may be maintained in the laboratory for a year or longer. However, sand Phyllactis will not live for longer than a week unless they can burrow in sand. If they are out of sand for more than a few days, the column begins to deteriorate. In the burrowed anemones there is little change in position or attitude from day to day. Occasionally a rock Phyllactis will extend its ruff above the substrate in a funnel-like shape. The greatest activity is seen when live brine shrimp are added to the water, at which time the tentacles are extended and become active. Phyllactis, whether or not they are buried in the sand, do no exhibit the occasional "buttoned up" attitude that is
typical of *Metridium*. Physiograph records show that buried anemones are not quiescent, but exhibit an arhythmic activity (Fig. 6).

**Walking or Creeping**

The terms "walking" and "creeping" have been used by various authors (Pantin, 1952; Stephenson, 1935) to indicate the lateral movements of anemones across several centimeters of hard or soft substrate. This activity also occurs in *Phyllactis*. Physiograph recordings and observations of the movements of the rock *Phyllactis* show that there is a great similarity between walking movements and digging movements, as shown in figures 5 and 9. Walking occurs when the column is more or less perpendicular to the substratum and is accomplished by rhythmic shortening of the column, with 5 minute intervals between contractions (Fig. 5A). The portion of the pedal disc that is leading as the anemone moves across a surface is the most inflated, and tone increases toward the back of the pedal disc. When the lead portion of the pedal disc is fully inflated and attached, there is a sharp contraction of the parietal muscles over this part of the disc, causing the column to bend forward. Parietal contractions then spread around the column in both directions from the original site of contraction and the whole column is shortened. Then a wave of
contraction, which deflates the pedal disc, starts at the trailing edge of the pedal disc and spreads around the sides and toward the center of the disc. The parieto-basilar muscles and other musculature of the pedal disc appear to play a part in this contraction which causes the back edge of the pedal disc to loosen its hold on the substrate and move forward. The contraction of the column is followed by a peristaltic wave that pushes water into the foot and causes the column to elongate. At this time the leading portion of the pedal disc begins to reinflate. This series of movements is repeated as the rock Phyllactis moves slowly across a surface with the lead portion of the pedal disc appearing to pull the anemone along, as it alternately inflates, attaches, deflates, and detaches. This behavior is not unusual for the rock Phyllactis in laboratory aquaria: one of these anemones placed on a rock in an aquarium with a sand substrate will often walk off the rock and burrow into the sand (Fig. 4). On some occasions rock Phyllactis in the aquaria have been observed to work their way out of the substrate in which they are buried, walk up the side of the aquarium to the water level, remain there for a few days, and then go down the side and burrow back in. Movements of an anemone walking up a wall do not appear to be different from those seen in an anemone moving across a horizontal surface.
Fig. 4. A Series of Photographs Showing the Various Phases of Pedal Disc Activity as a Rock Phyllactis Walks on a Rock.

A. The rock Phyllactis shortly after being placed on a rock.
B. Ten minutes later the anemone has moved sideways on the rock and the pedal disc is beginning to fill.
C. After a few minutes the pedal disc is nearly filled, and a contraction followed shortly.
D. Three minutes pass and the pedal disc is nearly deflated except for the lead portion on the left.
E. Ten minutes later the anemone shows marked progress in moving down the rock. The pedal disc is quite inflated.
F. Several minutes pass, the anemone has gone through the contraction and deflation stages, and the pedal disc is beginning to inflate again.
Fig. 4. A Series of Photographs Showing the Various Phases of the Pedal Disc Activity as a Rock Phyllactis Walks on a Rock. Elapsed Time Between A and F is Nearly 30 Minutes.
Walking or creeping on the pedal disc was observed less frequently in the sand *Phyllactis*. Usually, when this anemone moves, it will do so when lying on its column. It pulls itself along in an orally oriented direction by means of circular muscle contractions that pass up from the pedal disc to the mouth with a periodicity that varies with the animal and the circumstances. However, on one occasion a very large sand *Phyllactis*, that was well under way in its digging activity, walked when it was picked up and placed on a glass plate to determine if rhythmic activity would continue (Fig. 5B). The column contractions did continue, but they seemed to be involved with a movement of the pedal disc over the surface as the animal moved across the glass plate and started to burrow into the sand. This interruption of digging was repeated three times, and in all instances the animal made its way across about 3 cm. of glass until it was burrowing again into the sand.

The kind of locomotion exhibited under these circumstances is somewhat similar to that seen in the rock *Phyllactis*, the main difference being that all parietal muscles in the sand *Phyllactis* contract simultaneously. The leading edge of the pedal disc was more inflated and showed less tone than the trailing portion. Once the pedal disc was inflated, contractions of the parietal muscles occurred, the column shortened, and contraction of the
Fig. 5 Physiograph records of *Phyllactis* walking movements.

A. Rhythmic contractions of a rock *Phyllactis*. Reduction in amplitude and arhythmicity of contractions in the center tracing are due to this being the least inflated side and the contractions are not as distinct. Rhythmic contractions continue as the anemone moves off the plate, but the tension decreases on one side due to the movement, and the contractions are then recorded on just one side.

B. A combination of rhythmic digging and walking movements of a sand *Phyllactis*. At 1 the anemone walked off the glass plate and started to burrow. At 2 the anemone was placed back on the glass plate, but walked off just before 3. At 3 the tension of the myograph levers was readjusted in order to record the rhythmic contractions of digging. Note that the time scale from 3 on is different from that of the first three quarters of the record.
Fig. 5. Physiograph Records of the *Phyllactis* Walking.

A. Rhythmic Contractions of a Rock *Phyllactis* Walking.
B. A Combination of Rhythmic Digging and Walking Movements of a Sand *Phyllactis*. 
parieto-basilar muscles made the pedal disc deflate. In fact, it appeared that perhaps the contraction started in the parieto-basilar muscles and spread to the parietal muscles. The column began to elongate again as a band of circular muscle contraction passed down to the pedal disc and caused it to deflate. This deflation of the pedal disc appeared to release it from the surface to which it was attached, and then, as the leading edge of the disc reinflated, the pedal disc moved forward. On one occasion the lead was switched over to another portion of the pedal disc that was 90 degrees from the original location, and the animal moved off in another direction. The movements were rhythmic, with an interval of 5 minutes between contractions.

Substrate Selection

As indicated in the previous section, the two varieties of Phyllactis show an ability to move around or walk on the pedal disc. In order to see if this particular behavior is used in any sort of purposeful selection of substrate, a number of experiments was carried out. In these experiments Phyllactis were placed in a 5 gallon tank with four different substrates. The different substrates were laid out in triangles so that the apexes met in the middle. Two anemones were placed on the surface in the center of
each of the different substrate triangles and checked periodically from 3 days to 2 weeks to see what movements occurred. Four different sets of rock Phyllactis were tested, and even though some did not initiate digging movements for 24 to 48 hours, on most occasions they dug into the substrate on which they had been placed. In only two instances did two of the animals move from a very fine substrate, that is, a number 60 in one case and number 40 in another, to a coarser substrate. Once they were dug in and attached, these anemones stayed in place and did not move by pulling themselves along the glass bottom.

The sand Phyllactis showed more movement from one substrate to another. Six different sets of eight sand Phyllactis were tested. The anemones were left in the experimental tank for as long as 2 weeks to see how long it would take for them to stop moving. Most sand Phyllactis would burrow into the sand on which they were placed within 2 hours. The anemones that moved would either lie on the surface and move by inching along on the column as described in the previous section, or else move after they were buried by pulling themselves along on the glass bottom. Ordinarily about one-half (4) of the anemones would move before they buried, but only two of these would move to another substrate. On four different occasions animals moved from a coarser into a finer
substrate, and on three different occasions sand *Phyllactis* moved from a finer to a coarser substrate. No further walking movements occurred in most cases after 24 hours, but a few of the anemones took 48 hours to settle down.

From these experiments it does not appear that sand *Phyllactis* make a purposeful selection of a substrate of a specific grain size. Any movements prior to burrowing are random.

The Burrowing Anemone

**Sand Phyllactis**

A sand *Phyllactis* placed on any of a variety of substrates starts digging in a few minutes. The contractions of the muscles associated with digging are rhythmical, and there are at least three muscle systems intimately involved. In short, the actual digging appears to be accomplished by a shortening of the column which forces fluid into the inflated pedal disc and the disc into the sand. This is followed by an elongation of the column as the animal prepares for the next contraction. The anemone continues to dig until it reaches hard substratum, either a rock or a large shell or shell fragment. Temperature and composition of substrate affect the digging performance, but under laboratory conditions which come closest to those of the animal's environment, an
anemone will dig in completely within 3 hours. Once it is attached to the hard substratum, the rhythmic contractions cease (Fig. 6).

When an anemone is digging into the sand, it is possible to observe only parietal and circular muscle contractions. However, parietal-basilar activity can be seen as well if an actively digging sand Phyllactis is placed on a glass plate, since the same rhythmic contractions once initiated appear to continue. Also observations of parietal-basilar activity of the anemone may be made as it digs close to the glass side of an aquarium.

The various phases in burrowing behavior are diagrammed in figure 7 (bottom). The shortening of the column (Fig. 8A bottom) may be regarded as the first step in burrowing and at least three sets of muscles are involved. Typically, such a movement is said to be due to parietal activity (Pantin 1952; Batham and Pantin 1954). However, if the pedal disc is hooked up to one myograph and the column and ruff to the other two, physiograph records show that the first contraction in the pedal disc occurs approximately 30 seconds before any in the column and ruff (Fig. 7). This, along with observation of the burrowing anemone, would seem to indicate that the parieto-basilar muscles contract in unison first and this action is followed by a simultaneous contraction in the parietals. There
Fig. 6. Physiograph Record Showing the Completion of the Digging Activity of a Sand Phyllactis.

Arrow indicates a brief retractor response and the start of the arhythmic movements (spontaneous activity) typical of a buried anemone.
Fig. 7. A Physiograph Record of the Burrowing Activity of a Sand Phyllactis.

Lines 1, 2, and 3 indicate movements of levers attached to the upper part of the column, to the pedal disc, and to the ruff, respectively. Vertical lines have been drawn to facilitate the comparison of lines 2 with lines 1 and 3.
must also be a slow contraction of the retractors for the oral disc to pull down so symmetrically (Batham and Pantin 1954).

Following shortening there is an elongation of the column as the parietals and parieto-basilars relax and a peristaltic wave of circular muscle contraction moves toward the pedal disc (Fig. 8B bottom). The circular muscle contraction may appear as a discrete band moving down the column, or it may appear as a wave of increased tone passing down the column. The start of the circular muscle contraction is signaled by a slight tightening of the ruff around the column of the anemone.

When the circular muscle wave reaches the pedal disc, which is quite inflated during parietal contraction, the latter constricts and assumes a concave shape (Fig. 8C bottom). However, within 30 seconds to a minute the pedal disc begins to enlarge again and to assume a convex shape as water flows in and the parieto-basilar and circular muscles relax (Fig. 8D bottom). This latter movement detaches the pedal disc from any rock or shell to which it may have adhered during the contraction of the parietals. Once the pedal disc is fully inflated the parieto-basilar contractions reoccur, followed by the parietal contractions. Some records show an occasional quick contraction of the retractor muscles during digging (Fig. 9B). This is a random event which occurs after the
animal has started digging. Such a contraction forces water out of the column through the anemone's mouth and makes the anemone smaller. The smaller anemone settles into the larger hole. A quick contraction often occurs upon cessation of the rhythmic digging movements (Fig. 6).

Physiograph records of the digging movements of the sand Phyllactis show the time course and extent of movement during each phase of the digging behavior. Each tracing of the contraction and the subsequent elongation of the column may be divided into approximately five phases. Phase "A" in figure 8 (bottom) represents the shortening of the whole column as the parieto-basilar muscles and the parietals contract simultaneously. The subsequent change in slope, the first part of which is marked as "B", represents the relaxation of the parietals and the elongation of the column due to a peristaltic wave. There is a plateau at "C", sometimes with a slight peak. This represents the time when the anemone settles into the substrate as the peristaltic wave reaches the pedal disc and the latter deflates. "D" represents further elongation of the column as there is an increase in tone in the circular muscle and the pedal disc fills with water. This is the stage preceding the next parietal contraction. In some recordings there is a fifth phase "E" which represents a final elongation occurring immediately
Fig. 8. Diagramatic Representation of Movements of the Burrowing Phyllactis and Their Relation to the Physiograph Tracings.

before the contraction. The rhythmic quality of the contractions is shown in figure 9A, which, because of its length, is an unusual record. Nevertheless, a portion of it is representative of the sustained rhythmic activity in all digging anemones. Figure 9B is an expanded record which shows the simultaneous contraction of all parietal muscles in the sand Phyllactis during digging.

The physiograph records of the digging movements of the sand Phyllactis are quite consistent, not only with regard to pattern, but also as to time course. In more than thirty records, the most frequently measured time interval between parietal contractions was 4 minutes at 21°C. The interval between contractions may be somewhat longer or shorter at the beginning or end of the digging activity. The effect of temperature and other parameters on this interval is discussed below.

Sand Phyllactis were observed after they were released in Cholla Bay. When the anemones are placed in a small tide pool they begin to dig within 10 minutes. The mucous around the column soon makes it appear as if the anemones are in an envelope of fine sand. By the time an hour has passed the anemones are quite well dug into the substrate. As far as could be determined, the burrowing movements of these animals in their natural habitat were
Fig. 9. Physiograph Records from the Burrowing Phyllactis.

A. Record from a sand Phyllactis showing rhythmicity of the burrowing movements maintained for nearly 9 hours.
B. Record from a sand Phyllactis showing the simultaneous quality of the contractions. Points 1 and 2 indicate a sudden contraction of the retractor muscles.
C. Rock Phyllactis record. Tracings 1 and 2 are recorded from parts of the column with the strongest contractions (that is, those parts that are over the more inflated portion of the pedal disc).
the same as those of the anemones in the laboratory. Sand Phyllactis that were released in the moving waters of the bay were rolled about on the sand and were not able to dig in.

Rock Phyllactis

Rock Phyllactis will dig into a number of different substrates, but not into fine sand such as that which will pass through a U.S. number 60 sieve. Good digging records are more difficult to obtain from these anemones than they are from the sand Phyllactis. The rock Phyllactis are less apt to dig after being detached from the substratum, and thread loop attachments seem to be more inhibitory. The ruff of the rock Phyllactis is larger than that of the sand Phyllactis and consequently if the former anemone does dig, various movements of the column tend to be hidden from the observer. Nevertheless, many careful observations reveal that the digging behavior of the rock Phyllactis is basically the same as that of the sand Phyllactis, with contractions of the column forcing the partially inflated pedal disc into the substrate. However, in the rock Phyllactis there is not the simultaneous contraction of all parietal muscles which is seen in the sand anemone, but instead discrete parietal contractions progress around the column. The different movements associated with digging are shown diagrammatically in figure 8.
When a rock *Phyllactis* starts to dig, there is first an inflation of two-thirds of the pedal disc while the remaining one-third of the disc maintains its shape. This gives the anemone a rather lopsided appearance with a wedge-shaped foot (Fig. 8A). The portion of the pedal disc that is most inflated is not always the same. This was determined by placing four colored threads around the pedal disc, then pulling the animal up after it had started to dig and observing in which area the foot was most expanded. There did not appear to be any way to predict which part of the pedal disc would be most inflated.

The parietal contractions occur in a stepwise fashion about the column. Spread of this excitation around the column is rather slow: 3 to 6 seconds elapse before a contraction occurs one-third of the way around, and about 10 seconds before all the parietals have contracted. The area or "leader" where the contraction starts may be associated with the area of greatest inflation, but often the lead area will change, though there does not appear to be any predictable time interval or sequence for such a change. The contractions around the column are not of equal strength; the greatest contraction is always associated with that part of the pedal disc that is most inflated (Fig. 9C). It was determined a number of times that the increased tension on the physiograph transducer
did not bring about the greater contraction, since lowering the transducers as the animal dug in relieved the tension on the transducer spring only and had no effect on the extent of contraction. It is hard to observe the pedal disc of these animals as they dig, but in two instances it did appear that as the parietal contractions were occurring there was an increase in tone in the lower one-third of the column indicating a contraction of the parieto-basilar muscles.

Following contraction of the column the peristaltic wave, which may appear as nothing more than an increase in tone of the body wall, moves toward the pedal disc which is deflating endocoel by endocoel. The column begins to elongate at this time because of the relaxation of the parietals and the general increase in column tone due to the peristaltic wave (Fig. 8B, top). The progressive deflation of the pedal disc, due to the parieto-basilar and circular muscle contractions, starts in the region of greatest tone and proceeds around the pedal disc in both directions. The previously inflated portion of the pedal disc is drawn back from its former position in the substrate and the whole pedal disc assumes a concave shape (Fig. 8C, top). Within a minute the pedal disc begins to fill again endocoel by endocoel, starting with the least inflated
area; this results in further extension of the column of the anemone (Fig. 8D, top). Once the pedal disc is inflated to its maximum, the parietal contractions occur again.

The time course and pattern of various phases of the digging behavior in the rock Phyllactis can be clearly seen in different physiograph tracings. As with the sand Phyllactis, the tracings can be divided into five stages. This is illustrated in figure 8 (top). The first stage (designated as "A") appears in every record and represents the rapid column shortening which is due to parietal and probably parieto-basilar contractions. It is recorded as a sudden upward deflection of the physiograph stylus. It does not have two components: that is, it is not possible to separate the parietal and the parieto-basilar contractions.

The "B" stage is correlated with the relaxation of the parietals and the passage of the peristaltic wave down the column. The next phase (designated as "C") represents the 15-30 seconds during which the animal settles into the substrate as a result of the deflation of the pedal disc. "D" represents the extension of the column caused by the inflation of the pedal disc, further relaxation of the parietal muscles, and increase in circular muscle tone. A final portion, "E", is the upward movement of the ruff when the peristaltic wave originates in the sphincter prior to the contraction.
of the parietals. In some cases this last movement may be due to the final filling of the pedal disc. This whole series takes approximately five minutes. There is some variation in the amount of time required for each stage of column elongation.

As indicated above, the magnitude of contraction is not the same in all portions of the column. This is most clearly shown in physiograph records where pen excursions are of different amplitude in each of the three channels (Fig. 9C). Furthermore, with the shift in point of origin of parietal contractions there is a subsequent change in the strength of contractions recorded from any one part of the column. In most records there is one tracing that is associated with movements of the column on the side where the contractions are less extreme. This tracing (Fig. 9C, no. 3) differs from the other two in that the peak of contraction is not sharp; it appears rather broad and often there are two peaks. The relaxation between peaks is an indication of a strong contraction on the other side of the column, causing the opposite side to be lifted up temporarily.

The parietal contraction in any given area of a column is rhythmic, and in thirty different physiograph records of digging animals, five minutes was the most frequently measured interval
from one parietal contraction until the next at 21C. Deviations from this five minute interval occur in most cases at the start or finish of a digging record.

In some instances, as the anemone continues to dig into the substrate, it appears that more and more of the parietal contractions occur simultaneously. These unified contractions are similar to those seen in the sand Phyllactis and only occur in an animal that has started digging and has its pedal disc well into the substrate.

As indicated previously, physiograph recordings of a rock Phyllactis digging into a substrate are harder to obtain than those of a sand Phyllactis. However, there are a number of records, some as long as 12 hours, that show "typical" movements associated with digging, even though the anemone did not dig in. The factors which prevented the anemone from digging in are, at present, unknown.

The Effect of Various Parameters On Burrowing Behavior

Substrate

Anemones were placed on sands of different grain size, and recordings were made of their digging movements in order to determine if the burrowing performance was influenced by substrate composition. After a number of different trials it was evident that
for both kinds of Phyllactis the most consistent digging performance occurred in substrates that ranged from a rather coarse sand to one with medium-sized grains (U. S. numbers 4 through 20).

In sand as fine as U. S. number 60, the rock Phyllactis exhibited rhythmic contractions with the usual 5 minute interval, but the pedal disc scarcely penetrated the sand. However, sand Phyllactis were able to dig into such fine sand, though it appeared that they took longer to make the initial penetration than they would in coarser sand.

Both kinds of Phyllactis are able to burrow into smooth shell fragments that are from about one-third of an inch to 1 inch in diameter, but the digging records of the sand Phyllactis do not show the usual simultaneous parietal contractions, and movements seem somewhat distorted because of the different positions assumed by the anemone as it makes its way among the shell pieces. Visual observations indicated that the burrowing behavior was not greatly different from that of an anemone digging into sand.

**Temperature**

A few experiments were run to determine the general effect of a rising or falling temperature on the digging behavior of the
two varieties of *Phyllactis*. The cooling or heating of the water was started after the animals appeared to be well into their digging, and, in order to determine the effect on the most active digging phase, the temperature was changed with relative rapidity.

An increase in the water temperature from 20°C to 32°C over a period of 3 hours caused the interval between the contractions to shorten until it was one-half of the original interval shown by the two varieties of *Phyllactis*. At approximately 32°C the rock *Phyllactis* stopped digging even though it had not reached a firm substrate. The sand *Phyllactis*, even though attached to the substrate, would continue to contract rhythmically. When the water was cooled from 21°C to 10°C the anemones continued to dig, though the interval between contractions increased. By the time the water temperature was down to 10°C the rock *Phyllactis* stopped digging, and the contractions of the sand *Phyllactis* would be as much as 12 minutes apart, although digging continued. The digging activities of the rock *Phyllactis* appeared to stop whenever there was very much of an increase or decrease in the temperature; however, digging would resume again as the water temperature returned to 21°C.

Both varieties of *Phyllactis* were put into water of various temperatures to see if digging would be initiated at these
temperatures. At 28°C the rock *Phyllactis* dug into the substrate if left for 24 hours, but the sand *Phyllactis* just lay on the surface. At temperature as high as 33°C the rock *Phyllactis* showed some activity. When both *Phyllactis* were placed in 10°C water, they would not dig. However, when the water was warmed slowly, the sand *Phyllactis* started digging as the water neared 18°C, but the rock *Phyllactis* remained lying on the surface.

Not enough of these experiments were run to reach any valid conclusions. However, it appears that the interval between contractions decreases with increasing temperature, and that the ranges of temperature over which these animals are active are those of tropical anemones. The limits of digging activities are variable, but if these data show trends, they are that sand *Phyllactis*, once buried, are more active over a wider range of temperatures than the rock *Phyllactis*, but that the latter are more likely to initiate digging at warmer temperatures.

**Food**

Introduction of live adult brine shrimp into a tank with anemones that have not been fed for a week causes the buried anemones to become active. Within five minutes the ruff raises above the substrate and the tentacles extend further out from the
oral disc and show some movement. When a brine shrimp inadvertently makes contact with a tentacle, it sticks to it; probably it is impaled by nematocysts. Then the tentacle bends toward the mouth, which opens; the shrimp is caught up in mucous and ciliary activity, and is taken into the actinopharynx. As many as three or four shrimp may be caught in the tentacles at a time and each in turn will be pushed into the mouth. Anemones do not require live prey, however, and will consume bits of frozen fish or shrimp or even commercial shrimp pellets.

Five of fifteen sand Phyllactis buried in an aquarium were pulled up and allowed to start digging again. They had not been fed for a week. Once the 5 anemones started actively digging, about 100 adult brine shrimp were released in the water. Only the animals that were dug in showed feeding activities, and they would catch as many as 10 shrimp each before they stopped feeding. Brine shrimp that swam into the tentacles of digging anemones, on the other hand, would get stuck momentarily and then work free. Others just swam through the tentacles without being caught. A similar experiment was done with the rock Phyllactis. Once again, those anemones that were digging back into the substrate would not show any tendency toward feeding; whereas, those rock Phyllactis that were
buried would catch and feed on at least 5 to 10 brine shrimp. These experiments suggest that there is a change in threshold for nematocyst discharge during digging, possibly brought about by nervous inhibition.

**Interrupting Nervous and Muscular Pathways**

A number of rock and sand *Phyllactis* were cut in various parts of the column to see what effect this would have on digging. The cuts were made into the pedal disc, into the spinchter, one-third of the way around the column, and completely around the column, removing the oral disc and ruff. In all instances the rock *Phyllactis*, no matter what kind of cut had been made, would still be able to dig into the substrate, and the digging behavior seemed the same. In one case, a rock *Phyllactis* with oral disc and ruff removed dug in, and then grew a new oral disc and ruff and was still alive 10 months after the experiment. In the case of the sand *Phyllactis*, cuts into the pedal disc did not seem to inhibit or stop the digging activities, but after cuts into the column or removal of the oral disc these animals would lie on the surface and eventually die.
Electrical and Mechanical Stimulation of a Digging Anemone

It has been shown in previous sections that anemones pulled out of the sand after they had started burrowing would resume digging if placed back on the sand, or would continue contracting rhythmically if placed on a hard substratum such as a glass plate. In the latter instance, the rhythmic contractions became part of the walking behavior, allowing the anemone to move off the plate and dig back into the sand. The time between the removal from the substratum and the return to rhythmic activity was quite variable and depended somewhat on the kind of anemone and how much of a disruptive effect removal had on rhythmicity. In comparing the two populations of anemones, it was found that the rock Phyllactis were not as likely as the sand Phyllactis to resume digging immediately after being pulled out, and in some instances they stopped digging altogether.

Different strengths of mechanical stimuli applied with a glass rod elicit responses ranging from the slight twitch of a tentacle to complete withdrawal (the retractor response) of an anemone that is burrowed in. Stimuli given with a glass rod were ineffective in initiating burrowing in a loose anemone, and light touches did not affect the behavior of a digging anemone. On the
other hand, a strong stimulus would evoke a retractor response at any time. However, if the anemones were digging, they recovered from this stimulus quickly and continued their rhythmic activity.

On no occasion did it appear that any combination of electrical stimuli could elicit rhythmic digging behavior in an inactive anemone lying on the surface of the sand. Electrical stimuli did have some effect on burrowing animals. A series of stimuli were given to digging animals during various phases of the digging activity at a frequency and voltage (twice threshold) that would elicit either a parietal or a retractor response in a non-burrowing animal. The results show, in general, that a stimulus which normally evokes a parietal response when given in the interval between contractions, or a stimulus which normally evokes a retractor response when given during any phase of contraction or relaxation does not upset the rhythmic pattern of digging. But a stimulus of sufficient strength and frequency to produce a retractor response that is given during the "C" or relaxation phase of the column seems to increase the extent of relaxation before the next contraction.

These results show that an anemone's responsiveness to electrical stimuli is a function of the animal's attitude and position.
Electrical stimulation of an anemone that has just started to dig has more of a disruptive effect than stimulation of one that is well established in its digging routine, and an anemone appears to be less responsive while digging than when buried.
DISCUSSION

Burrowing and Its Relation to Other Activities

The burrowing behavior of the two varieties of Phyllactis represents another modification of the parieto-circular muscle sequence or column "action system" of the actinians. Pantin (1952) described a number of different functions for this well-defined mechanical system formed by the column, including maintainence of shape, movement in feeding, and locomotion by means of muscular waves in the pedal disc.

For the rock Phyllactis, walking and burrowing are very similar insofar as column activity and the movements of the pedal disc are concerned. In both types of behavior the lead portion of the pedal disc is highly inflated and there are rhythmic contractions of the parietal and circular muscles. The major difference is that in walking the lead portion of the pedal disc moves across the surface of the substrate, and in digging the lead edge pushes down into the substrate. The location of the rock Phyllactis with respect to the rocks and sand of intertidal habitat makes it appear that these anemones would be less likely to burrow than to walk along the surface of rock, pulling the column through the sand. However, in
contrast to other intertidal anemones, such as *Bunodosoma californica*, which remain attached to rocks or exposed ledges and show no inclination to burrow into a sandy substrate (personal observation), the rock *Phyllactis* is a burrowing anemone.

The usual mode of locomotion seen in large sand *Phyllactis* is not comparable to the digging behavior, although it does involve the parieto-circular muscle sequence. This anemone moves across the surface while lying on the side of its column, and alternate peristaltic waves and parietal contractions move it in an oral direction. In just one instance a record was obtained from a sand *Phyllactis* that was walking on its pedal disc in the manner of the rock *Phyllactis* (Fig. 5B). This pedal locomotion has been seen occasionally in very small sand *Phyllactis* that have come out of their burrows in the laboratory aquaria. However, the habitat of the sand *Phyllactis* is such that walking on the pedal disc is quite unlikely after the anemone is buried, and the anemone out of its burrow probably moves more readily across a sandy substrate by lying on its side than by walking on its pedal disc.

Batham (1965) has noted the similarity between walking and burrowing in the New Zealand anemone, *Mimetridium cryptum*, which walks readily and also burrows. She points out that burrowing is like walking in that there is a peristaltic activity of the
column in both instances, but that the leading lobe of the pedal disc in a burrowing animal is pointed downward instead of laterally. *Mimetridium* in its natural habitat is usually found half buried in the sand or mud and its pedal disc is attached to a shell or pebble.

Stephenson (1935) described burrowing in the anemone *Peachia hastata* which has a physa (a rounded aboral end which is used in digging) rather than a distinct pedal disc. At first, the anemone is bent in an arch and the physa rests vertically in the sand. Peristaltic waves pass down the column driving the water before them and distending the physa into a globular form. This distention pushes the sand away. The circular muscle contraction continues on down the column and diminishes the volume of the distended physa until the tip is introverted into the column. Another circular muscle contraction follows in a few seconds and distends the base again. The peristaltic waves alternately distend and contract the physa until the anemone is buried, and this takes about one hour. Stephenson did not mention whether or not contractions of the longitudinal musculature of the column accompanied the peristaltic contractions. Peristaltic waves are also seen in this anemone when it is merely lying on the sand, but it was not disclosed as to whether or not they were apparent in the anemone
that moved "aimlessly" about prior to burrowing. These anemones have no basal musculature, hence no pedal disc, so they cannot walk on the aboral end. They are normally buried in the sand with only the disc and tentacles showing.

According to the descriptions above it appears that in anemones that walk and burrow the two types of activity are very similar; but in those anemones that are primarily burrowers the digging activity is more specialized and more efficient, and locomotion is limited to the anemone's lying on its column and pulling itself along.

From brief descriptions of walking in Metridium (an anemone that does not burrow) it seems that this activity is very similar to that which has been observed for the rock Phyllactis. Batham and Pantin (1951c) and Pantin (1952) mention the high degree of coordination between all parts of the pedal disc and the column in the walking movements of Metridium, and the fact that it represents a complex modification of the parieto-circular muscle sequence in the column. However, they did not indicate that a distinct rhythmicity accompanied these parietal contractions. In the description of one kymograph record (Batham and Pantin, 1950c) mention was made of a locomotor phase and the greater frequency
of column contractions associated with it, but the drum speed was
too slow and the record of the individual contractions was not clear
enough to determine whether or not there was a rhythmic quality
to them.

Pedal disc locomotion is not common to all anemones. In
moving from one substrate to another some show very intricate
patterns of behavior. Calliactis, in order to transfer to shells
occupied by the hermit crab Dardanus, goes through a complex
behavioral routine involving the tentacles and whole column, and
Stomphia shows a similar activity in responding to the shells of
the mussel, Modiolus (Ross, 1965).

There are other features of the burrowing behavior that can
be compared with certain characteristics of the various anemones
that have been studied in detail. One such feature is the rhythmic
quality of the digging contractions, which may be maintained over
a period of hours. They have much in common with the rhythmic
inherent movements, which are "an observed property of the
anemone that does not arise from external stimulus" (Batham and
Pantin, 1950b). Batham and Pantin wrote three papers on
Metridium (1950b, 1950c, 1954) that are the basis for the under-
standing of some of the features of inherent slow movements in the
actinians. Needler and Ross (1958) and Ewer (1960) described a
similar rhythmic inherent activity in Calliactis. Pantin (1965) points out that knowledge of the importance of rhythmic phasic activity has now replaced early emphasis on facilitation and fast response and that many rhythmic activities are modifications of a basic sequence. An example of this is the stepwise parietal contractions that are part of inherent activity in the column of Metridium and occur at intervals of approximately ten minutes in these anemones (Batham and Pantin, 1950b). The contractions are not simultaneous, and some parts of the column follow the lead part by as much as one-half a minute. By using four attachments to the column, Batham and Pantin (1950b) observed that the parietal contractions did not necessarily progress around the column, for a part diametrically opposite the lead might contract before the intermediate region; so they surmise that a large part of the long delays in the contraction is of local origin, and is not due to slow progressive conduction across the whole animal. The parietal contractions are followed by a contraction of the marginal sphincter which in turn initiates a peristaltic wave. This is very similar to parietal activity in the burrowing or walking rock Phyllactis, and it would appear that a similar mechanism could control the two systems. In Phyllactis, only three attachments were used because of limitations in the number of recording channels, and
from three attachments the contraction pattern was not clear; however, there were delays of spread from one area to another that made it appear the conduction was not only slow but uneven. Even the time intervals between the contractions are nearly the same, because the recordings from Metridium were made in water that was about 15C, and the rock Phyllactis burrowing at this temperature showed intervals between contractions of thirteen minutes.

There is a similar inherent repetitive movement with a 10 to 15 minute interval at 15C in Calliactis, except that the column shortens evenly (Needler and Ross, 1958). The simultaneous shortening of the column in the burrowing sand Phyllactis is of the same sort that Needler and Ross (1958) describe as an "even shortening of the column and depression of the disc" in Calliactis. Also, the sand Phyllactis burrowing in 15C water would have nearly a 10 minute interval between contractions.

The Importance of Burrowing in the Natural Habitat

It is worthwhile to consider just how often in its lifetime a Phyllactis is going to need to burrow. Batham and Pantin (1950c) point out that the clonal arrangement seen in many groups of anemones makes it appear that the movement of these animals in
their natural environment is rare. *Phyllactis* show little movement in the laboratory aquaria. Once these anemones are in their burrows, and continue to be fed and maintained, they remain there for as long as a year, and even the best tended aquarium cannot be considered an optimum environment. It is difficult to imagine a very large *Phyllactis* leaving its original burrow and going to a new site. When these anemones are released in the open bay in three or four feet of water, they are constantly rolled and moved about by the water. It would seem that the only circumstance under which they could burrow into the sand again would exist if they were stranded in a small tide pool as the tide went out, and dug in while the water was calm. Should the environmental conditions of an anemone's habitat change by some shift of sand or movement of rocks or increase in temperature, a *Phyllactis* would probably leave its burrow and be carried by the current many feet. However, their success in burrowing in again might be small unless they were carried to quiet waters. Perhaps it is not necessary to account for the scarcity of the sand *Phyllactis* in the summer as being due to some sort of migration. The lowest tides occur during the day in the summer, and the anemones are much less likely to be fully expanded during the daylight hours. Sometimes in the laboratory aquaria, during the day the sand *Phyllactis* will be
drawn down slightly beneath the surface and be almost impossible to see. Burrowing appears to be a complex behavior that is innate in these anemones, and though it may be used only once in their lifetime it can be initiated in a very short time after the anemones have been dug up.

**Stimuli Involved in the Onset and Cessation of Burrowing**

In *Stomphia* swimming can be initiated by a specific stimulus, an extract of *Dermasterias* (Robson, 1961). *Calliactis* can be induced to move onto a new substrate by the presence of certain shell factors (Ross and Sutton, 1961). On the other hand, Batham and Pantin (1950c) feel that a locomotor phase in *Metridium* is initiated by a set of conditions, and not by a specific stimulus. Somewhat comparable to this is burrowing in *Phyllactis* which does not appear to be elicited by a certain stimulus, but instead by a set of conditions, albeit they are more specific than those for locomotion. The conditions necessary to bring about digging are lack of attachment of the pedal disc, absence of sand around the column, and a substrate to dig into. Placed on any substrate, from one-half inch shell fragments to very fine sand, *Phyllactis* will show digging activities. If the substrate sand is too fine, the
burrowing may not be successful, but the parietal contractions will
continue for about thirty minutes or so and stop, and then perhaps
start up again.

A soft substrate is more likely to cause the initiation of
digging activities than locomotion, but when the anemones do move
across the surface of the sand there does not appear to be any
purposeful substrate selection. The digging will usually continue
until the anemone is firmly attached to a hard substratum such as
a large shell fragment or the glass bottom of the aquarium.
However, the mere attachment of the pedal disc to a solid substrate
will not cause the rhythmic contractions to cease. This is seen in
anemones that are taken out of their burrows while digging and
placed on a glass plate; these anemones continue to show rhythmic
digging contractions. Another stimulus for the cessation of digging
must be the sand around the column. There are other unknown
factors as well. One very large sand Phyllactis continued to dig
for nearly nine hours, even though the pedal disc had probably
reached the bottom of the aquarium in the first two. Perhaps this
anemone was not "satisfied" with the extent to which its column
was buried.

Obviously there are a number of stimuli that are involved in
the initiation and the cessation of digging, and it appears that the
receptors for these stimuli are located in the pedal disc and column because an anemone without the ruff and oral disc can still bury.

The Control System

The burrowing behavior is innate and not dependent on environmental stimuli for each step. It is probably under the regulation of a system which controls the timing and sequence of every muscle contraction. The burrowing sequence, particularly the parieto-circular muscle contractions of the column in Phyllactis, is not unique, however, and though the pedal disc is not involved in the inherent activity of Metridium and Calliactis, it does seem to appear that control systems for such movements as burrowing and inherent activities are similar and are an integral part of the column "action system" of most anemones. The site of such a control system is hard to localize, but apparently it does not reside in the oral disc and ruff. Further, there is evidence that this control system not only initiates this behavior and acts positively to keep it going, but that it inhibits other activities as well. It inhibits nematocyst discharge and responses to low frequency electrical stimuli. Possibly this is because pathways in the nervous system which normally carry the information are occupied by information about digging behavior. However, some
messages do get through, and a retractor response may be evoked either mechanically or with electrical stimuli. Perhaps the mechanical stimulus and the higher frequency electrical stimuli recruit more units, or different ones, so that a response is evoked.

The Pacemaker

The interval between contractions is remarkably consistent in these burrowing anemones. For the sand Phyllactis at 21C the interval is always close to 4 minutes and for the rock Phyllactis at 21C the interval is 5 minutes. Not only is the interval consistent from anemone to anemone, but also it may be maintained for as long as 9 hours. As has been mentioned, the time interval is quite comparable to the time interval noted at the same temperature in the inherent rhythmic contractions of Metridium and Calliactis.

The first rhythmic behavior to be noted in Coelenterates was the rhythmic pulsations of jellyfish. After considerable study and debate, it was established that the jellyfish was the simplest animal with a true nervous pacemaker (Bullock, 1965). There is considerable variation in the intervals between beats in Aurelia, but the pulsations continue for hours. Stomphia is an anemone which has a behavior that is clearly pacemaker-controlled; Robson (1961, 1963) describes the parieto-basilar contractions that cause the column
bending or "swimming". The pacemaker is located in the middle of the column, perhaps in some multipolar cells that seem to be unique among anemones. The contractions in swimming last up to three minutes, and the intervals between the contractions are quite irregular. Often there are two quick contractions, then a pause. The two contractions are usually at diametrically opposite points of the disc. In contrast to the other pacemaker-controlled activities in the animals described above and in various other Coelenterates, Phyllactis exhibits an activity that is unique in its regularity and duration.

It is difficult to pinpoint the location of the pacemaker or pacemakers in Phyllactis. It has been shown at least that they are not in the oral disc or ruff. Multipolar cells of the sort that have been described for Stomphia are not obvious in the column of Phyllactis. The burrowing behavior is controlled by pacemakers, however, and is not a chain of reflexes in which each step in the behavior is dependent upon the completion of the previous step. The evidence for this is that rhythmic activity continues even when the anemone is pulled out of one substrate (sand) and put on another (glass). Furthermore, the interval between contractions is not affected by the size of the sand grain; and if the burrowing were controlled by a chain of reflexes and if one substrate could be
penetrated more rapidly than another, each step in the behavior would be completed sooner, and the interval between contractions would be shorter. The latter is not the case, and this fact is evidence of a pacemaker unaffected by external stimuli, except those that initiate the pacemaker's control of activity. The pacemakers may be of myogenic origin, since there does not appear to be any neuronal element which can be considered the source.

Pantin (1965) postulates that there might be local pacemakers in the normal parieto-circular contraction sequences in *Metridium*. In both *Metridium* (Batham and Pantin, 1954) and *Calliactis* (Needler and Ross, 1958; Ewer, 1960) the activity spreads from the sub-sphincter or pedal disc areas rather than from mid-column, but the morphological pathways for excitation of the column muscles are not known. Robson (1965) reports small multipolar cells in the sphincter region of *Calliactis* which are not strictly comparable to the much larger multipolar cells of *Stomphia*, and she feels it "is too early" to say whether or not these are concerned with autonomous activity. Ewer (1960) from his study of the rhythmic activity of the circular muscles of *Calliactis* suggests that rhythmic contractions arise from an inhibitory feed-back generated in some
manner by the contraction of the circular muscles. He felt that no pacemakers were involved since the rhythm of the contraction was not upset by an intercalated excitatory stimulus.

The burrowing behavior of *Phyllactis* represents a very consistent and predictable activity for an actinian, and this study presents primarily a description of the activity; the exact mechanism behind it remains to be determined.

**Comparison of the Two Varieties of Phyllactis**

Carlgren (1951) described two species of *Phyllactis* in the Gulf of California, *Phyllactis concinnata* and *Phyllactis bradleyi*. Cutress (personal communication) has tentatively classified both the sand *Phyllactis* and the rock *Phyllactis* as *Phyllactis concinnata*. The two anemones do represent at least two varieties. There are differences in the morphological features, such as the more fragile column in the sand *Phyllactis*, and there are subtle but distinguishable differences in color and structure in the overall appearance of the anemones as well. Also, these anemones are to be found in two different environments, and each appears to be well adapted to its own environment. However, no experiments were undertaken to see how one variety might fare in the habitat of the other. The sand *Phyllactis* is buried in the deep sand of Cholla Bay
and must burrow and remain in the burrow in order to maintain the integrity of the column. The rock Phyllactis has a very firm pedal attachment to a rock substrate, but it may move even though its less elongated column is surrounded by sand. The differences in the behavior of these anemones appear to be correlated with their respective environments. The rock Phyllactis exhibits a burrowing activity that is very similar to walking, and it would seem that in many instances this anemone pulls itself into the sand as it moves across the surface of a rock, rather than really burrowing. The sand Phyllactis, though, is a more efficient and predictable burrower and its usual form of locomotion is by pulling itself along the surface of the sand by peristaltic waves.

Further differences have been shown in biochemical tests (R. Pardy, personal communication). Electrophoretic separation of proteins has shown different patterns, indicative of differences in enzymes. However, species in anemones have been established primarily on morphological characteristics and great variation within a group that is identified as a single species of anemone is not unusual (Stephenson, 1935).

If the sand Phyllactis and the rock Phyllactis do indeed represent two varieties of the same species one would expect to find anemones that represent an "in between" group. Intermediates
do occur. There are slightly different Phyllactis anemones that are found occasionally near the reef outcroppings in Cholla Bay. These anemones are a little different color from the usual sand Phyllactis, the column is less elongated and has more of a tendency to hold together, and the ruff looks somewhat like that of the rock Phyllactis. On only two occasions were movements of these "in between" forms recorded. Efforts in the first instance were more successful than in the second, but the contractions of the column did not appear to be as consistently simultaneous as those of sand Phyllactis, and the pedal disc did not inflate evenly in the digging animal. In general appearance these "in between" anemones appeared to be more like the rock Phyllactis than the sand Phyllactis. It does seem, therefore, that the sand Phyllactis and the rock Phyllactis represent varieties of a species, and that the variations in anatomy, physiology, and behavior that have been noted are appropriate adaptations to their respective environments.
SUMMARY

The burrowing behavior of two varieties of the tropical anemone Phyllactis is described. The burrowing movements are similar to various other purposeful movements which require the parietal-circular muscle sequence. In the rock Phyllactis burrowing is a modification of walking, and the only difference in the two activities is that in burrowing the pedal disc is pushed downward into the substrate instead of moving laterally along the surface. The sand Phyllactis is the more efficient and seemingly specialized burrower of the two. This anemone seldom walks on the pedal disc, but when it does, it appears that the same muscular and coordinating systems are used as in burrowing. Ordinarily the sand Phyllactis moves along the substrate by lying on the side of its column and pulling itself along by peristaltic movements. Furthermore, there is a similarity between burrowing in the Phyllactis and various slow or inherent movements of the column that have been studied in Calliactis and Metridium.

The most unique feature of the burrowing behavior is the very consistent and predictable quality of the rhythmic contractions which can be maintained over a long period of time.
The general morphology of the Phyllactis is similar to that described for other anemones such as Metridium, Calliactis and Stomphia, except that the Phyllactis possess a ruff around the oral disc and very powerful retractor muscles. The nerve net on the retractors of the Phyllactis does not appear to be unique, and there are not multipolar cells in the column such as have been reported for Stomphia and Calliactis.

The two varieties of the Phyllactis anemone appear to be well adapted to their respective environments. Their adaptations are due to modifications of the rather limited morphological and physiological capabilities of the anemones. The most obvious adaptation of the Phyllactis to the water temperature of the region is their ability to remain active over a wide temperature range.
LIST OF REFERENCES


