# THE MECHANISM OF OPENING AND CLOSING OF *CALLIACTIS PARASITICA*

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(Text-figs. 1–4)

## Introduction

In a previous paper Chapman & Newell (1947) described the part played by the body fluid in the burrowing of the lugworm, and recorded the hydrostatic pressure occurring in the fluid contents of the coelom. The fluid-muscle system of this animal is completely closed, except for six pairs of nephridia which do not leak under pressures higher than those which occur naturally in the body of the worm.

It was considered of interest to inquire if the fluid-muscle system functions in the same way in an animal whose body cavity opens to the exterior by a wide aperture. *Calliactis parasitica* Couch was chosen as a large active animal whose normal or resting position is 'open'.

On the movements made by anemones, Hyman (1940) gives a few details of the method of working of the fluid-muscle system, but is obliged to quote Faurot's (1895) account of the burrowing of anemones into sand. Faurot describes only the outward appearance of the process in *Peachia* and says that 'il parait evident que le liquide qu'elles renferment est soumis à une compression'. Jordan (1935) gives an analysis of the properties of *Metridium* body wall, but does not describe the working of the muscular system as a whole. He demonstrates that 'muscle preparations' can be stretched by very small forces and that they do not spontaneously regain their original length when the forces are removed, but he does not distinguish clearly between the properties of muscle and those of mesogloea. Pantin (1940) states that 'on stimulation most anemones cover the disk by contraction of the longitudinal retractors and the parietal muscles of the mesenteries. The mouth, disk and tentacles are pulled in, and during this process some water is squirted out of the mouth. Full re-expansion subsequently requires the gastral cavity to be filled again with sea water. This is done by ciliary action of the stomodaeum and is a slow process. In *Calliactis*, closure is due primarily to the contraction of a powerful sphincter at the edge of the column just under the tentacles. There is little loss of contained water and re-expansion depends simply on the comparatively rapid relaxation of this muscle'. According to Stephenson (1928), water may be lost at the cinclides, through which the acontia are carried by water currents.

He considers that the cinclides may function as safety valves in preventing rupture of the body wall.

From the foregoing it can be seen that there is room for an investigation into the mechanism controlling the volume of contained water and the origin of the restoring force which brings about the 'rapid relaxation' of the sphincter during the movements of *Calliactis*. It would seem that some light could be thrown on the way in which anemones move by the measurement of internal hydrostatic pressure during various phases of movement coupled with observation of their movements and some knowledge of the distribution of their muscular tissues.

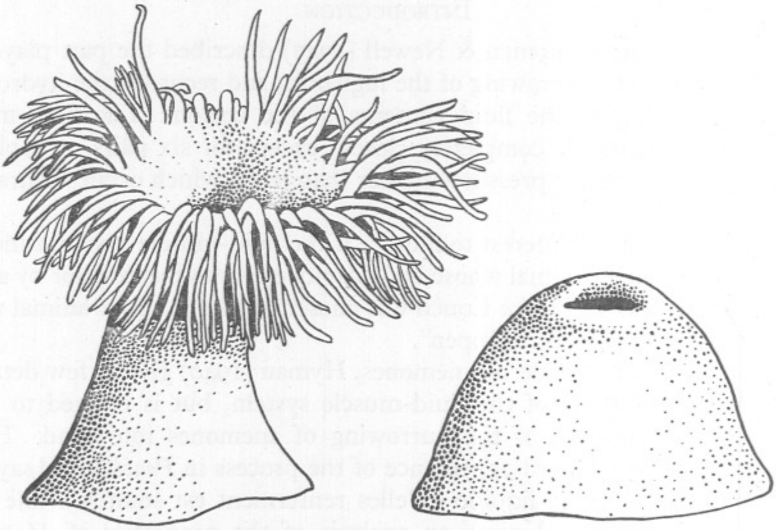

Fig. 1. *Calliactis parasitica* fully open and fully closed.

## Observations of Movements

When open, the tentacles of *Calliactis* are large, numerous, and well distended with water, and the disk is clearly displayed (see Fig. 1). On strong mechanical stimulation the animal can close rapidly and completely until its external surface is that of the column only (see Fig. 1). At the beginning of the contraction the tentacles diminish in size as their contents are expelled into the main gastral cavity, while the disk is retracted by the parietal muscles. A little later the powerful sphincter muscle at the edge of the disk just below the tentacles begins to contract so that the sides of the column are, as it were, drawn over the retracted disk until only a shallow depression indicates that the body wall is not continuous. The animal is now the shape of a bee skep and is firm to the touch, as if made turgid by the pressure of the muscular walls on the contained fluid. Even after strong stimulation this contracted posture is not long maintained, the sphincter usually beginning to relax in less than 2 min. Relaxation of the sphincter is followed by the expansion of the tentacles which are inflated by the inrush of fluid from the enteron of the column.

It seems unlikely that expansion as rapid as that shown by *Calliactis* could be accomplished by means of water pumped into the enteron by ciliary action. As mentioned by Pantin (1940) there is little loss of contained fluid, as was seen by putting a few drops of carmine suspension on to the opening of the stomodaeum of an expanded anemone and stimulating it to contract. Only when the sphincter had nearly closed was there any suggestion that water had been ejected from the animal, and at that stage of the contraction it might well have come from the liquid squeezed out from between the retracted disk and the enveloping sphincter. Conversely, carmine applied to a closed anemone showed that very little water, if any, was taken in during opening.

In addition, carmine suspension was placed near to the cinclides at the base of the column. Neither on normal contraction, nor on contraction strong enough to extrude the acontia, was any water seen to leave the apertures, even as the acontia were being expelled. It is unlikely that *no* water escapes during the extrusion of the acontia, but the amount must be very small.

A test was made to see if water was lost at each contraction by an amount small enough to escape observation but sufficient, when lost repeatedly, to affect the speed of opening and closing. A small anemone was stimulated mechanically twenty-two times in the course of 1 hr. 40 min., and at the end of the period was opening and closing rather more rapidly than at the beginning. The creature was stimulated strongly enough to cause complete closure but not sufficiently to cause the expulsion of the acontia.

Since the animal appears to behave as a closed system analogous to that of *Arenicola*, the stomodaeum being closed during movement, it might well be expected that there would be some considerable variations in pressure during different phases of muscular activity.

## THE INTERNAL HYDROSTATIC PRESSURE

An inclined capillary tube manometer filled with sea water was used to estimate the internal hydrostatic pressure, and was connected to the animal by a hypodermic needle of large bore. In use, the anemone formed the left-hand, and the capillary tube the right-hand, limbs of a manometer (see Fig. 2). Estimations were made by connecting the reservoir to the capillary tube until the level of the sea water in it rose to about 10 cm. above the level in the aquarium jar containing the animal. The tap was then turned so as to connect the anemone with the capillary tube and to cut off connexion with the reservoir. As preliminary tests had shown that less than 1 min. was required for the pressure in the animal and manometer to become balanced as shown by a stationary meniscus, scale readings were made 1 min. after the animal was connected to the manometer tube. Control tests, made with the needle free in the water of the aquarium jar, gave a correction to be deducted from the scale reading which allowed for the height of the water in the jar and for the small capillary rise of liquid in the manometer tube above the level in the aquarium. Finally, the scale reading, made to the nearest mm., was halved, since the slope of the manometer was such as to give a multiplication factor of 2.

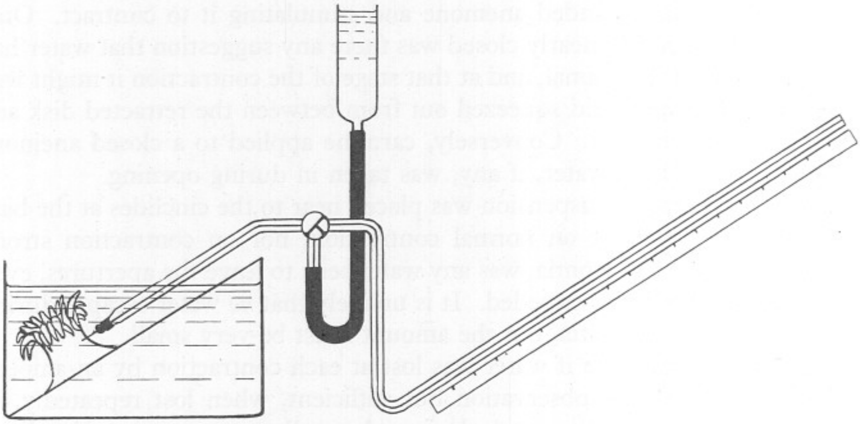

Fig. 2. Inclined capillary manometer.

TABLE I. MEAN PRESSURE IN CM. OF SEA WATER IN *CALLIACTIS*

| Test no. | Expanded | Contracted |
|---|---|---|
| 1 | 1·0 | 2·4 |
| 2 | 2·2 | 1·8 |
| 3 | 1·0 | 3·3 |
| 4 | 0·2 | 1·0 |
| 5 | 1·2 | 2·0 |
| 6 | 3·3 | 2·7 |
| 7 | 0·3 | 1·1 |
| 8 | 1·5 | 3·1 |

Several measurements were made on each animal both in the open and in the contracted state. Contraction was brought about and maintained by mechanical stimulation of the base of the column with a glass rod. Difficulty was sometimes experienced in keeping the animals contracted for a minute. The mean pressures measured by this method on the stock of eight animals are set out in Table I; detailed results are given in the Appendix.

The striking feature of Table I is the inconsistency of the readings, in spite of the fact that each figure represents a mean of between four and thirteen readings. Whilst, in general, the pressure in the closed animal is higher than it is in the open one, the amount of the difference is not constant, nor is the pressure in the open animals constant. A manometer was therefore made to give a continuous indication of the pressure changes inside the animal without, however, providing an exact measure of the pressures recorded, in order to show whether the instantaneous pressures previously recorded are representative of the normal pressure range.

## VARIATIONS OF THE INTERNAL PRESSURE

The apparatus, by which variations of internal pressure were shown (Fig. 3), consisted of a xylene-filled manometer connected to a very thin-walled rubber teat (*T*) at the end of a glass tube which could be manipulated and clamped with the teat in place in the enteron of the anemone. The air enclosed between the manometer and the teat could be put into communication with the exterior by a three-way tap, one position of which enabled the pressure within to be raised by blowing into it through a mouthpiece (*M*). The teat was made of rubber sufficiently thin to collapse when immersed in even 1 cm. depth of water, and hence was collapsed when it was quickly inserted into the stomodaeum of an open anemone. The glass tube bearing it was clamped into place and the teat was inflated by blowing gently into the mouthpiece until, at a pressure of 4 or 5 cm. of xylene, communication with the outside was cut off and the teat was left in communication with the manometer only. The apparatus was left for 5 min. to ensure that the air within the teat assumed the temperature of the water and hence remained practically constant during the course of the experiment. A scale was adjusted so that, at the beginning of the readings, the meniscus of the right-hand limb lay at zero. Readings of the pressure recorded by the manometer were made at 15 sec. intervals over

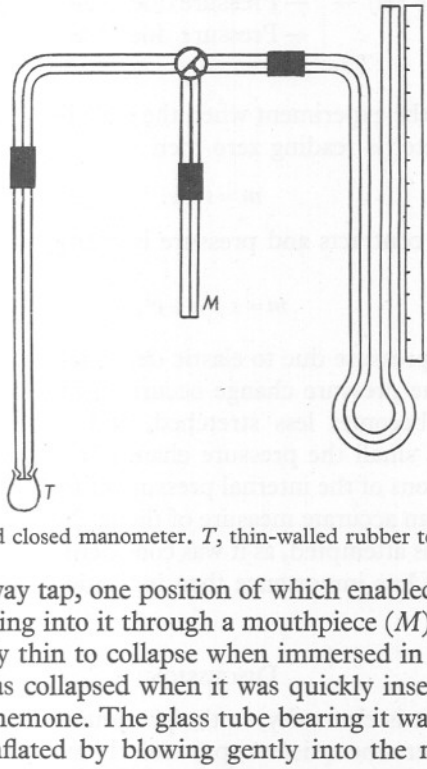

Fig. 3. Xylene-filled closed manometer. *T*, thin-walled rubber teat; *M*, mouthpiece.

periods of up to 40 min. duration. From time to time the animal was stimulated by prodding the column with a glass rod, and throughout the experiment its state, whether open or closed, was recorded with the manometer readings. The times at which mechanical stimulation was applied, together with a line representing the state of opening of the animal, were marked on the records. The results of three typical tests are represented graphically in Fig. 4.

It will be realized that the pressures recorded by the manometer are not equal to the pressures occurring in the animal, but are the reaction of the resultant of three pressures acting on the wall of the teat. They can be represented diagrammatically:

| | | |
|---|---|---|
| | \| | ← Pressure due to depth of submergence (*s*) |
| Manometric pressure (*m*) → | \| | ← Pressure due to elastic deformation of teat (*e*) |
| | \| | ← Pressure due to anemone (*a*) |
| | Teat wall | |

At the beginning of the experiment when the scale is set so that the right-hand limb of the manometer is reading zero then

$$m = s + e.$$

When the anemone contracts and pressure is exerted on the teat due to that contraction then

$$m = s + a + e^1,$$

where $e^1$ is the new pressure due to elastic deformation at the new size of teat brought about by the pressure change occurring in the anemone. As $a$ rises, therefore, the teat becomes less stretched, and $e$ is therefore diminished. Since, however, $e$ is small the pressure changes recorded by the manometer serve to show variations of the internal pressure of the anemone, even although they do not provide an accurate measure of them. No calibration or correction of the manometer was attempted, as it was considered that accuracy of pressure measurement was of less importance than indication of pressure change.

## DISCUSSION

From these records it is clear why, in the previous tests, measurements of the internal pressures were inconsistent, particularly in the closed animal.

From inspection of the graphs, and from observations made during the course of the experiments, it would appear that, on mechanical stimulation followed by closure, pressure rises rapidly, generally attaining a maximum within 15 sec. This maximum pressure is developed only momentarily and immediately begins to fall, during which time the anemone may remain contracted or may begin to open again. With the beginning of opening either the rate of fall of pressure is briefly arrested or a small rise in pressure may

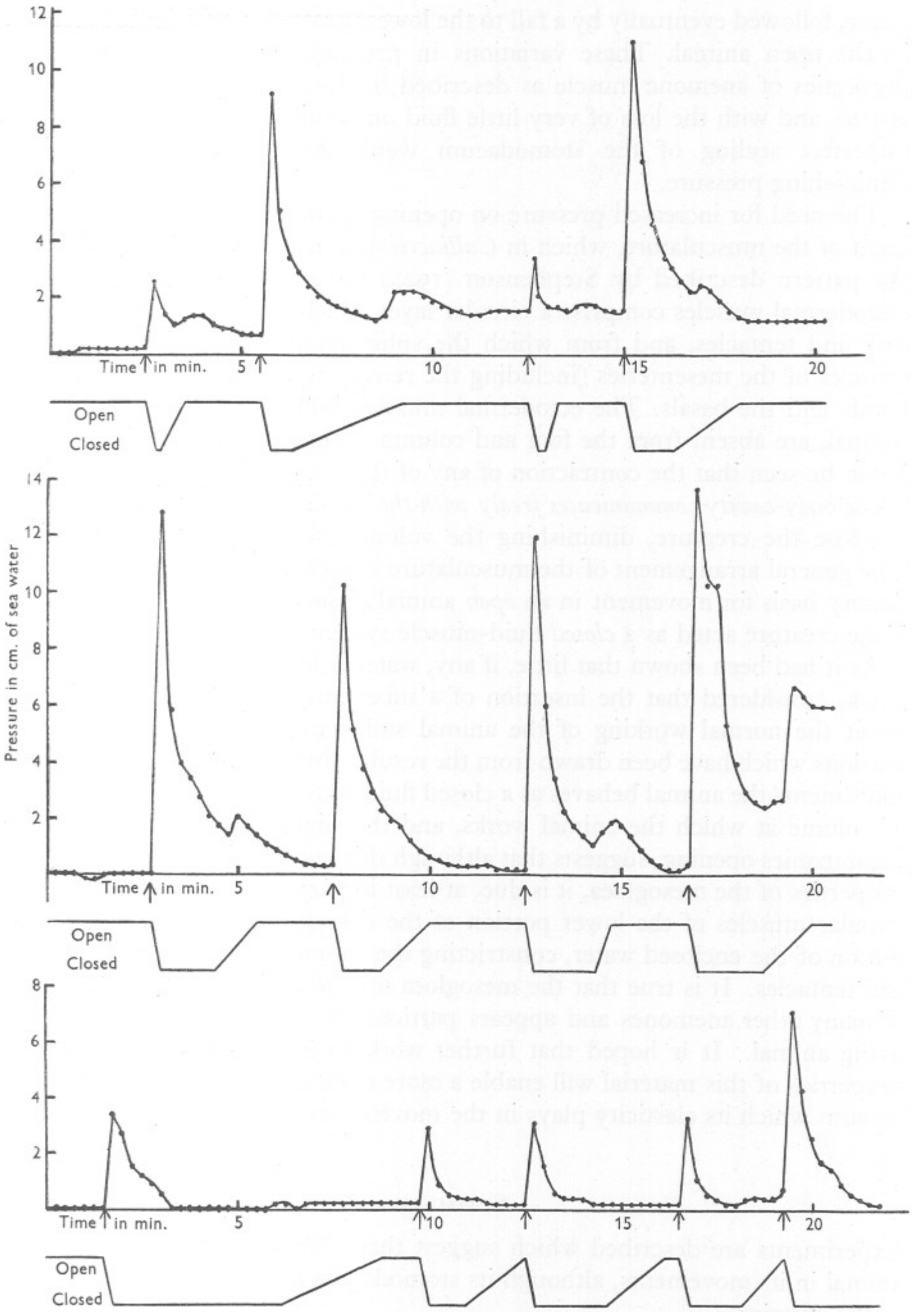

Fig. 4. Three records of the internal hydrostatic pressure changes in *Calliactis parasitica*. The animals were stimulated mechanically at the base of the column at the times marked by arrows; the line below each graph represents the opening and closing of the animal.

occur, followed eventually by a fall to the lowest pressures, which are recorded in the open animal. These variations in pressure are consistent with the properties of anemone muscle as described by Jordan (1935) and by Bozler (1936), and with the loss of very little fluid on contraction. Any loss through imperfect sealing of the stomodaeum would be reduced by a rapidly diminishing pressure.

The need for increased pressure on opening is connected with the arrangement of the musculature, which in *Calliactis* does not differ appreciably from the pattern described by Stephenson (1928) for anemones in general. The endodermal muscles comprise a circular layer which covers the foot, column, disk and tentacles, and from which the sphincter is derived as well as the muscles of the mesenteries (including the retractors of the disk), the parietobasals and the basals. The ectodermal muscles, which are, in general, longitudinal, are absent from the foot and column (Pantin, 1935). On inspection, it can be seen that the contraction of any of these muscle layers, *in an animal whose body-cavity communicates freely with the outside*, would be to contract or to close the creature, diminishing the volume of water which it contains. The general arrangement of the musculature is such as would provide a satisfactory basis for movement in an *open* animal if the mesogloea were elastic, *or* if the creature acted as a *closed* fluid-muscle system.

As it had been shown that little, if any, water is lost on normal contraction, it was considered that the insertion of a tube into the stomodaeum did not upset the normal working of the animal sufficiently to invalidate the conclusions which have been drawn from the results obtained, namely, that during movements the animal behaves as a closed fluid-muscle system. The constancy of volume at which the animal works, and the slight rise in pressure which accompanies opening, suggests that although this may be aided by the physical properties of the mesogloea, it is due, at least in part, to the contraction of the circular muscles of the lower portion of the column. These alter the distribution of the enclosed water, constricting the column and expanding the disk and tentacles. It is true that the mesogloea of *Calliactis* is stronger than that of many other anemones and appears particularly so when cut out from the living animal. It is hoped that further work on the structure and physical properties of this material will enable a more exact estimate to be made of the amount which its elasticity plays in the movements of the animal.

## SUMMARY

Experiments are described which suggest that *Calliactis* behaves as a closed animal in its movements, although its stomodaeum appears to be widely open to the exterior.

Observations of the movements of the animal are correlated with variations of the internal pressure. It is shown that expansion is not merely 'passive

relaxation', but is generally accompanied by a rise in pressure which is, however, much lower than that which accompanies rapid closing.

It is concluded that the fluid-muscle system of *Calliactis* behaves in a similar way to that of other soft-bodied invertebrates, but that the system works at a much lower pressure.

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## APPENDIX

### Details of Pressure Measurements in *Calliactis*

Pressures are given in cm. sea water to nearest 0·1 cm.

All readings made 1 min. after connecting animal with manometer tube.

All readings are corrected for capillary rise, height of water in aquarium jar and for slope of manometer.

| | Anemone 1 | | Anemone 2 | | Anemone 3 | | Anemone 4 | |
|---|---|---|---|---|---|---|---|---|
| | Open | Shut | Open | Shut | Open | Shut | Open | Shut |
| | 1·4 | 1·2 | 2·9 | 0·5 | 0·7 | 2·3 | 0·3 | 0·6 |
| | 2·3 | 3·1 | 3·0 | 1·5 | 0·9 | 5·0 | 0·2 | 1·1 |
| | 1·5 | 1·6 | 1·0 | 1·6 | 0·9 | 2·1 | 0·2 | 0·4 |
| | 0·8 | 3·7 | 2·9 | 2·0 | 1·1 | 3·7 | 0·1 | 0·9 |
| | 0·8 | 2·5 | 0·9 | 1·7 | 0·8 | 4·5 | 0·2 | 1·4 |
| | 0·5 | — | 3·4 | 1·9 | 2·1 | 1·9 | — | 1·0 |
| | 0·3 | — | 0·7 | 3·2 | 1·3 | — | — | 1·5 |
| | 0·3 | — | 3·6 | — | 0·7 | — | — | — |
| | — | — | 1·2 | — | 0·6 | — | — | — |
| | — | — | — | — | 0·9 | — | — | — |
| Mean pressure | 1·0 | 2·4 | 2·2 | 1·8 | 1·0 | 3·3 | 0·2 | 1·0 |

| | Anemone 5 | | Anemone 6 | | Anemone 7 | | Anemone 8 | |
|---|---|---|---|---|---|---|---|---|
| | Open | Shut | Open | Shut | Open | Shut | Open | Shut |
| | 1·7 | 3·1 | 1·7 | 3·8 | 0·8 | 1·0 | 1·6 | 3·0 |
| | 1·3 | 1·3 | 1·6 | 3·2 | 0·9 | 1·2 | 1·8 | 4·4 |
| | 1·3 | 1·3 | 2·1 | 1·2 | 0·4 | 0·7 | 1·7 | 3·7 |
| | 0·8 | 2·3 | 2·6 | 4·0 | 0·0 | 0·7 | 1·2 | 2·1 |
| | 0·6 | — | 4·3 | 1·5 | 0·0 | 1·9 | 1·8 | 4·5 |
| | 1·1 | — | 3·3 | — | 0·0 | — | 1·7 | 1·7 |
| | 1·3 | — | 3·0 | — | 0·0 | — | 1·1 | 1·5 |
| | 1·2 | — | 2·3 | — | 0·0 | — | 1·2 | 4·0 |
| | — | — | 4·7 | — | — | — | — | — |
| | — | — | 4·4 | — | — | — | — | — |
| | — | — | 6·5 | — | — | — | — | — |
| | — | — | 4·7 | — | — | — | — | — |
| | — | — | 2·3 | — | — | — | — | — |
| Mean pressure | 1·2 | 2·0 | 3·3 | 2·7 | 0·3 | 1·1 | 1·5 | 3·1 |