*Hommage de l'auteur*

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# The Evolution of the Chondrophora (Siphonophora-Disconanthae): New Evidence from Behavioural Studies

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### INTRODUCTION

THE problem of siphonophore evolution and relationships has long given grounds for controversy. The primary schism arose in the last century between those such as T. H. Huxley, Metschnikoff, Haeckel, and Hatschek who regarded the siphonophores as modified medusoid organisms giving rise by budding from the sub-umbrella to secondary medusae and polyps and, on the other hand, those such as Leuckart, Vogt, A. Agassiz, and Chun who regarded them as floating colonies of hydroid-polyps, showing specialization and division of labour, and budding off medusae. Within these two camps endless shades of opinion existed, as Leloup (12) has described. In the present century both views have continued to find adherents. Among the leading specialists, however, only Moser has supported the medusoid theory. In the special case of the Chondrophora, Leloup's demonstration (11) of the actinuloid nature of the conaria larva of *Vellela* and Garstang's detailed analysis (7) of the corymorphine affinites of the group have been influential in establishing the Chondrophora (*a*) as polypoid organisms and (*b*) as a fundamentally distinct group, possibly representing a line of evolution separate from that of the true siphonophores. In Totton's authoritative classification (20) the Chondrophora are established as a separate order within the Hydrazoa.

In spite of these advances, forms such as *Velella* and *Porpita* continue to be treated together with the true siphonophores and are, indeed, often thought to be typical members of the group. Furthermore, in the majority of modern accounts the medusoid hypothesis continues to hold sway, the float (pneumatophore) being viewed as a modified medusa from beneath which the polypoid members are budded. A noteworthy exception is Hardy (9) who follows Garstang's interpretation.

Since the present paper provides evidence supporting the tubulariid affinites of the Chondrophora, a brief comparison of the gross morphology and development of the two groups is a necessary preliminary.

### CHONDROPHORE STRUCTURE AND HOMOLOGIES

*Porpita* hangs at the surface with the oral aperture (Fig. 1 D, *o*; Plate I) facing down. The upper portion of the disc is above water level. The mantle
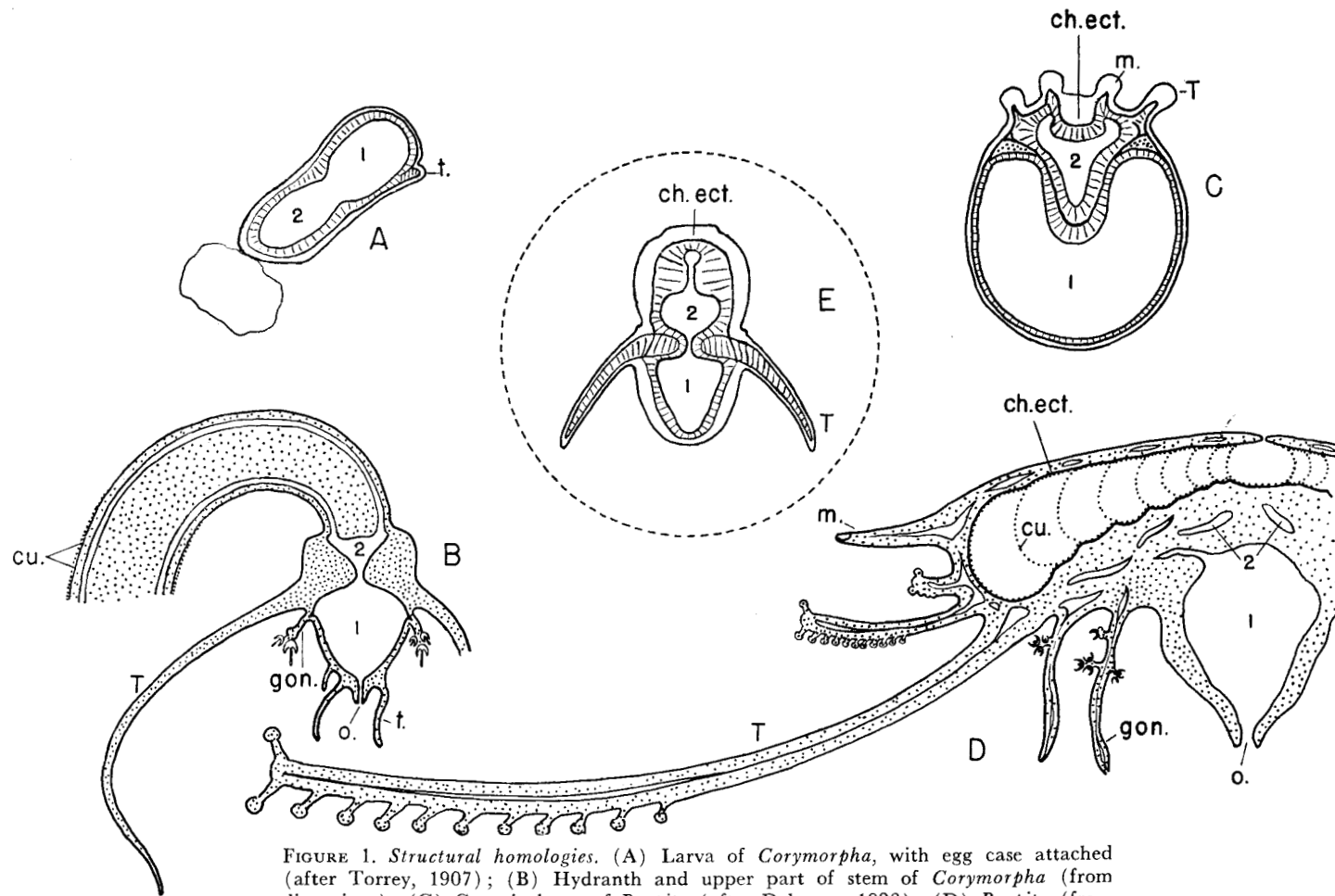
FIGURE 1. *Structural homologies.* (A) Larva of *Corymorpha,* with egg case attached (after Torrey, 1907); (B) Hydranth and upper part of stem of *Corymorpha* (from dissections); (C) Conaria larva of *Porpita* (after Delsman, 1923); (D) *Porpita* (from dissections); (E) Actinula larva of *Tubularia* (after Leloup, 1954). *ch.ect.,* chitin-secreting ectoderm; *cu,* (dotted line) chitinous cuticle in B, float chamber wall in D; *gon,* structures bearing medusa buds; *m,* mantle flap; *o,* mouth of hydranth; *T,* tentacles (proximal tentacles in *Corymorpha*); *t,* distal tentacles; *1,* oral chamber of hydranth; *2,* aboral chamber.
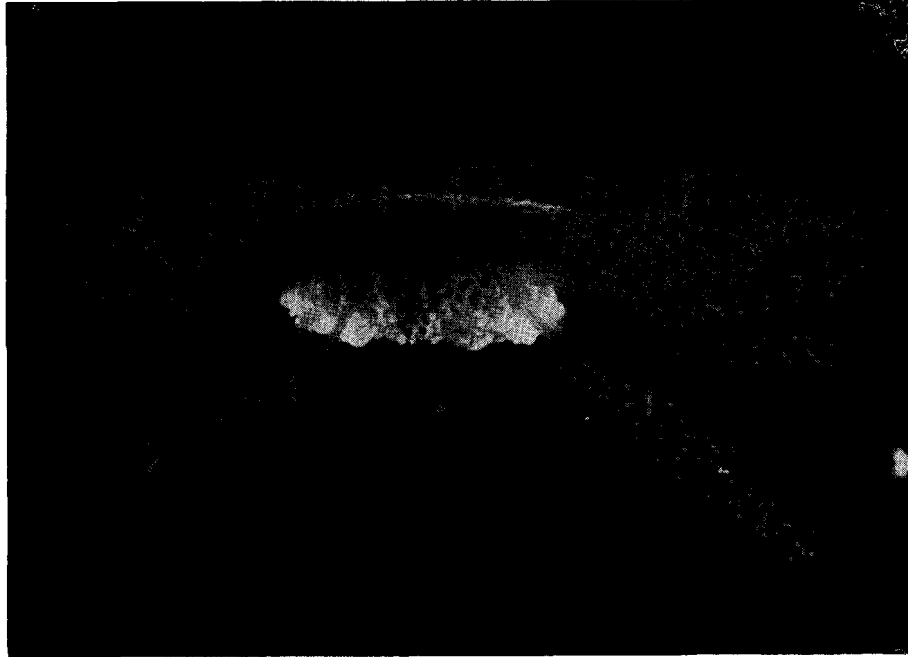
PLATE I. *Porpita porpita* L. (Photo by A. K. Totton)

flap (Fig. 1 D; Fig. 2 *m*) lies flat on the surface. Figure 1 illustrates the morphological homologies between *Porpita* and a sessile hydroid such as *Corymorpha*. The larvae of the two forms are shown in Fig. 1 C and 1 A respectively. Both can be regarded as actinula derivatives. An actinula, that of *Tubularia*, is shown in the centre (Fig. 1 E). While the larva of *Corymorpha* leads only a very short free existence and never shows the typical actinuloid facies, that of *Porpita* is free-living and comparable in fundamental structure to the actinula. This was first shown by Leloup (11) for the conaria larva of *Velella*, which is similar.

The homologies between the adults will be clear from the illustrations. In the development of *Corymorpha* the aboral region grows out forming the stem, the ectoderm producing a thin cuticle around it. In the development of *Porpita*, this region grows inwards, the ectoderm sinking in and secreting the cuticle as a series of concentric air-filled chambers which form the float. The float is therefore really an invaginated cuticle secreted as a succession of concentric layers like the perisarc of many hydroids.

The mature *Porpita* is a hydranth compressed in its main axis into a wide flat disc, with the aboral region invaginated as a float. If the hydranth is defined as the region from (and including) the proximal tentacles $(T)$ to the mouth, then in the mature *Porpita* the mantle flap $(m)$, upper part of disc, and invaginated portions can be viewed as stem-counterparts. As will be seen, the mantle flap has a muscular structure and behavioural properties comparable to the stem in *Corymorpha*.
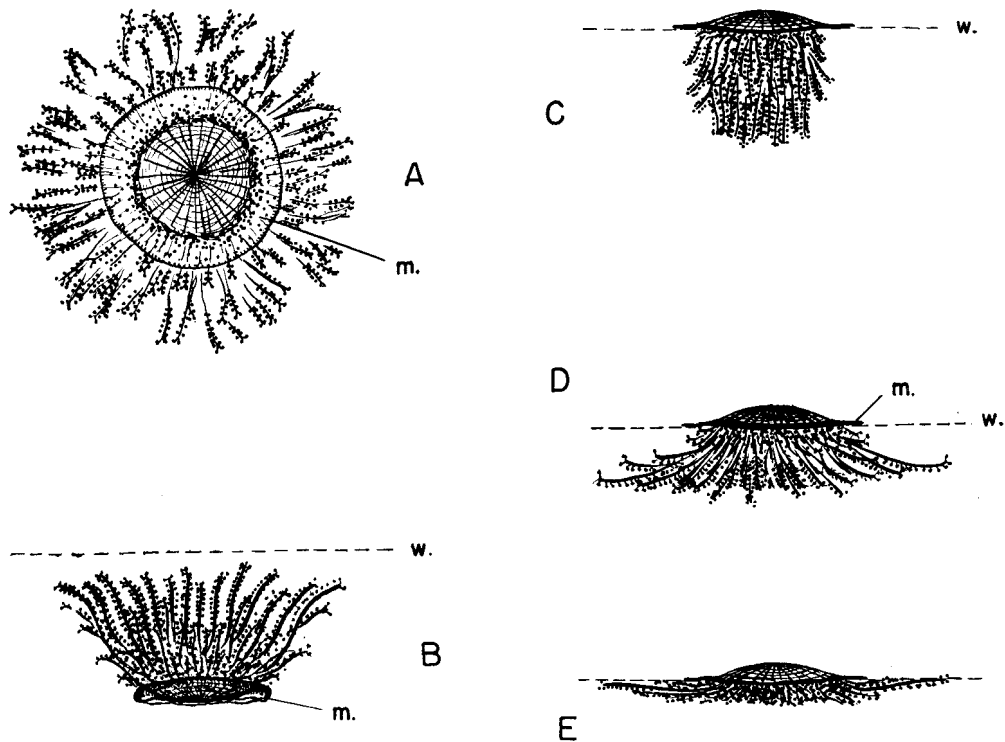
FIGURE 2. *Behaviour* (from photographs and sketches made in the field): (A) *Porpita* in resting position, from above; (B) Righting activity, from the side; (C) Food collecting behaviour, tentacles fully lowered; (D) Resting position, from the side; (E) Aboral, or protective response. *m,* mantle flap; *w,* water surface.

The proximal tentacles (*T*) in Corymorpha correspond to the tentacles (*T*) in *Porpita*, but in the latter they are budded through life, young and old ones being present in the same animal. Tentacles were seen to undergo autotomy when the animals were treated roughly; this doubtless occurs in natural conditions, the loss being made good by outgrowth and downgrowth of replacements.

The mouth opening (*o*) at the tip of the hydranth of *Corymorpha* corresponds to the opening in the central "zooid" (really the distal part of the hydranth) in *Porpita*. Distal tentacles (*t*) are present in *Corymorpha*, appearing in the early larva; they are not present in *Porpita*.

The structures (*gon*) bearing the medusae in *Corymorpha* find their counterparts in *Porpita*. In the latter they have mouth openings and ingest food (10). Presumably this makes them "zooids"; they are, in fact often referred to as "gonozooids." It would seem, however, that they have acquired individuality secondarily by the process of developing an opening in the tip of what was originally a simple outfolding of the hydranth wall. The existence of the "gonozooids" is the only reason for calling *Porpita* a colonial

coelenterate. The marginal tentacles are no more "dactylozooids" than are those of *Hydra*.

The homologies of the coelenteric cavities are harder to follow. The distal cavity of the hydranth (1) is a large digestive chamber in both cases. The proximal cavity (2) in *Corymorpha* is not represented as such in the adult *Porpita*. In larval development it is broken up into canals by the ingrowth of ectodermal tissue (5). Endoderm canals with frequent anastomoses run in the stem of *Corymorpha* and in the mantle and aboral region (stem homologues) in *Porpita*.

It will be clear, therefore, that there is no trace of "medusoid" organization in a form such as *Porpita*. Further, as Agassiz (1) stressed, the animal resembles a siphonophore less than it does a sessile tubulariid hydroid.

## MECHANICAL ORGANIZATION

Field observations, dissection, and histological study have been carried out by the author in order to elucidate the mechanics of movement in *Porpita* and *Velella*. The mantle flap, the tentacles, and the organs of ingestion are the only movable parts.

The mantle flap is an outfolding of the body wall which forms a collar around the disc. It is a mobile structure, capable of curling up aborally and of uncurling again into its normal flat position. Radially arranged, unstriated muscle fibres occur in the ectoderm on either side of the mantle. These can be regarded as the homologues of the longitudinal muscle system in the stem of the sessile hydroid. The mantle contains a thick collagenous mesogloea which serves as a support for the muscle fibres. Collagen was identified by the X-ray diffraction technique by Dr. K. M. Rudall, who kindly examined some of the author's material.

The tentacles possess longitudinal muscle fibres in the ectoderm; these fibres are particularly strongly developed in the basal part. The endodermal lining of the tentacles consists of enormous vacuolated cells closely packed together. Cells of this type occur frequently throughout the coelenterates and are known to be skeletal in character, providing a certain stiffness and resilience. The tentacles of *Porpita* do not shorten appreciably when the muscles contract, but bend at their bases. Flexion is in the vertical plane, either towards the mouth or away from it. Lateral movements are slight. The antagonism to muscular contraction in the tentacles evidently resides in the skeletal properties of the endodermal "box-cells." In an anaesthetized specimen, a tentacle can be pressed down or up from its normal resting position but when released it springs back. The more the tentacle is bent, the greater is the resistance and resilience. Endodermal circular muscle is inconspicuous or absent. The box-cells must so reduce the capacity for changes in length that circular muscle cannot play an important part. In *Velella*, by contrast, the box-cells are somewhat smaller, circular muscle is present, and the tentacles (according to Vogt) are in continual movement, writhing and changing in length. The movements of the tentacles in *Porpita* are spas-

modic, sharp, flicking flexions in the vertical plane, with skeletal, not muscular antagonism. The organs of ingestion are mobile, extensible structures with both longitudinal and circular muscle systems. They perform independent, writhing, searching movements.

The distribution of nerves in *Porpita* has been described by Conn and Beyer (4). The system is widespread throughout the ectoderm, but there are no fibre bundles such as occur in the margin of medusae, nor are there any local, ganglionic aggregations of nerve cells. Silver preparations made in the course of the present study show that the fibres are orientated chiefly in the radial direction in the upper side of the disc, becoming more circular round the mantle edge. In *Velella* (14) I have found a double nervous system in the ectoderm, consisting of a system of large fibres which run together forming net-like configurations and an open system of smaller fibres which retain their independence despite frequent close juxtapositions with other fibres. The *Porpita* preparations do not give quite such a clear picture of the relationships between the fibres, but I am confident that the arrangement is essentially the same in the two forms. The "accessory neurons" which I described in my thesis (Oxford, 1956) I now believe to be the counterparts of the open-system fibres in *Velella*. I have not been able to confirm my suggestion that polyploid neurons occur in the *Porpita* nerve net.

### BEHAVIOURAL STUDIES

The material used in this investigation consisted of specimens collected at Arrecife in the Canary Islands. The animals were recovered from tidal pools following periods of strong onshore wind. Several dozen specimens were examined, and some in apparently perfect condition were transferred to observation tanks in a cool room, where they continued to be active and responsive over the period of study. The specimens were of moderate size, measuring 10–15 mm. across the disc.

#### (a) Vertical Movement

It has been claimed (6; 8) that chondrophores can expel air from the float and so sink below the surface, rising again by resecretion of gases. It is hard to find any first-hand evidence for this. Field observations by Kölliker (10) and Vogt (21) led them to deny that the process took place. The specimens examined in the Canary Islands showed no such tendency, and in the author's opinion, based on histological study, they lack the musculature necessary to expel air in large quantities. In the case of true siphonophores such as *Physophora* the process does, however, definitely occur. It is possible that in the larval chondrophore some such capacity exists, disappearing later (2).

#### (b) Food-Collecting Movements of the Tentacles

The downwards or orally-directed movements of the tentacles in *Porpita* exhibit several degrees of complexity and occur spontaneously as well as in response to tactile stimulation. In an early account Lesson (13) describes

how the movements serve to sweep food particles down into the oral region, where the organs of ingestion pick them up. Observations made in this study also suggest that food-collection is the primary if not the sole purpose of the activity. There appears to be no basis for the statements of some writers that the movements are locomotory. *Porpita* lacks organs of locomotion, drifting passively on the surface. In *Velella*, by contrast, a sail is present. Chun (3) claims that the tentacular movements assist in forcing air out of the stigmata on top of the float, in a sort of breathing process. However, Schneider's experimental investigation (18) of the breathing theory casts serious doubts upon its plausibility. Being at the time of the investigation ignorant of Chun's theory, the present author did not investigate "breathing."

If a tentacle is lightly stimulated by a soft blow from a glass rod, after one or two seconds it will flex a few times in the oral direction, each flexion carrying it a little lower. Unless the stimulus is repeated, the activity dies out after four or five flexions. Each flexion is a sharp jerk. The amplitude, that is, progress achieved by each jerk, decreases the lower the tentacle goes. Presumably this is because skeletal resistance to flexion increases the more the tentacle is bent.

If two or more tentacles are stimulated and respond, their flexions are synchronized whether they are near together or not. The degree of bending, however, is variable. No exceptions to this rule of synchrony were observed.

Small groups of tentacles behave like single tentacles, only a few flexions normally occurring. When a larger number of tentacles is stimulated (how large was not exactly determined) the response takes on a new and distinctive character. All (or nearly all) tentacles, whether stimulated or not, take part and the series of flexions, instead of dying out after four or five, carries on without any outside help for forty or more. The whole response (here called "concerted") has an unmistakable pattern. As with the simple responses, all active tentacles show synchronized flexions (although the degree of depression, and hence the amplitudes of contraction, are not uniform). There is evidently a threshold, to be thought of in terms of numbers of tentacles aroused rather than of strength of stimulation, below which the response is elementary and above which it becomes self-propagating. Once evoked, the concerted response is usually complete, However, in a few instances "false starts" were observed; the concerted response seemed to have begun but failed to develop beyond two or three jerks.

In the experiments the concerted response was usually evoked by bouncing the animal in the water by a light blow on the top of the disc. Mild disturbance of a large enough number of tentacles, whether achieved in this way or by tactile stimulation applied directly to the tentacles sets the response in motion. It was not established whether the "mild disturbance" is effective because it excites touch receptors on the surface of the tentacles or because it bends the tentacles slightly and excites stretch receptors; both may possibly be involved. There is usually a perceptible time lag between stimulus and response, but there is no gradual build-up to the full response; it is concerted

from the outset, the first contraction appearing simultaneously in the whole corps of tentacles (except in the case of "late-starters" mentioned below).

The series of jerking flexions comprising the concerted response has a characteristic pattern. The tentacles are swiftly lowered below the disc (7 contractions in a typical case) ; they are held there (18 contractions) jerking rapidly (about 200/min.) at very low amplitude. Then decline becomes apparent and the tentacles ascend to the resting position (20 contractions). The jerks usually fade out when the tentacles are about half-way back to the resting position. The three phases of the pattern are really continuous and the number of contractions comprising each phase varies in different performances and between different specimens. Figure 2 D shows the resting position; Fig. 2 C shows the fully lowered position of the tentacles.

The jerking movements evidently represent a conflict between the series of muscular contractions pulling the tentacles downwards and the elasticity of the tentacles resisting flexion and tending to pull them back between flexions. The endodermal box-cells are probably chiefly responsible for these skeletal properties, although the aboral-side musculature might conceivably function passively as elastic tissue. It is unlikely that it is *actively* concerned, because when it does actively contract it produces a much more vigorous type of movement and one which eliminates the concerted, downwards response (see below, p. 16).

In the first part of the cycle, as the tentacles are being brought down, the tempo of contraction increases. As the return takes place it decreases. There appears to be an appropriate frequency (as well as amplitude) of contraction for each degree of inclination. This is evidently related to the varying skeletal resistance. When the tentacle is descending, each muscular jerk encounters greater resistance and achieves less progress than its predecessor. At the same time, the recoil effect in the interval between contractions progressively increases. Thus the accelerating tempo of contraction is adjusted to the increasing strength of recoil: the more powerful the latter becomes, the less time is allowed to it. Downward progress continues in the face of increasing resistance and resilience; it does so not, apparently, because the contractions become stronger but because they become more frequent. When the tentacles are fully lowered resistance is at its maximum. The amount of movement produced by each contraction is so slight, and the frequency of contraction is so high, that the tentacles appear almost motionless. This state of affairs does not last long (four or five seconds). Then the muscular contractions cease to hold their own; the tentacles jerk their way back to the resting position. The contractions are no longer strong enough, or are not of sufficient duration, or are not frequent enough to hold the tentacles down against their own inherent elasticity.

The decline is a gradual one for the further back the tentacles move the weaker become the antagonizing forces. Consequently, there is a progressive lightening of the load on the muscles. The fact that equilibrium is not achieved suggests that the muscular activity continues to weaken right up to

the end despite the lessening of the opposition. By "weakening" is meant simply the lessening in the effects of muscular contraction.

The absolute nature of the synchronization is one of the most striking features of the food-collecting movements. In one specimen, a number of tentacles at one side of the disc seemed unable to achieve the fully lowered position. They beat in a partially depressed position. However, they did not beat at the rate "proper" to their degree of inclination, but showed the rapid tempo of the main group, which were fully depressed. In another specimen a few tentacles were seen to start late in the concerted response. They were motionless until the main group were well down; then they suddenly sprang into life and in two or three rapid, almost continuous flexions reached the position which the main group had achieved only after 6 or 7 flexions.

So far we have dealt with responses to mechanical stimulation. The food-collecting movements may, however, occur spontaneously. Individual tentacles may suddenly become active, without any obvious cause. A more striking type of spontaneous activity also occurs, involving the complete performance of concerted food-collecting cycles at regular intervals. For about five minutes, a typical specimen performed feeding cycles spontaneously at approximately half-minute intervals. The concerted activity lasted about ten seconds, and was followed by about twenty seconds of quiescence. Then, without warning, a new cycle would begin. The concerted performances were identical to those elicited by external stimulation. The regular repetition of the cycles did not endure, but after about five minutes the performances became less frequent. and finally disappeared. The concerted activity could still be evoked experimentally, however. Chun (3) records regular performances of what he believed to be breathing activities, involving movements of the tentacles and other regions. These, he states, occur seldom more than twice a minute. It seems probable that he was observing the same type of activity, although his explanation in terms of breathing is open to doubt.

The spontaneous repetition of the concerted cycles must be regarded as the highest expression of food-collecting behaviour. At the most elementary level we have individual tentacles reacting to local stimulation; then, with two or more tentacles active at the same time we have synchronization of the contractions: then, with a sufficiently widespread stimulus, the response affects all tentacles, whether stimulated or not, and becomes self-propagating through forty or fifty contractions; finally, these concerted performances become self-evoking as well as self-propagating. We have here an illustration of the principle expressed by Pantin (15) : "As we go from simpler to more complex behaviour patterns we must always be prepared to find new physiological properties utilized to build up the machinery of behaviour."

Lacking an investigation with physiological equipment one cannot venture a detailed interpretation of these movements on a neuro-muscular basis. The synchronized series of tentacular flexions could be explained theoretically on

a basis of the summation of sensory data arising from stretch-receptors in the tentacles, the sharp resilient backward movement following each contraction causing the stretching. The increasing tempo of contraction as the tentacles descend would thus be linked with the increasing strength (or sharpness) of the resilient recoil movements. The synchronization of tentacular activity indicates that each motor nervous discharge (possibly a single nerve impulse) is through-conducted to all regions. No evidence for decremental spread of impulses was found. The nervous system of *Porpita* would seem to act like a condenser, building up to discharge level by the accumulation of sensory data from all active sources. In spite of the superficial resemblance of the series of step-like contractions to phenomena such as *Calliactis* sphincter closure, it is hard to envisage the mechanism in *Porpita* in terms of facilitation. With regard to the spontaneous outbursts of concerted activity, the absence of localized aggregations of nervous tissue would make it unlikely that a specific pacemaker exists. As in the case of *Arenicola marina* (22) where one of the "pacemakers" is only an ill-defined area of the ventral nerve cord, we may here be dealing with the whole nerve plexus or a large part of it. The term "uncentralized" is so often applied to the coelenterate nervous system that one forgets that it could equally be described as "all-centre."

### (c) Protective Response

It was explained above that the flexions performed in the oral direction (food-collecting movements) follow mild disturbance or gentle agitation of the tentacles. If a stronger blow is inflicted, or if a tentacle is pinched with forceps a different, though likewise through-conducted, response is evoked. All the tentacles flex in the *aboral* direction. The flexion brings the tentacle tips up to the surface of the water (Fig. 2 E). They are held there stiff and immobile for about two seconds and then the muscles relax.

This reaction has not previously been described and in naming it "protective" the author invokes certain assumptions: (1) that the position of the tentacles flattened against the surface would increase stability and (2) that it would reduce the vulnerability of the animal by presenting to best advantage the armament of nematocysts that are arranged on the knobs along the oral and lateral surfaces. The reaction follows abrupt stimulation such as a predator might inflict.

In no case were partial degrees of response observed. Response follows stimulation without a time lag perceptible to the naked eye. Tentacles remote from the point of stimulation flex in the same moment as the stimulated tentacle. The aboral response is a single sustained flexion, not a series of short jerks. If the stimulus is repeated, the response is sustained for longer.

Administration of a suitably sharp stimulus to an animal engaged in concerted food-collecting behaviour evokes the protective response. The downwards movements are eliminated, and are not resumed following completion of the response.

An interesting phenomenon associated with the aboral response was observed: following the response, the tentacle at which the stimulus had been applied would pass straight through the resting position into a short series of flexions in the oral direction. In experiments on an isolated segment it was found possible to evoke the complete cycle of downwards flexions indirectly by this means (p. 18).

### (d) Righting Behaviour

Agassiz (1) records the following observations for *Porpita*: "It can, by bringing its tentacles together over the disk, and throwing up the free edge of the mantle in a given direction, then expanding the tentacles of one side far over on the opposite direction beyond the central part of the disk, it can thus readily change the centre of gravity and tilt the disk back again into a normal attitude, should it for any cause have been set afloat with the tentacles uppermost."

Righting behaviour was observed independently in the course of the present study. Overturned specimens embark on a series of unified jerking flexions, of the same type as occur in food-collecting behaviour. Each flexion pushes the tips of the tentacles against the surface of the water, forcing the disc downwards (Fig. 2 B). In the Canary specimens, though not in those studied by Agassiz, flexions were equilateral. Also, the tentacles usually reached equilibrium, jerking to and fro within the 50°–70° range of inclination from the horizontal. The frequency of contraction in this position was 60–80/min., and the rhythmic beating was sustained for periods over a minute. At the same time as the tentacles are engaged in these movements the mantle flap slowly curls up in the aboral direction. As soon as righting is achieved, the tentacular movements cease and the mantle flap uncurls again, coming to rest parallel to the water surface.

It is clear that the mantle forms a stabilizer when in the extended position. It is normally held flat on the surface, its upper side dry. The curling up which follows overturning would reduce its stabilizing properties, making righting easier. The simultaneous activity of the tentacles would also lessen
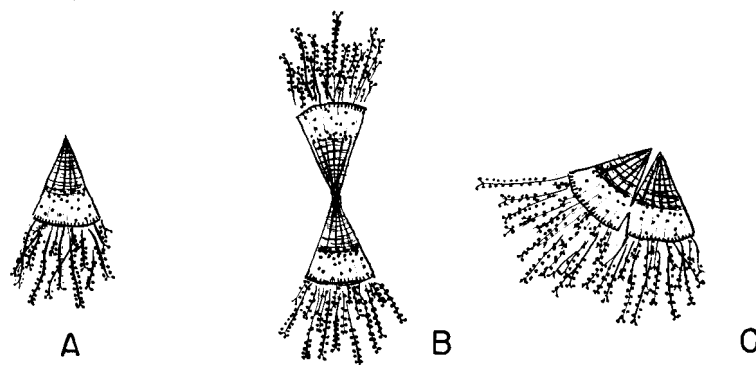


A                                        B                                C

Figure 3. *Incision experiments.* Explanation in text.

stability in the inverted position. This was demonstrated to the author's satisfaction by manipulation of righted and overturned specimens in the laboratory.

### (e) Behavioural Results from Incision Experiments

In Fig. 3 A an isolated 45° segment is shown. In such a piece, concerted food-collecting cycles were obtained by mild tactile stimulation. The protective response was also obtained, but it was followed by concerted feeding behaviour. Small segments were not studied.

Figure 3 B shows two 45° segments connected only by a 4 mm. wide bridge. It was found that movements on either side were co-ordinated. Food-collecting behaviour on both sides could be stopped by a strong stimulus (evoking the protective response) applied to one side.

The 100° fragment shown in Fig. 3 C was incised radially from either side, so that a narrow bridge of tissue was all that connected the two parts. The tentacles in the two halves showed synchronized behaviour. Concerted feeding cycles occurred spontaneously on two occasions in this preparation, the activity beginning at the same moment in the two halves. Thus the behaviour of isolated or partially isolated fragments resembles that of the intact animal.

In order to establish that co-ordination depends on actual tissue continuity and not simply on mechanical contact, a segment was removed from a specimen and its tentacles were thrust in among those of the parent piece. No co-ordination was exhibited between the behaviour of the two portions.

### Behavioural Resemblances Between Corymorpha and Porpita

The activities of *Corymorpha* have been studied by a number of workers, the most detailed account being that of Parker (16). Portions of this account are reproduced in his book *The Elementary Nervous System* (17).

The proximal tentacles of *Corymorpha* have an endodermal axis of large vacuolated cells, which Parker refers to as a "plastic skeleton"; following flexion their "elasticity returns the tentacle to its original position," exactly as in *Porpita*. There is longitudinal but not circular muscle in the tentacles. The tentacles respond to mechanical stimulation by flexing in the oral direction. There is a time lag between stimulus and response of "a second or so." In all these respects, *Porpita* is comparable. When kept in quiet water *Corymorpha* exhibits spontaneous food-collecting activities lasting about a minute, with about two minutes quiescence between performances. In *Porpita*, spontaneously repeated activity cycles occur more frequently, but the time ratio of activity to quiescence is similar, *viz.* 1 : 2.

In these food-collecting cycles, the proximal tentacles of *Corymorpha* exhibit "two or three convulsive efforts," which bring them in around the mouth. In *Porpita*, six or seven such flexions may be necessary for full lowering. The accounts do not explicitly state that the convulsive efforts are synchronous nor that all tentacles take part, but it is implied that such is the case, that is, that the activity is concerted and synchronized, as in

*Porpita.* It would be interesting to find out whether the short series of contractions in *Corymorpha* exhibits acceleration or not, and whether, while the tentacles are being held in around the mouth, they are motionless or are in a state of tetanus, as in *Porpita.*

If a specimen of *Corymorpha* is laid on its side, the stem performs righting movements, bending into a U-shape, and then straightens out as it approaches the upright position. Parker performed experiments showing that the longitudinal muscles of the stem are responsible for these movements, and that the response is a geotropic one. *Porpita* also shows what appears to be a gravity response (in the mantle flap) when overturned. From their location and orientation, the muscles concerned in the two responses can legitimately be viewed as homologous.

Against these resemblances we must place some differences. Nothing comparable to the aboral response of the tentacles in *Porpita* has been described in the proximal tentacles of *Corymorpha.* The distal tentacles (lacking in *Porpita*) take part in food-collecting activity. Bowing movements of the stem also accompany feeding. Most important of all, when a proximal tentacle of *Corymorpha* is stimulated, the response spreads from one tentacle to others with increase in the strength of stimulation. In *Porpita* on the other hand, flexions in the oral direction could be evoked in one tentacle by mild tactile stimulation, but if the stimulus was made sharper the response did not spread to other tentacles; instead, a different response, the aboral one, was called forth.

In spite of their differences it will be seen that the two forms show numerous points of comparison both in the mechanics of movement (for instance, the jerking, orally directed flexions) and in the general character of the behaviour patterns. The spontaneous performance at regular intervals of feeding cycles in both groups is a particularly striking feature. The occurrence of a gravity response in the mantle muscles of *Porpita* and in the homologous aboral musculature of *Corymorpha* shows how a basic functional property can be manifested in widely different ways and yet, on analysis, contribute evidence of relationships.

It may seem at first surprising that the behaviour of the two forms has not diverged to a greater extent. However, the seemingly great differences in habitat and mode of life of the two forms are more apparent than real. We are not dealing with sessile versus free-swimming modes of life. Although *Porpita* moves at the surface of the water it does so passively. It cannot move vertically like a medusa nor alter its spatial relations except by righting itself following overturning. It could be described as sessile with respect to the surface of the water, being attached at the underside of the surface by its float (which is the structural homologue of the stem which attaches *Corymorpha* to the sea floor). It is, in fact, an inverted sessile hydroid with the water surface as its "sea floor." In both *Corymorpha* and *Porpita* there are budded from the hydranth free-swimming medusae which can move vertically in the water and presumably benefit from the dispersal effects of ocean currents different from those encountered by the sessile stage.

## ACKNOWLEDGMENTS

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