# Analysis of Locomotion in a Siphonophore Colony

G. O. Mackie

*Proceedings of the Royal Society of London. Series B, Biological Sciences*, Volume 159, Issue 975 (Jan. 14, 1964), 366-391.

Stable URL:
http://links.jstor.org/sici?sici=0080-4649%2819640114%29159%3A975%3C366%3AAOLIAS%3E2.0.CO%3B2-I



*Proceedings of the Royal Society of London. Series B, Biological Sciences*

# Analysis of locomotion in a siphonophore colony

By G. O. Mackie

*Department of Zoology, University of Alberta, Canada*

(*Communicated by Sir Alister Hardy, F.R.S.—Received* 9 *November* 1962—*Revised* 8 *May* 1963)

The siphonophore *Nanomia cara* swims forwards and backwards by means of its nectophores. Reverse swimming is a through-conducted response in which the circular muscle in each nectophore contracts and radial fibres ('fibres of Claus') in the velum simultaneously shorten, deflecting the water jet emitted through the velar opening forwards. Forward-swimming contractions may be synchronized initially in all nectophores or may be asynchronous, but in both cases colonial control is involved. The fibres of Claus do not contract in forward swimming. Synchronized forward swimming ('*F*') is through-conducted from the siphosome at a velocity estimated at 75 to 150 cm/s. It may also be evoked by stimulation of posterior (older) nectophores. Stimulation of anterior (younger) nectophores or of the float elicits only reverse swimming ('*R*'). Stimulation of nectophores in a 'transitional' zone may evoke either *F* or *R* complete in all nectophores, but never responses intermediate between the two. Evidence is given that nectophores undergo sensory transformation during life, initially serving for the evocation only of *R*, later only for *F*. The basis of this transformation is not understood. No comparable change in motor capacity occurs. Use of excess $Mg^{2+}$ in various concentrations shows that striated muscle action is suppressed more readily than that of unstriated muscle and that both are suppressed more readily than is transmission of excitation between nectophores and stem. Surgical operations on whole specimens and on detached nectophores show that there is a single conduction route for the *F* response, histologically identified as an exumbrellar nerve tract. Transection of this tract obliterates *F* conduction without affecting the *R* response. It is shown that transmission of the latter must occur in the entire exumbrellar ectoderm of the nectophore or in special conducting elements (undetected) associated with it. Neither mesogloeal nor endodermal conduction appear to be involved in locomotory responses. The existence of two separate conduction systems in the stem, connected with those demonstrated in the nectophores, is inferred. *Nanomia* responds to sudden illumination of the siphosome by *F* behaviour. Nectophores and float, however, are not photosensitive. Autotomy of nectophores is a highly organized process, involving compensatory stem adjustments. The locomotory behaviour of siphonophores and chondrophores is reviewed and new information is provided for several species. Co-ordination of activities is widespread. The locomotory behaviour of *Nanomia* is typical of the long-stemmed Physonectae.

## 1. Introduction

Most animal colonies are fixed and immobile but in a few groups locomotory capacity has been evolved. Certain ectoprocts and sea-pens can crawl slowly on the bottom or on submerged objects. The free-swimming habit is shown only by the pelagic tunicates and by some members of the order Siphonophora. Polymorphism is carried to a higher degree in the latter group than in any other colonial animals and it is well known that certain Siphonophora swim with the aid of specialized medusoid members, the nectophores. It is to be expected then that locomotory behaviour will be highly organized in such forms, in keeping with their morphological elaboration, but such information as exists on the subject has never been collected and discussed in one place and no experimental investigation has hitherto been attempted. In the present account an attempt has been made to bring together existing information concerning locomotion in siphonophores and to correlate it with and extend it by further original studies in the field. These studies began in Naples in 1954 and have continued intermittently to the present time.

Not until recently at the Friday Harbor Laboratories of the University of Washington was it possible, however, to bring the analysis down to matters of detail. The form used in this investigation was *Nanomia cara*, a member of the Sub-order Physonectae, now in the centenary year of its first description by Agassiz (19 November 1862).

## 2. Material

The taxonomy of *N. cara* Agassiz (*Cupulita sarsii* Haeckel) and of the related *N. bijuga* Delle Chiaje (*Halistemma tergestinum* Claus; *Cupulita picta* Haeckel) is still in an unsatisfactory state (Totton 1954); the view has on occasion been expressed, and is discussed by Bigelow (1911), that only one species is involved. At present, however, it appears necessary to recognize both species. *N. cara* is typically a northern form occurring on the coast of Norway, along the Canadian maritime and New England shores and in the Vancouver Island region. '*Stephanomia bijuga*', described by Berrill (1930) from Salcombe, Devon, is evidently *N. cara* as currently defined. *N. bijuga* has been recorded from Misaki but is best known from the Mediterranean and other warm waters. Berkeley & Berkeley (1960) recorded both species from the Vancouver Island area on the basis of determinations by the present writer. Study of specimens subsequently taken from these waters has, however, made it appear probable that only one species (*N. cara*) is present, the determination of earlier material as *N. bijuga* being based on the seemingly erroneous, though prevailing, assumption that the presence or absence of a basal vesicle in the palpon and of certain patterns of pigment distribution are characters of diagnostic value in the taxonomy of this genus. All specimens used in the present study were *N. cara*.

The specimens were collected at the surface off the floats at the Friday Harbor Laboratories during May, June and July 1960–62 where, though never abundant, they occurred with fair regularity. It was found easiest to collect the specimens at night with the aid of a light immersed in the water. Methods of keeping siphonophores in the laboratory are described by Mackie & Boag (1963). With regular feeding, *Nanomia* can be kept in good condition for weeks and will grow in size. Autotomy of nectophores cannot be avoided entirely, but there is continual replacement by budding.

In the nomenclature of parts and in general concepts concerning the morphological organization of the colony this account owes much to Totton (1954), the most important general work on the siphonophores now available. The names of the siphonophores studied at Naples by Boag and the author are those used by Totton. Almost without exception, a long list of synonyms could be appended to each modern name and study of the earlier literature is impeded by the necessity for lengthy investigation into the identities of forms described.

## 3. Experimental techniques

### *A. Anaesthetic and surgical procedures*

A solution of crystalline magnesium chloride at 67·1 g/l. in glass-distilled water was used in mixture with sea water. The stock solution was kept at the same

temperature as the sea water and was aerated. One part of it to two of sea water gives a mixture in which lengthy operations can be carried out without cytological deterioration occurring in the animal. Weaker mixtures (1:5, 1:7·5, 1:15) were used for special purposes. *Nanomia* is small enough to fit into a Petri dish and operations can be carried out under the dissecting microscope at magnifications up to about × 40. For sectioning nerve tracts or for abrading epithelia the finest sort of entomological pins ('minuten Nädeln') mounted on bamboo shafts were used. Needles were sharpened under the microscope to a point, blade or scraper, using a small electric grinder as used for dental instruments. The tendency of nectophores to autotomize can be substantially reduced by anaesthesia but is hard to eliminate entirely. The scope of operations in the nectosomal region is thus limited.

### *B. Electrical stimulation*

A Grass S.M. 6 stimulator was used in conjunction with platinum electrodes. A pulse duration of 1·0 ms was used. Single or repeated shocks were used as appropriate. The voltage was arbitrarily adjusted to a point just above the minimum required to give a shock.

### *C. Methylene blue staining*

The rongalit methylene blue method (Pantin 1948) was used with slight alterations suggested by Dr E. A. Robson (personal communication). Permanent preparations were not attempted and all observations were carried out on water-immersed material.

## 4. Natural activity

Kept in large tanks in dim light with fresh, cool, filtered sea water, specimens of *Nanomia* remain quiescent for long periods with their tentacles extended (figure 1). Occasional sudden contractions are shown by the tentacles followed by slower relaxation. In specimens which have recently fed, pumping of fluids to and fro between gastrozooids and palpons via the stem canal goes on steadily, with occasional interruptions for the elimination of wastes by one or other of the digestive members. These and other 'vegetative' activities are described more fully elsewhere (Mackie & Boag 1963).

Various external factors can bring about locomotion, but it may also occur spontaneously, i.e. in the absence of identified external stimuli. The first indication that locomotion is about to begin is a general shortening of the tentacles, tentillae and siphosome stem. This is quickly followed by the actual swimming movements which are performed by several or all of the nectophores. Sometimes activity begins simultaneously in all the nectophores so that there is a sudden, powerful thrust forward (figure 2*B*) after which the nectophores usually continue to pulsate, but no longer synchronously. At other times activity is asynchronous from the beginning (figure 2*C*), usually appearing first in anterior (upper) nectophores and spreading down to lower ones. Where swimming begins with a synchronous thrust the colony leaps forward by about 7 to 10 cm in typical instances, this distance being traversed in about $\frac{1}{3}$ s. A second synchronized thrust is never seen so this

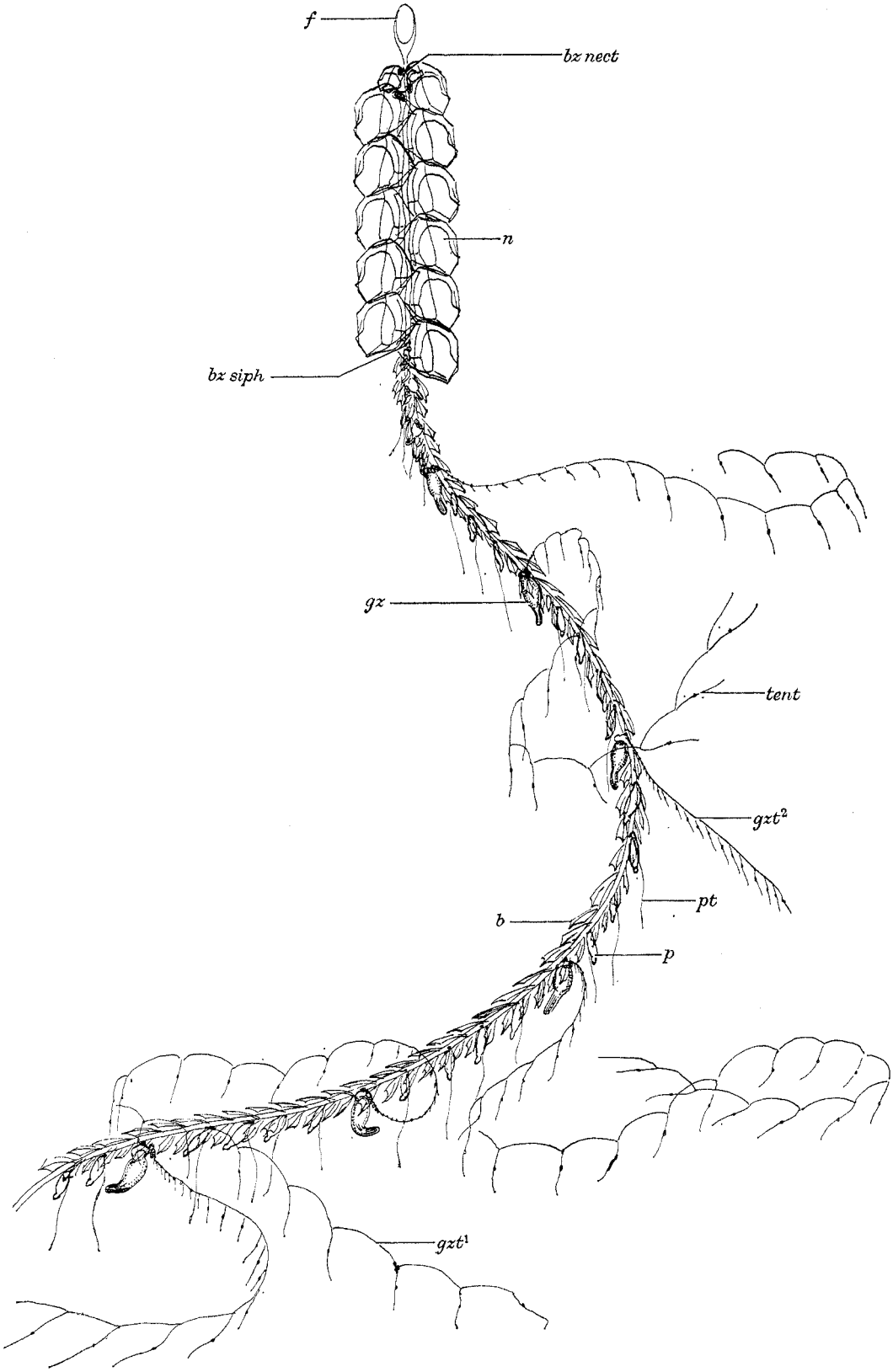


FIGURE 1. *Nanomia cara*. Upper two-thirds of colony with eleven nectophores at rest. *b* bract, *bz nect* nectosome budding zone, *bz siph* siphosome budding zone, *f* float, *gz* gastrozooid, $gzt^1$ extended tentacle of gastrozooid, $gzt^2$ contracting tentacle, *n* nectophore, *p* palpon, *pt* palpon tentacle, *tent* tentillum.

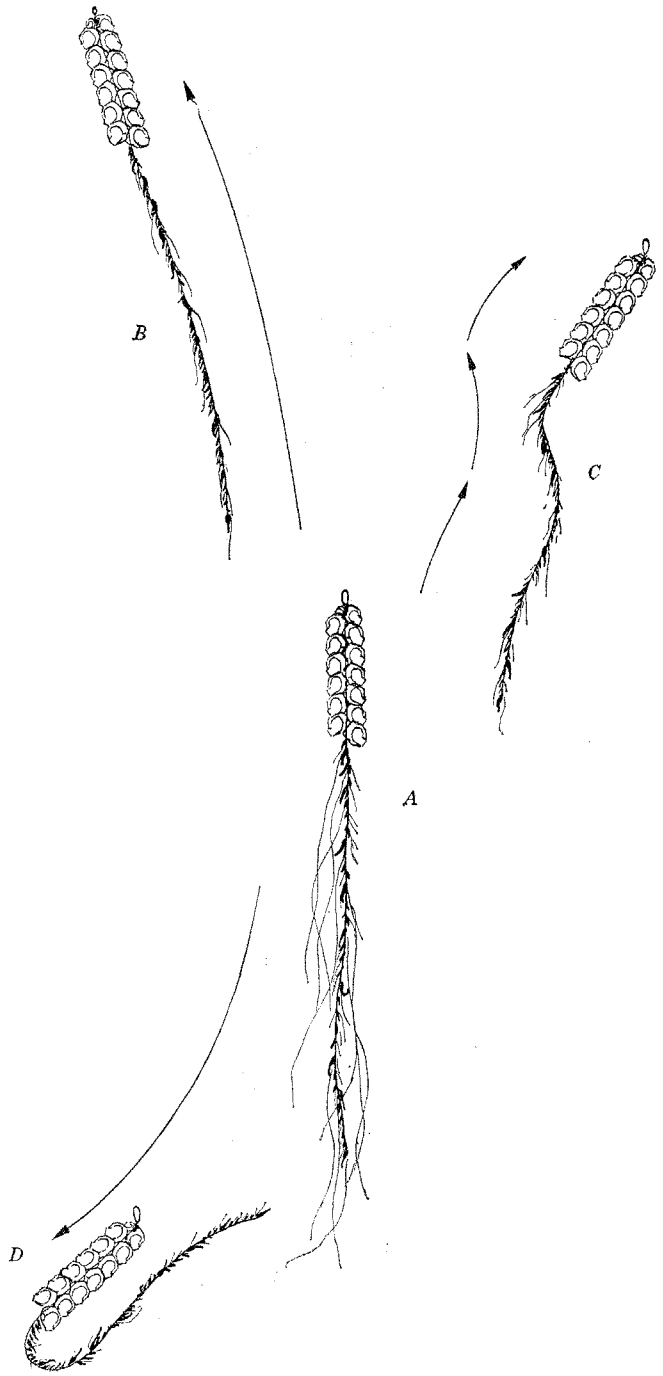


FIGURE 2. Locomotory behaviour. *A*, *Nanomia* at rest. *B*, Synchronized forward swimming thrust. *C*, Zigzag swimming, nectophores contracting asynchronously. *D*, Reverse swimming.

type of movement is not maintained at a regular velocity. However, the overall velocity from a standing start over the first $\frac{1}{2}$ s can be given as 20 to 30 cm/s. After the synchronized thrust the colony either glides to a halt or continues to swim by asynchronous pulsations. Specimens with 12 to 15 nectophores now show approximate velocities of 8 to 10 cm/s. Berrill (1930) estimated a velocity of 8 cm/s for this species. In the larger and less streamlined *Forskalia contorta* the velocity is 30 to 50 cm/min (Leloup 1935). Pulsation frequencies in the nectophores vary inversely with size. In *Nanomia* the fully grown nectophores show frequencies of approximately 4/s (Berrill 1930) with younger ones showing higher frequencies. Leloup indicates pulsation frequencies of 120 to 150/min in *Forskalia.*

Whereas the initial synchronized thrust shoots the colony directly forwards, the activity of the nectophores when not so synchronized has the effect of driving the colony in a somewhat zig-zag pathway, particularly in specimens with only a few nectophores. Agassiz (1865), for instance, whose specimens had only 4 to 6 nectophores, describes locomotion in *N. cara* as 'a sort of alternating motion . . . throwing the whole of the upper part of the community violently from side to side'. In specimens with larger nectosomes movement is much smoother as there are usually several alternating blocks of nectophores at different levels of the column pulsating in varying combinations and working at different frequencies. However, zigzagging is usually shown in some degree. Contractions often pass down in unilateral series from upper to lower nectophores, whether the wave begins at the top of the column or at some distance down it. This fact was noted by Sars (1846) in some brief but very perceptive behavioural notes on a siphonophore which was almost certainly *N. cara.* (Sars's figures for '*Agalmopsis elegans*' include components of two distinct siphonophores now known as *Agalma elegans* and *Nanomia cara.* It is the latter which dominates the figures and is chiefly referred to in the text—Totton (1954, pp. 36, 63).) Thus one cannot separate forward locomotion into two categories, one in which the nectophores pulsate in concert, the other in which they act independently, for in both cases there is evidence of colonial control. Vogt (1854) has likened the movements to those of soldiers performing drill. The analogy is apt for the synchronized initial thrust but in the asynchronous activity, where the nectophores function in unilateral and bilateral combinations of varying size and duration, one is reminded more of the shifting and complex movements of ballet.

When the siphonophore is at rest the buoyancy of the float holds it more or less vertical in the water and consequently, when locomotion ensues, it is initially in the upwards direction. However, the propulsive force exerted by the nectophores is easily sufficient to counteract the tendency of the float to hold the colony vertical and if, for instance, during the zigzag forwards movements a block of nectophores on one side becomes more active than those on the other, the colony will move round in an arc and may swim directly downward. Hyman (1940, p. 48) saw '*Halistemma*' (probably *Nanomia*) 'dart about vigorously, often executing loop-the-loop curves', and it is clear that the organism has the capacity for swimming at any angle and in any plane. What is less clear is whether or not the colony can *control* the angle and plane of locomotion, and if so to what extent.

The foregoing observations refer only to locomotion in the forward direction. The siphonophore is also capable of swimming in reverse (figure 2*D*). If, during forward locomotion, the front of the colony comes in contact with any resistant object, including the air–water interface, the nectophores may show one or occasionally a series of two synchronized contractions in which the jets of water issuing from the velar openings are directed *forwards* so that the colony is propelled *backwards*. This response has evidently been seen by some previous writers but without a true recognition of the nature of the process. Sars (1846) simply states that the siphonophore 'draws back rapidly'. According to Leloup (1935) the backwards movement is achieved by means of rapidly alternating shortenings and extensions of the stem (*Stephanomia rubra*). However, close observations on *Nanomia* and other forms clearly show that more than stem contraction is involved, that it is a form of swimming in which the nectophores are active participants (see below, p. 374). The effect of such a single concerted thrust is to propel the nectosome some 10 to 15 cm in the reverse direction. This displacement is greater than the 7 to 10 cm provided by the initial synchronized thrust in the forward swimming but whereas in the latter much of the force is expended in overcoming the inertia of the siphosome, in the reverse response the siphosome merely doubles upon itself, exerting little initial drag. Where two consecutive reverse thrusts are exhibited, the interval between them is about $\frac{1}{3}$ s.

A mere verbal description can give little idea of the agility and vigour with which the colony moves. It will be seen below (p. 377) that the synchronized forward swimming response is evoked by any abrupt contact of objects with the hinder areas of the colony, that a through-conduction pathway is involved, rapid propagation along which ensures that reaction follows stimulus with very slight delay; and it has been noted above that the effect of the response is to remove the entire colony immediately to another area. In other words, this is a typical 'escape' response. The effectiveness of the reverse (withdrawal) response is also very clear when one observes the success and speed with which the organism repeatedly extricates itself from corners of the tank and other traps in which many large planktonic forms, e.g. Hydromedusae, ctenophores, tend to lodge. Very few animals which swim by jet propulsion have the ability to control the jet in such a way that movement may be forwards, sideways *and backwards* and it would seem that the potentialities of this method of locomotion have been fully developed only in the cephalopod molluscs, with the physonectid siphonophores running a close second. The observations also support a view long ago expressed by C. Vogt, that 'il y a une volonté commune à la colonie qui dirige les mouvements des cloches natatoires' (Vogt 1854).

## 5. Mechanics of the nectosome

### *A. The column*

The nectophores are budded from the stem immediately below the float (figure 1). While young, they are protected by projecting portions of the more mature nectophores. As they grow in size they move downward relative to the budding zone

and the lowest nectophores are thus the oldest. Growth ceases early in the life of a nectophore; consequently the column tapers only near the top. The nectophores are jointed together very compactly and in a way predetermined by the morphology of their exumbrellar ridges and depressions. There is only one way in which a nectophore will fit comfortably with respect to other nectophores and to the stem. Muscular tension in the stem holds the nectophores tightly together in this position. Under deep anaesthesia the stem may relax to the extent that the column of nectophores loses its compactness and disarticulation occurs.

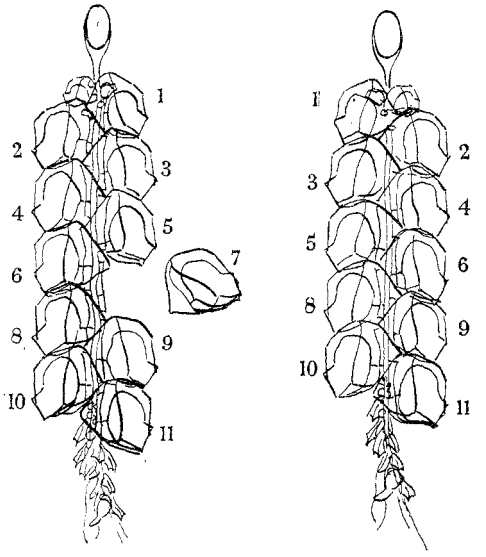


FIGURE 3. Readjustment of nectosome following autotomy of a nectophore. The upper part of the column rotates through 180°; simultaneously the stem shortens.

Nectophores are frequently autotomized. The loss of a nectophore is potentially dangerous, not so much because it reduces propulsive capacity, but because a gap is created on one side which would cause asymmetry, loss of compactness and disarticulation of the column. This disruption is avoided in the following way: immediately following autotomy, and possibly as a continuation of the same sequence of muscular contractions, the stem rotates through 180° in a clockwise direction as seen from above, and the nectophore next in order above comes to fill the gap (figure 3). Over the next few hours, cytological repair must occur for the scar is eliminated and torsion folds disappear. However, specimens which have lost many nectophores suffer from looseness and disarticulation of the nectosome which, in turn, may lead to further autotomy. Production of new nectophores by budding may result in replacement of a damaged nectosome in whole or in part. The new nectophores may be smaller than the original set, no doubt because conditions in the laboratory are less favourable for growth than are those of the natural habitat. The specimens caught at Friday Harbor rarely had more than fifteen mature nectophores, but Fewkes (1888) describes specimens from eastern Canadian waters with twice this number.

### *B. The individual nectophore*

The nectophore is a sterile, astomate, atentaculate medusoid in which the primary radial symmetry is replaced by a nearly perfect bilateral symmetry. The single imperfection in *Nanomia* is that the lower nerve tract (*lnt*) passes to one side of the pedicle attachment, instead of passing up both sides (figure 6*B*). The elaborate sculpturing of the exumbrellar surfaces and the extension of the subumbrellar cavity into lateral pockets are conditions related to the articulation of the nectophore with others in the series and with the stem. Attachment to the stem is by

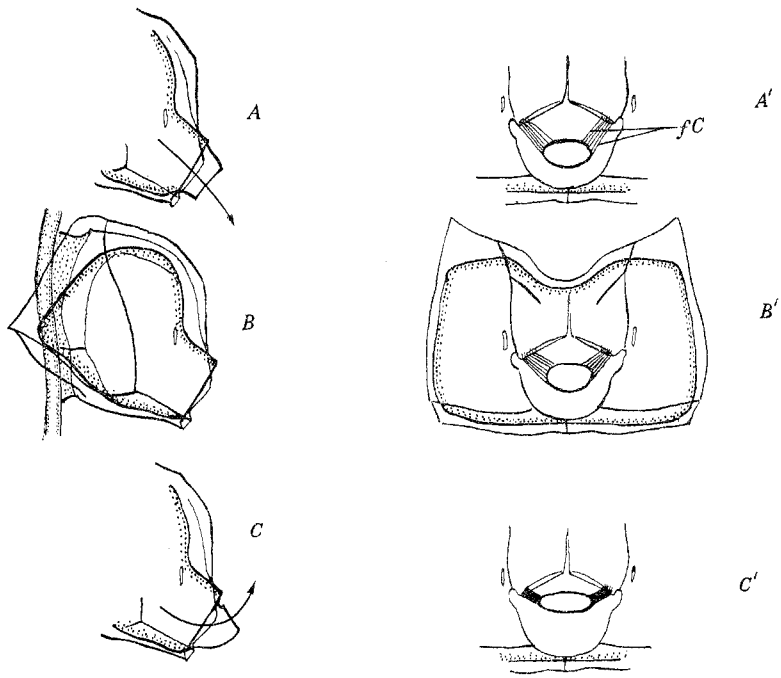


FIGURE 4. Velar mechanics. *A–C* lateral views, *A′–C′* abaxial views of nectophores. *A*,*A′* in forwards locomotion; *B*,*B′* at rest; *C*,*C′* in reverse locomotion. In forwards locomotion the fibres of Claus (*fC*) do not contract. In reverse, they contract, deflecting the water jet upwards (forwards).

means of a muscular pedicle (*ped*) through which passes an endodermal canal (pedicular canal, *c ped*, figure 6) to the subumbrella at the point of origin of the four radial canals. The whole subumbrellar cavity and the inner side of the velum are lined with striated muscle, running chiefly circularly. Contraction of this system is responsible for the constriction of the nectosac and consequent ejection of water through the velar aperture which is the basis of swimming. In addition to this system, there is a radial system of smooth muscle fibres located in the superior-lateral corners of the velum on the subumbrellar side, first described in *N. bijuga* (*'Halistemma tergestinum'*) by Claus (1878). These will be referred to as the 'fibres of Claus' (*fC*). Their role in deflecting the water jet is illustrated in figure 4. In forwards locomotion the fibres do not contract and the nectophores

are so orientated that the water jet is directed obliquely backwards. In reverse locomotion the fibres of Claus contract at the same moment as the swimming contraction occurs with the result that the velar opening is pulled upwards with consequent deflexion of the jet. It has never been observed, and there is no reason to suppose, that asymmetrical contraction of the two groups of fibres ever occurs or that the water jet can be directed sideways. In addition to the circular muscle system and the (radial) fibres of Claus, a third set of muscle fibres is present (not illustrated). These consist of very fine, smooth muscle fibres arranged radially on the exumbrellar side of the velum. They probably function antagonistically to the circular system on the subumbrellar side of the velum, restoring the velar opening to a certain shape and size following each swimming contraction.

### *C. Distribution of nerves in the nectosome*

Using the osmic-acetic maceration method, Schaeppi (1898) studied the distribution of nerves and muscles in the nectophores of several siphonophores. In addition to the circular muscle of the subumbrella and the radial fibres of the velum, Schaeppi records the presence of a bundle of fibres, orientated circularly, running round the margin on the exumbrellar side near the base of the velum. He notes that the fibres are exceptionally fine, winding in and out among the bases of the cells; he considers the possibility that they are nerve fibres, forming an exumbrellar nerve ring, but rejects this possibility in favour of the view that they are muscle fibres. In the mid-line on both upper and lower sides, the circular fibre bundle gives off a strand radially on the exumbrella towards the stem. Schaeppi regards these radial tracts as predominately muscular, but he notes that nervous elements are associated with them. In the lower tract, nerve fibres accompany the muscle fibres all the way from margin to stem in both *Halistemma* and *Physophora*, with minor differences of detail. In the upper tract the nerve fibres are intermingled with the muscle fibres, but neither extends as far as the stem. Schaeppi further found an open type of nerve net in certain regions of the exumbrella, forming connexions with neurones in the radial tracts. This nerve net also contributed cells and fibres to the circular muscle bundle in the margin, but no well-delineated, consistently orientated, thick collection of nerve cells was found of the type forming the exumbrellar nerve ring of hydromedusae.

In studying nectophores from *Forskalia edwardsii* and *Stephanomia rubra*, two of the species investigated by Schaeppi, I have arrived at the conclusion that Schaeppi's original impression was the correct one, and that the fibres forming the principle component of the circular and radial tracts are nerve fibres, not, as he eventually described them, muscle fibres. Some of the evidence for this statement has been set forth elsewhere (Mackie, thesis) but new, unpublished support has been obtained since. It is intended to publish this in another paper, but as the sections of the present account dealing with the functional organization of nectophores will involve reference to the histological arrangement of nerves and muscles in these members, a summary of my main findings will be presented here, with an indication of the points in which there is a conflict with Schaeppi's interpretations.

From study of silver-stained strip preparations and teased preparations of

exumbrellar tissue stained with haematoxylin I find that the fibres of the circular bundle originate from two types of cell, the first of which lies near the surface, has a rounded, compact form with little cytoplasm, and carries a hair at the free surface, projecting to the exterior, the second type being a compact cell lying deeper, often in the middle of the fibre bundle, and lacking a hair. The first type is a typical hydrozoan neuro-sensory cell and the second is a bi-polar ganglion cell. The thin, winding fibres show an affinity for silver in Holmes's silver preparations, and are distinguishable from muscle fibres in the same preparations, which show less affinity for the stain. Conversely, in iron-haematoxylin preparations of Bouin-fixed material, where the muscle fibres stain an intense black, the fibres in the circular bundle hold little of the stain. Thus my findings indicate that the circular fibres are neurites, not muscle fibres, and I regard the fibre bundle as an exumbrellar marginal nerve ring homologous and very similar to that of hydromedusae. With regard to the two radial tracts, my findings again indicate that the predominating tissue is nerve, not muscle. I have found no muscle fibres in the radial strands, although some cnidoblasts may be present, in addition to the neurons.

In *Nanomia*, I have done no more than carry out preliminary studies in order to ascertain whether or not the histological picture accords with the results from *Forskalia* and *Stephanomia*. These studies bear out the earlier findings, and it can be stated that the arrangement in the three genera is very similar. I have extended my observations on *Nanomia* by using methylene blue on living tissue, and have been able to follow the distribution of nervous tissue in the exumbrellar in more detail than was previously possible. I find, like Schaeppi, that the lower nerve tract (Schaeppi's 'lower muscle tract') runs all the way to the pedicular attachment point, terminating in a swelling adjacent to the pedicle. The upper tract (figure 6*C unt*), likewise consisting of nerve cell-bodies and fibres, arises from the circular fibre bundle as a thick band, but, as it ascends the exumbrella, it splits up into smaller tracts and eventually resolves itself into a mass of individual neurons which straggle away into the surrounding ectoderm. Schaeppi does not state whether any of these processes makes contact with the pedicle. In my methylene blue preparations, I found that the fibres failed to penetrate to this region, but were confined within the superior and abaxial areas. In addition to the upper and lower radial nerve tracts and the outlying neurons connected with the former, exumbrellar nervous tissue occurs in the two patches (Claus's 'seitlichen Zapfen') which project from the velar base out over the exumbrella on either side, but here too, as with the upper nerve tract, no nervous connexion with the stem is in evidence. Thus the only nerve pathway from stem to margin appears to be the lower of the two exumbrellar radial tracts.

In investigating the distribution of nerves on the subumbrellar side of the nectophore, my findings have been in agreement with Schaeppi's. There is no general plexus over the subumbrellar muscle sheet (a phenomenon I have commented upon elsewhere—Mackie 1960*a*), instead, the nervous tissue is confined to the subumbrellar marginal nerve ring.

It was at one time claimed (Korotneff 1884; Schneider 1892) that a central nervous system existed in the stem, but Schaeppi states that the structure in

question is merely an outgrowth from the endoderm of the central canal. According to Schaeppi, ganglion cells occur in the stem and nectophore lamellae, but they are not concentrated into multicellular tracts.

## 6. Experimental analysis

### *A. Evocation of locomotion*

Application of a fine glass probe to various parts of the siphosome evokes local muscular contraction in the region stimulated. A light touch to a tentacle evokes first purely regional contraction but if the stimulus is repeated the whole tentacle shortens. Gastrozooids may become active when their tentacles are stimulated, the activity consisting of elongation and writhing (Mackie & Boag, 1963). The activity may spread to neighbouring gastrozooids without, however, causing contraction of the intervening stem. All of these activities are of the type usually described as 'facilitated' (following Pantin (1935)) on the assumption that excitation is spreading progressively across a synaptic nerve net with repeated stimulation, each wave of excitation facilitating the synaptic passage of subsequent waves. With prolonged gentle agitation of the siphosome, it is occasionally possible to evoke the asynchronous type of forward swimming referred to earlier, and this may also be regarded as a facilitated response. However, it is much more common for locomotion to ensue suddenly in the form of synchronized forward swimming, an activity with sharply definable characteristics. In freshly captured specimens the siphosome is so sensitive that local and facilitated responses are hard to obtain, or are shown momentarily and are then superceded by the synchronized swimming. After a period in captivity the siphonophore becomes less excitable, but a sharp tap applied to any region of the siphosome immediately evokes the synchronized response. The response is characterized by general contraction of the siphosome and by a single synchronized contraction in all the nectophores. Reaction follows stimulus with barely perceptible delay even where the stimulus is applied to the posterior end of a long specimen. The contraction of the nectophores is not the culmination of a wave of contraction running up the stem. It occurs actually before the tentacular shortening is visible in some cases. After the initial swimming contraction, nectophoral activity may continue asynchronously and the siphosomal contraction may be completed while the colony swims. The writhing activity of gastrozooids does not normally form part of this general response but may be exhibited concurrently if it has been initiated prior to evocation of the general response. The general contraction plus synchronized swimming are evoked together on an all-or-nothing basis, in sharp contrast to the facilitated activities referred to earlier. All-or-nothing reactions can be explained by assuming that excitation passes to the responding regions by nervous through-conduction from the point stimulated; thus a single stimulus of sufficient intensity to 'fire' the through-conduction system should evoke the full response every time. This can be demonstrated in *Nanomia* by electrical stimulation. Delivery of a single shock to a bract, gastrozooid, palpon or lower nectophore evokes the full response. A single shock to the tentacle of a fresh specimen usually evokes the full response, but sometimes the

response is local and a second shock is needed to discharge the through-conduction system. The muscular responses of individual nectophores are strictly all-or-nothing and there is no resemblance to the various types of stepped contractions exhibited elsewhere in the phylum.

To sum up the foregoing observations it may be said that there is clear evidence for responses both of the facilitated and of the through-conducted type, the differentiation of the two depending on the type of stimulation employed. To say that 'mild' stimulation evokes the one and 'strong' the other does not greatly clarify the picture but is unfortunately all that can be said at the present. Unless electrical activity engendered in the conduction system can be recorded and correlated with the stimuli, one cannot define either quantity or quality of stimulation with accuracy. An electrical shock functions here as 'strong stimulation' but whether because it excites receptors over a wide area, gives rise to prolonged repetitive discharge from receptors or gives rise to some specially patterned type of discharge it is impossible to say.

An attempt has been made to measure conduction rate up the stem in the through-conducted response, the interval between stimulus and nectophore response being measured by eye and ear 'calibrated' against a flashing light and signal marker adjusted to known frequencies. This method may be thought crude, but siphonophores do not lend themselves willingly to attachment of recording apparatus such as neurophysiologists customarily employ for such estimations. Repeated observations on the longest available specimens (20 to 25 cm) suggest that the conduction rate must be between 75 and 150 cm/s at 14 °C and is probably at least 100 cm/s. In a specimen 25 cm long, this means that the reaction time (of the siphonophore) is about $\frac{1}{4}$ s.

Reverse swimming occurs, as noted above, when anterior parts of the colony strike some resistant object during forward swimming. Use of electrical stimulation shows that a single shock applied to float or anterior nectophores evokes the response. Again, the response of the nectophores is all-or-nothing and follows a single stimulus, so through-conduction is to be inferred. Siphosome contraction may also be exhibited but this may be incomplete and we cannot speak of through-conduction below the level of the nectophores in this instance. As noted above, a second synchronized response in the nectophores, also of the reverse type, may sometimes be exhibited.

Experiments on the sudden illumination of dark-adapted specimens showed that light can act as a stimulus evoking neuro-muscular activity. Sudden exposure to daylight of 150 ft.c evokes synchronized forward swimming and its accompanying stem contraction. The response, however, is not immediate, but occurs after approximately 1·5 s delay during which local muscular activity is seen in the siphosome. There is a distinct resemblance here to the prelude to spontaneous forward swimming where, as noted earlier, the first indication of activity is in the siphosome. It would appear that the initial response to light excites the facilitation pathways and, on reaching sufficient 'strength' becomes through-conducting or 'sparks over' into through-conducting pathways. If the specimen is incompletely dark-adapted, or if the intensity or duration of illumination is lower, or if it is

applied to a restricted locality, only facilitated responses may be exhibited. The sensitivity of specimens to light of a particular intensity is of brief duration, perhaps in the order of 15 s, after which they settle down. Reverse swimming cannot be evoked by photic stimulation, even when a very bright light is focused on the areas where tactile and electrical stimulation elicit the response. Systematic study of the whole colony area by area with a focused beam showed that photo-sensitivity is confined to the siphosome (figure 5). It may be noted incidently that

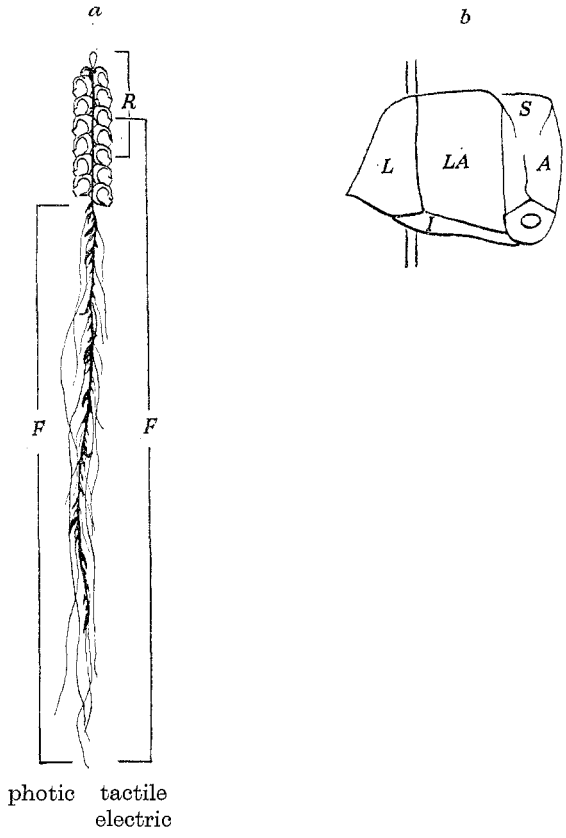


FIGURE 5. *a*, Regional sensitivities. Reverse locomotion is evoked by tactile and electric stimulation in the region *R*, forward locomotion by photic (left) or by tactile and electric (right) stimulation in the regions *F*. *b*, A nectophore showing exumbrellar zones referred to in the text. *A* abaxial zone, *I* inferior, *L* lateral, *LA* lateral-abaxial, *S* superior.

*Nanomia* shows a second response to light, chromatophore movements (Mackie 1962), but this appears to be an unrelated phenomenon. Chromatophores occur in the nectophores and float, these areas showing no photo-sensitivity where the evocation of muscular responses is concerned. The nature of the siphosomal photo-receptors is unknown, but this is true of a number of coelenterates which respond to light (North & Pantin 1957; Passano & McCullough 1962). It is possible that the receptive structures are neurones, for neuronal photosensitivity has been demonstrated in a number of invertebrates, e.g. *Aplysia* (Arvanitaki & Chalazonitis, 1961 and earlier papers).

*B. Differentiation of responses in the nectosome*

It has been seen that electrical stimulation of lower nectophores evokes the synchronized forward response (which will be referred to as $F$) while stimulation of anterior nectophores and float evokes the reverse response ($R$). It is possible to show that there are really three sensory zones in the nectosome, an anterior ($R$-evoking), a posterior ($F$-evoking) and a transitional region where either $F$ or $R$ responses may be evoked. Study of a specimen with eight nectophores, each stimulated by a single shock on ten separate occasions gave the results shown in table 1. A shock evokes either the complete $F$ of the complete $R$ response in the whole nectosome or a local response (unspecified) in the nectophore stimulated ($L$).

TABLE 1. NECTOSOMAL RESPONSES OBTAINED BY STIMULATING INDIVIDUAL NECTOPHORES, NUMBERED FROM THE TOP OF THE COLUMN

Reverse ($R$), forward ($F$) and local ($L$) responses are enumerated.

| nectophore | $R$ | $F$ | $L$ |
|---|---|---|---|
| 1 | 10 | 0 | 0 |
| 2 | 10 | 0 | 0 |
| 3 | 5 | 5 | 0 |
| 4 | 1 | 8 | 1 |
| 5 | 0 | 9 | 1 |
| 6 | 0 | 6 | 4 |
| 7 | 0 | 4 | 6 |
| 8 | 0 | 7 | 3 |

The table shows that the two anterior nectophores are $R$-evoking and propagate so readily that no $L$ responses are given while the four posterior ones, though more prone to give $L$ responses, evoke only $F$ responses when they do propagate to the colony. Nectophore 3 was strictly intermediate, giving $F$ and $R$ in equal numbers, while nectophore 4 was predominantly $F$-evoking, but with residual $R$-evoking capacity. Four other colonies were analyzed but autotomy of nectophores prevented completion of data. It was found, however, that transitional zones of 3 to 5 nectophores occurred, the total number of nectophores being over 12 in each case, and that the transitional zone, instead of being near the top of the column as in the original specimen was near the centre. Figure 5 illustrates the transitional zone as it appeared in these specimens. The original specimen had probably lost one or two anterior nectophores before the tests were begun.

The reactions of transitional nectophores appeared generally stable over the periods of study (up to 1 h) but in a few cases there appeared to be some reversion from $F$ to $R$ predominance, possibly associated with excessive stimulation. In speaking of 'residual' $R$-evoking capacity and 'reversion' to $R$ predominance it is assumed that a nectophore during its growth and passage down the column undergoes a transition from $R$- to $F$-evoking capacity. This assumption is supported by preliminary observations of specimens over periods of several days. The observations were begun late and time did not permit completion. In the most complete test, a specimen was deprived of all its mature nectophores. It was segregated and fed regularly. After 5 days it had four mature nectophores, all of which were

purely *R*-evoking. After 7 days it had five nectophores, the top four of which were *R*-evoking, the lowest being now transitional, orientated 6:4 in favour of *R*. If it had been possible to complete the experiment, one supposes that the lowest nectophore would become *F*-evoking, that others moving down from above would become transitional and eventually the pattern as shown for perfect specimens would be produced. A further implication from this line of reasoning is that old nectophores are shed from the bottom of the column, so maintaining the balance between *F* and *R* areas. This, however, has not yet been demonstrated.

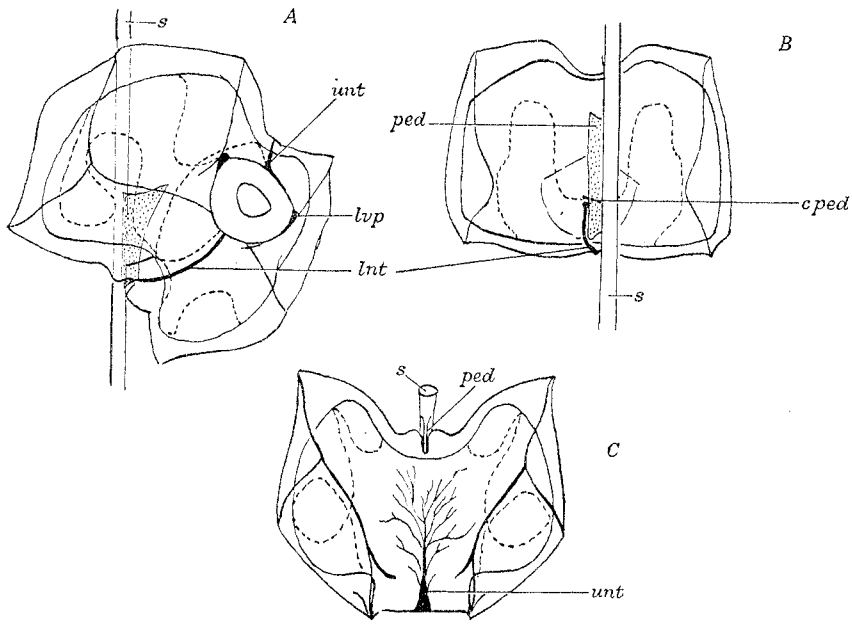


FIGURE 6. Nectophores seen from various angles to show nerve tracts. *A*, lateral-abaxial view of nectophore tilted to one side. *B*, Axial view. *C*, Superior-abaxial view. Broken lines show pathways of radial canals. *c ped* pedicular canal, *lnt* lower nerve tract, *lvp* lateral velar patch, *ped* pedicle, *s* stem, *unt* upper nerve tract.

An attempt was made to ascertain whether, in transitional nectophores, *F*-evoking and *R*-evoking capacities were differentiated spatially on the exumbrellar surface. The question has not been satisfactorily answered but preliminary studies suggest that there is such spatial zonation, the abaxial and superior-abaxial zones retaining *R* sensitivity longer than other regions, *F* sensitivity appearing first and spreading up from the inferior-lateral areas (figure 5*B*).

Finally, it should be made clear that the transformation of the nectophore as a sensory unit from the *R*-evoking to the *F*-evoking condition does not in any way affect the nectophore's capacity as a motor unit to take part in *R* locomotion. Similarly, the anterior nectophore, direct stimulation of which always evokes the *R* response, takes part in *F* locomotion and, in fact, as Sars long ago observed, is often more active in the asynchronous swimming than are posterior nectophores. Any age change in motor capacity then is simply in the direction of reduced excitability. The changes in sensory capacity are, by contrast, qualitative.

*C. Responses of specimens under partial anaesthesia*

Specimens in 1:15 isotonic $MgCl_2$:sea water show reduced excitability, but the *R* and *F* through-conduction mechanisms still operate and responses, though sluggish, are not altered essentially. In 1:10 solution, certain nectophores, particularly posterior ones, fail to contract in the *F* and *R* responses. This disturbance is evidently motor, for the inert nectophore will continue to transmit excitation to the colony when stimulated, even though failing to contract itself. Another effect of anaesthesia at this level is the partial blocking of siphosomal muscular contraction, hitherto a component of the *F* response. The siphosomal conduction pathways remain functional, however, and *F* swimming can be evoked by stimulation of the siphosome, even though the latter shows no muscular activity, or contracts only after repeated shocks have been delivered. The observation that muscle action is blocked by magnesium anaesthesia before nervous transmission is in accordance with observations on other coelenterates (Ross & Pantin 1940; Bullock 1943; Josephson 1962).

A specimen in 1:7·5 solution no longer gives the *F* response in any form. The *R* response can, however, still be obtained in a curiously altered and attenuated form. The anterior nectophores may respond normally, but in the posterior ones, the only sign that excitation is still arriving at the margin is the twitching of the fibres of Claus. The circular muscle contraction has been selectively eliminated. In one anaesthetized specimen approximation of the electrodes to an anterior nectophore with shocks at 1/s evoked synchronized twitchings of the fibres of Claus all the way down the nectosome of fourteen nectophores. Usually, however, a few anterior nectophores continue to show the circular muscle component, so vestigial *R* behaviour is exhibited.

Specimens in a 1:5 solution show general suppression of both *F* and *R* responses. Local twitching of the fibres of Claus can be obtained by direct application of the electrodes to the overlying tissue, but no transmission occurs to other regions or, if it does, there is no motor response. Autotomy of nectophores can still be obtained by persistent stimulation of a nectophore which indicates that conduction is not completely blocked at this level. The exact quantity and quality of stimulation required to elicit autotomy of nectophores has not been investigated and is in any case outside the scope of the present account. It may be noted that the nectophores and bracts are the only members which autotomize; some writers have seemed to suppose that autotomy occurs in all the appendages but fortunately this is not so.

*D. Localization of conduction pathways in the nectophore*

It will be clear from the preceding remarks that excitation can pass either way between nectophore and stem. It has also been noted that a nerve tract is histologically demonstrable connecting the margin and stem over the lower side of the exumbrella. A first step in the investigation of conduction routes was clearly to ascertain the function of this lower nerve tract; other experiments suggested themselves as the investigation proceeded.

*Expt.* 1. The lower nerve tracts of all the (six) mature nectophores in a specimen were abraded over a distance of 500 to 1000 $\mu$m with as little damage to surrounding tissues as possible. On recovery of the specimen from anaesthesia, it was found that it no longer gave the swimming component of the *F* response following stimulation of the siphosome. The siphosome still contracted, and an immature nectophore (which had not been operated on) showed the *F* response. Direct stimulation of posterior nectophores evoked *L* responses, except in a small number of cases when one or more nectophores on the opposite side showed contractions immediately afterwards. At first sight this appeared to indicate that *F* excitation could still be propagated from posterior nectophores in spite of the operation to the nerve tract. However, investigation showed that the response of opposite nectophores was never simultaneous with that of the one stimulated (as in the propagated *F* reaction) and that most of the nectophores showed no response. It can be assumed then that the 'response' seen was evoked mechanically. If a jet of water is directed against its velum a nectophore frequently shows a local response. Similarly, when the nectosome is suddenly displaced sideways by the contraction of a nectophore on one side, those on the opposite side experience a sudden flow of water against the velum which would act in the same way as the experimental jet and evoke a local contraction. The experiment then shows that section of the lower nerve tract eliminates the passage of *F* excitation both ways between stem and nectophores. By contrast, the *R* response is not affected and can be evoked in the usual way by stimulation of the anterior nectophores or float.

*Conclusion.* The integrity of the lower nerve tract is not essential either for local nectophore responses or for the transmission of the *R* response but it is essential for the transmission of the *F* response from nectophore to stem and vice versa.

*Expt.* 2. In several nectophores of a fresh specimen the area where the four radial canals join was destroyed by means of a needle inserted through the mouth of the nectophore. This obliterates the only connexion between the endoderm of the stem and that of the nectophore. On recovery of the specimen, these nectophores showed no alteration in their behaviour.

*Conclusion.* There is no evidence that excitation is transmitted by the endoderm. If transmission occurs at all it is not essential for either *F* or *R* responses.

*Expt.* 3. In several nectophores on one side of a specimen both upper and lower nerve tracts were sectioned near the margin. This operation led to the obliteration of the *F* response in the denervated nectophores as in Expt. 1. Since these were all on one side, this specimen performed *F* swimming in circles. By contrast, *R* swimming was unaffected and symmetrical.

*Conclusion.* Integrity of the upper nerve tract is not essential to transmission of the *R* response.

*Expt.* 4. The upper and lower nerve tracts of a nectophore were sectioned and an attempt was made to abrade a complete ring of ectoderm from around the nectophore, so isolating the marginal region from the intact tissue on the side of the stem. This operation was carried out on five different specimens. In two cases *R* excitation could still pass between stem and margin. In the other three it was abolished. *F* excitation was eliminated as in previous experiments.

*Conclusion.* Uncertain as far as the *R* response is concerned, although the abolition of *R* conduction in three cases strongly suggests that the exumbrella provides the normal conduction pathways for the response. In the cases where conduction persisted, it is possible that some tissue continuity remained after the operation. Further study of the *R* conduction pathways was called for and was carried out on detached nectophores.

*E. Responses of detached nectophores; determination of* R *conduction routes*

Following autotomy a nectophore usually performs a lengthy series of swimming contractions in which the fibres of Claus may or may not take part; thus *F* and *R* types of activity are shown. Attempts to correlate the predominance of *F* and *R* activity of isolated nectophores with their characteristic *F*- or *R*-evoking capacity prior to detachment gave inconclusive results. It seems that the character and amount of locomotory activity shown by a detached nectophore is fairly meaningless in terms of its previous behaviour. This may be because autotomy involves violent tissue disruption and consequent unpredictable disturbance to the conduction mechanisms in the exumbrella. It was observed that detached nectophores show diminishing ability to give purely *F* contractions the longer they have been isolated, even if prior to detachment they were strongly *F* orientated. In such nectophores, *R* responses (either complete or confined to the fibres of Claus) are evoked by stimulation of any area of the exumbrella surface. It is hard to know how to interpret these phenomena, for the detached nectophore is unreliable experimental material, but certain clear deductions can be made: (*a*) the capacity for *R* transmission in the exumbrella must never be wholly extinguished even in posterior nectophores; (*b*) *R* sensitivity is dispersed all over the surface and is not confined to the areas from which, by their accessibility, the *R* response is obtained in intact specimens; (*c*) it may also be noted that the circular muscle of the nectophore, earlier seen to be more susceptible to anaesthesia than the radial fibres of Claus, is quicker to show functional deterioration following autotomy. Several experiments were carried out on detached nectophores in order to ascertain the location of *R* conduction pathways.

*Expt.* 5. In a nectophore which gave the *R* response to stimulation at any point on the surface an area of exumbrellar tissue about 2 mm wide was abraded from one lateral surface (figure 7*A*). Application of the electrodes to this denuded area gave no response, although surrounding areas were still sensitive.

*Conclusion.* Excitation cannot be conducted via the mesogloea.

*Expt.* 6. In another *R*-sensitive nectophore an island of intact tissue was created on the axial surface surrounding the pedicular attachment region, by abrading a ring of ectoderm (figure 7*B*). Stimulation of this area gave no response, although surrounding regions were still sensitive.

*Conclusion.* Excitation cannot be conducted by the endoderm or mesogloea in the pedicular attachment region (confirms Expt. 2).

Several other experiments along these lines had similar results and it appears that *R* excitation is propagated exclusively by the exumbrellar ectoderm or by conducting elements in it and that all parts of it can conduct. It will be recalled

that the histological study with methylene blue revealed nervous tissue only in restricted areas of the exumbrella. This result has to be reconciled with the evidence that all regions can conduct. As in *Cerianthus* (Horridge 1958) two possibilities appear open: either nerve elements are more widely distributed than the histological investigation showed or conduction occurs in elements other than nerves, in this case presumably the cells of the exumbrellar epithelium. Although this matter cannot be decided without further study, certain comments can be made (see Discussion, p. 389). Another unsolved problem concerns the role of the upper nerve tract. It has been shown that the tract is not essential to either *R* or *F* responses, although it could still be concerned in one of them (presumably the *R* response) in a restricted role. It will be recalled that *R* sensitivity appears to be retained longer in the superior and abaxial areas of transitional nectophores, than it is elsewhere on the exumbrellar surface. (p. 381). These are precisely the regions in which the upper nerve tract and its outlying processes lie.

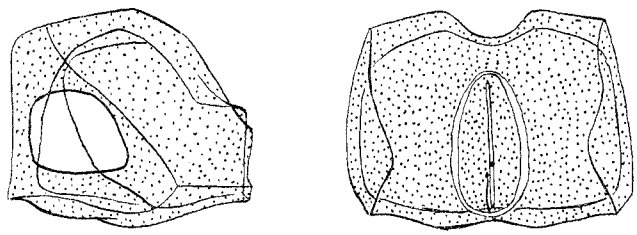


FIGURE 7. Typical abrasion experiments on detached nectophores. Intact exumbrellar tissue is stippled. In *A* (Expt. 5) an area has been abraded from a lateral surface. In *B* (Expt. 6) a ring of ectoderm has been abraded from around the stem attachment region.

### *F. Models for motor and sensory connexions*

The experiments clearly show that, in the nectophores, *F* excitation is transmitted along a separate conduction pathway to *R* excitation, that the route for the former is the lower nerve tract, that there is no single localized route for the latter but that it is carried all over the exumbrella. Intermediate responses are never observed and it may be deduced that excitation cannot spread from one system to the other, that the two conduction routes are separate and insulated from one another. Contraction of the circular swimming muscle is a component of both responses while the contraction of the fibres of Claus is a component peculiar to the *R* response. On the basis of these observations we can construct a diagram of the motor connexions as in figure 8. For convenience, the *R* conduction routes are represented by a single (broken) line.

With regard to sensory connexions, it has been shown that stimulation of the nectophore surface may give rise to propagated excitation evoking in other nectophores either *R* or *F* responses but not mixtures of the two nor responses intermediate between the two. This suggests that there are probably separate conduction systems for the two responses not only in the nectophores but in the stem as well. This point has not been verified directly but it has been assumed in constructing

the 'wiring' diagram (figure 9) that separate conduction pathways exist in the stem, as this seems most likely.

A highly interesting feature of the sensory mechanism is the apparent transformation with age of a nectophore from the *R*-evoking to the *F*-evoking sensory

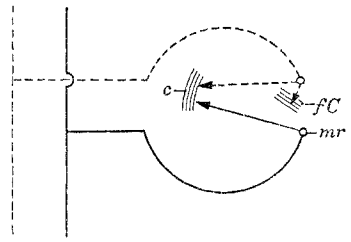


FIGURE 8. Motor connexions in a nectophore. Broken line: conduction pathways for reverse swimming; solid line: conduction pathways for forward swimming; *c* circular muscle, *fC* fibres of Claus, *mr* marginal nerve ring.

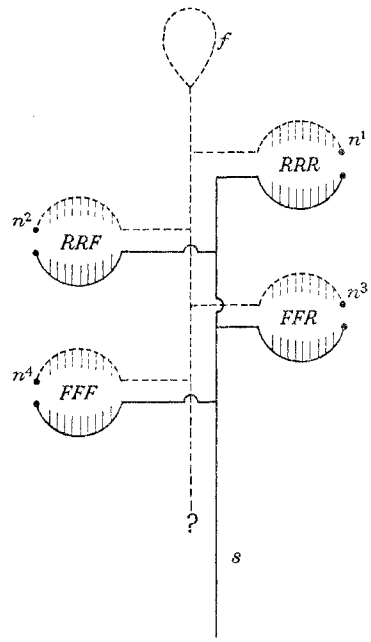


FIGURE 9. Nectosomal sensory connexions in a model colony of four nectophores. Conduction pathways (as in figure 8): broken line for reverse swimming and solid line for forward swimming. The letters *RRR*, *RRF*, *FFR* and *FFF* respectively indicate the relative exumbrellar sensitivities in the four nectophores in regard to stimulating reverse (*R*) or forward (*F*) swimming. *f* float, $n^1$–$n^4$ nectophores, *s* siphosome.

condition. The letters in figure 9 represent the extent to which excitation originating in the exumbrellar tissue is channelized into (or is patterned in such a way that it is propagated by) one or other of the two conduction systems. The nature of this channellization or patterning is completely mysterious.

Stimulation of a nectophore elicits either the *F* or *R* activity not only in the nectophore stimulated but in nectophores both anterior and posterior to the one stimulated; there is thus no evidence for polarized conduction in either system.

Stimulation of the float excites the *R* conduction system and stimulation of the siphosome excites the *F* conduction system; these features are incorporated in the 'wiring' diagram. It is not certain that there are two separate conduction systems in the siphosome; if there are, one of them would certainly carry *F* excitation, but the other would appear to have no functional connexion with the *R* system in the nectosome. The *R* conduction pathway in the diagram, therefore, ends posteriorly in a question mark.

### 7. Conduction and co-ordination in other Siphonophora

Study of two other members of the Sub-order Physonectae suggests that co-ordination of nectophoral activity occurs very much as in *Nanomia*. Hardy (1956, p. 117) cites observations by the present author on *Forskalia edwardsii* Kölliker, including the first reference to the role of nectophores in reverse swimming. These observations have since been extended by D. A. Boag (notes made available from studies at Naples, 1960). In both *Forskalia* and *Stephanomia* (*S. rubra* Vogt) forward swimming may be initiated by a single synchronized thrust or it may start in one or two nectophores, nearly always anterior ones, and spread to others as in *Nanomia*. Boag describes the forward progress of *Stephanomia* as 'sinuous and snake-like' when the nectophores are acting asynchronously; in the synchronized response movement is in a straight line. In *Forskalia* the asynchronous response causes slow progression in a helical pathway, the synchronous response causing rapid movement straight ahead. Reverse locomotion substantially as described in *Nanomia* has been observed by Boag in both these species. Velar responses and the action of the fibres of Claus appear closely similar in all three genera. It is probable that the information given for *Nanomia* will prove applicable with relatively slight modification to all the long-stemmed Physonectae. The situation in short-stemmed forms such as *Physophora* is another matter and few details of locomotory behaviour here are available. In 1775 Forskål (trans. C. Vogt 1854) described the vigorous swimming actions of this form; Totton (1954) provides some interesting observations on the activity of the long and prehensile palpons of *Physophora* and further notes that unified contractions occur in the nectophores on one side during horizontal locomotion and that swimming activity may begin in a young anterior nectophore, later becoming general. No mention is made of reverse locomotion, however, and it is not known whether the fibres of Claus are developed. If they are, then it may be assumed that reverse locomotion is possible. The curious physonect *Athorybia rosacea* lacks nectophores and swims 'by energetic movements of the bracts' (Kölliker 1853). Totton (1954) also saw movements of the bracts but of a somewhat less energetic character. Haeckel (1888) states that *Nectalia loligo* can raise and lower its corona of bracts. It does not appear to swim with them, although the two long lateral bracts may assist swimming indirectly either by acting as 'lee-boards' or by helping the moving colony avoid obstacles (Garstang 1946). No other siphonophores are known to possess mobile bracts, although a sheet of muscle is invariably present in the base, serving for autotomy. This muscle could no doubt evolve into a locomotory role. Keferstein & Ehlers (1861) show that the muscle is strongly developed in the

locomotory bracts of *Apolemia* but in location and shape it is not dissimilar to the autotomy muscle of bracts in other physonects. Further study of this interesting adaptation is much to be desired.

The Sub-order Cystonectae, including *Physalia* and *Rhizophysa*, require little comment. They have no capacity for locomotion. Through-conducted and local responses have been noted in *Physalia* (Mackie 1960*b*). *Rhizophysa* is said to have a very contractile stem and to be sensitive to stimulation.

Nectophoral locomotion, undirectional in all known cases, occurs throughout the Sub-order Calycophora. Miscellaneous notes on swimming postures, frequencies and general behaviour are provided by Totton (1932), Leloup (1935), Jacobs (1937) and others. Mackie & Boag (1963) describe a peculiar form of behaviour associated with spreading of the fishing filaments in *Muggiaea atlantica*. Recent observations on this form at Friday Harbor show that a nerve tract, hitherto undescribed, runs in the hydroecial ectoderm connecting stem and nectophore margin. There is reason to expect that this nerve will prove to be present in all the Diphyinae. Preliminary experiments with electrical stimulation show that in both *Muggiaea* and *Lensia* (*L. conoidea* K. & E.) conduction occurs both ways between nectophore and stem, but whether conduction is dependent on the integrity of the nerve tract has not yet been ascertained. *Hippopodius hippopus* Forskål has six or more nectophores but synchronized locomotory contractions are not observed. Activity begins in the small anterior nectophores and spreads to others; if it reaches the lowest two, which alone are capable of propelling the colony, a slow and somewhat erratic type of locomotion occurs (Boag 1960). The nectophores also show a radial response in which smooth muscle fibres located in the pseudovelum contract, curling the whole marginal region inward; this response may be exhibited simultaneously throughout the colony following stimulation. Contrary to the arrangement in the Diphyinae, *Hippopodius* lacks localized nervous connexions between stem and nectophores. Indeed, there appears to be no exumbrellar nervous system, although the usual marginal nerve rings are present. This absence of exumbrellar nervous tissue again raises the question of neuroid transmission in the ectoderm and of possible significance here is the well-known but little investigated phenomenon of 'blanching' shown by this form. The exumbrellar tissues become opaque, waves of opacity spreading over the colony from a point of stimulation. Possibly this optical effect is an accompaniment of excitation capable of evoking muscular activity. Korotneff (1884) claims that the opacity seen by day appears as luminescence by night. At all events, it is to be hoped that this interesting phenomenon will be studied further; *Hippopodius* is probably the commonest of the surface-living siphonophores of the Mediterranean.

*Porpita* and *Velella* (O. Chondrophora, Totton 1954) are phylogenetically remote from the true siphonophora, with which, however, it is traditional to treat them. They may show elaborate behaviour (Mackie 1959) but are incapable of locomotion. In *Velella* two histologically distinct neurone systems were described (Mackie 1960*a*) without, however, there being much to indicate their functions. It has since been possible to carry out some simple experiments on the living *Velella* and it was found that delivery of a single shock of one millisecond duration to any

point on the exterior evokes simultaneous, immediate contraction of the feeding zooids (gonozooids) sometimes accompanied by unified tentacular movements. It seems highly probable that the syncytial giant fibre net (closed system) is responsible for propagation of the through-conducted response, the second neurone system (open system) being presumably concerned with local activities.

The evidence available, though still incomplete, does bear witness to the ubiquity and sophistication of co-ordinating mechanisms in the Siphonophora. These mechanisms are exhibited most strikingly in the locomotory and 'escape' responses, but nervous influences are in evidence in a number of humbler activities of the vegetative kind and it will probably be found that very few activities are organized on a purely local basis.

## 8. Discussion

While answering some of the more general questions concerning the mechanics and co-ordination of locomotion in physonects, this study has opened fresh problems which cannot be discussed here in detail but which it may be useful to list. Questions of somewhat specialized interest are concerned in the mechanism and control of autotomy and of the asynchronous forward swimming response, the nature of the photosensitive elements in the siphosome and the structure, distribution and interconnexions of the neural elements in the stem. Possibly of wider interest is the conduction system for the *R* response where, it has been suggested, epithelial transmission may be involved. The physiological observations have been confined to visible (muscular) behaviour and no direct information is available on electrical activity carried on in the nervous system. We know, however, from recent work (Josephson 1961*a*, *b*, 1962; Passano & McCullough 1962) that overt behaviour of a hydroid, like that of a higher metazoan, is merely the 'exposed top of the iceberg'. The simple *Hydra*, for instance, proves to have two through-conduction systems, photosensitive pacemakers, inhibition and feedback mechanisms. Any attempt to draw more than the most general conclusions from observed behaviour alone would, in the case of the much more complex siphonophore colony, be injudicious. To the extent that such deductions can be made, they have already been made in presenting the results. Only in one case is additional comment called for, the matter of epithelial conduction in the exumbrella which, though not proven, appears to the author to be worth serious consideration. In seeking a precedent for conduction of the proposed type we may call to mind the case of vertebrate cardiac muscle where conduction is both non-nervous and all-or-nothing. Woodbury & Crill (1961) give evidence of electrotonic spread in atrial muscle and it is likely that local circuit current flow accounts for transmission in the heart. Heart muscle is almost certainly not syncytial (Sjöstrand & Andersson-Cedergren 1960) but the passage of excitation across the cell membranes evidently presents no difficulties.

Non-nervous conduction, whether decremental or all-or-nothing, is hard to investigate but may, with the application of modern recording methods, prove to be quite common and to co-exist in some situations with nervous conduction of

various sorts. Pantin (1956) effectively argues that 'the importance of the evolution of the nervous system was not that it superseded a primitive mechanism [local organization of effector action] but that, added to it, the combination had far greater potentiality for complex activity and response'. One may suppose, however, that in most places where they survived at all non-nervous phenomena would continue to be exhibited in purely local roles, for the nervous system is inherently better suited to co-ordinating effector responses over long distances. In the locomotion of *Nanomia*, however, an unusual problem is involved, that of providing two through-conduction systems, topographically co-existent but physiologically separate. In a higher animal differentiation of sensory and motor connexions could satisfy the requirements easily, but any such refinements in a coelenterate would have to be developed *de novo* from the elementary nerve plexus. Arguments such as these lead us to suppose that evolution may here have developed the conduction potentialities of the general ectoderm for one of the systems, reserving the nervous system for the other.

Work at Naples in 1954 was carried out while the author held the Oxford Naples Scholarship and a Research and Maintenance grant from the Department of Scientific and Industrial Research of the U.K.; subsequently financial assistance has been provided by the University of Alberta General Research Fund and by the National Research Council of Canada. Without this aid the study could never have been attempted; it could scarcely have been carried through successfully without the co-operation of the Directors and Staff of the Stazione Zoologica at Naples and of the Friday Harbor Laboratories of the University of Washington; and it was at all times greatly assisted by the help and encouragement of the author's wife. Mr D. A. Boag's generosity in making available for publication here his notes from Naples is recorded with gratitude. Dr D. M. Ross has kindly read the manuscript and many of his suggestions have been incorporated.

## References

Agassiz, A. 1862 *Proc. Boston. Soc. Nat. Hist.* **9**, 180–181.

Agassiz, A. 1865 North American Acalephae. *Ill. Cat. Mus. Comp. Zool. Harvard*, no. 2.

Arvanitaki, A. & Chalazonitis, N. 1961 Excitatory and inhibitory processes initiated by light and infra-red radiations in single identifiable nerve cells. In *Nervous inhibition* (ed. Florey), pp. 194–231. London: Pergamon Press.

Berkeley, E. & Berkeley, C. 1960 Some further records of pelagic Polychaeta . . . together with records of Siphonophora. *Canad. J. Zool.* **38**, 787–799.

Berrill, N. J. 1930 On the occurrence and habits of the Siphonophore, *Stephanomia bijuga* (Delle Chiaje). *J. Mar. Biol. Ass. U.K.* **16**, 753–755.

Bigelow H. B. 1911 The Siphonophorae. *Mem. Mus. Comp. Zool. Harvard*, **28**, 2, 173–402.

Boag, D. A. 1960 Notes made available from studies at Naples.

Bullock, T. H. 1943 Neuromuscular facilitation in scyphomedusae. *J. Cell. Comp. Physiol.* **22**, 251–272.

Claus, C. 1878 Über *Halistemma tergestinum* n.sp. nebst Bemerkungen über den feinern Bau der Physophoriden. *Arb. zool. Inst. Univ. Wien.* **1**, 1–56.

Fewkes, J. W. 1888 On certain medusae from New England. *Bull. Mus. Comp. Zool. Harvard*, **13**, 209–240.

Garstang, W. 1946 The morphology and relations of the Siphonophora. *Quart J. Micr. Sci.* **87**, 103–193.

Haeckel, E. 1888 Report on the Siphonophorae. *Rep. Sci. Results H.M.S. 'Challenger' Zool.* **28**, 1–380.

Hardy, A. C. 1956 *The open sea. Its natural history: the world of plankton.* London: Collins.

Horridge, G. A. 1958 The co-ordination of the responses of *Cerianthus* (Coelenterata). *J. Exp. Biol.* **35**, 369–382.

Hyman, L. H. 1940 *The invertebrates: Protozoa through Ctenophora.* New York: McGraw-Hill.

Jacobs, W. 1937 Beobachtungen über das Schweben der Siphonophoren. *Z. vergl. Physiol.* **24**, 583–601.

Josephson, R. K. 1961*a* Colonial responses of hydroid polyps. *J. Exp. Biol.* **38**, 559–577.

Josephson, R. K. 1961*b* Repetitive potentials following brief electric stimuli in a hydroid. *J. Exp. Biol.* **38**, 579–593.

Josephson, R. K. 1962 Spontaneous electrical activity in a hydroid polyp. *Comp. Biochem. Physiol.* **5**, 45–58.

Keferstein, W. & Ehlers, E. 1861 *Zoologische Beiträge 1; Beobachtungen über die Siphonophoren von Neapel und Messina.* Leipzig: Engelmann.

Kölliker, A. 1853 *Die Schwimmpolypen oder Siphonophoren von Messina.* Leipzig: Engelmann.

Korotneff, A. 1884 Zur Histologie der Siphonophoren. *Mitt. Zool. Sta. Neapel.* **5**, 229–288.

Leloup, E. 1935 Les siphonophores de la rade de Villefranche-sur-Mer (Alpes Maritimes, France). *Bull. Mus. Roy. Hist. nat. Belg.* **11**, 1–12.

Mackie, G. O. 1956 Thesis for degree of D.Phil., Oxford.

Mackie, G. O. 1959 The evolution of the Chondrophora: new evidence from behavioural studies. *Trans. Roy. Soc. Can.* (3) **53**, 7–20.

Mackie, G. O. 1960*a* The structure of the nervous system in *Velella*. *Quart. J. Micr. Sci.* **101**, 119–131.

Mackie, G. O. 1960*b* Studies on *Physalia physalis* L. (by A. K. Totton & G. O. Mackie). Part 2: Behaviour and histology. *Discovery Rep.* **30**, 369–408.

Mackie, G. O. 1962 Pigment effector cells in a cnidarian. *Science* **137**, no. 3531, 689–690.

Mackie, G. O. & Boag, D. A. 1963 Fishing, feeding and digestion in Siphonophores. *Publ. Staz. Zool. Napoli.* (in the Press).

North, W. J. & Pantin, C. F. A. 1958 Sensitivity to light in the sea-anemone *Metridium senile* (L): adaptation and action spectra. *Proc. Roy. Soc.* B, **148**, 385–396.

Pantin, C. F. A. 1935 The nerve net of the Actinozoa. 1. Facilitation. *J. Exp. Biol.* **12**, 119–138.

Pantin, C. F. A. 1958 *Notes on microscopical technique for zoologists.* Cambridge University Press.

Pantin, C. F. A. 1956 The origin of the nervous system. *Pubbl. Staz. Zool. Napoli*, **28**, 171–181.

Passano, L. M. & McCullough, C. B. 1962 The light response and the rhythmic potentials of *Hydra*. *Proc. Nat. Acad. Sci. Wash.* **48**, 1376–1382.

Ross, D. M. & Pantin, C. F. A. 1940 Factors influencing facilitation in Actinozoa. The action of certain ions. *J. Exp. Biol.* **17**, 61–73.

Sars, M. 1864 *Fauna littoralis Norvegiae* 1. Christiania: Dahl.

Schaeppi, T. 1898 Untersuchungen über das Nervensystem der Siphonophoren. *Jena. Z. Naturw.* **32**, 483–550.

Schneider, K. C. 1892 Einige histologische Befunde an Coelenteraten. *Jena. Z. Naturwiss.* **27**, 377–462.

Sjöstrand, F. S. & Andersson-Cedergren, E. 1960 *The structure and function of muscle* (ed. Bourne). New York: Academic Press.

Totton, A. K. 1932 Siphonophora. *Sci. Rep. Gr. Barrier Reef Exp.* **4**, 10, 317–374.

Totton, A. K. 1954 Siphonophora of the Indian Ocean. *Discovery Rep.* **27**, 1–162.

Vogt, C. 1854 Recherches sur les animaux inférieures de la Méditerranée. 1. Sur les siphonophores de la Mer de Nice. *Mém. Inst. nat. genev.* **1**, 1–164.

Woodbury, J. W. & Crill, W. E. 1961 On the problem of impulse conduction in the atrium. In *Nervous inhibition* (ed. Florey), pp. 124–135. London: Pergamon Press.