Communication présentée le 28 mai 1960.

THE NEMATOCYST OF HYDRA (Part III).

THE MIGRATION PATHWAYS OF NEMATOCYSTS IN HYDRA

by

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ACKNOWLEDGEMENT.

This work was supported in part by a post-doctoral grant awarded to the senior author by the National Science Foundation of the United States of America. This grant allowed the author to work in the laboratory of Dr. Paul Brien at the Université Libre de Bruxelles for a period of one year.

The author would like to express his sincere thanks to his colleagues in the Zoology Department at the Univertsité Libre de Bruxelles for the kind reception which they have given him and for their general helpfulness and encouragement during his stay in Brussels.

INTRODUCTION.

In 1907, HADZI, after experimenting with *Tubularia* and *Campanularia,* presented strong evidence for the fact that nematocysts are manufactured in areas far removed from the tentacles and reach their final destination in the tentacle batteries only after an active migration from the site where they were developed. According to HADZI, nematocysts which are contained in cnidoblast cells in the gastric epidermis are capable of traversing the mesogloea and the gastrodermis and then migrating through the gastrovascular cavity to the tentacles, where, by a

process not completely understood, the cnidoblasts penetrates the tissues of the animal and orients itself in the epidermis. BRIEN (1942) demonstrated that a similar process occurs in *Cladonema radiatum*.

This observation was generally accepted by the scientific world and applied to coelenterates in general. Although no one had been able to witness such a phenonemon occurring in hydra because of the opaqueness of the animal, many scientists, notably KEPNER et al. (1937) and JONES (1941) presented histological evidence which supported the hypothesis that nematocysts in hydra, like those in *Tubularia*, migrate via the gastrovascular cavity from the gastric region to the tentacles. This idea has been promulgated by most introductory textbooks of zoology in America for the past twenty years.

However, in 1950 BRIEN proposed a theory concerning nematocyst migration in hydra which was in contradiction to our traditional notions concerning this process. This author demonstrated quite conclusively in 1949 that hydra possesses a growth region just under the hypostome where a constant cell proliferation produces cells which force older cells distally to the tentacle tips and proximally to the basal disk where these cells atrophy and are sloughed off. Thus, hydra is constantly renewing its tissues from a single active growth center and is essentially immortal. BRIEN's demonstration of a growth center in hydra has been confirmed by BURNETT (1959) working on the brown hydra, *Pelmatohydra oligactis* (*Pallas*), and by BURNETT and GAROFALO (1960) in *Chlorohydra viridissima*.

As a result of his observations of the growth pattern in hydra, BRIEN hypothesized in 1950 that it is not necessary to assume that nematocysts in hydra must migrate through the gastrovascular cavity to reach the tentacles. Since nematocysts are continually formed in the growth region of the animal, it appeared quite conceivable that nematocysts could simply be pushed into the tentacles through normal growth processes. Nematocysts at the extremities of the tentacle would be sloughed off along with the epidermal cells, but a fresh supply of these structures would be furnished each day to the base of the tentacle. Thus, an entirely new concept of nematocyst migration was advanced.

SEMAL-VAN GANSEN (1951) rigorously examined and confirmed BRIEN's hypothesis. She found that if a vital dye is applied to the base of a tentacle of hydra, the dye moves slowly towards

the extremities. Such a phenomenon would be expected if normal growth processes were responsible for the migration of nematocysts. The time of passage of a vital stain from the base of a tentacle to the tip is approximately one week. SEMAL-VAN GANSEN also studied the cnidoblast cells in the vicinity of the growth region and gave an excellent account of the distribution of the different types of nematocysts found in the epidermal cells which would eventually enclose a nematocyst battery. According to this author, nematocysts are formed along the entire gastric epidermis. A single epidermal cell may contain many nematocysts representing all the types of nematocysts found in hydra. As the epidermal cell is pushed through growth processes towards the tentacles, it becomes more flattened, and by the time it has reached the lower $^1/_3$ region of the tentacle it is nearly spindle shaped. This flattening process forces the enclosed cnidoblast cells (which now may be referred to as nematocytes since their enclosed nematocysts are fully sculptured) to take their characteristic positions in the nematocyst battery. Thus, it appears that nematocyst migration in hydra follows a pattern unlike that commonly believed to be operating in coelenterates in general.

However, LENHOFF (1959) employing techniques of radioautography presented strong evidence which is in contradiction to the theory of BRIEN (1950) and SEMAL-VAN GANSEN (1951). This author was able to incorporate radioactive $^{14}CO_2$ selectively into developing nematocysts. He states that after 16 hours, hydra who have been exposed to the radioactive material have their radioactivity « confined to small but discrete loci throughout the upper $^2/_3$ of the body tube. Few, if any, of these loci were present in the tentacles ». LENHOFF further found that if similarly treated animals were then allowed to remain for 48 hours in a non-radioactive medium, many of the loci would appear in the tentacles. Furthermore, if a radioactive proximal or lower portion of a hydra is grafted to a non-radioactive hypostome and tentacles, radioactive loci would appear subsequently in the tentacles. Obviously these nematocysts would not be able to reach the tentacles through growth process which would force them proximally rather than distally.

Thus, we have two conflicting schools each presenting strong evidence in favor of their theories. The present study will be an attempt to resolve this conflict by means of grafting techniques and histochemical techniques applied to whole animals.

Materials and Methods.

The animals employed in the following studies were adult specimens of the common brown hydra, *Pelmatohydra oligactis*. They were reared after the method of Loomis and Lenhoff (1956).

During the course of these studies many animals were stained at various p.H's in a methylene blue solution and prepared as whole mounts. The rapid procedure for the staining of whole hydra is explained in the previous paper, *The Nematocyst of Hydra*, Part II.

It was also necessary to perform several grafting experiments throughout the course of this research. The grafts consisted of a stained proximal portion of one animal (including the basal disk, peduncle, and budding region) grafted to the unstained distal region (tentacles, hypostome, and growth region) of another animal. Methylene blue was selected as a vital stain. The method of applying this stain to the tissues of hydra, plus techniques involved in grafting procedures are explained in detail in a previous paper (See Burnett, 1959).

Methylene blue may be considered to be a selective stain for nematocysts, found in living animals, since these structures concentrate the stain to a much greater extent than any other structure or cell in hydra. However, not all nematocysts in the hydra will stain after vital staining. On the average about two in every five stenoteles located in the gastric region will concentrate the dye. Nevertheless, this method provides an excellent means of studying the migration pathways of nematocysts in living animals.

Several hydra were examined histologically at various intervals after the initiation of the feeding process in an effort to determine the nematocyst distribution of animals which had presumably depleted their supply of nematocysts while subduing prey. The hydra employed for these purposes were prepared for whole mounts and stained at various p.H's. This preparation is described in detail in the previous paper (See *The Nematocyst of Hydra*, Part II).

Observations and Discussion.

In the previous paper, *The Nematocyst of Hydra*, Part II, it was clearly demonstrated that there are chemical differences in the capsular contents of nematocysts located at different levels

in the tentacles. There is a p.H gradient extending from the extremities to the bases of the tentacles, and even into the growth region of the animal where nematocysts are formed. As nematocysts migrate from the base towards the tips of the tentacles, they become increasingly more acid and show a simultaneous increase in metachromasia. This observation led to the suggestion that nematocysts reach the tentacles from the growth region of the animal through the force exerted upon nematocytes by rapidly dividing cells in the growth region. For, if it is assumed that nematocysts located in the tentacles are formed in the body region and migrate to the tentacles through the gastrovascular cavity, then nematocysts freshly arrived from the gastric region, nematocysts which do not stain at p.H 8, should be found along the entire length of the tentacle. This does not appear to be the case. As has been previously demonstrated, the stenoteles in the distal ¾ of the tentacles all stain at p.H 8. On the other hand, hydra stained at p.H 5 reveal that only the stenoteles in the body or gastric region concentrate the dye; stenoteles located in the tentacles do not stain at this p.H. If a nematocyst migrated from the body region to the tentacles via the gastrovascular cavity one would expect to find nematocysts in the tentacles which stained at p.H 5. Over fifty animals were stained at this p.H and examined closely, and in only three cases were stained stenoteles found in the distal ¾ region of the tentacles. However, it must be stressed that all of these hydra had not been fed for a period of 24 hours. Therefore, it is quite possible that nematocysts had migrated to the tentacles immediately after feeding was complete, undergone a rapid increase of acidity within their capsules, and were not detectable at the time of staining.

It appeared that the only definite way by which to determine whether nematocysts reach the tentacles through growth processes and not through an active migration via the gastrovascular cavity would be as follows : if a method could be developed whereby it would be possible to suppress the formation of nematocysts while allowing for growth processes to continue, one would expect to find animals which contained in early stages nematocysts only in the distal ¾ of the tentacles, later in the distal ½ region, and finally only at the extremities of the tentacles.

A method has been developed recently which produces an inhibition of nematocyst formation to a great extent without

interfering with the growth processes of the animal. This method will be described in detail in the following paper, *The Nematocyst of Hydra*, Part IV, but it might be mentioned at this time that hydra in all of the stages just described were observed. This observation is taken as concrete evidence for the fact that nematocysts manufactured in the growth region of hydra normally reach the tentacles, not through an active migration process via the gastrovascular cavity, but are pushed to the tentacles as a result of normal growth processes in the animal. This finding is in complete agreement with the theories of Brien (1950) and Semal-Van Gansen (1951).

However, one may consider, on the other hand, a hydra which has had its nematocyst supply greatly depleted by rich feeding. If the animal must depend upon normal growth processes to furnish new nematocysts, several days would elapse before the stock of nematocysts in the tentacle is renewed. Repeated observations have revealed that hydra, normally, do not greatly deplete their nematocyst supply during the feeding process. A hydra is capable of killing or immobilizing a *Daphnia* with three or four stenoteles. A single large *Daphnia* each day will provide the hydra with sufficient nourishment to allow the animal to bud normally. In the laboratory, however, it is possible to greatly deplete a hydra's nematocyst supply by pulling the prey from the tentacles as soon as the prey has been immobilized. It has been demonstrated (See *The Nematocyst of Hydra,* Part I) that hydra is easily capable of killing over 100 *Artemia* if this process is carried out. The specific strain of hydra used for the present experiments contained an average of 100 stenoteles per tentacle. After killing 100 *Artemia* the hydra contained an average of 20 stenoteles per tentacle. Such rich feeding would be an extremely rare phenomenon in nature, but presumably it could occur in ponds containing dense blooms of *Daphnia* or copepods which would be battering the tentacles of hydra 24 hours a day.

In order to study the results of rich feeding upon nematocyst migration, the following experiment was conducted. Ten hydra were placed for two hours in a small dish containing several hundred *Artemia.* Another group of ten animals were fed *Artemia* individually; the *Artemia* were pulled from the tentacles immediately after they were killed. This process was repeated until each hydra killed at least 100 *Artemia.* A third group of ten animals were given approximately twenty *Artemia*

apiece and allowed to ingest them. The first group of animals represents a group of hydra that might occur in ponds containing dense blooms of crustaceans. The second group, of course, represents a situation which could only occur in the laboratory, but one which assured the investigators that the nematocyst supply of the animal had been greatly depleted. The third group of hydra represents animals which have undergone a slightly heavy, but not abnormal, feeding process.

After feeding the hydra were removed from their dishes and placed in water containing no *Artemia*. The animals were then excised through their stomach regions. The distal portions of these excised animals were then grafted to proximal portions of normal animals which had been stained vitally with methylene blue.

After 24 hours all thirty animals were squashed lightly under a coverslip and examined with the aid of an oil immersion objective. The results of these observations were as follows : 2 hydra which had undergone heavy feeding contained two or three stained stenoteles in the nematocyst batteries of the tentacle; 7 of the ten hydra which had been fed artificially, i.e., were not allowed to ingest their prey, contained stained stenoteles in the nematocyst batteries of the tentacles (minimum 2 — maximum 5 stenoteles); hydra which had undergone normal feeding contained no stained nematocysts in their tentacle batteries.

Clearly all of the stained nematocysts which were sighted in the nematocyst batteries of the tentacles must have reached this area through an active migration process because growth processes would tend to force the colored nematocysts towards the basal disk of the animal. It must be stressed that during the examination of these hydra it was necessary to exercise great precision. In all three groups of animals studied, nematocysts containing methylene blue were found, often in abundance, in the gastrodermal cells of the tentacle rather than in the nematocyst batteries of the epidermis. It is quite possible that several of these nematocysts might eventually pass into the epidermis, but it cannot be assumed. SEMAL-VAN GANSEN (1951) has demonstrated very clearly that nematocysts which are found in gastrodermal digestive cells are in the process of being digested rather than distributed to various parts of the body of the hydra. The authors have, to a great extent, confirmed the observations of SEMAL-VAN GANSEN. Serial sections through animals which have

not fed for twenty-four, forty-eight, or seventy-two hours will all reveal an abundance of nematocysts in gastrodermal cells; critical examination reveals that the nematocysts are indeed being digested by the gastrodermal digestive cells. The appearance of nematocysts in the gastrodermis have induced many previous investigators to hypothesize that these nematocysts would eventually be deposited into the epidermis of the animal.

The present paper is not able to explain why some nematocysts apparently are transferred from the gastrodermis to the epidermis while others are digested within the gastrodermis. However, a few reasonable hypotheses may be offered. Probably many of the nematocysts undergoing digestion in hydra arrived at their final destination in the digestive cells, not through an active migration from the epidermis, but were brought into the animal along with the prey. Each *Artemia* which passes through the mouth of a hydra contains usually three or four stenoteles. These stenoteles, of course, are of no use to the hydra. They are phagocytized along with the digested tissues of the *Artemia* and their capsules are digested. There are nematocysts, however, in the digestive cells which have not been discharged and are still within their cnidoblast cell. It is hypothesized that these nematocysts reached the gastrodermis by means of an active migration on the part of cnidoblast cells enclosing them. Probably the cnidoblast migrates between the gastrodermal cells and passes out into the gastrovascular cavity. From this point on, the migration process is purely a random one, i.e., any digestive cell in the animal is capable of ingesting the cnidoblast. Quite possibly many cnidoblasts are ingested in the gastric region of the animal; since there are no nematocyst batteries in this region to receive the ingested nematocyst, it is held within the digestive cell. Eventually the cnidoblast perishes and digestion of the nematocyst begins. On the other hand, many cnidoblasts will reach the tentacles, because a single strong contraction of a hydra will force a great amount of particulate matter in the gastrovascular cavity into the tentacles. These cnidoblasts are then ingested by digestive cells in this area and are passed on to the giant, flat epidermal cells which house the nematocyst battery. The authors have sighted many stained cnidoblast cells both within the gastrovascular cavity and digestive cells of the epidermis. However, it is not certain that every cnidoblast which is ingested by a gastrodermal digestive cell in the tentacles will be passed on to an epidermal cell.

When the nematocyst battery contains its normal number of nematocysts there is literally no room for another stenotele, for example. It was not uncommon during these studies to find a single gastrodermal digestive cell in the tentacles which contained two stained cnidoblasts containing stenoteles. Often, the nematocyst battery adjacent to the digestive cell contained a full complement of nematocysts. An epidermal cell which houses a nematocyst battery is greatly stretched and the nematocysts are nearly touching one another. It would be quite impossible to force additional stenoteles into the battery. However, if a nematocyst happens to be ingested in an area where there is a depletion of nematocysts in the battery, the nematocyst can easily be passed to the epidermis.

On the surface, the preceding experiment indicates that hydra which have had their nematocysts supply greatly depleted by rich feeding replenish their nematocyst supply because of an active migration on the part of the cnidoblasts from the gastric region of the animal, whereas during normal feeding there is no migration of nematocysts since there is no nematocyst depletion in the batteries in the tentacles. The authors do not believe that this is the case. A living hydra, if examined critically under oil immersion during various time intervals after feeding extending through a five day starvation period, will be found to contain cnidoblast cells in its gastrovascular cavity and in the gastrodermal cells of the tentacle. This appears to be the normal state of the animal; nematocysts which are not oriented into a nematocyst battery in the growth region or at the bases of the tentacles are capable of traversing the middle lamella and passing into the gastrovascular cavity. Many of these nematocysts are picked up by gastrodermal digestive cells in the tentacle. If the nematocyst supply in the tentacle is depleted by rich feeding, some gastrodermal cells, those adjacent to a nematocyst battery which has had its nematocyst supply depleted, will pass their nematocysts to the epidermis. The fact that during the present experiments no stained nematocysts were sighted in the tentacle batteries of hydra which had killed only twenty *Artemia* can be explained simply; by a pure chance process the gastrodermal cells adjacent to these batteries did not contain any nematocysts. It must be remembered that only two in about 5 stenoteles stain with methylene blue when the dye is applied vitally; this explains why animals which had their nematocyst supply greatly depleted by rich feeding con-

tained only two or three colored nematocysts in their batteries. Many nematocysts involved in the migration process would not be recognizable by the present methods. Therefore, the chances of finding a colored nematocyst in the batteries of an animal which had undergone a normal feeding would be slim. Further support for this hypothesis comes from the observation of hydra which had undergone rich feeding but had not killed as many animals as hydra which were not allowed to ingest the prey. The former animals contained less colored nematocysts in their batteries than forms that had killed one hundred or more *Artemia,* but contained more nematocysts than forms which had undergone normal feeding.

Thus, it appears that hydra furnishes nematocysts to its tentacle batteries by two methods. A nematocyst may be carried inside its cnidoblast cell to the tentacles via the gastrovascular cavity or it may reach the tentacles through normal growth processes of the animal. It appears quite obvious from the foregoing experiments that under normal conditions growth processes suffice to provide for the upkeep of nematocyst supply in the tentacles.

A final experiment was conducted in order to ascertain whether nematocysts are always found in the gastrovascular cavity of hydra or arrive there only after the supply of this organelle in the tentacle was depleted. This experiment was also designed to indicate roughly the origin of these migrating nematocysts.

A group of fifty hydra were offered *Artemia* until each hydra had killed approximately 50 animals. These hydra were fixed at various intervals after the feeding process in groups of ten. The times of fixation were one hour after feeding, 2 hours, 4 hours, 24 hours, and 48 hours. Five animals in each group were stained in a methylene blue solution buffered at p.H 5; the remaining five were stained at p.H 8. A stained nematocyst (colored at p.H 5) found in a nematocyst battery which was located in the distal ¾ region of the tentacle must have originated in the growth or gastric region of the animal (See *The Nematocyst of Hydra,* Part II). In all of the hydra examined, several stenoteles were sighted in the digestive cells of the gastrodermis of the tentacles; animals fixed at any given time interval after feeding contained no more nematocysts in their gastrodermal cells than animals fixed at any other time interval after feeding. Approximately ¾ of the stenoteles found

in the digestive cells of the tentacles stained at p.H 8 indicating that they had their origin either in the peduncle or the tentacle epidermis. The remaining ¼ of the stenoteles did not stain at p.H 8 and did stain at p.H 5. This indicates that these nematocysts had their origin in the gastric region of the animal. Most of the stenoteles sighted were in various stages of digestion or disintegration, but several of them appeared to be perfectly normal.

It is concluded from these experiments that although a great percentage of the stenoteles sighted in the gastrodermis stained at p.H 8, these stenoteles may well have had their origin, not in the tentacles, but in the gastric or growth region. It has been demonstrated previously (See *The Nematocyst of Hydra*, Part II) that a stenotele originating in the gastric region becomes more acid very quickly once it is under the influence of the tentacular or peduncular regions. Therefore, it is quite possible that these stenoteles migrated to the tentacles from the gastric region, underwent a fast chemical change, and stained similarly to the stenoteles in the nematocyst batteries. On the other hand, the fact that there were several stenoteles which did not stain at p.H 8 and did stain at p.H 5 is a definite indication that these structures had their origin in the growth or gastric regions of the hydra. However, the authors do not rule out the proposition that it is possible for a stenotele, located in a nematocyst battery, to be forced back into the gastrodermis.

These experiments also indicate that a depletion of stenoteles in the tentacles of the animal is not responsible for a migration of these structures from lower regions of the animal. A hydra examined 2 hours after feeding contains no more stenoteles in the gastrodermal cells of the tentacles than an animal examined at 48 hours. It has been previously stated any hydra, regardless of its state of nutrition, will contain cnidoblasts in the gastrovascular cavity.

Furthermore, it must be mentioned that several nematocysts of the stenotele variety which stained at p.H 5 were found in the nematocyst batteries of the tentacles of animals examined 2 and 4 hours after the feeding process was complete. Usually there were only 2 or 3 stained stenoteles per animal; in one exceptional case 10 stained stenoteles were sighted. In general, these results are in agreement with the results obtained after staining vitally with methylene blue.

The following paper will present further evidence for the fact that nematocysts are capable of migrating from the growth region to the tentacles via the gastrovascular cavity. For the present. it will suffice to say that a hydra which contains no nematocysts in its tentacles when grafted to a proximal portion (stomach, budding, and peduncular regions) of a normal animal, will be found to contain several dozen nematocysts in its tentacle batteries after 24 hours. Since there were originally no nematocysts in the tentacle, except at the extremities, every nematocyst ingested by a gastrodermal cell of the tentacle will be passed directly to the epidermis.

It is hoped that these foregoing experiments will resolve the differences of opinion expressed by LENHOFF (1959) and SEMAL-VAN GANSEN (1951). LENHOFF has stated that the uptake of labelled CO_2 into the developing nematocysts was not in the tentacles of the hydra but in the body region. However, if one examines LENHOFF's photographs carefully, he will immediately see that that the radioactive loci are concentrated in the tentacle bases and growth region, exactly the regions where BRIEN and SEMAL-VAN GANSEN stated that nematocysts are formed and subsequently pushed by growth processes towards the extremities of the tentacles. LENHOFF also stated that if a radioactive proximal region of a hydra is grafted to a non-radioactive distal region, radioactive loci are found eventually in the tentacles. It must be stressed that LENHOFF was not able to determine whether the radioactive nematocysts were in the gastrodermal digestive cells of the tentacles or in the tentacle batteries. The presence of radioactive nematocysts in the tentacles does not mean that these nematocysts will be employed by the hydra, in fact, under normal conditions practically all of them will be digested.

SUMMARY AND CONCLUSION.

It has been demonstrated conclusively that nematocysts in the tentacle batteries of hydra normally do not migrate to the tentacles through the gastrovascular cavity, but reach the tentacles through the normal growth processes of the animal. A constant cell duplication in the growth region of the hydra forces nematocysts proximally towards the basal disk and distally towards the tentacles. In the bases of the tentacles the nematocysts become arranged into the characteristic nematocyst battery of hydra.

However, it has also been demonstrated that under conditions of stress, i.e., when hydra's nematocyst supply has been greatly depleted by rich feeding, nematocysts may be passed from the gastrodermis of the tentacles to the epidermal batteries. Nematocysts, inside their cnidoblast cells, are always found in the gastrovascular cavity of hydra. Many of these nematocysts are ingested by gastrodermal cells of the tentacle. If the epidermal cell, adjacent to a tentacle digestive cell which has ingested a nematocyst, has a full complement of nematocysts there is no passage of nematocysts from the gastrodermis to the epidermis. On the other hand, if such a nematocyst battery is deprived of a nematocyst, it will accept a nematocyst from the gastrodermal cell adjacent to it.

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