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ATTACHMENT OF CALLIACTIS PARASITICA TO
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well as by external factors, e.g. food extracts as used by PANTIN (1942) and EWER (1947). HYMAN (1946) and PANTIN (1942) state that the nematocysts of well-fed coelenterates fail to discharge against food animals. On this point two recently completed studies are in direct contradiction. M^{lle} BOUCHER (1961), a student of prof. WEILL, working with Hydra attenuata, presents evidence in support of HYMAN and PANTIN's view: « si les nematocystes indifférents ne se déclenchent pas que par les pendants des tentacules, il est manifeste au niveau de tous les tentacules. Ainsi le déclenchement de la décharge nématocystique implique un phénomène physiologique général ». On the other hand, BURNETT, LANTZ and WARREN (1960), working with *Pelmatozoum obliquum*, present evidence that the fully fed animal is capable of discharging nematocysts and subduing prey.

**THE REMOTE CONTROL
OF NEMATOCYST-DISCHARGE
IN THE ATTACHMENT OF *CALLIACTIS
PARASITICA* TO SHELLS OF HERMIT CRABS**

By D. DAVENPORT (1), D. M. ROSS (2),
and L. SUTTON (2)

INTRODUCTION

The subject of the control of nematocysts has greatly interested zoologists for almost a century. A number of early workers (CHUN, 1881; CHAPEAUX, 1892; GRENACHER, 1895, etc...) believed that they are under nervous control, but PANTIN (1942) has summarized more recent views thus : « The balance of histological evidence is against the presence of nerves running to the cnidoblasts (PARKER and VAN ALSTYNE, 1942; WEILL, 1934). The physiological evidence points fairly clearly to the cnidae being independent effectors... it is not possible to obtain a cnida response by the conduction of excitation from a distant stimulus... There is neither conducted excitation nor inhibition ». Yet in his 1952 Croonian Lecture he said : « Perhaps... nervous action is indirect and may raise or lower the threshold of such structures to direct stimulation even though it cannot cause their discharge ».

The problem is still by no means settled. It has been said that the threshold of discharge of nematocysts is affected by internal factors and the general condition of the animal, as

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well as by external factors, e.g. food extracts as used by PANTIN (1942) and EWER (1947). HYMAN (1940) and PANTIN (1942) state that the nematocysts of well-fed coelenterates fail to discharge against food animals. On this point two recently completed studies are in direct contradiction. M^{lle} BOUCHET (1961), a student of prof. WEILL, working with *Hydra attenuata*, presents evidence in support of HYMAN and PANTIN and says : « si les nématocystes représentent effectivement des « effecteurs indépendants » dont la décharge ne peut être déclenchée que par des facteurs agissant directement sur eux ou sur leurs nématoblastes, cette décharge peut être inhibée par un contrôle, de nature encore inconnue, mettant en jeu un facteur qui dépend de l'état général de l'animal et qui se manifeste au niveau de tous ses tentacules. Ainsi le déclenchement de la décharge nématocystique implique non seulement des facteurs physiques et cytophysiologiques, mais des phénomènes corrélatifs de la physiologie générale de l'organisme... » On the other hand, BURNETT, LENTZ and WARREN (1960), working with *Pelmatohydra oligactis*, present evidence that the fully fed animal is capable of discharging nematocysts and subduing prey.

Other workers have speculated that external factors may cause a coelenterate to « inactivate » its nematocysts, in particular in the well-known symbioses between coelenterates and fishes (BAERENDS, 1957, p. 252). But although this possibility is interesting, evidence of such a phenomenon is to date completely lacking. Up to the present time it has never been conclusively demonstrated that information is transmitted to the nematocysts within the animal (1).

In the course of recent work by one of us (ROSS, 1960) on the behaviour of the actinian *Calliactis parasitica* and its host *Pagurus bernhardus*, it has been shown that « a chemical stimulus contained in the organic deposits which normally exist on a hermit-crab shell is an essential ingredient in the sensory situation which elicits the attachment behaviour of *Calliactis* ». FAUROT (1910, 1932) described this behaviour of *Calliactis* in its association with the crab *Dardanus arrosor* (= *P. striatus*), in which partnership attachment is usually assisted by the crab. ROSS (1960) was able to give a fuller account of the anemone's behaviour, since *P. bernhardus* does not assist attachment in any way, and *Calliactis* attaches readily to large empty *Buccinum* shells, making observation of the attachment process much easier. ROSS says that the

(1) We have recently learned of an unpublished observation by PICKENS that a nudibranch which feeds on the tentacles of the Siphonophore *Physalia* is paralyzed and killed if the tentacle on which it is feeding is severed some inches proximally to it.

first step in the process of attachment is that «... the tentacles explore the surface of the shell very actively and many of them adhere to the shell, perhaps by glutinous nematocysts, forming an attachment firm enough to hold the anemone on the shell even when the crab moves about ».

The work to be described here arose out of later observations by ROSS and SUTTON (unpublished). Not only is the described neuromuscular response relatively « specific for shell » but so also is the tentacular « sticking » or attachment. Moreover, judged subjectively, the « stickiness » of the tentacles to this specifically-acting « shell-factor » *changes in time* in accordance with changes in the situation of the anemone. This is shown by the fact that free anemones readily stick to host shells if the shells are brought into contact with their tentacles, whereas anemones which have already settled on shells rarely stick to another shell in this way. Apparently the attachment process is inhibited when an anemone is settled on a shell.

We wished to find out whether the subjective judgement that nematocyst attachment to shell is inhibited when the anemone is already on the shell could be supported by conclusive quantitative evidence. In what follows we present such evidence and show that for at least one type of nematocyst in one actinian, the firmly held belief that nematocysts are independent effectors (e. g. NICOL, 1960) can no longer be maintained.

MATERIAL AND METHODS

For our first experiments six *C. parasitica* living on *Buccinum* shells inhabited by *P. bernhardus* were used. These animals had been transported from Plymouth to Banyuls and thrived in the laboratory circulation at 15°-16°. Our second and third series of experiments were conducted with 60 *C. parasitica* attached to the shells of gastropods of several genera inhabited by *Dardanus arrosor*.

A standard test consisted of touching with a physiologically active shell a series of ten tentacles selected at random in each experimental anemone. When testing *Calliactis* from Plymouth the tip of the spire of an active *Buccinum* shell was brought carefully into contact with the tip of a tentacle. The tentacles of *Calliactis* from Banyuls were similarly tested with the spire of a *Cassis* shell or the tip of the spine of a *Murex* shell. A positive response (+) was recorded if contact by the tip of the shell to the tip of the tentacle resulted in any adhesion whatever. Immediate

retraction or no adhesion was recorded as a zero (o). Although it was not possible to record the fact numerically in the data, the typical response of a single « shell-sensitive » tentacle was to adhere strongly to the shell without eliciting any neuromuscular response of the disk or of neighbouring tentacles other than a slight waving of the tentacles which occasionally occurred in highly sensitive animals. Controls tested by glass rods drawn to a fine bead, which had been washed in detergent, distilled water, 70 % alcohol, absolute alcohol and alcohol/ether usually gave no response whatever, although in highly sensitive animals occasional adhesion would occur. Controls by similar rods, the tips of which had been dipped in food juices (*Mytilus*) and dried, invariably resulted in powerful adhesion, clumping of neighbouring tentacles and partial retraction of the margin of the disk. The total response to stimulation by shell of a single tentacle of an animal « sensitized to shell » is therefore subjectively quite different from its response to food.

THE OBSERVATION OF ATTACHMENT BY NEMATOCYSTS

It was not impossible that the tentacles adhered to the shell by some other means than by nematocyst discharge. Therefore, it was necessary to find some way of observing the discharge of nematocysts from the living tentacle in response to shell. Firstly, isolated tentacles were tested with shell and although such tentacles occasionally gave bursts of nematocyst discharge to strong stimulation by small pieces of active shell, the discharge provoked did not seem great enough to accomplish strong adhesion. It was noted, however, that stimulation by pieces of shell often resulted in the release of strings of mucus of considerable tensile strength and that one could often move the isolated tentacle by a string of mucus extending to it from the piece of shell. But the production of the mucus strings by an isolated tentacle under such stimulation was not fast enough to effect the rapid and apparently « triggered » attachment that had been observed in « sensitized » animals on contact by shell to the tentacles *in situ*.

Finally, while observation was made under the dissecting microscope at 100 X, a small piece of active shell was held by fine forceps and brought carefully into contact with the tentacle tips of a « sensitized » animal. Under these conditions rapid, « triggered » attachment occurred to the piece of shell and on withdrawal the tip of the tentacle was seen clearly to be attached

by threads to the shell so that the tentacular surface gave the exact appearance of a typical nematocyst response to active substances pictured by PANTIN (1942, fig. 2 A), in which the surface of the tentacle is raised into « peaks » by the tension of the nematocyst threads. In addition small pieces of shell were further divided to the size of small sand grains and « salted » into liquid Cutex on a slide. The slide was then dried and used as an « artificial shell ».

Control slides carrying dried Cutex alone did not adhere to tentacle tips, but those carrying bits of shell adhered to them. This gave the observer the opportunity to cut off an adhered tip and observe its attachment under high power. Masses of nematocyst threads were thus observed to connect the tip of the tentacle to the small pieces of shell cemented onto the slide.

There is therefore no doubt that typical shell attachment is effected by nematocysts, although the behavioural acts of tentacular exploration and neuromuscular attachment may also be reinforced by the secretion of mucus of high tensile strength.

EXPERIMENTS

No. 1. Our first experiment was exploratory in that several situations were tested somewhat empirically. We report it in full because it gave broad indication of the possible variability to be expected, and thus made it possible for us to design the more crucial tests of experiments No. 2 and No. 3. The results may be observed in fig. 1. The experiment consists of a series of scores from tests of ten tentacles selected at random from each of six Plymouth *Calliactis*, for a total of 60 «tentacle contacts» per score. These scores were done at varying intervals under the different conditions described in what follows. All tests were conducted with an active *Buccinum* shell.

At 1200 on Oct. 28 the animals, four of which were on empty *Buccinum* shells and two of which were on inhabited shells, were scored. The total positives were 15/60 (A). Immediately after this score, the test shell was brought into contact with the entire tentacular crown of each anemone in the belief that such treatment might sensitize the tentacles. An immediate count conducted after this treatment resulted in a drop to 6/60 (B). At this point the anemones were carefully peeled from their host shells and allowed to remain free in the aquaria. At the end of 2½ hours they were all expanded and unattached, and were scored to give 27/60 (C). Immediately thereafter they were again massively stimulated by contact of the entire crown of tentacles with the shell, and this treatment resulted in a second marked drop in the number of

positives to 8/60 (D.). Again the animals were allowed to remain unattached, and after another hour (1630) were scored. The positives had risen to 38/60 (E.). A third immediate massive contact with shell resulted in another drop in sensitivity to 12/60 (F.). After this, there being evidence that massive contact with

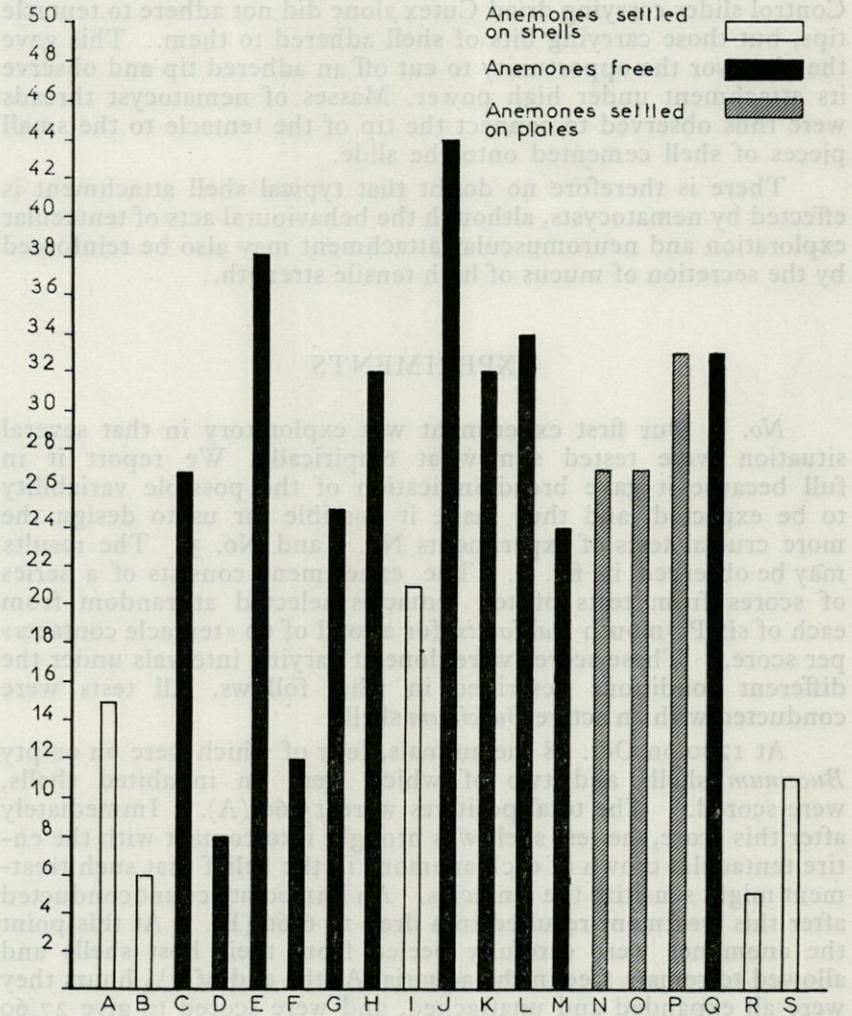


Fig. 1. — Experiment No. 1. Vertical = positive scores out of 60 «tentacle-contacts». Horizontal = time (intervals between scores not constant). For the conditions of each score, see the text.

shell resulted in an immediate steep drop in sensitivity, such treatment was discontinued for the series. At 1730 the unattached anemones were again counted to score 25/60 (G) and at 2100 gave a score of 32/60 (H). At this time the animals were allowed to climb onto shells and remain on them overnight. Scored on the morning of Oct. 29 at 0900 they gave a score of 21/60 (I). They were then again removed from the shells and allowed to remain free and unattached to surfaces. After opening they gave at 1200, 1600, 1800, and 2000 scores of 44/60 (J), 32/60 (K), 34/60 (L), and 24/60 (M). The animals were then placed in an aquarium overnight where they were given an opportunity to attach themselves to glass plates. On the morning of Oct. 30 when firmly settled on the plates they were counted at 1000, 1200, and 1400 to give scores of 27/60 (N), 27/60 (O) and 33/60 (P). At 1400 they were removed from the plates and allowed to remain free and unattached. Tested at 2000 when they were expanded they scored 33/60 again (Q). Finally the animals were once more allowed to climb onto shells and the next morning (Oct. 31) were scored on the shells to give at 1000 and later at 1400 5/60 (R) and 11/60 (S) only.

Examination of the results of this experiment (fig. 1) indicated to us that the level of sensitivity of the tentacles to shell when the animal is attached to shell (A, I, R, S), is lower than when it is unattached to a surface (C, E, G, H, J, K, L, M, Q). There was also evidence that the sensitivity of tentacles when animals are attached to glass plates (N, O, P) is not very different from that of free animals. It also appeared that the level of sensitivity may change with considerable rapidity, since massive contact of shell with the tentacular crown effected much lower scores if the animals were immediately scored thereafter (B, D, F). The data also indicated that there may be rhythmic sensitivity-changes during the day, but that there may be marked differences in sensitivity affected by different conditions at the same time of day could be noted when we compared the scores for the animals made on Oct. 29 and 30 at 1400 when unattached, 44/60 (J) and 33/60 (P), with those made for the same hour on Oct. 31 when the animals were attached to shells, 11/60 (S).

No. 2. The above experiment showed the necessity of designing further ones which would exclude any effects of internal rhythmic changes and which might provide conclusive evidence that the tentacles of *Calliactis* are much more sensitive to shell when the animals are unattached than when they are *in situ* on their host's shell. Two such experiments follow, the data for the first of which are presented in detail in table I.

TABLE I
EXPERIMENT No 2A

Anemone n°	TENTACLE CONTACTS										TENTACLE CONTACTS									
	On shells at 1300										Free at 1700									
	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
1	0	0	0	0	0	0	0	0	0	0	+	+	+	+	+	+	+	+	+	+
2	0	0	0	0	0	0	0	0	0	0	+	0	+	+	+	+	+	+	+	0
3	0	0	0	0	0	0	0	0	0	0	+	0	+	+	+	+	+	+	0	+
4	0	0	0	0	+	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	+	0	0	+	+	+	+	0	+	+
6	+	0	+	0	+	0	0	0	+	0	+	+	+	0	+	0	+	0	+	+
7	+	0	0	0	0	0	0	0	0	+	0	0	0	0	+	+	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	+	+	+	+	0	+	+	+	+	+
9	+	+	0	0	0	0	0	0	0	0	+	+	+	0	+	0	0	+	+	+
10	0	0	0	0	0	0	0	0	0	0	0	+	+	+	+	0	+	+	0	+
	Positives 9/100										Positives 62/100									
	Free at 1300										On shells at 1700									
11	0	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0
13	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	+	0	+	+	0	+	0	+	+	0	0	0	0	0	0	0	0	0	0
15	+	0	0	+	+	0	+	+	+	+	+	+	+	0	0	0	0	0	0	0
16	+	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	+	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0
18	+	0	+	0	+	0	+	+	+	+	0	0	0	0	0	0	0	0	0	0
19	+	0	+	0	+	+	+	+	0	+	+	0	0	0	0	0	0	0	0	0
20	+	+	+	+	+	+	0	0	0	0	0	0	0	0	+	0	+	0	+	0
	Positives 36/100										Positives 10/100									

On Oct. 31 (experiment No. 2. A), a sample of 20 recently collected *Dardanus arrosor* with anemones were selected. Ten of the *Calliactis* were removed from shells and placed in several aquaria. Ten of the hermits with anemones were placed singly in aquaria so that the anemones would open without disturbance from other crabs. By 1300 the next day, Nov. 1, all the anemones were expanded and ready for scoring. Meanwhile, the anemones which had been removed from their hosts had been prevented by occasional manipulation by a glass rod from settling by their bases on the surfaces of their aquaria. As in the preceding experiment scores were made by testing at random ten tentacles from each anemone. Table I indicates that the scores for the ten anemones (1-10) on the shells of their hosts totalled 9 positives out of 100 « tentacle-contacts », while the score for their unattached counterparts (11-20) totalled 36 positives out of 100 contacts.

Immediately after these counts the samples of anemones were placed in a reverse situation, anemones 1-10 being separated from their hosts' shells and 11-20 being allowed to climb on shells. By 1700 these animals were ready for scoring. Animals 1-10, which at 1300 when on their hosts had given a score of 9/100, now gave a positive score of 62/100, and animals 11-20, which when free had given a score of 36/100, now gave a score of 10/100.

Meanwhile on Nov. 1 (Experiment No. 2 B) a second series of fresh animals were selected for a duplicate experiment. At 1000 anemones 21-40 were selected, 21-30 being allowed to remain on hosts, while 31-40 were carefully removed from their shells and allowed to remain free in aquaria. By 2100 all anemones were open and ready for counting. The score for animals 21-30 which were on shells gave 1/100, while the score for the free animals (31-40) gave 35/100. Immediately after this test the situation of the animals was reversed, animals 21-30 being freed and 31-40 allowed to climb on shells. At 0900 the next day when all animals were expanded and ready for testing, animals 21-30 which had given a score when on shells of 1/100 now gave a score of 50/100, while animals 31-40 which had given a count of 35/100 when free, now when attached gave a score of 2/100.

No. 3. Experiment No. 1 gave evidence that there was no great difference in sensitivity to shell between the condition when animals were free and their condition when settled on glass. We wished to determine whether the mere act of attachment by the pedal disk to any substratum resulted in a marked raising of the threshold of discharge by shell or whether for this rise to occur settlement on shell (and implied « shell-recognition ») was indeed necessary.

On Dec. 1 a fresh series of 20 animals were collected. Ten *Calliactis* were removed from shells and allowed to attach themselves firmly by their pedal disks to chemically clean Petri dishes. A second ten were allowed to remain on their hosts' shells. Both sets of animals were tested on Dec. 4, immediately after which the situation of the animals was reversed, the sample which had been on shells being removed and allowed to settle on dishes and the sample which had been on dishes allowed in turn to climb onto shells. On Dec. 7 the animals were again scored.

Fig. 2 shows the results. As can be seen, the ten animals which on Dec. 4 when on dishes had given a score of 47/100,

now on Dec. 7, when on shells gave a score of 9/100, while the ten which on Dec. 4 on shells had given a score of 14/100, now on Dec. 7 when on dishes gave a score of 35/100.

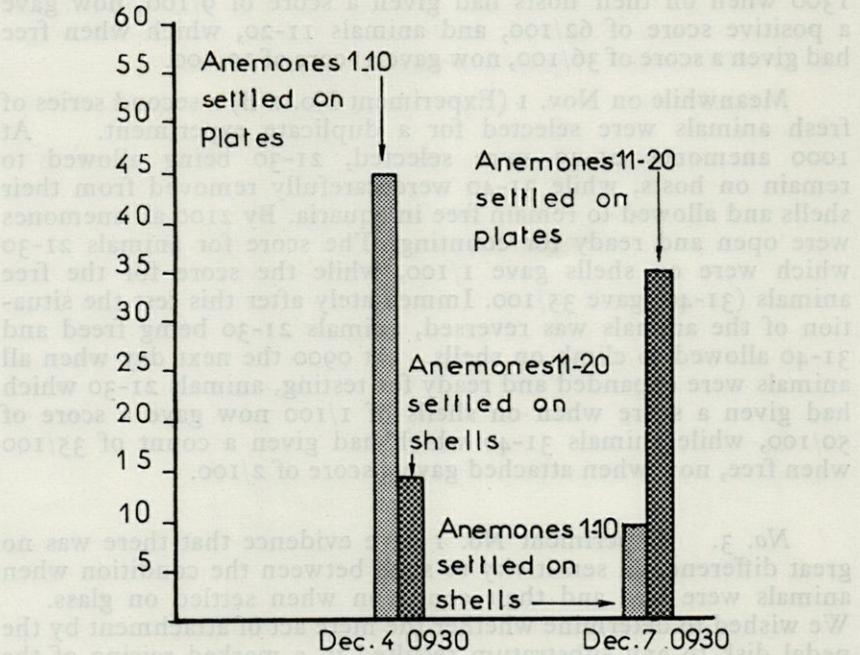


Fig. 2. — Experiment No. 3. Vertical = positive scores out of 100 «tentacle-contacts». Horizontal = date and hour of scores.

DISCUSSION AND CONCLUSIONS

The above experiments give quantitative evidence that there is a marked change in threshold of discharge of those nematocysts which are concerned in shell attachment during the course of events which occur when an anemone climbs onto its host's shell. Free anemones or those that have settled on clean, smooth surfaces (Petri dishes) show in general a low threshold of discharge, while anemones *in situ* on shell generally have a high threshold. This accords with the observation that when several animals are together in one aquarium, one rarely sees the tentacles of an anemone which has settled on one shell adhering to another shell.

The only conclusion that can be drawn from these observations is that an anemone receives information from the contact of the pedal disk with the shell which alters the state of the shell-specific mechanism of nematocyst attachment. The source of this information cannot be specified as yet. It could be received from chemoreceptors in the pedal disk responding to organic material on the shell. This might explain why the threshold is much higher when the animal is firmly settled on shell than when on clean glass. We know already that the tentacles are sensitive to some alkali-destroyable substance on the shell rather than to the shell surface as such (ROSS, 1960). But the information might come from some other sense organs responding to the roughness or shape of the shell as compared to smooth glass or plastic surfaces. It should be possible to test these alternatives using anemones settled on alkali-cleaned shells and suitably roughened or shaped glass or plastic surfaces.

Experiment No. 1 gave information that immediately after massive contact with shell via the crown of tentacles, there is a marked rise in the threshold of discharge. This observation along with other subjective ones carried out during routine testing indicates that the time element concerned in the transmission of information may not be long, perhaps, a matter of minutes at most. But because one must wait for the tentacles to expand before testing, long periods usually elapse after detachment or settling before the threshold of nematocyst discharge can be determined. Therefore one cannot gain information about the method of control from the time scale of threshold changes. At present one can only state that the nematocysts concerned in attachment can no longer be regarded as independent effectors and must leave the physiological mechanism whereby they are controlled to be elucidated later. Likewise, the micro-anatomical characteristics of the nematocysts concerned remain to be investigated by a specialist in these structures. That they are not the same as those concerned in feeding seems obvious from their response specificity. If they are proven to be different, a further conclusion follows logically. Those sensitive to food generally have a low threshold to food when the animals are *in situ* on the hosts' shells, while, as shown, those sensitive to shell have a high threshold to shell. The anemone « discriminates », one type of nematocyst being inhibited when the other is not.

Two final subjective observations should be reported which may have some bearing on future investigations. In the course of several hundred « tentacle contacts » made during these experiments it was frequently observed that groups of tentacles on the disk of the anemone would be « shell-sensitive » when others in their

vicinity would not. Likewise one could get a subjective impression of whether an anemone would or would not have a low threshold to shell by observing its state of expansion and general tentacular activity. It was clear at the outset that many factors affected the threshold of discharge both quickly and over a longer period of time, and for this reason it was necessary to employ a statistical approach to the problem. Later work may indicate experimental conditions which will give more nearly all-or-nothing performances by the shell-sensitive nematocysts.

In conclusion, the authors wish to express their appreciation to the Director and members of the staff of the Laboratoire Arago, Banyuls-sur-Mer, for their generosity and kind assistance in making these investigations possible.

SUMMARY

1. The method whereby *Calliactis parasitica* attaches itself to the shell of its host hermit-crab by means of shell-specific nematocysts has been investigated.
2. Evidence is presented that the threshold of discharge of these nematocysts changes markedly in accordance with the attachment behaviour of the animal, the threshold of discharge being low in free animals and high in animals *in situ* on shells.
3. Evidence is presented that the state of discharge is controlled by the receipt of specific information by the anemone from contact with the host's shell. The nature of this information and the mechanism of its transmittal remain to be investigated.

RÉSUMÉ

1. Le mécanisme par lequel *Calliactis parasitica* se fixe sur la coquille de son hôte par l'intermédiaire de nématocystes réagissant spécifiquement au contact de la coquille a été étudié dans ce travail.
2. Le seuil de décharge de ces nématocystes varie de façon marquée suivant l'état de l'animal : ce seuil de décharge, très bas chez des animaux libres (c'est-à-dire fixés sur un autre substrat que sur une coquille), devient très élevé chez des animaux en place sur une coquille.
3. Enfin, il est démontré que la décharge est commandée par la réception par l'anémone d'une information spécifique lors d'un contact avec la coquille de son hôte. Il reste à étudier la nature de cette information et sa transmission.

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