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Notes on the Physiology of *Charybdea rastonii.*

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With 5 Text-figures.

Late in the summer the little inlet in front of the Misaki Biological Station abounds with hundreds of the interesting cubomedusa, *Charybdea rastonii.* They are often so numerous that they cause not a little annoyance to the bather. To the student of cœlenterates, however, the circumstance affords excellent opportunity for investigation.

Although the morphology of cubomedusæ has been studied to such an extent that further investigation seems scarcely necessary, yet our knowledge of their physiology is very poor, the only works on this subject being the two papers by Conant ('98) and by Berger ('00), and no doubt much is to be done in future along that line. It was in the summer of 1915, August 28–September 2, that I performed at Misaki a few simple experiments upon *Charybdea rastonii.* In August of 1916 some of these were repeated with the same results. In the following pages I shall briefly describe the results of my experiments and observations on this interesting medusa.

I. Light reaction.

Charybdea rastonii behaves in response to photic stimulus quite differently from *C. xaymacana* observed by Conant. The Jamaican species manifested a sudden change in swimming activity when transferred to direct sunlight from the diffused. Most of them ceased to pulsate and settled to the bottom (Berger '00 p. 5), though some did not do so (Berger '00 p. 26). If the glass vessel containing *Charybdea rastonii* be brought into the sun, none of it becomes quiescent. The medusæ swim about just as calmly as in diffuse daylight. It need hardly be mentioned that they prefer weak to strong light as do other species of cubomedusæ, since in their natural habitat they come near the surface of the sea only in the morning and towards evening, most of them going down to a little deeper part during the rest of the day. I do not know where they are at night. This difference in light reaction between the two species may stand in relation to the fact that *C. xaymanaca* lives in deeper water than *C. rastonii*.

II. The rhopalium in relation to pulsation and swimming activity.

As to the rhopalium it suffices to say that, contrary to Haake's description ('86 p. 555 and '87 pp. 602, 603), the paired eyes persist throughout life in *C. rastonii* of Misaki, as has been pointed out by other authors in the same species occurring in other localities.

As was observed by Conant (Berger '00 p. 8 and p. 29) the part of the rhopalium loaded with the calcareous concretion lies always lowermost, whatever position the medusa may assume during swimming. This can be seen to best advantage by watching from without with a hand lens a medusa, which is held vertically against the inner side of a glass vessel. In rotating the animal so as to bring the mouth upwards it is noticed that shortly before the rhopalium stalk takes the inverted position, say

165°–170°, the main part of the rhopalium turns and hangs down, to the opposite side. That this is due to the presence of the concretion is shown by the fact that, after extraction of that body, the longitudinal axis of the rhopalium always remains straight in whatever position the jellyfish may be held. Since the extraction of the concretion does not affect in the slightest degree the swimming activity, the concretion seems to serve simply as a weight for keeping the rhopalium properly suspended as was suggested by Berger ('00 p. 8). The rhopalium, as a whole, therefore, can hardly have any value as an organ of equilibrium.

The taking off of one, two (opposite or adjacent) or three rhopalia exercises no influence whatsoever upon the mode of swimming nor upon the balancing of body. Neither does a momentary paralysis take place after such operations. In this respect *C. rastonii* differs from *C. xaymacana*, in which species, while no permanent paralysis takes place after removal of one or two rhopalia, yet it did occur after a third one was removed, though this result does not seem to be constant (Berger '00 p. 8). One thing I noticed in *C. rastonii* deprived of three rhopalia is the fact that it shows a tendency to swim with the side of the remaining rhopalium turned downwards, though this is by no means the rule. The influence of the extirpation of the rhopalia upon the number of pulsations I have not as yet satisfactorily worked out, owing to the difficulty of dissociating it from the effect of the shock caused by the operation.

If a single rhopalium be kept intact, the medusa is of course able to pulsate. As has been shown in other forms, the jellyfish cut into a strip by a spiral incision continues to pulsate, provided a single rhopalium be present. It does not matter whether or no the pedal ganglion remains in the strip.

If all the rhopalia be extracted, the animal instantly ceases to pulsate and remains still on the bottom of the vessel. In a few cases the jellyfish thus operated resumed pulsation for a short length of time, and even tried to swim up. But they did not seem to have strength enough to pull up the relaxed tentacles. In the above cases the cutting off of four pedal ganglia did not stop pulsating. Very seldom do the medusæ deprived of all the rhopalia lift themselves up and swim for a short distance. It may be added that by pinching the tentacles (even at the distal end) weak pulsations may be aroused in the medusæ destitute of all the rhopalia.

It is evident that from the above experiments as well as from those of previous authors, that the pulsation center is localized in the rhopalium. Now the question naturally arises as to what part of the organ sends out stimuli to the subumbrellar muscles to cause pulsation. In dealing with the problem the concretion can *a priori* be left out of consideration, since it has nothing to do with nervous function and moreover its extraction from all the rhopalia does not in the least impair the swimming activity of the medusa (Berger '00 p. 8). To decide the question the following simple experiments were performed. Three rhopalia were pulled off, and from the remaining one only the eye part together with the concretion was cut off. Pulsation continued without any impairment. Only when the part near the stalk was excised, the jellyfish became motionless (Fig. 1). From these experiments it may be concluded that the pulsation center is located in the part next to the stalk. And I think that this conclusion is born out by the

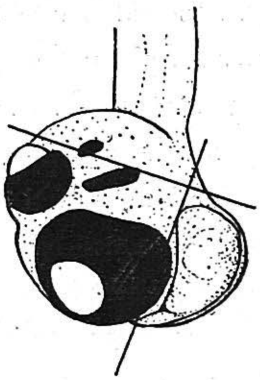

Fig. 1.

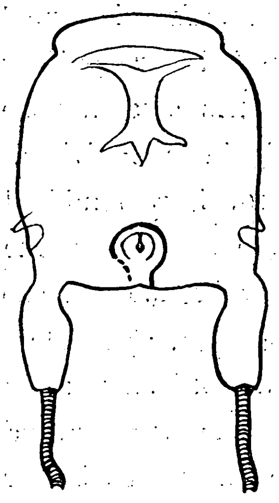

Fig. 2.

histological findings obtained by previous writers.

To determine the course of nervous stimuli from the rhopalium the following experiments were tried. Three rhopalia were taken off and an incision was made starting from the bell edge and going upwards around the rhopalium niche as shown in the accompanying diagram (Fig. 2). The medusa thus operated could swim about. Then the cut was extended farther down, *i. e.*, to a point a little above the velarium, pulsation stopped. This seems to show that the narrow area just above and along the velarium lacks the nerve plexus.

From the experiments on pedalium reflex, which is to be described in the next section, it will be seen that the nerve stimuli do not reach the upper third of the bell. Although I have no knowledge of the distribution of nerve plexus in the *Charybdea* bell, yet from these experiments it may be taken for warranted to conclude that the bell is devoid of nerve plexus in the upper third of its extent as well as near the velarium.

III. Rhopalium-pedalium reflex.

As was noted by Conant (Berger '00 p. 12 and p. 31) *Charybdea* has an interesting reflex, which may be called the rhopalium-pedalium reflex. It consists in this, that, if a rhopalium is lightly stroked all the tentacles contract and all the pedalia are simultaneously bent into the bell cavity. Extraction of three rhopalia does not make any difference at all. Undoubtedly this reflex is adaptive; for the moment the enemy tries to seize the jellyfish and comes in contact with any rhopalium (the only pigmented region of the medusa), the tentacles and the pedalia are quickly drawn in and the animal sinks to the bottom, thus increasing the chance of escape from being preyed upon. Only in one individual out of some hundred specimens I have examined, it was noticed that one pedalium did not respond at all to the stroking of the rhopalium, while the other three did. This may be due to some congenital defect in the reflex mechanism.

In order to see how soon fatigue comes to the pedalial muscles three rhopalia were cut off and the fourth one was stroked several times in succession as soon as the pedalia relaxed after contraction. In one individual the bending became difficult after twelve or thirteen stimulations, and to the sixteenth stroking the pedalia did not respond at all. In another medusa the contraction became weak after seven or eight stimulations, and the fourteenth did no longer cause bending at all. But it is hardly necessary to add that a stronger stimulus, *e. g.*, the pinching of the basal part of rhopalium or the sensory niche with a pair of forceps, will call forth response even in such fatigued medusæ.

In passing it may be mentioned that by means of the rhopalium-pedalium reflex, the course of the nerve impulse from the rhopalium to other parts of the body was determined. Three rhopalia were cut off and the lower half of the bell was bisected by two opposite incisions, as shown in Fig. 3. Then the rhopalium was stroked. This experiment was per-

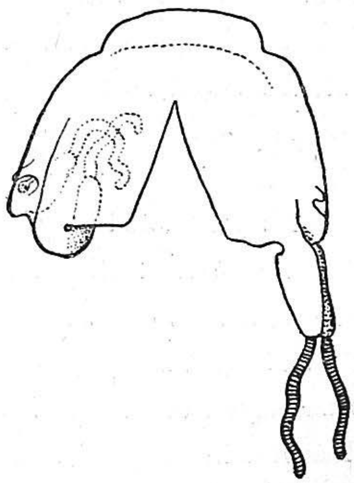

Fig. 3.

formed upon several individuals changing the length of the incision. In five cases the length of incision, by which the reflex was stopped in the two pedalia opposite the stroked side, was determined to be as follows:

Height of bell	21, 5 mm	25 mm	26 mm	25 mm	26 mm
Length of incision	13	17	14	17	15

In a few cases, instead of three rhopalia only two opposite ones were extirpated, and the above experiments were repeated with precisely the same result. From these experiments, as has already been alluded to, one cannot escape from the conclusion that the upper third of the *Charybdea* bell does not transmit nerve stimuli notwithstanding the presence of the subumbrellar muscles due in all probability to the absence of nerve plexus there.

It should be noted that the pedalium is also bent into the bell cavity by stimuli originating from a place other than the rhopalium. If the outer edge of a pedalium, where there are many patches of nematocysts, be stroked, then that pedalium alone contracts, the other three remaining relaxed, as was observed by Conant (Berger '00 p. 31). This reaction is seen in the individuals deprived of all the rhopalia and also in the ring of bell margin made by a circular cut a little below the level of the sensory niches. Such a ring was cut at one place and spread open on the bottom of a vessel containing water. Various places of it were pinched to see how the pedalia acted. In case the pinched place was half way between any two pedalia, these alone contracted. If, however, the place was nearer to one pedalium, that pedalium alone usually contracted, but sometimes two on either side responded. Very seldom three or four pedalia were bent by the pinching at one place. As the upper edge of such preparation is below the sensory niches, the main nerve connections between the rhopalia and pedalia have of course been severed. How pinching stimuli are transmitted in this region, I could not make out, especially in view of the fact deduced from the experiments already mentioned, that the nerve plexus do not seem to be present in the immediate neighborhood of the velarium.

IV. Oral arm reaction.

Various parts of the medusa were stimulated to see how the oral arms respond. Only when the subumbrella close to the velarium was stroked, the oral arms performed a peculiar groping movement without "pointing." Neither the touching of the oral arms nor of the inner surface of the stomach produced any effect at all. In *C. xaymacana*, it may be noted, the removal of one or all rhopalia induced a strange movement of the oral arms (Berger '00 p. 11). In the Japanese form the oral arms do not respond to such a stimulus.

V. Phacellae.

The phacellae of *C. rastonii* was described by Bigelow ('09 pp. 17 and 18) from preserved specimens as follows: "the filaments of each phacella have become collected into three or four groups, each group arising from a distinct stalk. The filaments, furthermore, arise from the stalk at different levels and some of them are apparently branched, so that they

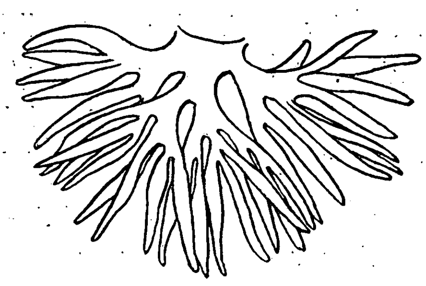

Fig. 4.

present a tree-like appearance." His figure is here reproduced (Fig. 4). In *C. arborifera* of Maas, which is supposed to be the same species as *C. rastonii*, the phacellae are said to be dendritic, all the tufts arising from a single stalk (Maas '97 Pl. 14, Fig. 9). The phacellæ of Japanese *Charybdea* present an entirely different aspect from the above description, especially when they are examined in living medusae. The filaments are clustered in four groups on the interradial sides of octagonal gastral cavity. They number nine or ten in each group and are disposed at irregular intervals. Each filament is composed of a stalk and a terminal tuft. Some stalks have a side branch, it is true. But the whole structure can hardly be called dendritic (Fig. 5). The phacellæ show a slow squirming movement, as was observed by Fritz Müller ('58 p. 543) and also by Conant ('98 p. 14). The filaments can best be studied by holding a medusa with food in its stomach against the inner side of a glass vessel and by examining it with a handlens from the outside.

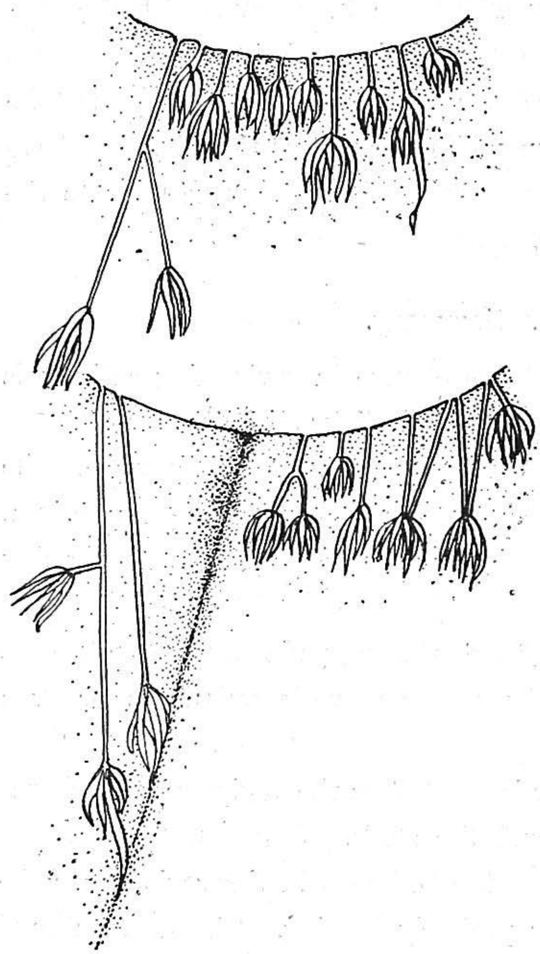

Fig. 5.

Parenthetically the mode of ingestion may here be mentioned. If a piece of fish meat be brought to a tentacle, the latter encircles the piece and contracts. The edge of the oral arms begins to flare out to receive both the tentacle and the meat. After these are drawn into the gastral cavity, the tentacle is slowly pulled out. It is then that the phacellæ commence to display their activity. The stalk elongates four or five times its ordinarly length or sometimes even more. The terminal tufts are very sticky and also distensive. Some tufts frequently come in contact with the perradial lip furrow. They glide up and down that furrow. Often a filament, or two, which are very much stretched out, may be found adhering to the furrow, while the rest of the filaments have already detatched themselves from the gastral surface due to the contraction of the stalk (Fig. 5).

VI. Summary.

1. In *Charybdea rastonii* no change in swimming activity is noticeable, if brought in the sun from diffused light.

2. Whatever position the medusa may assume, the concretion is always at the lowermost end of the rhopalium. Its extraction does not cause any change in swimming activity.

3. Medusæ deprived of all the rhopalia usually cease to pulsate, but very seldom may perform weak pulsations or even swim for a short distance.

4. The pulsation center is located in the region of the rhopalium between the eye part and the stalk.

5. In the upper third of the bell and in the region near the velarium the nerve plexus is probably lacking. The nerve stimuli are not transmitted in those regions.

6. Fatigue comes to the pedalial muscles after 14–16 contractions as tested by the rhopalium-pedalium reflex.

7. The mouth edge spreads out, if the lower region of the subumblella near the velalium is stroked.

8. The phacellæ of *Charybdea rastonii* are 9–10 in number in each interradial corner of the gastral cavity and are arranged at irregular intervals. Each is not dendritic, but is composed of a very elastic stalk and a terminal tuft.

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