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Studies on Regeneration of Coelenterata. 3rd part: Hydromedusae, Charybdea and Coeloplana.

By

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With 9 Text-figures

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Regeneration of Radial Canals in Hydromedusae.

If a hydromedusa be cut into small pieces, as has been done by C. W. HARGITT (1897–98), T. H. MORGAN (1899) and G. T. HARGITT (1902), each piece, provided it contains a part of the margin, will develop into a complete small medusa. The little medusa develops in a few days. According to MORGAN E. HAECKEL has observed even a single tentacle, if it contains at its base a small part of the bell margin, giving rise to a new medusa. C. W. HARGITT shows that the excised portions of the bell margin regenerate promptly and each divided piece of the disc becomes an "independent and perfect" medusa. But this regeneration according him is "a recovery of form and function rather than regeneration in the strict sense of that term."

The new medusa is in most respects similar to the original, though, of course, of smaller size. Neither HARGITT nor MORGAN could find any regeneration of additional radial canals, which would be necessary to complete the original symmetry.

Experiments repeated by G. T. HARGITT on the same species of Gonionemus and by myself on the Japanese species, *Gonionemus depressus* always confirm the fact that pieces of the jelly-fish as small as one fourth of the whole, or even smaller, have a remarkable recuperative power, leading to the production of the bell-shape. In this case the presence of a bit of the bell margin in the piece may be necessary, but it was not found that the radial canals were indispensable. Even a piece which contained neither the radial canals nor the bell margin, showed a tendency to become bell-shaped. With regard to the fact that the new medusa does not often regenerate additional radial canals, C. W. HARGITT (1898) states that "this does not seem to be an important matter, since there does not seem to be a special necessity for a definite number".

However, MORGAN observed that the new medusa underwent a certain amount of regeneration, and in some cases a new canal-like scar was formed along the line where the cut edges fused together. According to G. T. HARGITT the ends of the marginal canal fuse and a new radial canal does form along the line fusing the cut edges of the bell. V. NEPPI (1918) experimentally demonstrated regeneration of the radial canals in two Neapolitan hydromedusae, *Obelia geniculata* and *Phialidium variabile.* Instead of dividing the medusae, NEPPI made insertions in the jelly of the disc and by this method he derived supernumerary radial canals, in addition to the original four that cross at the centre of the bell.

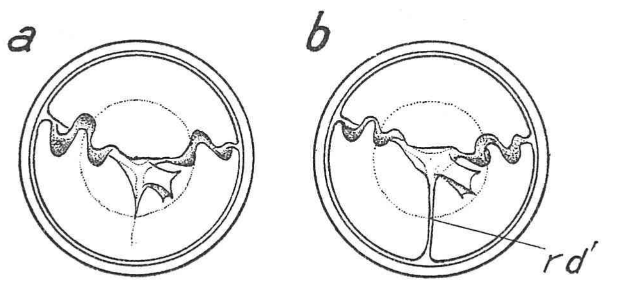

Fig. 1.

Medusae from 1/2 umbrella of one and the same individual of *Gonionemus depressus* GOTO, ventral view. *rd'* additional radial canal.

The regeneration of the radial canals is, therefore, beyond dispute. They always appear on the line along which the cut edges of the disc fuse together. But this regeneration is not constant. Even among pieces of one and the same individual, there is much variation, so that in two pieces of the same disc additional canals may be formed in one and not in the other (see fig. 1).

Regeneration of Mouth Part.

If instead of being cut in two in the vertically radial plane, the disc of a medusa be cut in a horizontal plane, one piece will be bell-shaped and the other a ring. In some cases, especially when the plane of section is not too low in respect to the height of the disc, the latter develops into a new medusa. In all cases the cut edges gradually contract till they are touching. As soon as they meet they begin to fuse, and at the same time bring the cut edges of the radial canals into the middle of the subumbrellar space of the new medusa. The mouth part then appears. It is always formed from the part where the last fusion of the radial canals occurs, and there is almost no exception to this rule.

The mouth part is formed more quickly and more easily in the pieces cut radially. In this case the position of the new manubrium varies, sometimes it is just at the centre of the bell cavity and sometimes more or less peripheral, according to the position where the proximal cut edges of the radial canals meet together, as well as to the condition whether or not additional radial canals are formed. Such a variation is especially distinct in one-fourth pieces, containing a single radial canal (see fig. 2). MORGAN states that the new manubrium develops from the proximal end of the old radial canal, and since this end is often carried to one side during the closing-in of the piece, the new manubrium lies, not at the top of the subumbrellar space, but quite to one side. Perhaps no regeneration of an additional canal occurs in that case.

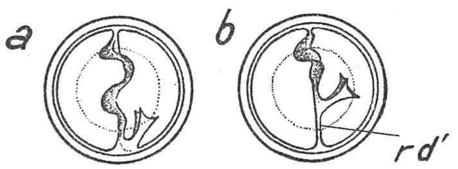

Fig. 2.

Medusae from 1/4 umbrella of the same individual of *Gonionemus depressus* GOTO, ventral view.

Coming back to the form developed from the ring-like jelly, first of all the proximal cut edges of the radial canals fuse all together and then a gastric pouch is formed. This, as has been pointed out by G. T. HARGITT, is simply a large space into which the radial canals lead, and at first it has no opening to the exterior. The mouth opens afterwards. MORGAN removed from the oral side of the disc the entire stomach and its attached manubrium, as well as the immediate proximal ends of the radial canals, leaving the exumbrellar part intact. He hoped by this means to find out if, under those circumstances, a single manubrium would develop, or if a manubrium would sprout forth from each of the proximal ends of the radial canals. As a result, the endoderm grew forwards over the region previously occupied by the stomach, and out of it was formed a stomach from which a single manubrium grew out. However, according to G. T. HARGITT the formation of a double or bifurcated manubrium is not quite uncommon in such cases. It is reported that in his four sets of experiments, 21 per cent. developed double manubria.

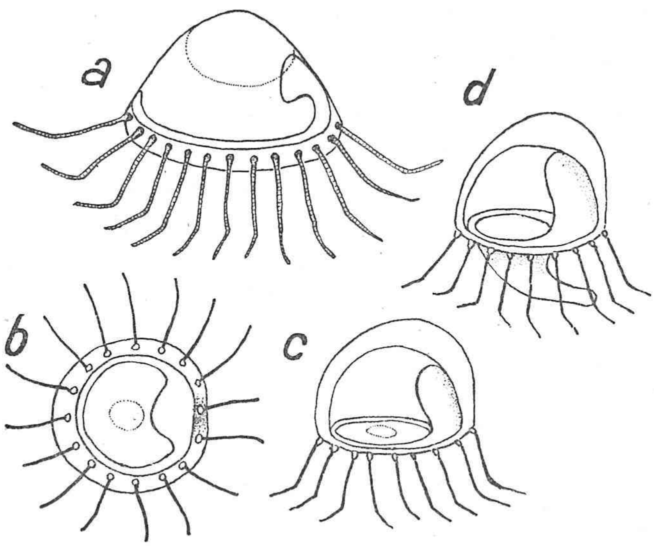

Fig. 3.

Form-recovery of an umbrella less than 1/4 the whole and without the radial canal (*Gonionemus depressus* GOTO) ; *a* one day old (lateral view), *b* the same specimen after a week (ventral view) and *c* in the lateral view. *d* another specimen of the same age with a hypertrophied velum.

Now turning to another question, it may be asked whether the mouth organ can be also derived from the marginal ring canal as from the radial canals. For this purpose it is necessary to cut out pieces of the jelly, smaller than one fourth of the whole disc so that they do not contain any element of the radial canals. Such pieces of Gonionemus, as shown by MORGAN, can live well and still show the power of assuming the bell-like shape. I have cut out similar pieces of jelly from the disc of the Japanese Gonionemus, and have got many pieces closed in and the old tentacles form a ring encircling the margin (fig. 3 b). In some specimens a manubrium-like organ was found coming out from the centre of the closed bell margin as shown in fig. 3 d. But a closer examination of the specimens soon revealed that the organ in question was not a true mouth part. It is a fused velum, which attains a particular development and grows out of the bell margin. Its cavity is continuous with the subumbrellar cavity of the closed jelly and not with that of the ring canal. The latter shows, however, a certain degree of hypertrophy and swells on the side where the cut edges have joined together (fig. 3 c, d.).

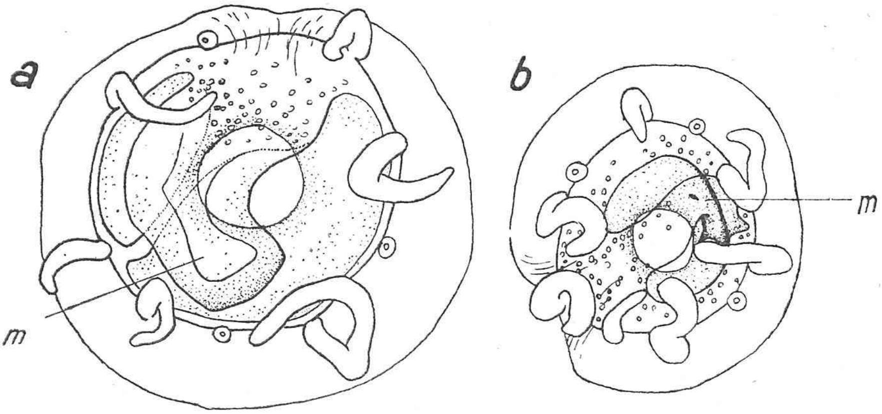

Fig. 4.

Regeneration of the manubrium from the ring canal in umbrellae less than 1/4 the whole of *Scolionema gemmifera* KISHINOUYE (× 40), *a* with a single radial canal and *b* without the radial canal, both in ventral view. *m* new mouth part from the ring canal.

During the process of the form-regulation mentioned above the cut edges of the ring canal were carried more or less upwards, but no mouth opened from this part of the canal. Nevertheless, that this enlarged part of the ring canal represents the gastric cavity of the new medusa, from which the mouth part will arise, there can be no doubt, since from a similar enlargement of *Scolionema gemmifera* a new manubrium does actually develop (see fig. 4).

Regeneration of Bell Margin.

C. W. HARGITT and T. H. MORGAN reported that when the entire margin was removed new tentacles regenerated, though in their investigation they remained rudimentary and bud-like. G. T. HARGITT repeated the same experiment and confirmed the regeneration of tentacles. In all cases the cut edges contract more or less. The process continues till the edges nearly meet and the bell becomes again spherical, so that the bell margin after this regulation of form is diminished according to the extent of the area originally cut.

According to my further observation, when the bell margin was scraped off instead of being cut off in two vertically radial planes in one quadrant, the cut surface gradually diminished and finally disappeared as the wound closed in; the bell became somewhat ovoid, narrowing on one side. Two radial canals on this side approached each other and joined to the ring canal at one point. There was almost no space remaining in the fused part for the formation of new tissue. Without doubt there was no regeneration of the missing tentacles in such a case (fig. 5 a).

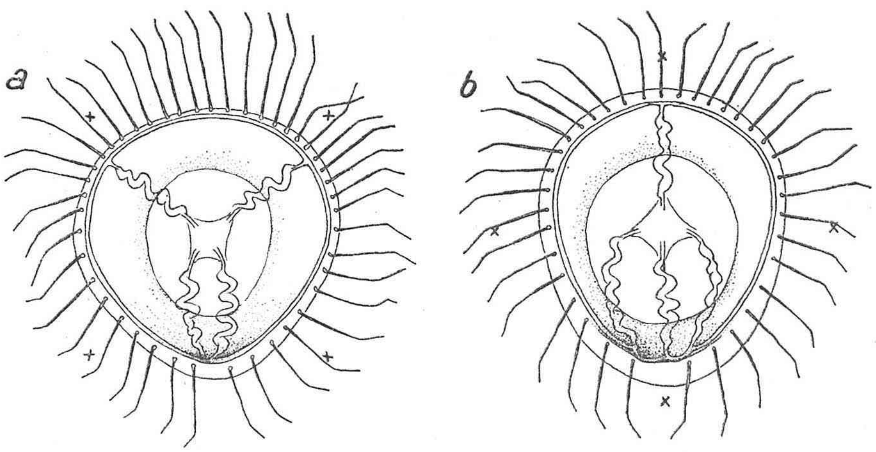

Fig. 5.

Form-regulation in medusae, (*Gonionemus depressus* GOTO) after their margin has been scraped off *a* in one quarter and *b* in two quarters. × indicates the original position of the radial canals.

If two quadrants of the bell margin were scraped off, the edges of the injured surface approximated from all sides, and the wound closed in the same way as before. Diminution of the bell margin took place to an even greater extent. The bell gave rise to a typically ovoid shape, the narrow side containing three radial canals joined to the ring canal at nearly the same point. A small amount of new tissue was formed at this time, but still no additional tentacles were formed (fig. 5 b).

Finally, the entire margin of the bell was cut off just inside the ring canal. This resulted in good regeneration of the bell margin, including the ring canal and tentacles, if not in their original number. From other experimental data it seems highly probable that the reduction of the number of tentacles is connected with the diminution of the margin of the bell after the regulation of form, and is not due to incomplete regeneration of the tentacles themselves. The fact may well be compared to the regeneration of the sensory bodies in the excised bell margin of Mastigias shown in a former paper (1927, p. 451–).

In another set of experiments, in which the bell margin was removed by four cuts, each diagonal to two radial canals, one or two tentacles appeared first at each angle, other tentacles being gradually

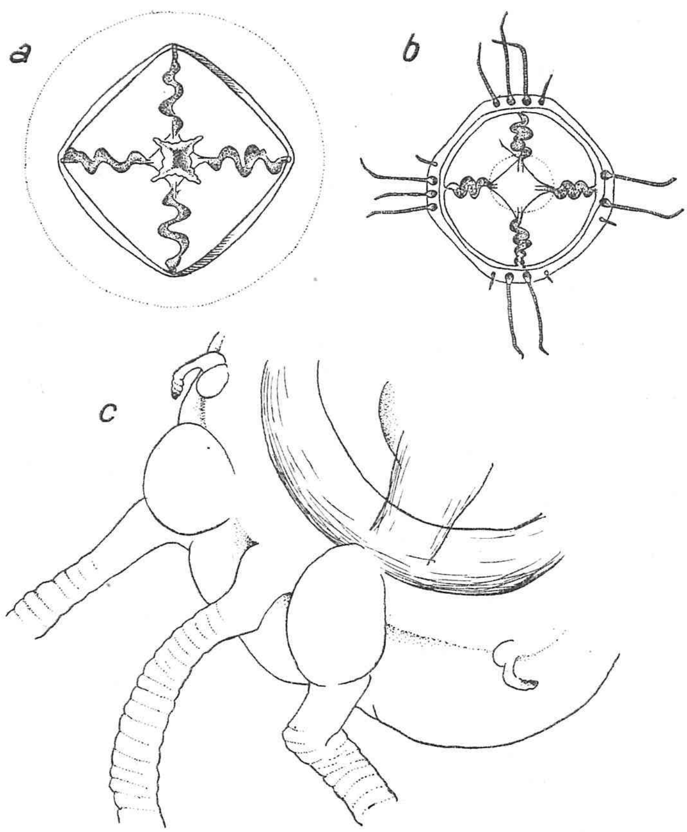

Fig. 6.

Regeneration of tentacles: *a* the initial condition of an operated animal, *b* the same at the end of a week; *c* magnification (× 30) of one edge of a similarly operated specimen. All ventral views (*Gonionemus depressus* GOTO).

added on both sides of those (fig. 6 b), as in the case of development of these organs in some hydromedusae such as *Spirocodon saltatrix* (ref. OKADA 1926, p. 81). In the latter case the tentacles commence to form from the four points where the radial canals run into the marginal ring canal, and the others are added gradually on both sides of the one that has first appeared. But the question is still open, whether or not the tentacles in the regenerating specimens might have started from the four angles simply because of these points being in a more peripheral position than the other points in the excised bell, as in the regeneration of tentacles of Cerianthus or some other sea-anemones after oblique sectioning of the stem. Unfortunately the discs, the margins of which were cut in four planes each parallel to two radial canals, died before tentacles appeared in the new medusae, and there was no opportunity of repeating this experiment.

Regeneration of Reproductive Organs.

The further development of the gonads and ripening of the reproductive products were little affected by cutting into or dividing the disc, but if the organs or parts of them were removed, there was no sign of regeneration of them, and this was so even when the radial canals were reformed. If regeneration of reproductive organs does take place, it would undoubtedly occur slowly and at a later period in the process of regeneration.

Regeneration in Charybdea.

This aberrant scyphomedusa has a tall dome-shaped bell, with four perradial, marginal sense-organs or rhopali, situated within niches upon the side of the bell, and four interradial tentacles. Four wide perradial sacs extend outwards from the central gastric cavity into the interstitial space of the bell. These sacs are incompletely separated one from another by four narrow interradial septa or frenulae. There are eight gonads, each of which is leaf-like and attached only on one side to an interradial septum, from which it extends outwards into the gastro-vascular space. The bell margin is not cleft into lappets, and unlike most scyphomedusae, its subumbrella forms an annular diaphragm, which partially closes the opening of the bell cavity like the velum of the hydromedusae. There are, further, four groups of gastric cirri or phacellae in the interradial corners of the central stomach at the inner edge of the four interradial septa.

If the medusa with the structure described above be cut into two halves by a longitudinal cut, each piece gives rise to a half-sized, narrowly elongated medusa (fig. 7 d) having two tentacles, two rhopali etc., as in the half pieces of Gonionemus. The cut edges approximate

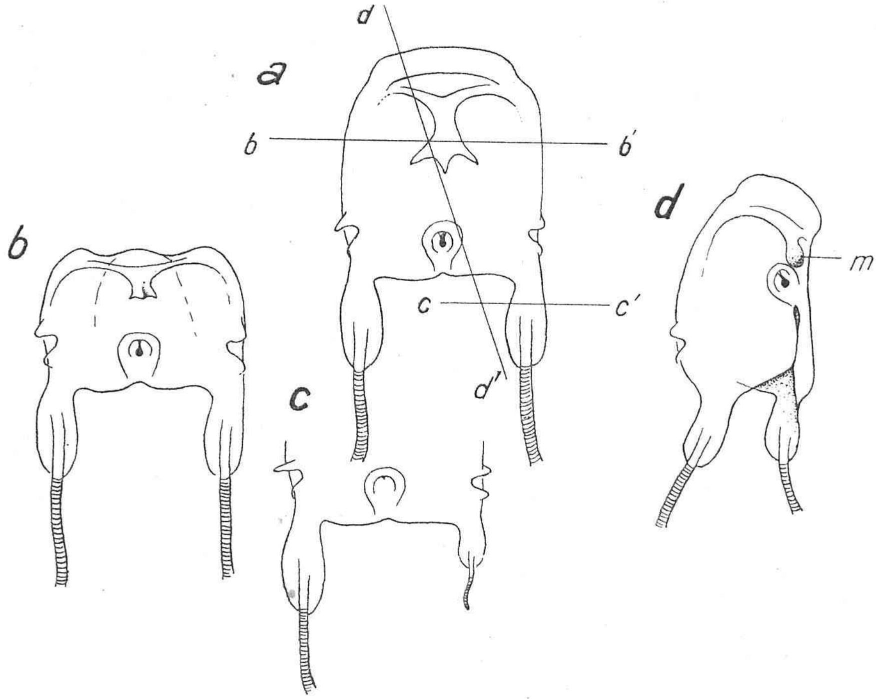

Fig. 7.

Form-recovery and regeneration of organs in *Charybdea rastonii* HAACKE. *a* lateral view of an entire animal, with indication of the directions of the cuts, *b* recovery of the upper part in a horizontally divided umbrella, including the gastric pouch and manubrium, *c* regeneration of tentacle, *d* regulation after a longitudial cut, with formation of the new mouth apparatus.

from both sides to the middle and fusion takes place. Although these partial medusae could be kept alive for several weeks, only very little regeneration was found. The mouth part was generally regenerated in spite of the degree of the original injury. The missing tentacles were also replaced by new ones (fig. 7 c), but the latter were never formed from the bell proper.

Form-regulation takes place in the half Charybdea just as in the half Gonionemus, and fusion of the cut edges always commences at the bell margin, which is carried more or less upwards. This process of fusion proceeds gradually upwards towards the top of the bell. Therefore, after a certain period the new medusa may have a small slit-like opening near the bell top, while fusion is complete in the lower parts. In one of my former papers (1927 a, p. 248), I have put forward the suggestion, based upon this experimental observation that the problematical "Stielkanal", in which a young Charybdea is said to be attached to a certain form of scyphostome (ref. W. HAACKE, 1887), might be rather due to some such accidental production during the early phase of its metamorphosis.

At any rate, from the above description alone Charybdea appears to possess a very limited power of regeneration. But it should not be forgotten that the experiment represents only one side, that following longitudinal cuts. It is, therefore, important next to examine the effect of transverse cuts.

If the dome-shaped bell of Charybdea be cut in a horizontal or horizontally oblique plane of section, the ring-shaped lower part can close the opening of the top, and gives rise to a new medusa of a low dome-shape as shown in fig. 7 b. The gastric cavity and mouth part are replaced, and these are quite normal in structure as well as in position in the bell cavity. This experiment of horizontal cutting was repeated by Prof. N. YATSU on the same material at the same place (at Misaki), and the regenerative changes can be well followed chronologically in six figures in the Dobutsugaku Zasshi (Zool. Mag. Tokyo), Vol. 34, p. 326.

When the bell is divided into an upper and a lower part by a horizontal cut, gradual constriction appears at the level of the cut in the subumbrella of the lower ring part, and the wound-opening diminishes by and by, but does not close completely as in the case of the hydromedusae. After a time there appears a square, horizontal plate from the subumbrella with a central hole, while the wound of the exumbrella remains widely open. According to YATSU this condition of the regenerating medusa is seen as early as seven hours after the operation, and the formation of the square plate is explained simply as a mechanical production, due to muscular contraction at the cut level of the subumbrella. (The same contraction does not take place on the lower cut-edges of the upper piece, in spite of their being of the same constitution as the upper cut-edges of the lower piece.)

According to my own observation, the square plate in question does not appear so quickly, and its formation is not so simple as to be merely mechanical and due to a muscular contraction. Certainly true regeneration with production of new tissue is concerned in its formation. The fact is most evident in YATSU's fig. 3 and 5, which are reproduced here in fig. 8 with his kind permission. The section shown in fig. 8 *a* belongs to a six-hour specimen, and even in such an early phase of regeneration the formation of new tissue on the subumbrellar edge is unmistakable. Nevertheless, the recovery of form by the operated medusa is largely subject to the mechanical action of muscular contraction, especially on the subumbrellar edges. Thus each radial surface of the subumbrella soon forms a semicircular flap

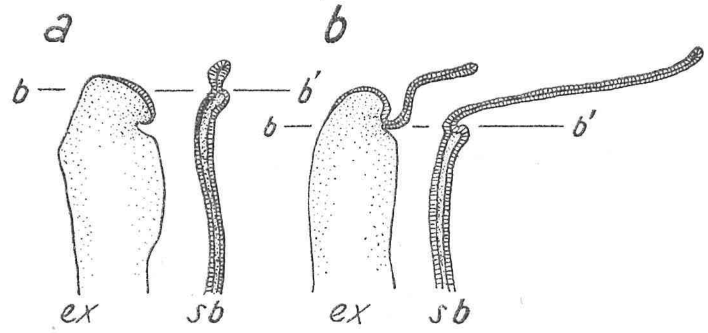

Fig. 8.

Tissue proliferation from cut edges of the ex- and subumbrella of *Charybdea rastonii* HAACKE (after N. YATSU 1922). *a* section of 6 hours old specimen. *b* a later condition about 20 hours from the beginning. *b–b'* indicates the initial revel of the cut.

turned into the bell cavity. The flaps grow at the same time through the further addition of new tissue to the free ends and come together at the interradial lines, on which are the septa connecting the ex- and subumbrella, but fusion does not take place at the centre. The regeneration of the exumbrella is very slow, perphaps owing to mesogloea being incomparably thicker than in the subumbrella, so that at a certain period there is produced a stage in which the operated medusa consists of a square, horizontal subumbrella having a central hole and an unclosed exumbrella.

By the time the exumbrella is closed, the square plate of the subumbrella, owing to the continuous addition of new tissue and to its growing faster than the exumbrella, is carried down almost vertically, leaving a wide space behind. The central part having the central hole is transformed directly into a new mouth. The new manubrium of Charybdea is produced in this way and the space left between the closed ex- and subumbrella represents henceforth the gastric cavity, in which the gastric cirri alone are still waiting to be regenerated.

Incompleteness of Regeneration in Medusae.

Returning to the point where we started, it is maintained that in nature and in the laboratory the regeneration of the divided disc of medusae is quite limited and imperfect. This fact is generally accepted as established, and is frequently cited as a good example of incomplete regeneration. One may suppose that this must be due to the fact that medusae, which represent the sexual individuals of hydroids, have a smaller power of regeneration than polyps. It is true that medusae exhibit less regenerative activity than polyps, but this does not supply the reason for the limited regeneration of the medusae. The facts so far as learned in the preceding experiments sufficiently show that they still preserve a strong regenerative power in each separated part, and if this power be allowed to develop freely, without any disturbance by other part or parts, the missing tentacles, mouth parts, radial canals and other organs are readily replaced by new ones. The regenerative power of medusae is by no means limited, and their regeneration is imperfect only when the process takes place as a whole, a full manifestation of the power of each separated part being in that case checked. In a former paper (1927, p. 539) I have explained this incomplete regeneration of the disc in a Rhizostom-medusa, *Mastigias papua* as being rather conditioned by the direction of the cut and not by the degree of injury, two forces, *regulative* and *reparative*, working in this case antagonistically to each other: "La faculté réparatrice agit, semble-t-il, en raison inverse de l'épaisseur du tissu enlevé, c'est-à-dire de la profondeur de la plaie, la formation du nouveau tissu étant presque stationnaire à tous les niveaux de section; tandis que la faculté régulatrice agit en raison directe de la profondeur de la plaie, mais indépendamment de la longueur de la bordure sectionnée." It is now well proved that the same rule holds also true in the disc of hydromedusae and Charybdea.

It still remains to elucidate why in the divided disc after the wound is completely closed, remoulding of the original plan of the radial structure is imperfect. Although similar phenomena have been reported in other types of animals, there seems to be as yet no adequate explanation of them. In medusae, this checked regeneration appears to be most probably connected with the strong development of the mesogloea between two dermal layers. According to S. HATAI this gelatinous substance, which may be allied in composition to chitin or cartilage, may serve as a store of food for the animal in case of starvation (ref. A. G. MAYER 1917, p. 180).

However, chitin and cartilage are quite different in compositions, the former being supposed to be a polymerised monoacetyl glucosamine, while the latter is $CaCO_3$ with some PO_4 plus proteins such as scleroproteins. So far as I know, chitin could not possibly be used as a store of food, and I doubt whether cartilage and mesogloea could be so used. On the other hand I am quite aware that medusae in a starved condition undergo a certain amount of regeneration, and the mesogloea is accordingly diminished, especially where regeneration is taking place. That regeneration occurs in starved tissues is not without example in the animal kingdom, and the diminution of the jelly in the regenerating area can be explained rather as the mechanism of form-regulation working on that part. This regeneration takes place very slowly compared with the recovery of the divided pieces to their original disc-shape. Hence, if there is any form of Coelenterata in which the mesogloea does not strongly develop or can be easily reorganized, a typical regeneration is expected. I have found such a form in an aberrant Ctenophore, Coeloplana.

Regeneration of Coeloplana.

Here in fig. 9 a series of regeneration processes is illustrated. The first sketch represents the condition of an isolated piece 5 minutes after operation. The cut edges approximate from each side, and the piece rounds up (fig. 9 a). This gives rise to an irregular disc-like body in the course of 10 hours, the edges of the cut surface coming together all around. About a week later the normal structure of a Coeloplana is completed. Practically, there is no formation of new tissue and the disc shape of the piece is simply due to the process of form-regulation, that we have already met with in the divided disc of medusae. However, regeneration went a step further in this case, and in the piece shown the entire organization of the animal is reproduced on a smaller scale by the method of internal reorganization or morphallaxis.

There is sometimes a narrow strip behind the line of fusion of the cut edges, which is distinguished from other parts by its darkly coloured condition (fig. 9 c). One of the tentacles is always formed on this line, and the other develops in accord with it, on the opposite side in the old tissue, with a sensory organ between their bases in the centre of the disc (fig. 9 e).

A. KREMPF (1921), who has observed the regeneration of Coelo-

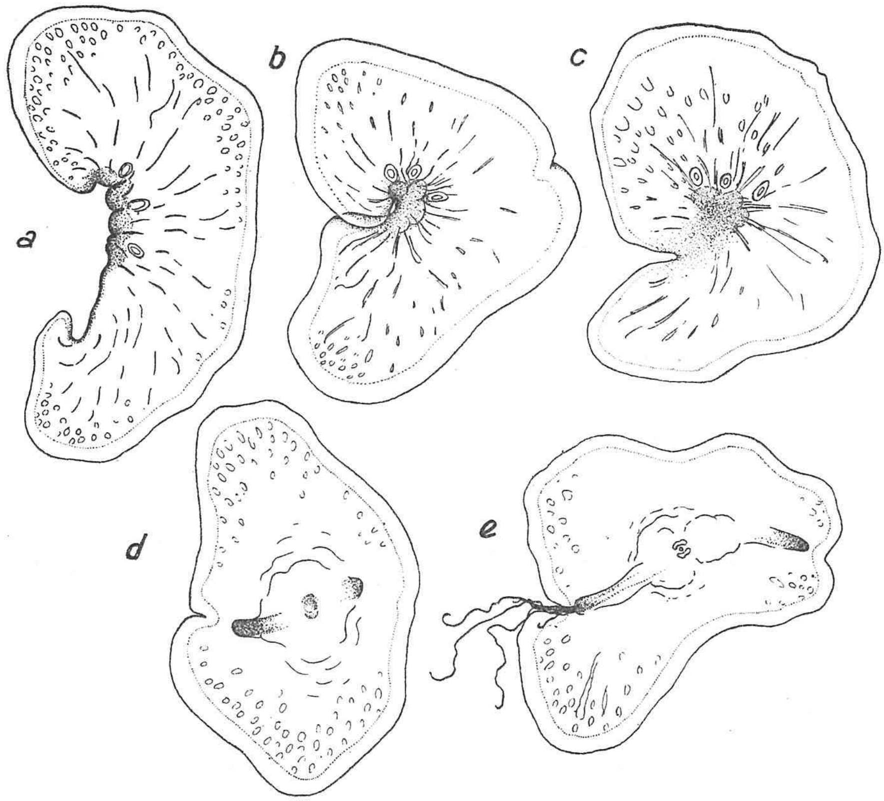

Fig. 9.

Serial representation of regeneration in a piece of *Coeloplana bockii* KOMAI, *a* 5 minutes, *b* one hour, *c* 5 hours, *d* 24 hours, *e* 5 days after the operation (dorsal view, mag. about 30 times).

plana, states that "the animal does not regenerate the two antagonistic elements of its biradial symmetry, i. e. its dorsal and ventral centres, at the same time. From this disharmony of time result forms which have only one tentacle and one 'enterotoxille', and have lost their radial symmetry. They are asymmetrical. But from the alteration of their original radial harmony comes out a new harmony. The form originally provides two antagonistic centres, and from there biradiality is reduced to a single centre and becomes bilateral." KREMPF compares this asymmetrical regeneration of pieces of Coeloplana to the unitentacular, pelagic, larval ctenophore, *Thoë paradoxa* of Chun, and revives the old theory :

"ce Cténaire se présente avec un tentacule unique et Chun a fait preuve d'un grand esprit de finesse et de pénétration en comprenant immédiatement le parti que l'on pouvait tirer de cette disposition pour la comparaison des axes des Cténophores avec ceux des Métazoaires bilatéraux ; il a considéré, avec raison, cette forme comme traduisant une tendance à l'atrophie de l'une de ses deux structures radiaires opposées et se plaçant à un point de vue identique à celui auquel j'ai été amené moi-même par l'étude des Anthozoaires, il a homologué le plan tentaculaire de *Thoë paradoxa* au plan de symétrie bilatéral, c'est-à-dire au plan sagittal ou plan dorso-ventral des bilatéraux."

But before we can appreciate this comparison between the simple morphological structure found in the regenerating pieces of Coeloplana and the unilateral structure of the larval ctenophore in question, we should require a more careful consideration of the process of reorganization in the former.

As is quite clear in the sketches of fig. 9 there is almost no proliferation of new tissue, and the regeneration is apparently due to a direct transformation of the old material to the new so as to complete the model of the original animal, but without any increase in the size attained at the time when the cut edges fused together. In such a case it is generally observed that while ectoderm remains in its dermal arrangement, the endodermic and mesogloeal elements are reduced first into an unorganized condition, in which new organization arises secondarily.

Assuming this method of reorganization to occur in the regenerating pieces of Coeloplana, we must then ask whether the process commences at the same time in the parts near the cut edges as it does in the parts far away from those edges, or whether it is not more probable that the process commences first of all near the cut edges and then progresses gradually into the other parts? If the latter alternative be true, the asymmetrical structure in the regenerating piece of Coeloplana would not be of much value in considering the phylogeny of the bisymmetry of the metazoa higher than Coelenterata. We may be dealing with nothing more than a case of difference in the time of regeneration between one side and the other in the same body. Indeed one of the tentacles is always found on the side where the cut edges come together or even on the line of fusion. *The tentacular axis is thus first determined in the regenerating pieces of Coeloplana notwithstanding the direction of the original plane of the cut.* On the other hand the asymmetry of larval ctenophores may be due to an isolation of blastomeres or to an injury in the developing egg, with subsequent incomplete regeneration of the missing half.

I leave further elaboration of the regeneration in Coeloplana to my friend and pupil Mr. Hideo TANAKA.

Summary

1. Divided pieces of a medusa can recover the original bell-shape without tissue proliferation from the cut surface. This form-regulation, however, checks the regeneration of the missing organs such as radial canals and tentacles.

2. The incomplete regeneration of medusae can not, therefore, be explained as due to their imperfect power of regeneration. Any organ can be caused to regenerate on condition that its free development is not checked.

3. Gastric pouch, manubrium and mouth are produced almost in every case and in any conditions. They are always produced from the proximal end of the remaining radial canal or if the latter is missing even from the marginal ring canal. The regeneration of tentacles, sensory organs and radial canals is conditioned by the direction of the cut as well as the degree of the wound.

4. In Coeloplana this regeneration goes a step further and complete regeneration in addition to the recovery of form takes place by means of internal reorganization.

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