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EXPERIMENTS ON THE POLARITY OF A  
STALKED MEDUSA *THAUMATOSCYPHUS*  
*DISTINCTUS* KISHINOUE

BY

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(With 23 Text-figures)

Since CARLGREN's findings (1909) on the strong capacity for reconstitution in *Lucernaria quadricornis*, the stalked medusae have been an interesting object of experimental work as a scyphozoan of strong capacity for reconstitution. From CARLGREN's experiment on the reconstitution of tentacles and manubrium it has been shown that the medusa indicates a remarkable physiological gradient. After him, however, no experimental works of this kind were carried out on the Stauromedusae until CHILD (1933) published a work on a Japanese stalked medusa, *Halicystus auricula* CLARK. He reported that the capacity of reconstitution of tentacles is different according to the levels of the body at which horizontal or oblique sections were made and also that the pieces of the medusa from various levels have differential susceptibility to the reactions of reagents as KCN, or indophenol. CHILD concluded from his experiment, "Data on differential susceptibility and on the indophenol reactions, as well as those on reconstitution at different levels indicate the presence of a physiological gradient, at least in the umbrella region. The distal margin of the umbrella and the distal end of the manubrium represent the highest end of this gradient."

During the summer of 1932 the present writer at the suggestion of Prof. Tohru UCHIDA engaged in an experiment on a Japanese stalked medusa *Thaumatocyphus distinctus* KISHINOUE at the

Akkeshi Marine Biological Station. The experiment was repeated in the next summer with results slightly different from those obtained with *H. auricula*.

Before proceeding further the writer wishes to acknowledge his deep indebtedness to Prof. Tohru UCHIDA for his constant guidance throughout these experiments and also to Prof. Y. K. OKADA of the Kyoto Imperial University for his valuable suggestions on many points.

### Material

*Thaumatocyphus distinctus* KISHINOUE is abundantly found attached to *Zostera marina* and other sea plants in the vicinity of the Akkeshi Marine Biological Station. The largest individual found by the writer was about 25 mm in length and 10 mm in diameter when extended; the smallest one 8 mm in length and 3.5 mm in the width of calyx. Smaller individuals were used for experiments, because younger ones proved much better reconstitution than those of larger size. In general the animals lived in the laboratory up to four weeks after operation. Several individuals were kept in finger bowls covered with glass plates, together with the sea grass to which they attached in standing sea water. No feeding was attempted. To avoid rising of temperature of water the bowls were always placed in running tap water, nevertheless operated animals often died for some unknown reasons. The operation was done at least within a few hours after collection without narcotizing. In graft experiments pieces of the stalk from various levels of different medusae were connected by piercing along their long axes with a fine glass needle. Thus connected pieces were slightly pressed on both ends with small pieces of paper, so that the cut surfaces of the stalks come into contact with each other. In the next morning they were found fused in the desired manner. Individuals used for histological observations were fixed with BOUIN's solution, imbedded in paraffin, sectioned in 10  $\mu$  and stained with Haematoxylin and Eosin.

## Experiment

The anatomy of the present medusa was described in detail by UCHIDA and HANAOKA in 1933. Only the important structure concerned in this experiment will be noted in the following. Fig. 1 shows the diagrammatic outline of the medusa. The distal margin of the calyx is divided into eight adradial arms each bearing a cluster of tentacles of various numbers. The eight perradial and

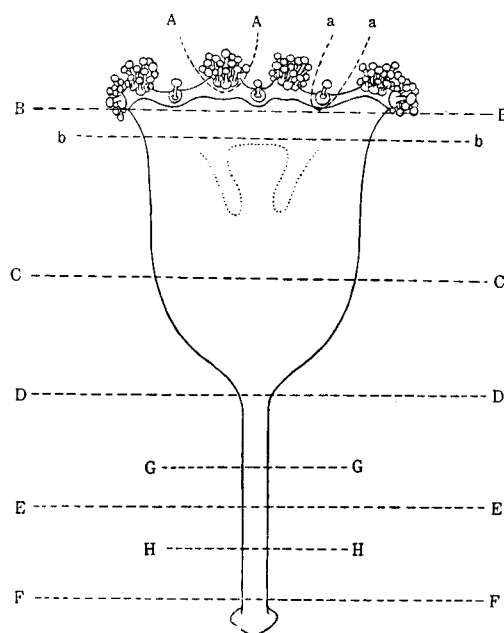


Fig. 1. Diagrammatic outline of *Thaumatoscyphus distinctus*. AA, aa, Lines of section in cases of removal of tentacle arm and primary tentacle. BB-HH, Various levels of transverse section.

interradial primary tentacles are similar in form to the three tentacles standing outermost on the adradial arms and are provided with a shield-like covering on the abaxial side. Just outside the tentacle clusters and primary tentacles there is an undivided band of coronal muscle along the bell margin causing a high ridge of mesogloea. The peduncle is cylindrical with an adhesive pedal disc at its proximal

end. The knob of the tentacle consisting of many slender cells arranged in several rows is covered with a layer of rod-shaped nematocysts. No ovoid nematocysts are found among them. The ectodermal muscle fibres of the stem are embedded in the mesogloea. The shield-like covering of the primary and secondary tentacles is composed of gland cells with an elliptical vesicle and granulated cells arranged in several radial rows. There are no nematocysts in the covering. The coronal muscle fibres are found only on the adaxial side of the slender cell lamella which limits the abaxial end of the marginal structure. On the axial side of the primary tentacles there is a sensory organ for light, which is blackly pigmented and composed of exceedingly narrow cells arranged in a row. The entoderm cells of the tentacles are large, high and characterized by deeply stained granulated bodies at the innermost portion. There are many wedge-shaped solitary gland cells among them. The experiments were directed to the three ends; namely, to determine I) the reconstitutive potency of tentacles and the adhesive foot disc at various levels of calyx and peduncle; II) the reconstitutive potency of heteromorphic tentacles in pieces sectioned at both ends at various heights; III) the influence of the adhesive foot disc upon pieces of stalk grafted on the distal end.

I) *Reconstitution of tentacles and peduncle at various levels of calyx and peduncle.*

A) *Reconstitution after the removal of a tentacle arm or of primary tentacles* (from the line A-A or a-a in Fig. 1). The removal of an arm with a tentacle cluster is followed in a few days by reconstitution of a new arm bearing four or five tentacles which increase in number as the reconstitution proceeds (Fig. 2, A). The similar rapid reconstitution occurs after the removal of a primary tentacle, but the new tentacle sometimes deviates a little in position from the original one (Fig. 2, B). In some individuals in which the margin was irregularly cut at the operation, new tentacles ap-

peared there in excess (Fig. 2, C). The formation of primary and secondary tentacles, however, takes place not only after removal of the tentacles but also mere injury on the margin of calyx brings about the formation of supernumerary tentacles as shown in Fig. 2, D.

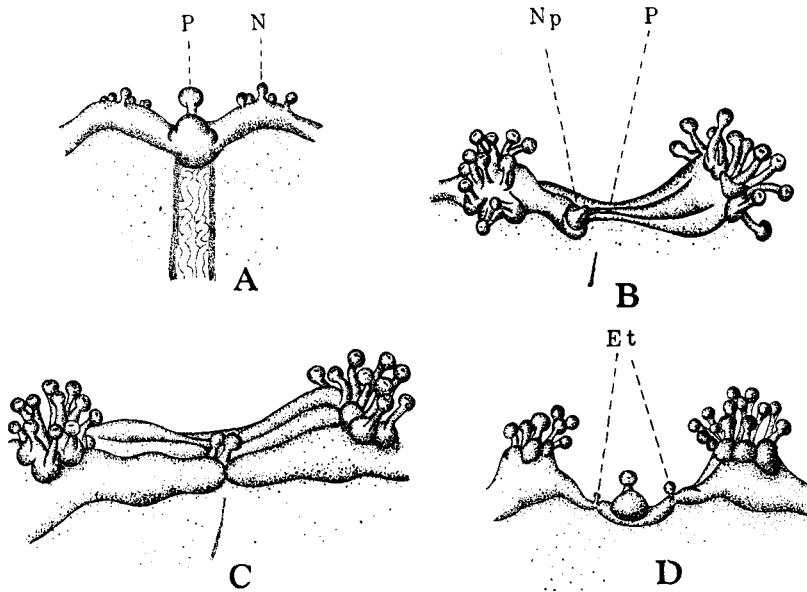


Fig. 2. Reconstitution at the bell margin. A, Reconstitution after removal of two tentacle arms, P primary tentacle, N new tentacle arm. B, Reconstitution after removal of primary tentacle, Np new primary tentacle, P pigment of the photosensitive organ of the removed primary tentacle. C, Formation of two tentacles after removal of one primary tentacle. D, Formation of supernumerary tentacles (Et) after the injury of bell margin.

B) *Reconstitution at the levels between manubrium and marginal organs (at the level B-B or b-b in Fig. 1).*

i) Reconstitution in the proximal pieces. A total of about 50 animals were sectioned horizontally at the level between the manubrium and marginal organs, and in about 80% of the proximal pieces reconstitution of lost marginal organs occurred in 4-8 days after operation. It is very interesting to note that the reconstitution at the level just below the marginal ridge is quite different from

what occurs at the more proximal levels. From the level just below the marginal ridge the arrangement of new tentacles is generally similar to those of the normal medusa, that is, they are arranged in several groups, though not strictly in eight, and primary tentacles are often clearly distinguished from secondary ones (Fig. 3, A).

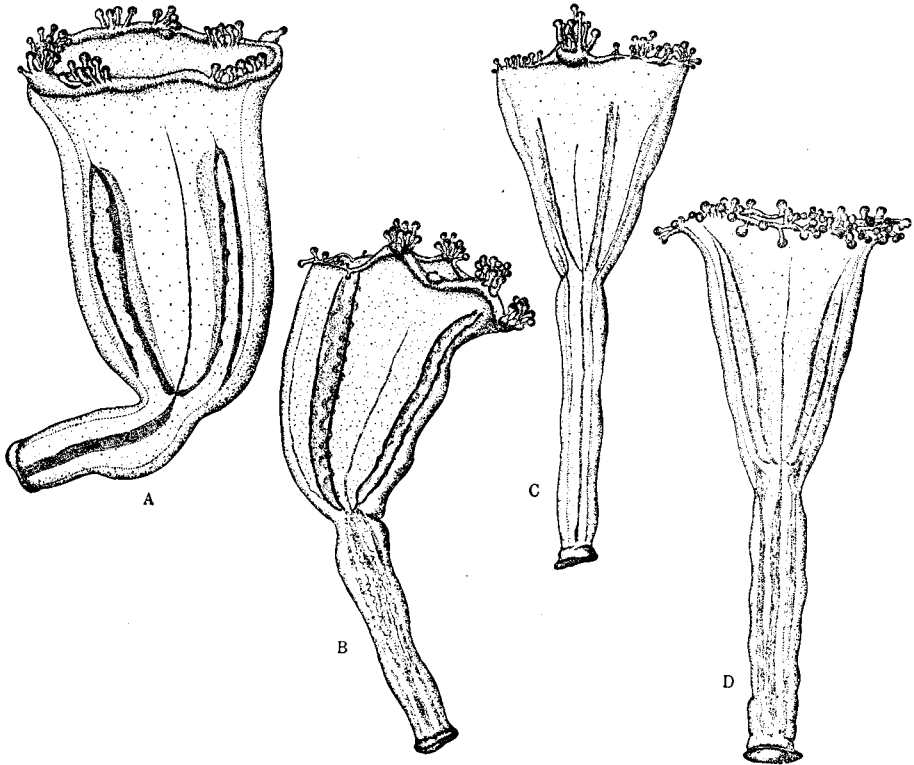


Fig. 3. Reconstitution after section between manubrium and bell margin. A, New tentacle cluster reconstituted. B, Tentacle cluster reconstituted on the half-circle of the cut surface. C, Only one tentacle cluster reconstituted; other tentacles evenly distributed on the new margin. D, All tentacles reconstituted evenly distributed on the new margin.

But when sectioned at levels near the manubrium, the tentacles regenerate evenly from the margin and hence no distinction of the primary and the secondary tentacles (Fig. 3, D). In practise, however, it is very difficult to section the living animal just below the marginal ridge. Sometimes the section was made at

a level too proximal and sometimes the cut was a little oblique; the mode of appearance of new tentacles was different according to the levels of section, some appearing in groups and others being dispersed (Fig. 3, B, C). The reconstitution of the tentacles is as

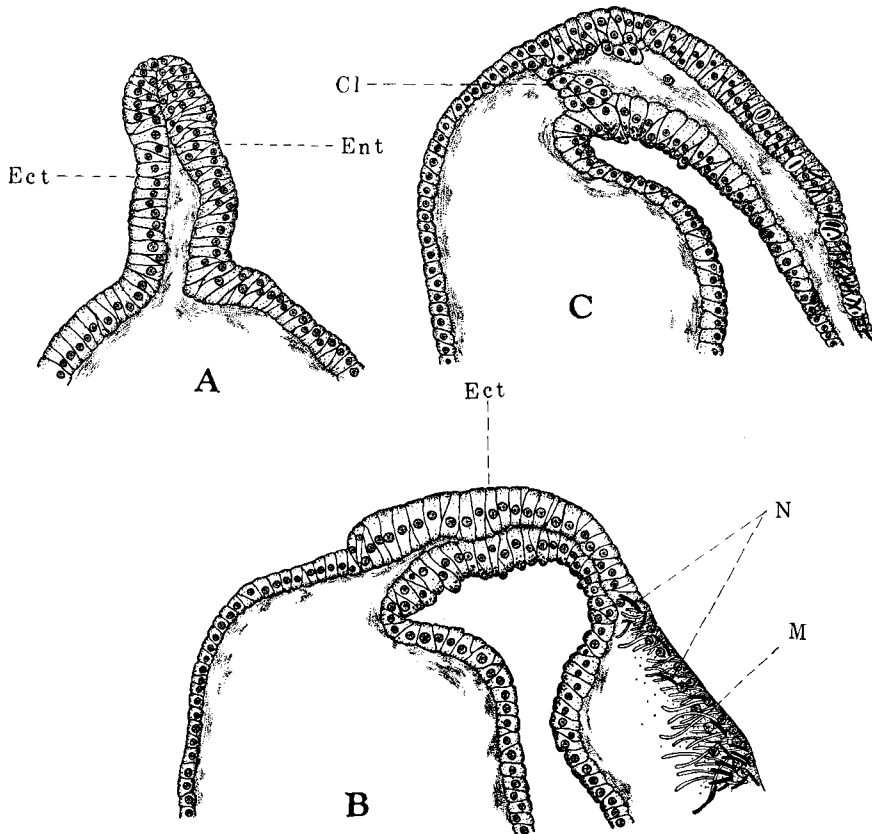


Fig. 4. Development of tentacle. A, Cut end of exumbrella one day after operation, Ect ectoderm, Ent entoderm. B, New margin of the cut umbrellae 2 days after operation, Ect high ectoderm cells forming the future tentacles, N migrating rod-shaped nematocyst, M muscle fibres. C, Formation of cell-lamella (Cl) in the new margin of the cut umbrellae.

follows. Within several hours after the operation the ectoderm and entoderm cells of the cut surfaces become fused in both the exumbrella and the subumbrella. The cells on the new margins acquire the embryonal character and form new ridges without mesogloea



in a few days (Fig. 4, A). These ridges both of the exumbrella and subumbrella gradually extend and finally unite to form the new bell margin (Fig. 4, B). In the meantime the mesogloea is deposited between the two cell layers. The cells on the abaxial side of the cell lamella gradually differentiate to become large and high. In the

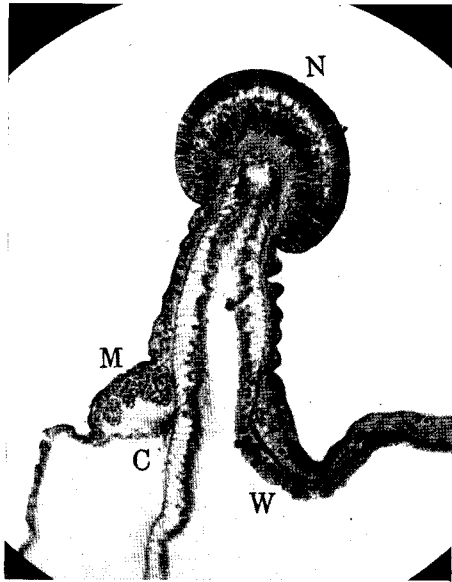


Fig. 5. Photomicrograph of reconstituted tentacle, N nematocyst layer, M coronal muscle fibres, C cell lamella, W wedge-shaped gland cells in the endoderm.

reconstitution of a new tentacle the cell lamella appears first and limits the abaxial end of the marginal structure. The new tentacle, at first represented by a mere marginal knob covered with rod-shaped nematocysts, becomes equipped with numerous rod-shaped nematocysts which have migrated from the adradial portions of the abaxial and side wall of the infundibula. The ectoderm and endoderm cells at the base of the knob then form a tubular stalk and thus the reconstitution of a new tentacle is completed. Along with the reconstitution of the tentacles the ectoderm cells proliferated in the mesogloea differentiate into coronal muscle fibres, and some of the tentacles become provided at the adaxial base of the stalk with a shield-like cushion covered with vesiculated and granulated gland cells. In the endoderm cells of the tentacles solitary wedge-shaped gland cells appear and muscle fibres develop in the ectoderm of the stalk (Fig. 5).

ii) Reconstitution in the distal pieces. The distal cut margin becomes contracted and fused in a few days in the center to form a disc-shaped fragment (Fig. 6). The fragment lived in the

laboratory up to one week or more but no further reconstitution of the proximal structure was observed. The ectoderm of the fused surface of the calyx was uniformly composed of the original cubical cells.

C) *Reconstitution at the level below the manubrium* (at the level C-C in Fig. 1).

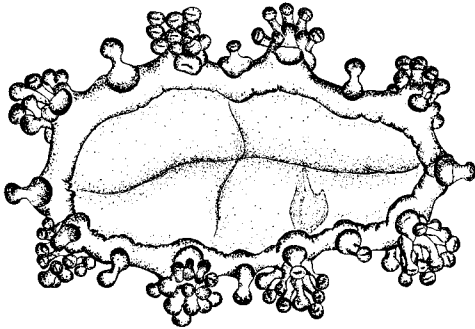


Fig. 6. Reconstitution of distal piece sectioned between manubrium and bell margin.

i) *Reconstitution in the proximal pieces.* A total of about 30 animals were sectioned at the level below the manubrium and in about 50% of the proximal pieces reconstitution occurred within 8 days or more after operation. Fig. 7. represents one of the specimens showing the reconstitution at this level. The distal end has grown to a considerable extent and the tentacles are distributed universally along the new margin. The mode of development and the microscopical structure of these tentacles are similar to those regenerated from the more distal levels, but the nematocysts covering the tentacle knob are less dense and the coronal muscle fibres are more faint than those from the distal levels. The manubrium of the proximal piece is reconstituted at the expense of gonad cells

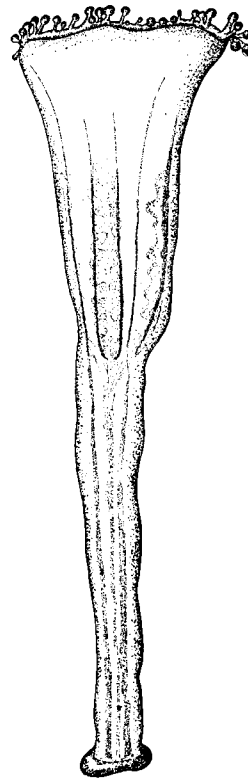


Fig. 7. Reconstitution after section below manubrium.



Fig. 8. Photomicrograph showing the reconstitution of manubrium, G tissue of gonad, M new manubrium.

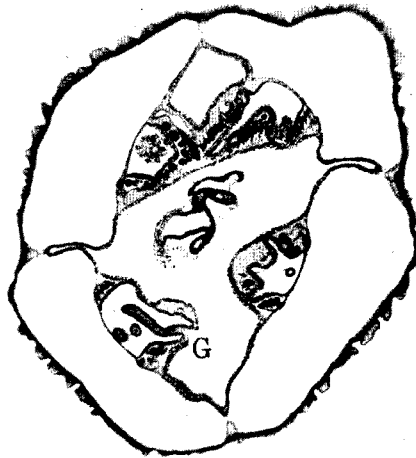


Fig. 9. Cross section through the new mesogonial pocket, G gastral filament arranged in the mesogonial pocket.

and cells consisting the walls of the stomach cavity. The cells composing these parts are once dissociated before the reconstitution and reorganize a new manubrium. Fig. 8 shows a manubrium developing at this level. The reconstitution of mesogonial pockets is most interesting. In *T. distinctus* they extend from the margin downwards and are connected in the lower part with the stomach cavity. In the section at the level below the manubrium the proximal piece is deprived of the mesogonial pockets. But in 10 days or more after operation mesogonial pockets are formed in the proximal pieces by the union of the radial walls of the stomach cavity and consequently the interradial gastral filaments are arranged in the new mesogonial pockets as shown in the photomicrograph of Fig. 9.

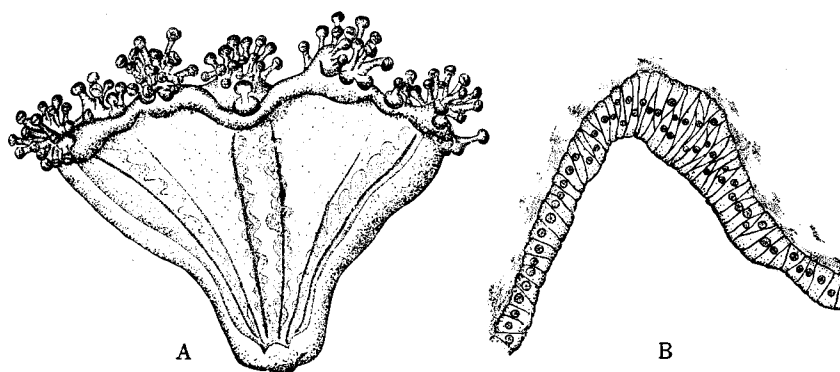


Fig. 10. A, Reconstitution of distal piece after section below the manubrium. B, High ectoderm cells at the proximal new end of piece of A.

ii) Reconstitution in the distal pieces. The distal pieces at the proximal cutting all contract and fuse in the center to form a cup-like fragment in a few days (Fig. 10, A). Although no sign of the stalk was observed at the proximal end of these pieces within the following 10 days, the ectoderm cells of the calyx are exceedingly high at the proximal end; the fact probably indicates the first step of the reconstitution of the foot disc (Fig. 10, B).

D) *Reconstitution at the junction of the calyx and peduncle.* (at the level D-D in Fig. 1).

i) Reconstitution in the proximal pieces. About 30 animals were sectioned at the junction of the calyx and the peduncle. The reconstitution of tentacles in the proximal pieces occurred in 8 days or more in about 50% of the operated animals. The new tentacles were slender and small in number (Fig. 11). Most of the specimens lack the shield-like covering but they do have a slight elevation of ectoderm cells at the base of some tentacle stalks. The coronal

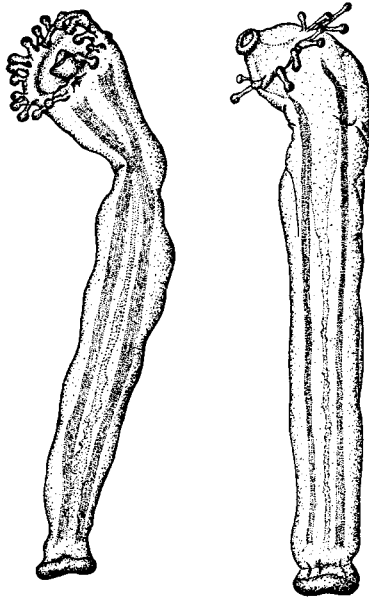


Fig. 11. Reconstitution after section at the junction of calyx and peduncle.

muscle are very weak and some of the specimens have no coronal muscle fibres at all. The stalk of the tentacles is very short, wedge-shaped gland cells are not found in the endoderm. The arrangement of the rod-shaped nematocysts of the tentacle knobs is very slow; then many ovoid nematocysts are irregularly intermingled among the rod-shaped nematocysts. Sometimes the outer surface is covered exclusively by the ovoid nematocysts. The four radial pockets of the peduncle unite in the distal end into a large stomach cavity. The manubrium is reconstituted by the endoderm cells lining the radial pockets (Fig. 12,

A). In some specimens the manubrium was reconstituted more distally than marginal structures.

ii) Reconstitution in the distal pieces. The reconstitution of the stalk at the proximal end of the distal pieces occurs in a much higher degree than in the pieces sectioned at the more distal levels. In these pieces the lower end of the calyx grows a little and forms a small knob with mesogloea newly secreted there (Fig. 12, B). The

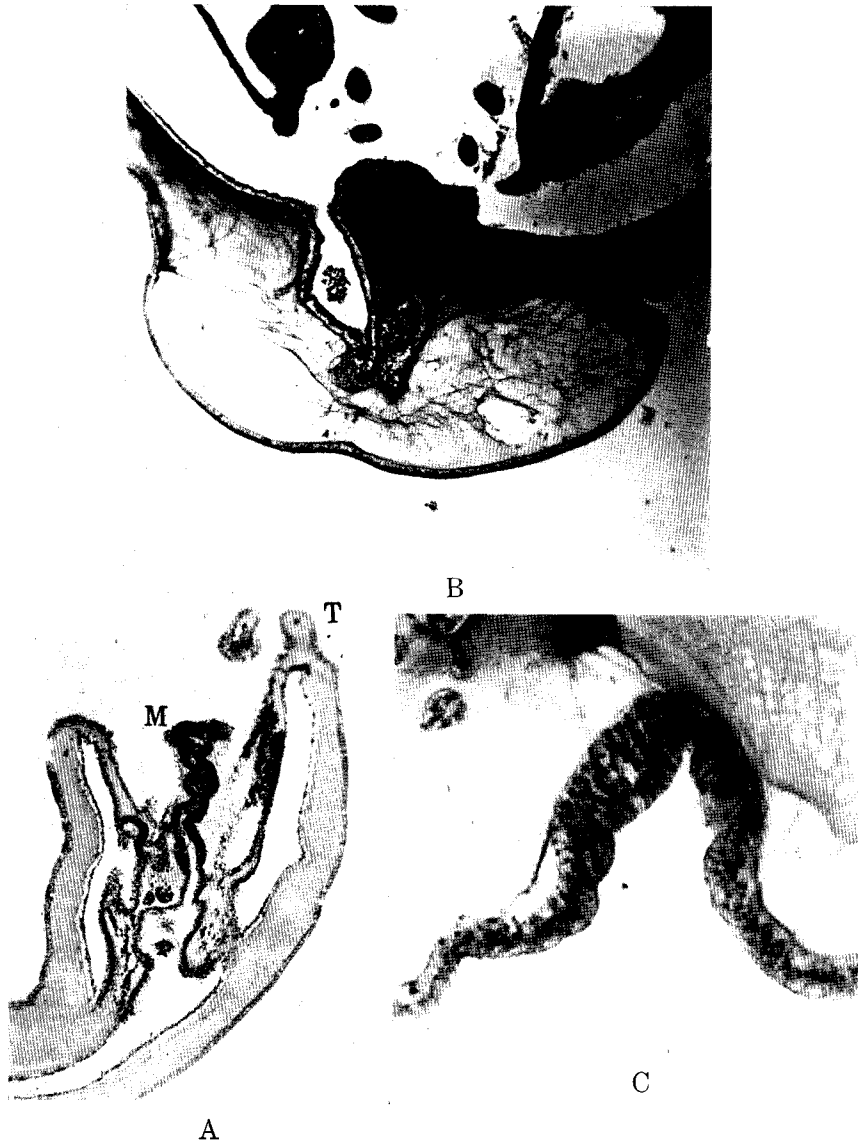


Fig. 12. A, Reconstitution of manubrium from the entoderm cells of peduncle, M manubrium, T tentacle. B, Sagittal section of peduncle reconstituted at the junction of calyx and peduncle. C, Ectoderm layer at the proximal end of the specimen of B.

endoderm cells extend into the stalk-bud and the ectoderm cells at the most proximal apex of the knob become large and columnar, yet they are not differentiated into mucous gland cells and fibrous cells (Fig. 12, C).

E) *Reconstitution at the middle level of peduncle* (at the level F-F in Fig. 1).

i) Reconstitution in the proximal pieces. In about 50% of the operated animals, tentacle reconstitution occurred with similar rapidity to that in the sections at the junction of peduncle and calyx

(Fig. 13, A). But the microscopical structure of the new tentacles is quite different from the original tentacles. The nematocyst layer of the knob is exclusively composed of ovoid nematocysts and in the tentacle stalk no muscle fibres are found. Between the cell lamella and the tentacles there are neither coronal muscle fibres, nor shield-like covering which is situated at the base of the tentacles in the normal medusae.

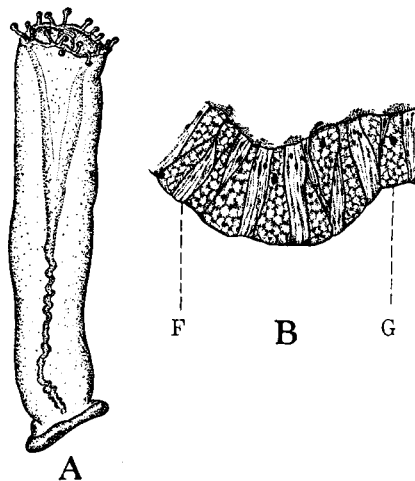


Fig. 13. A, Reconstitution of tentacles at the middle level of the stalk. B, Ectoderm cells at the proximal end after section at the middle level of stalk, F fibrous cell, G gland cell.

pieces are incomplete in structure, the structure of the adhesive foot disc newly formed in the distal pieces resembles very much the normal one. The cells of the new disc are very large and differentiated into mucous gland cells and fibrous cells as in a normal disc (Fig. 13, B).

F) *Reconstitution at the proximal level of the peduncle* (at the level F-F in Fig. 1).

ii) Reconstitution in the distal pieces. While the tentacles reconstituted on the proximal

i) Reconstitution of tentacles. Reconstitution occurred in about 30% of the thirty operated animals within 10–15 days after operation. (Fig. 14). These reconstituted tentacles are each

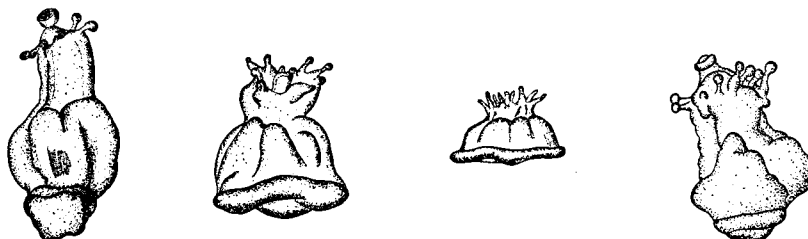


Fig. 14. Reconstitution of tentacles from the proximal part of stalk.

represented by a mere marginal knob containing on the surface a few ovoid nematocysts, which are even then sometimes absent. All other marginal organs such as cell lamella, coronal muscle fibres and shield-like covering did not develop in the margin reformed at this level.

ii) Reconstitution of the foot disc. The reconstitution of the foot disc in the distal pieces is complete at this level. The differentiation of mucous and fibrous cells is clearly seen and in the specimen represented in Fig. 15 the foot disc was functional.

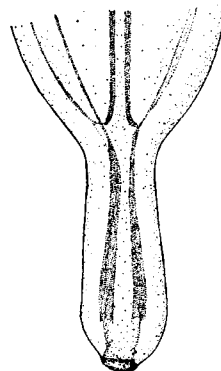


Fig. 15. Functional foot disc reconstituted at the proximal end of piece consisting of umbrella and distal two thirds of the stalk.

G) *Reconstitution after an oblique section through the calyx with removal of all or some of the marginal organs.*

In the experiment on *H. auricula*, CHILD found that after oblique sectioning through the umbrella with removal of all parts of the original margin the rate of reconstitution on the oblique surface of section decreases towards the proximal part; reconstitution at the more proximal levels is more or less inhibited by dominant potency of reconstitution at the distal levels and at the most proximal levels of the oblique surface this inhibition is the greatest.



In *T. distinctus*, however, when oblique sections were made in the same way as by CHILD, no inhibiting influence by the more distally developing tentacles upon those at the more proximal levels was observed except a slight decrease of the rate of reconstitution

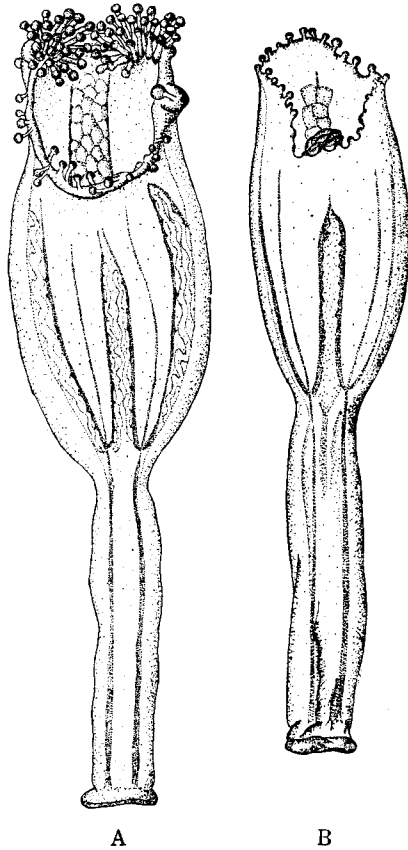


Fig. 16. Reconstitution of tentacles after oblique sectioning through calyx with removal of all marginal organs (A) or through calyx leaving two tentacle arms.

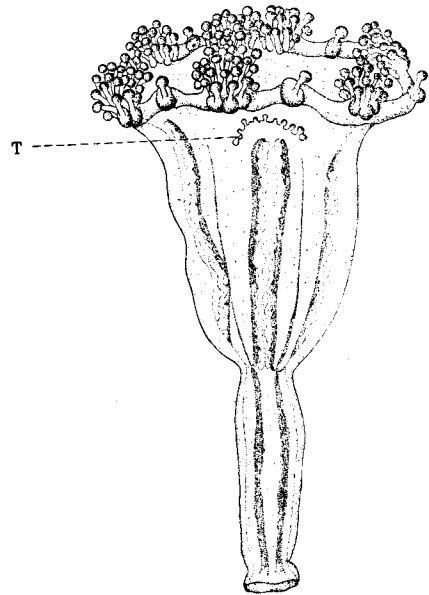


Fig. 17. Reconstitution of tentacle (T) after horizontal injury on the calyx.

at the more proximal levels (Fig. 16, B). Even when some of the marginal organs were left in the sectioning the remaining marginal organs did not arrest development of the tentacles at the more proximal levels on the oblique surface. (Fig. 16, A). In addition

to the experiment of oblique sectioning a horizontal injury was made at various levels of the calyx. The injury was followed by the formation of tentacles fewer in number compared with those which appeared on the corresponding levels in the preceding experiments (Fig. 17). These facts indicate that the inhibiting influence of the more distal tentacle upon development of the more proximal tentacles is not so great in *T. distinctus* as in *H. auricula*.

II) *Reconstitution of heteromorphic tentacles in pieces from various heights sectioned at both ends.*

To determine the reconstitutive potency of the heteromorphic tentacles in pieces sectioned at both ends from various heights, the animals were sectioned at the levels B-B, C-C, D-D, E-E, G-G, H-H, shown in Fig. 1 into five pieces.

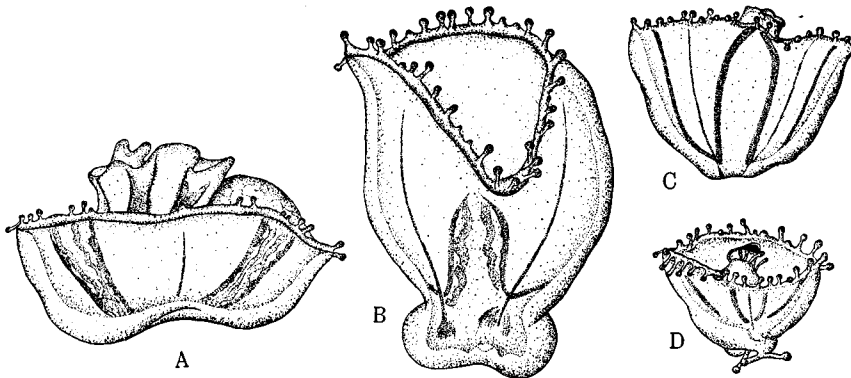


Fig. 18. Reconstitution of tentacles in the pieces obtained from various levels of calyx. A, from the level between BB-CC, B and C, from the level between CC-DD in Fig. 1. D, piece with heteromorphic tentacles from the proximal one third of the umbrella.

In the pieces sectioned at the levels between B-B and C-C no heteromorphic tentacles developed. The proximal end of these pieces contracted in the center to form a calyx base and at the distal end the tentacles appeared on the new margin (Fig. 18, A). In most pieces obtained from the heights between C-C and D-D a similar

reconstitution occurred (Fig. 18, B, C). But in a single specimen illustrated in Fig. 18, D, three small tentacles developed on the proximal end of the calyx in addition to the distal tentacles on the new margin. No heteromorphic tentacles could be found in the pieces

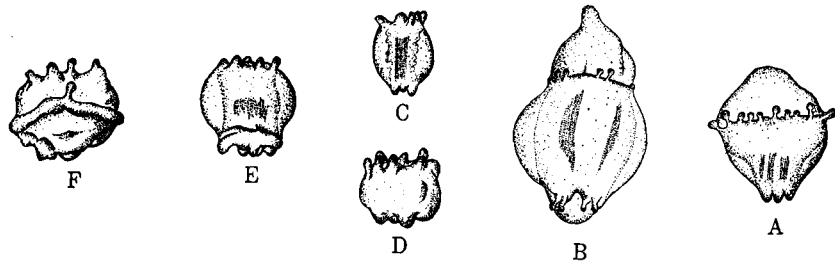


Fig. 19. Formation of heteromorphic tentacles in the pieces from the middle one third of the peduncle.

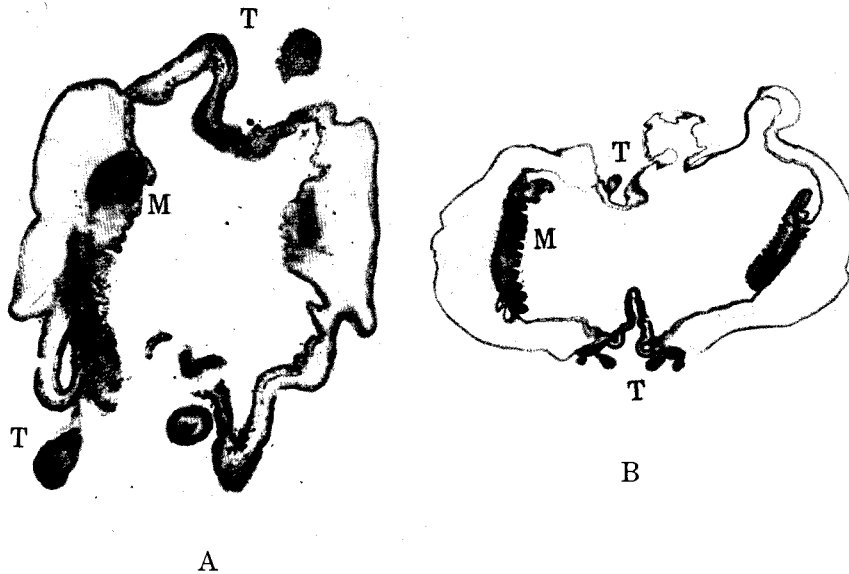


Fig. 20. Sagittal section of the pieces A and B in Fig. 19.  
T, tentacle. M, muscle fibres.

from the levels D-D and G-G, but in the pieces from the heights G-G and H-H six specimens were obtained with tentacles at both ends of section. (Fig. 19). In some of these specimens the tentacles

of the proximal end were apparently irregularly formed, but microscopical observation proved in them the tentacular structure of the ectodermal nematocyst layer as it appeared at the corresponding levels in the former experiments (Fig. 20, A. B). In one specimen (Fig. 19, F) one of the proximal tentacles is directed distally. In the pieces sectioned at the most proximal level only one specimen was obtained with such heteromorphic tentacles. In most pieces without heteromorphic tentacles the one end is closed by the contraction of the cut surface and the other end has new tentacles (Fig. 21, B, C). Some specimens

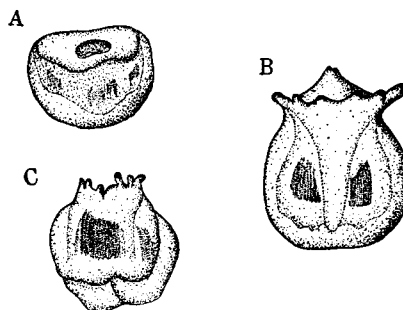


Fig. 21. Reconstitution in the pieces from the middle one third of peduncle.

destitute of tentacles at all, had only an opening at the distal end (Fig. 21, A) or were spherical in form with both ends closed. This spherical fragment lived over 10 days in the laboratory.

### III) Influence of terminal foot disc upon the grafted stalk piece.

Grafts were made after the method described under the heading, Material. To avoid the disorder of direction of grafted pieces the following method was available; when a graft of opposite direction was desired, a graft of two pieces each with foot disc was first made with the discs pointed in the opposite directions (Fig. 22, A) and after the fusion of the two pieces one of the foot discs was removed (Fig. 22, B); when the graft in the same direction was to be made, a piece with a small part of calyx was used on one side and the calyx was removed after the fusion. Grafting of a stalk piece on another piece bearing the foot disc easily succeeded in any direction. Repeating the method one can make a chain of pieces of stalks from different individuals (Fig. 22, C). These stalk-chains lived

over one week in the laboratory. Regardless of the direction of graftings two pieces always united perfectly to each other and a mouth opened without fail at the distal end of the united animal.

These chains of stalks lived sometimes up to two weeks but to the regret of the writer he could not find any reconstitution of marginal organs on the grafted pieces.

### Conclusion

The results obtained from the series of experiments above described indicate that the present medusa also represents an axial gradient in regard to the reconstitution of tentacles and stalk. The potency for the reconstitution of tentacles on the distal end of the cut surface decreases as the level of section moves proximally. When sectioned at the level just below the bell margin, new tentacles appear in 4-8 days on the distal surface. This rate of reconstitution is postponed to 8-, 8-, 10-, 10-15 days towards the proximal parts as the level of sectioning moves downwards to the levels C-C, D-D, E-E, F-F, G-G. The similar case is also observed in the percentage of animals which reconstitute tentacles after the operation, *i.e.* when the animals were sectioned at the level of B-B, the reconstitution

of tentacles is found in about 80% of the proximal pieces of the operated animals. This percentage of animals bearing reconstituted tentacles decreases to 50%, or 30%, as the level of sectioning moves

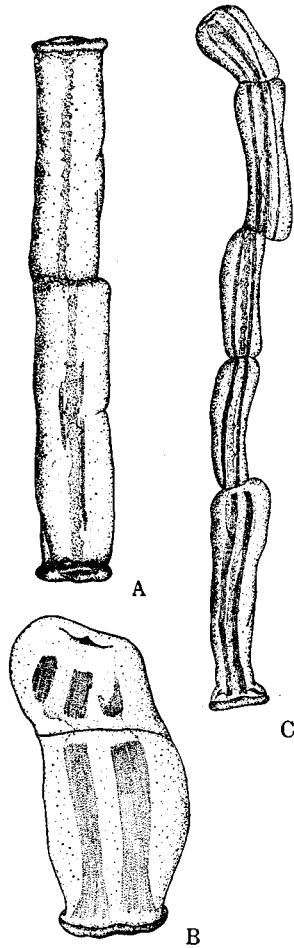


Fig. 22. Fusion of stalk pieces. A, two pieces fused in opposite directions. B, terminal disc of the one piece removed. C, chain of stalk pieces from many different individuals.

downwards to C-C, D-D, E-E, F-F. These facts indicate the presence of an axial gradient in this medusa. The axial gradient is also shown in respect to arrangement and histological difference of tentacles reconstituted. Near the distal level new tentacles appear in cluster on the cut surface, though not exactly grouped in eight. On levels a little proximal new tentacles are not arranged in cluster but are

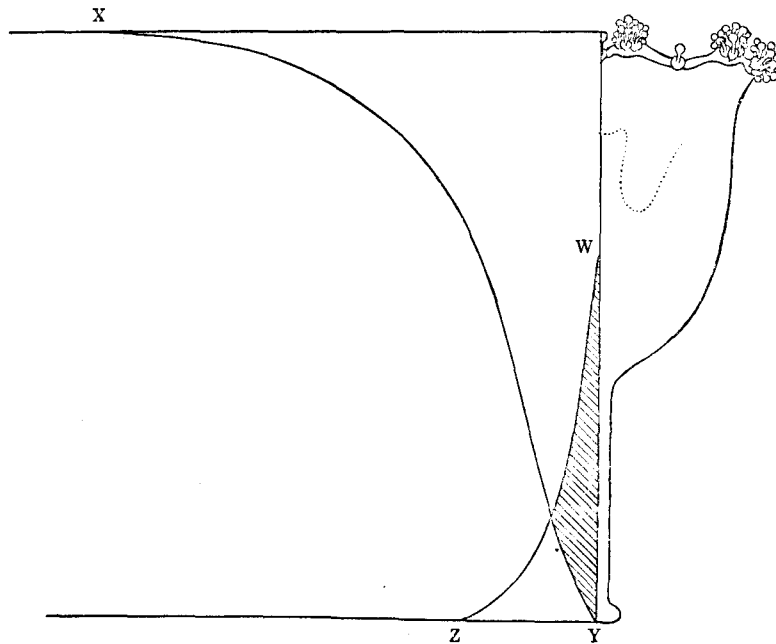


Fig. 23. Diagram showing the potency of reconstitution of tentacle and foot disc.

evenly distributed on the margin, but these tentacles are similar in structure to the normal ones. Near the proximal one third of the stalk, however, new tentacles are represented by mere small knobs containing a few ovoid nematocysts instead of rod shaped ones and sometimes with no nematocysts at all. In the tentacles reconstituted from the middle length there are several intermediate forms according to the heights of the level of the section. As in the tentacles rod-shaped nematocysts are gradually replaced by ovoid nematocysts

as the level moves downwards, also the development of coronal muscle fibres becomes slow and faint. This potency of ectoderm to reorganize the muscle fibres disappears completely in the proximal half of the stalk. The similar case is also observed with regard to the reconstitution of the shield-like covering. The potency of reconstitution here mentioned in the medusa is approximately graphically represented by the curve X-Y in Fig. 23.

In contrast to the reconstitution of the distal organs that of the proximal organ, foot disc, shows another axial gradient which is quite opposite in direction. When sectioned a stalk near the pedal disc new functional pedal disc reconstitutes on the distal end of the cut surface. As the level of section moves upwards the formation of the foot disc is more incomplete and finally on levels between the manubrium and marginal ridge no indication of reconstitution of foot disc. This potency for foot disc formation is approximately expressed by the curve Z-W in Fig. 23. In connection with these two gradients of reconstitution it must be noticeable that occurrence of the aboral heteromorphic tentacles takes place only in pieces from the peduncle and from the proximal end of calyx; the region corresponds to the part expressed in the graph as the common zone in which the two curves X-Y and Z-W are fallen on. CHILD making experiments on *H. auricula* also reported a specimen with a reconstituted foot-like structure at the aboral end of the distal piece consisting of the umbrella and the distal half of the stalk, and also a stalk piece sectioned at both ends, bearing new tentacles on both ends in bipolar form.

The writer regrets that he could not determine the effects of the foot disc upon grafted pieces of stalks, because no reconstitution of tentacles took place.

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