ON THE MORPHOLOGY OF A STALKED MEDUSA, *THAUMATOSCYPHUS DISTINCTUS* KISHINOUYE

BY

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(*With Twenty Text-figures*)

The medusa was first reported by KISHINOUYE (1910) who examined two specimens collected from Shimushiri, the northernmost island of the Kuriles. Unfortunately he seemed to have cut no section and therefore briefly described the gastric cavity as follows: "The central stomach cavity is long and prismatic." Taking into consideration this description, MAYER (1910) referred the medusa to the Eleutherocarpidae = Haliclystidae. In 1929 the senior author, who investigated sections made from a specimen of the medusa collected from North Saghalien, transferred the species from the Haliclystidae to the Cleistocarpidae on account of the presence of four mesogonial pockets. At that time, however, only a preserved specimen was at his disposal, and therefore only a half of its calyx was used for making sections and the peduncle was not studied in detail. Recently we found that the medusa occurs abundantly in the vicinity of the Akkeshi Marine Biological Station, Hokkaido during July-August. Moreover, few papers have been published dealing with the morphology of the stalked medusae, probably on account of their comparative rarity. Such being the case, it seems to us to be not unnecessary to publish our observations. Other papers on regeneration and the early development of the species are now in preparation by the junior author.

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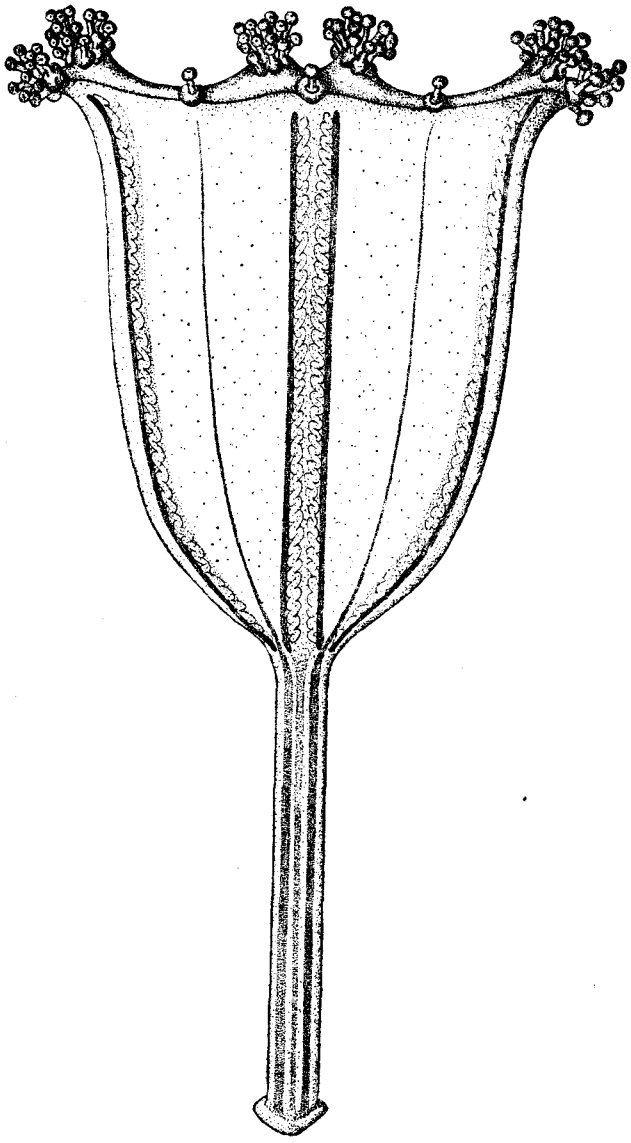

Fig. 1. *Thaumatoscyphus distinctus* KISHINOUYE

External characters. The body is goblet-shaped, with a cylindrical peduncle which is comparatively long in smaller specimens. The calyx is higher than wide, generally about 10 mm by 8 mm, almost quadrate in cross section, narrowing towards the proximal portion and somewhat abruptly widened close to the margin. The mesogloea is fairly thick and rigid. The exumbrella is rather smooth, though beset with sparsely scattered nematocyst clusters. There are 12 pigment stripes, a narrow one in each perradius and a wide pair in each interradius. Close to the margin runs a furrow encircling the marginal exumbrella. The umbrella margin is divided into eight short adradial arms, making four pairs with respect to the interradii, and separated by exceedingly shallow perradial clefts. Each arm is provided with a terminal cluster of tentacles which are variable in number according to the developmental stage. These tentacles are short and capped, each with a concavity in the center of the distal cap. The three outermost tentacles are comparatively small and each are mounted upon a cushion-like base which takes sometimes the form of a shield-like covering on the abaxial side. The primary tentacles are considerably modified and are somewhat similar to the outermost secondary tentacles just mentioned, provided with a discoid head, a short stalk, an axial canal, and mounted on a cushion-like base which becomes often shield-like in form. At the axial base of these primary tentacles there exists a blackly pigmented spot which probably serves as an organ standing in relation to light. Just outside the tentacle clusters and the primary tentacles there is an undivided band of coronal muscle along the bell margin, causing a high ridge of mesogloea.

The subumbrella is provided with numerous longitudinal ectodermal muscle fibres, regularly arranged. In each interradius there is a bag-like swelling sprinkled with numerous white conspicuous nematocyst clusters. The gonads, contained in these swellings, are laterally folded generally about 20–30 times, making paired longitudinal rows, extending from the interradial portions of the bell margin to the base of the calyx, and narrowing towards both the

ends. Corresponding to the rows of the gonads, run four interradial pairs of pigment stripes. The mouth is four-sided. The stomach suddenly becomes narrow some distance below the lips and considerably crisped transversely for several millimeters. The gastral filaments are numerous, arranged in four interradial paired rows. The stomach cavity is divided into four radial and four mesogonial pockets.

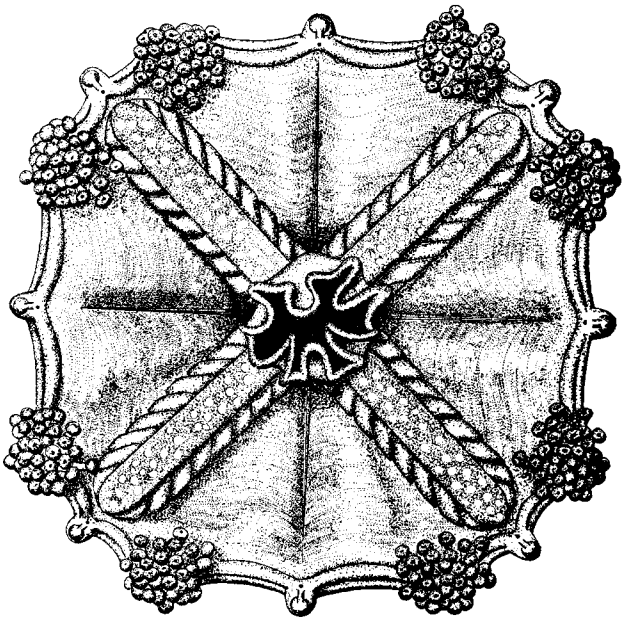

Fig. 2. *Thaumatoscyphus distinctus* KISHINOUYE ; oral view.

The peduncle is cylindrical, quadrate in section, with a terminal disc which is somewhat rectangular in shape and furnished with a small furrow in the central portion of the aboral side. The peduncle is considerably variable in length in the living state and may be stretched out to about twice the length of the calyx. The cavity of the peduncle is divided only near the calyx into the four perradial chambers on account of the confusion of the four interradial taenioles, but for the most part it is single-chambered and cross-shaped in transverse section, since the taenioles are separated.

Measurements of four specimens in different developmental stages are as follows :

Specimen	Length of calyx	Width of calyx	Length of peduncle	Number of secondary tentacles in each adradius
A	15 mm	10 mm	11 mm	26
B	12 mm	8 mm	10 mm	25
C	7 mm	4 mm	8 mm	15
D	3 mm	3.5 mm	5 mm	13

The colour is somewhat variable; calyx brown or greenish with scattered fine black flecks and white spots, which are especially conspicuous in the interradial subumbrellar parts. Peduncle generally light brown or green. Marginal tentacles brown. Gonads brown. Eight adradial longitudinal black streaks running from the bell margin to the base of the calyx, together with four interradial ones, more slender than the former and extending near the bell margin to the end of the peduncle, are characteristic in the species.

Microscopical anatomy. The ectoderm cells of the exumbrella are generally similar; low and cylindrical, and there are sparsely distributed several exumbrellar thickenings into the jelly, especially numerous near the margin, which contain a congeries of cells of several kinds, such as ovoid nematocysts, granulated gland cells and vesiculated cells of irregular forms. The ovoid nematocysts situated

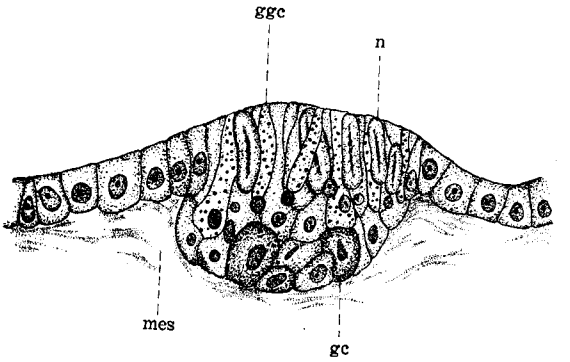

Fig. 3. Section of exumbrella. ×3333; gc gland cell, ggc granulated gland cell, mes mesogloea, n nematocyst.

in the outer part of the congeries seem to be more slender than those found in the nematocyst sac (Nesselsack) in the interradial mesogloea. The gland cells intervenning between the nematocysts are slender, provided with a nucleus in the lower portion, full of fine granules deeply stained by haematoxylin, and open externally. In the lower half of the congeries there are aggregated cells of different forms and sizes, containing vesiculated cells and glandular ones. At the bottom of the exumbrellar thickenings there are always found one or two massive gland cells with a somewhat degenerated nucleus and plasma well stained by haematoxylin. The ectoderm cells of the basal part of the peduncle are exceedingly modified; these cells are very high and contain mucus well stained by aniline blue. By virtue of these cells the medusa can attach to the substratum. Almost alternative in position with these cells, are present slender cells which seem to be fibrous in structure and are well-stained by acid fuchsin. The subumbrellar ectoderm is generally thicker than that of the exumbrella and contains many gland cells and, especially in the adradial portions just outside the base of the gonads near the perradii, numerous rod-shaped nematocysts. In the portion provided with numerous rod-shaped nematocysts there are found many granules of dark brown pigment.

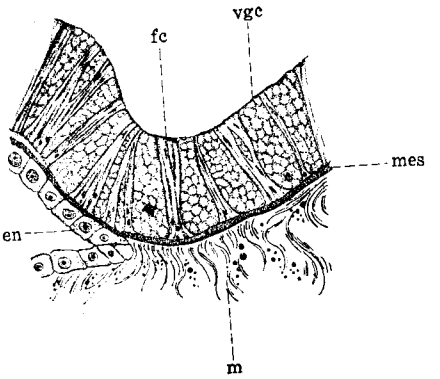

Fig. 4. Section of pedal disc. ×3333; en endoderm, fc fibrous cell, m muscle, mes mesogloea, vgc vesiculated gland cell.

The mesogloea is fairly rigid like that of *Haliclystus steinegeri*, being provided especially in the exumbrella with long fibres in spiral forms and running generally perpendicularly to the ectoderm layer. In the interradial mesogloea just inside each mesogonial pocket are imbedded several nematocyst sacs, in which many ovoid nematocysts

are contained. The longitudinal muscle bundles in the mesogloea are confined to the interradii in the lower portion of the calyx and in the peduncle, but they spread out gradually towards the perradii in the upper portion and each eventually becomes divided into two, making eight adradial muscle banners. In the marginal portion just below the anchors there runs a well developed coronal muscle bundle which makes a circular ridge on the exumbrella. Inside the coronal muscle there is in the jelly a cellular lamella made of flat ectoderm cells arranged in a row.

The endoderm cells of the radial pocket are glandular and cubic, while those of the mesogonial pockets and the canals of the peduncle are far higher than the former. However, the endoderm cells situated in the axial portion of the mesogonial pockets are low like those in the radial pockets. The endoderm cells in the tentacles will be described later on.

From the morphological point of view, the peduncle of the stalked medusae is divided into two types; one being single-chambered and the other four-chambered. So far as we are aware, the peduncles belonging to the latter type are always four-chambered in their whole length except only the upper (oral) part near the point of junction with the calyx, which is often single-chambered on account of the incomplete fusion of the taenioles. With regard to the morphology of the peduncle, *Thaumatoscyphus distinctus* seems to be unique in the Stauromedusae. According to KISHINOUYE (1910), "The cavity in the peduncle is divided into four chambers by fusion of the well-developed interradial taeniolae." Concerning the peduncle of *Brochiella hexaradiatus* which is most probably referable to the genus *Thaumatoscyphus*, BROCH (1907) states, "Der Stiel (Fig. 6) ist rund, einkammerig, innen mit sechs longitudinalen Muskeln, die im Querschnitt in der Regel ein hufeisenförmiges Bild zeigen." So far as we have been able to observe, the peduncle of *T. distinctus*, though at first single-chambered in the short part near the calyx, is in its main part four-chambered by the confusion of four taenioles, but, in a way dissimilar to that of other medusae, it becomes again single-chambered in the

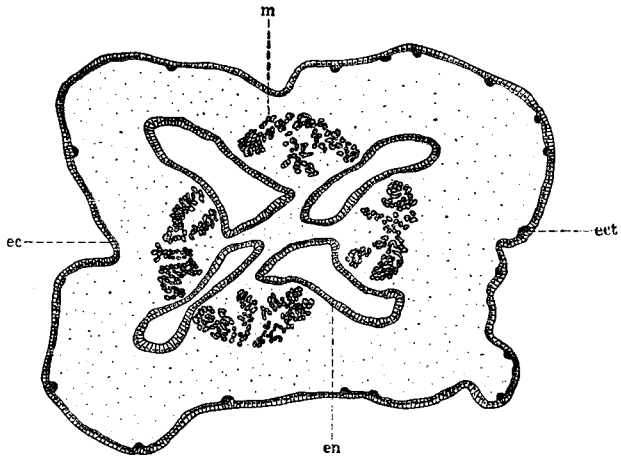

Fig. 5. Horizontal section of peduncle. ×150; ec ectoderm, ect ectodermal thickening, en endoderm, m muscle.

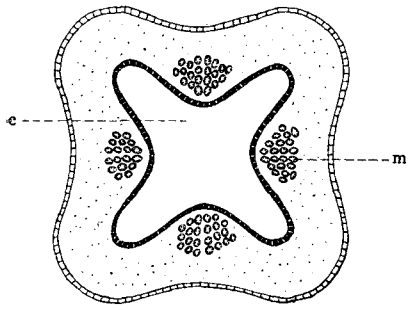

Fig. 6. Schema of horizontal section through lower portion of peduncle; c cavity, m muscle.

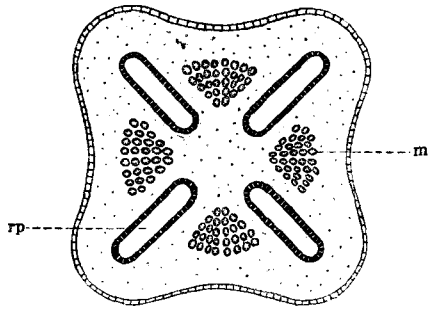

Fig. 7. Schema of horizontal section through middle portion of peduncle; m muscle, rp radial pocket.

basal portion. The mesogloea is fairly thick, rigid and provided with four interradial muscle strands, each consisting of many well developed longitudinal muscles arranged in loose bundles in cross section.

According to the level of cross section, the calyx differs greatly in structure, as shown in Figs. 8–11. There are in the calyx twelve longitudinal canals, which may be divided into three groups; four infundibula, four radial and four mesogonial pockets. The infundibula are lined with an ectoderm layer and extend from the level of the

manubriuem to the end of the calyx, gradually becoming narrow towards the proximal part (near the peduncle). The ectoderm cells in the upper portion are generally similar to those of the exumbrella, while in the lower portion they are higher than the latter, and, especially in those on the axial side, granulated. The radial pockets surrounded by cubic granulated glandular cells of similar form are connected in the lower (basal) part with the interradial canals of the peduncle. These pockets are somewhat of the

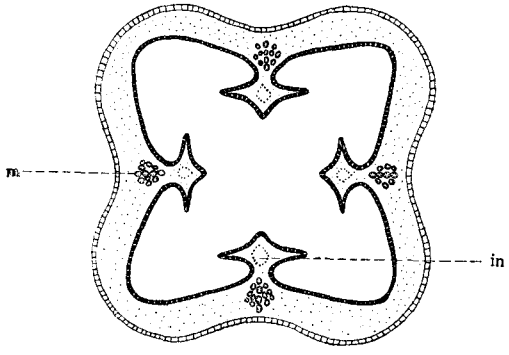

Fig. 8. Schema of horizontal section through lower portion of calyx; in infundibulum, m muscle.

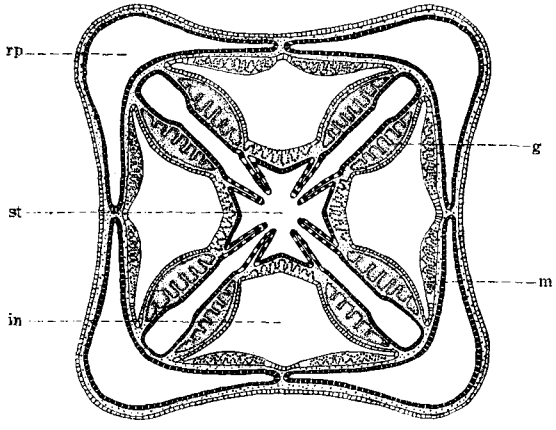

Fig. 9. Schema of horizontal section through middle portion of calyx; g gonad, in infundibulum, m muscle, rp radial pocket, st stomach cavity.

form of an extremely laterally compressed cone, with the apex near the peduncle. The mesogonial pockets extending from the margin downwards are connected in the lower part with the stomach cavity. The endoderm cells demarcating the pockets are higher than any

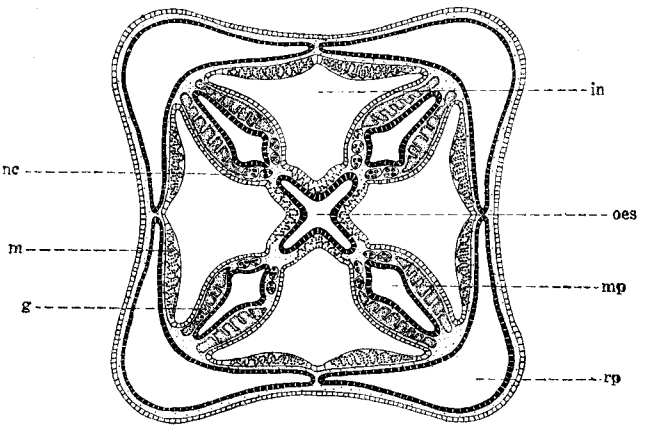

Fig. 10. Schema of horizontal section of calyx much higher than Fig. 9; g gonad, in infundibulum, m muscle, mp mesogonial pocket, nc nematocyst sac, oes oesophagus, rp radial pocket.

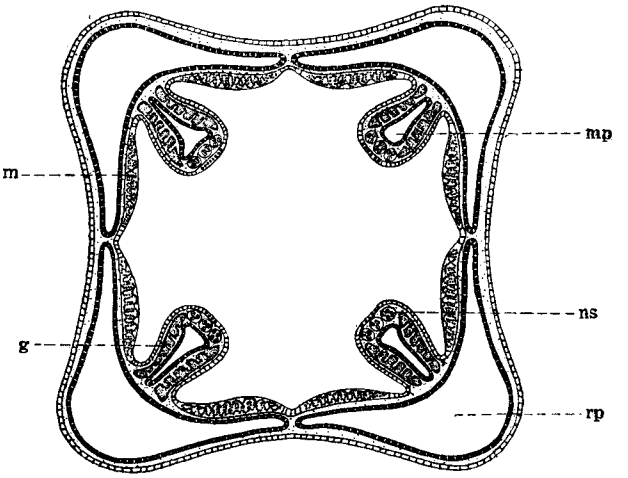

Fig. 11. Schema of horizontal section through upper portion of calyx; g gonad, m muscle, mp mesogonial pocket, ns nematocyst sac, rp radial pocket.

endoderm cell in other places and contain vesiculated cells, granulated gland cells and wedge-shaped gland cells which consist of an elliptical granulated basal part and a narrow distal neck opening into the pockets. The eight longitudinal muscle strands, which unite in the peduncle into four interradial strands, extend laterally in cross section in each adradius, covering almost the whole length of the abaxial mesogloeal wall of the infundibula. A similar type of longitudinal muscles is reported by GROSS (1900) for *Craterolophus tethys* and *Haliclystus octoradiatus*, and by UCHIDA (1929) for *Haliclystus steinegeri* and the medusa here considered.

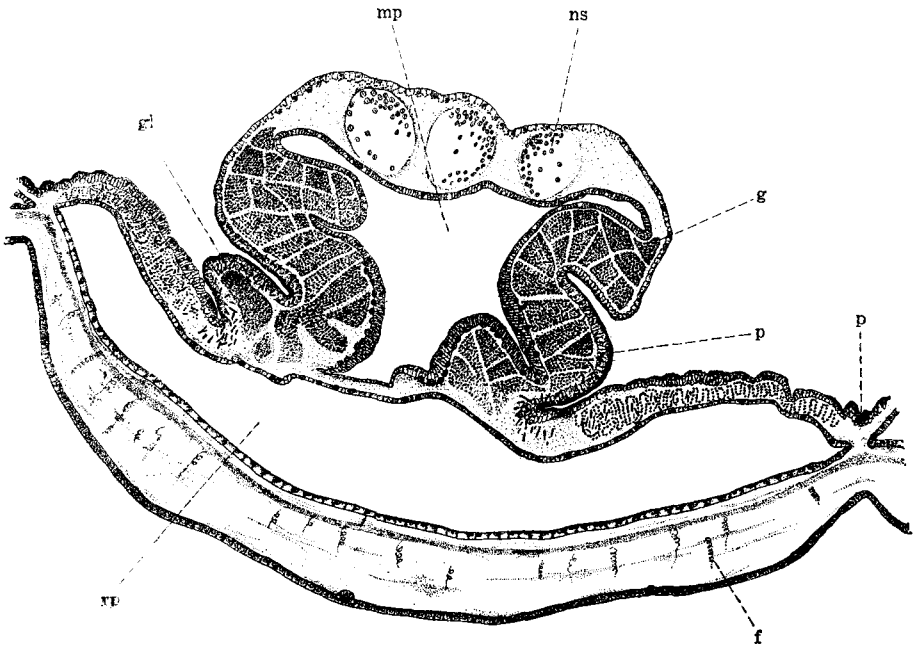

Fig. 12. Horizontal section of a quadrant of calyx. ×167; f fibre, g gonad, gl glutinante, mp mesogonial pocket, ns nematocyst sac, p pigment, rp radial pocket.

The presence of the rod-shaped nematocysts (glutinantes) in the abaxial ectoderm wall of the infundibula is known in *Craterolophus tethys* by GROSS (1900, p. 615), KASSIANOW (1901, p. 309) and LEUSCHEL (1932, p. 369), in *Haliclystus octoradiatus* by WIETRZYKOWSKI (1912,

p. 54) and WEIL (1915, p. 1) and in *Lucernaria quadricornis* by LEUSCHEL (1932, p. 369). *Thaumatoscyphus distinctus* is also provided with numerous glutinantes in the adradial portions (in the perradial portions in the lower part) of the abaxial and the side wall of the infundibula so as to protect the gonads in each adradius. In the endoderm cells, in which the glutinantes are found, are contained abundant pigment granules. The glutinantes are also found imbedded in mesogloea in the neighbourhood of the pigmented areas.

It is generally known that the stalked medusae have many nematocyst sacs (Nesselsack) in the perradial mesogloea of the subumbrella. These nematocyst sacs are arranged in two rows in cross section near the margin, but they are generally arranged in a row, their sizes being censiderably variable. The nematocysts contained in these sacs are all similar and of ovoid type (penetrantes), showing different developmental stages. The process of their metamorphosis agrees with LEUSCHEL's descriptions of *Lucernaria quadricornis*. On the periphery of the nematocyst sacs there are found nematocysts now in the process of metamorphosis, nuclei of ectoderm cells which took part of the nematocyst formation, and irregularly shaped plasmoid masses. The latter two are residia of ectoderm cells used in the formation of the nematocysts. The nematocysts already formed are present in loose aggregation in the nematocyst sacs and some are observed to migrate into both the ectoderm and the endoderm. Contrary to the general opinion that the nematocyst sacs are formed by the process of invagination of the subumbrellar ectoderm cells, LEUSCHEL (1932) recently indicated that they are due to delamination of the latter, giving several actual evidences Though we could not observe the process of the formation of the nematocysts sacs, we have often met with ectodermal cell heaps which are situated above the nematocyst sacs and composed of cylindrical cells somewhat obliquely arranged so as to show the remnant of the delamination (or invagination). Several investigators, such as KEFERSTEIN (1862), KLING (1879) and KASSIANOW (1901) are of the opinion, that the nematocyst sacs are organs for defence as well as attack, and they

are able to escape outside of the sacs by pressure through a narrow slit between the ectodermal cells. According to LEUSCHEL (1932), the opening is not present and the nematocyst sacs are nothing but a place to form ovoid nematocysts. About *Craterolophus tethys* he gave a figure of the "Stiel" in the ectoderm layer, which is situated just above the nematocyst sac. According to him the "Stiel" is represented by ectoderm cells irregularly arranged but there is no

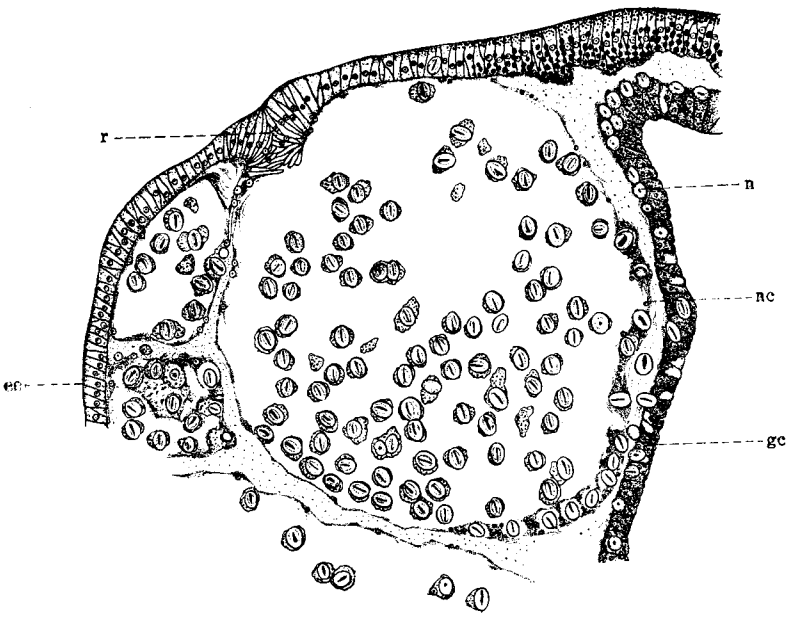

Fig. 13. Horizontal section of nematocyst sacs. ×1000; ec ectoderm, gc gland cell, n nematocyst, nc nucleus of cell took the part of formation of nematocyst r remnant of delamination (or invagination).

opening from the sac leading outside. Judging from LEUSCHEL's descriptions and figures, the "Stiel" seems to correspond to the remnant of the delamination of *Thaumatoscyphus distinctus* above mentioned.

The manubrium, consisting of outer ectoderm, an intermediate mesogloea and inner ectoderm, is furnished with four crisped lips of which cross sections show complicated foldings. The inner ectoderm

cells are mostly glandular and provided with a pyriform vacuole with a deeply stained fleck at its narrow bottom, probably a coagulum. Besides the glandular cells and supporting cells, there are scattered in the ectoderm ovoid nematocyst cells. The outer ectoderm cells are of various heights, all faintly granulated and provided with ill-developed muscle fibres which are often imbedded in the mesogloea. The stomach is cross-shaped in transverse section in the upper portion, but communicates with the mesogonial pockets in the lower part. The gastral filaments are, more or less, long elliptical in cross section, and covered on one side with tall granulated cells well stained by hæmatoxylin and on the other with smaller cubical cells, these two sorts of cells being connected by small polygonal cells arranged in about two rows. There are sparsely distributed ovoid nematocysts between these cells.

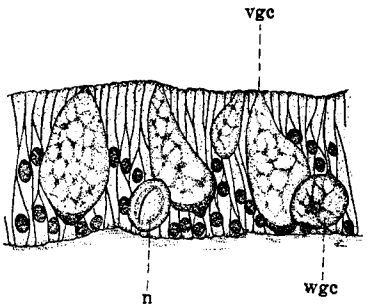

Fig. 14. Horizontal section of lip. ×3333; n nematocyst, vgc vesiculated cell, wgc wedge-shaped cell.

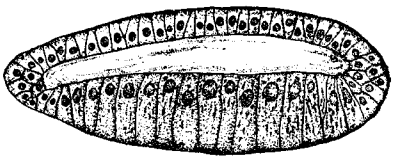
Fig. 15. Cross section of gastral filament. ×3333.

The terminal knobs both of the primary and secondary tentacles are covered with numerous rod-shaped nematocysts closely arranged in a layer and are provided with many slender cells which are glandular and radially arranged in several rows, containing a few rod-shaped nematocysts among them. The ovoid nematocysts are not present. The stem of the secondary tentacles except those standing in the outermost portion is made of similar cubical ectoderm cells, which are provided with muscle fibres arranged in the mesogloea, making many shallow foldings in cross section; the muscle fibres are absent in the portion of the stem imbedded in the jelly. The endoderm cells of the tentacles are considerably larger and

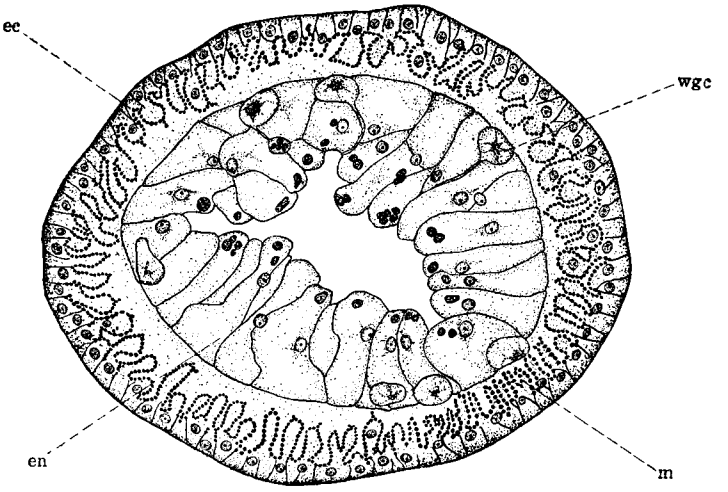

Fig. 16. Cross section of secondary tentacle. ×1667; ec ectoderm, en endoderm, m muscle, wgc wedge-shaped cell.

higher than the ectoderm cells and generally vesicular, each with a nucleus in the middle and several deeply stained granulated bodies at the innermost portion. There are also some wedge-shaped, solitary gland cells with a widened base containing a well-stained coagulum and a slender neck opening into the lumen of the tentacles. The stem of the primary tentacles and a few secondary tentacles situated in the outermost portion, though similar in general to that of the ordinary secondry tentacles in the distal portion, are characterized on the abaxial side by the presence of many ovoid vesicular gland cells, each with a deeply stained fleck at the bottom, and by the absence of muscle fibres. Furthermore, these tentacles have on the abaxial side a covering composed of gland cells with an elliptical vesicle and granulated gland cells arranged in several radial rows. The nematocysts are not found there. On the axial side of these tentacles there is a sensory organ for light which is blackly pigmented and composed of exceedingly narrow cells arranged in a row. Just inside the organ, rod-shaped nematocysts gather in several groups in the jelly. They are probably wandering towards the tentacle knobs.

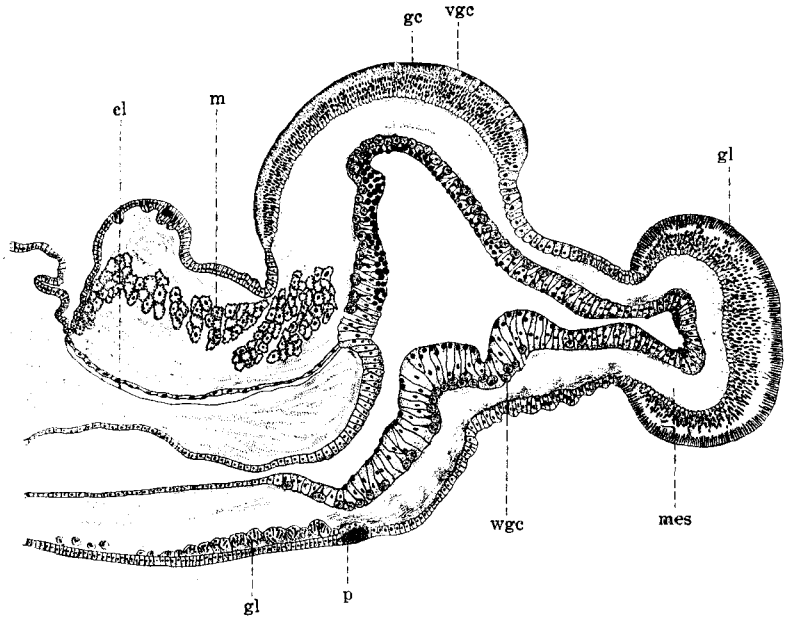

Fig. 17. Sagittal section of primary tentacle. ×333; cl cellular lamella, gc gland cell, gl glutinante, m muscle, mes mesogloea, p pigment, vgc vesiculated gland cell, wgc wedge-shaped gland cell.

Abnormalities. Though the stalked medusae are normally tetramerous and generally provided with four pairs of gonads, four pairs of the secondary tentacle clusters and eight anchors (which are lacking in a few genera), there are several records in regard to their abnormal symmetry. In 1907 BROCH reported a haxamerous stalked medusa under the name of *Stenoscyphus hexaradius*, from a specimen collected on Fosheims Peak. On the basis of its six-rayed structure, KRUMBACH (1925) proposed a new genus *Brochiella* for it. UCHIDA (1929) regarded the medusa as an abnormal specimen of *Thaumatoscyphus* with 6 instead of 4 rays, since the medusa agrees with *Thaumatoscyphus* in several important points, and furthermore he (1928 & 1929) found several hexamerous individuals of *Sasakiella cruciformis* which is normally a tetramerous stalked medusa. The abnormal hexamerous specimens of *S. cruciformis* observed by him were mostly regularly six-sided, but some had arms of unequal

sizes, two of them had two adjacent arms which were smaller than the rest and fused at the base, representing an intermediate form between four-armed and six-armed condition. Among the specimens of *Thaumatoscyphus distinctus* examined by us, five are abnormal as shown in the following table.

Specimen	Number of gonad	Number of anchor	Number of tentacle cluster
A	5 pairs	11	11
B	6 pairs	11	11
C	5 pairs	10	10
D	8 pairs	14	14
E	4 pairs (On account of confusion of two gonads in lower part, there are only 3 pairs of them.)	8	8

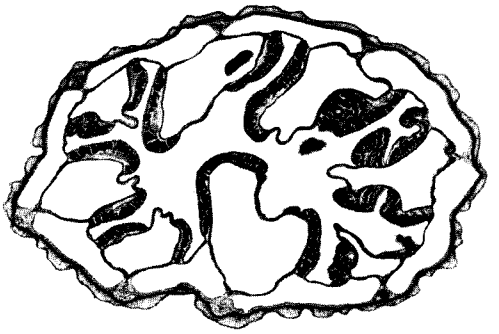

Fig. 18. Horizontal section of calyx of abnormal specimen (D). ×21, YAMAGUCHI photo.

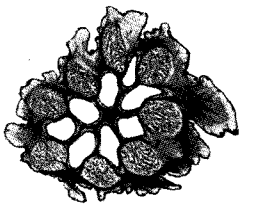

Fig. 19. Horizontal section of peduncle of abnormal specimen (D). ×21, YAMAGUCHI photo.

In these specimens the internal structure agrees with the external one; the number of canals or muscle strands of the peduncle corresponds to that of the pairs of gonads as shown in sections made from the specimen D. Besides these species, UCHIDA examined several individuals of *Haliclystus auricula* collected near the Asamushi Marine Biological Station, which had abnormal numbers of symmetry.

Habits. The medusa is found attached to *Zostera marina* by means of the basal disc, generally with its mouth downwards. The leech-like locomotion is mainly due to the basal disc, the tentacle knobs and the longitudinal muscle strands. The contraction is characteristic; it is always commenced with a coiling movement of the peduncle. The food contained in the stomach cavity is mostly copepods. A known enemy of the medusa is a pycnogonid belonging to the genus *Ammothea* which is abundantly found in Akkeshi Bay. The arachnoid is commonly found as a temporal parasite to the subumbrella of an anthomedusa *Polyorchis karafutoensis*[1] during July-August and also often attacks the stalked medusa. Therefore, we occasionally come across the stalked medusae with a damaged bell margin. In these medusae we can see several small secondary tentacles newly regenerated on the injured part of the bell margin. A similar case is quotted by PRELL (1909, p. 26), who has already reported his observation made in an aquarium for a Norwegian pycnogonid (*Phoxichilidium femoratum*) which devours a stalked medusa (*Lucernaria* sp.[2]).

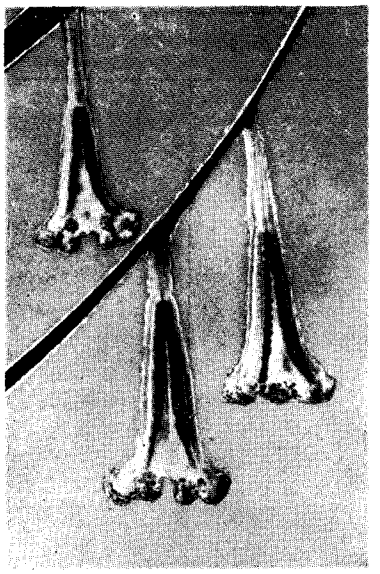

Fig. 20. *Thaumatoscyphus distinctus* KISHINOUYE from life, somewhat enlarged, YAMAGUCHI photo.

Localities. Shimushiri, in the Kurile Islands (KISHINOUYE, 1910); Cape Moshita, North Saghalien (UCHIDA, 1929). As new localities the following two will be reported; off the coast of Honto, South Saghalien (from the specimens given by Mr. S. MAKINO), Akkeshi, Hokkaido.

1) Those collected from the same medusae of North Saghalien are perhaps eligible for the same pycnogonid. Jap. Jour. Zool., vol. 1, p. 89.
2) The medusa is probably referable to the genus *Haliclystus* on account of the presence of anchors.

LITERATURE

1) ANTIPA, G. 1891. Die Lucernariden der Bremer Expedition nach Ostspitzbergen im Jahre 1889. Nebst Anhang über rudimentäre Tentakel bei Lucernariden. Zool. Jahrb. Abt. Syst., Geog. u. Biol. Tiere. Bd. 6, p. 1–20, Taf. 1–2.

2) BROCH, H. 1907. Hydroiden und Medusen. Report of the Second Norwegian Arctic Expedition in the "Fram" 1896-1902. No. 12, p. 1–11, Taf. 1–11.

3) CARLGREN, O. 1930. Die Lucernariden. Further Zoological Results of the Swedish Antarctic Expedition 1901–1903 under the Direction of Dr. OTTO NORDENSKJÖLD, vol. 2, p. 1–18.

4) GROSS, J. 1900. Zur Anatomie der Lucernariden. Jen. Zeit. Naturw., Bd. 33, p. 611-624, Taf. 23-24.

5) KASSIANOW, N. 1901. Studien über das Nervensystem der Lucernariden nebst sonstigen histologischen Beobachtungen über diese Gruppe. Zeit. Wiss. Zool., Bd. 69, p. 1–93, Taf. 22-25.

6) KEFERSTEIN, W. 1862. Untersuchung über niedere Seethiere. Zeit. Wiss. Zool., Bd. 12, p. 1–26, Taf. 1–11.

7) KISHINOUYE, K. 1910. Some medusae of Japanese waters. Jour. Sci. Coll. Tokyo, vol. 27, art. 9, p. 1–35, pl. 1–5.

8) KLING, O. 1879. Ueber *Craterolophus tethys*. Ein Beitrag zur Anatomie und Histologie der Lucernarien. Morph. Jahrb. Bd. 5, p. 141–166.

9) KRUMBACH, T. 1925. Handbuch der Zoologie, Bd. 1, p. 522–576.

10) KRUMBACH, T. 1930. Scyphozoa. Die Tierwelt der Nord- und Ostsee. Bd. 111, Lief. 17, p. d 1–88.

11) LEUSCHEL, H. 1932. Beiträge zur Histologie und Physiologie der Lucernariden. Zool. Jahrb., Bd. 52, p. 338–388, pl. 3–4.

12) MAYER, A. G. 1900. Medusae of the world, vol. 3, p. 499–735, pl. 56–76.

13) PRELL, H. 1909. Beiträge zur Kenntnis der Lebensweise einiger Pantopoden. Bergens Mus. Aarbok, 1909, No. 10, p. 1–30.

14) TASCHENBERG, O. 1877. Anatomie, Histologie und Systematik der Cylicozoa LEUCKART, einer Ordnung der Hydrozoa, p. 1–104, Taf. 1–4.

15) UCHIDA, T. 1928. Short notes on medusae. 1. Medusae with abnormal symmetry. Ann. Zool. Jap., vol. II, p. 373-376.

16) UCHIDA, T. 1929. Studies on the Stauromedusae and Cubomedusae with special reference to their metamorphosis. Jap. Journ. Zool., vol. 2, p. 103–193, pl. 3–5.

17) WEIL, R. 1925. Foyers de formation et voies de migration des nématocystes de *Haliclystus octoradiatus* CLARK. Existence, sur leur parcours, de réservoirs sélectifs. C. R. Acad. Sci. Paris, t. 180, p. 327–330.

18) WIETRZYKOWSKI, W. 1912. Recherches sur le développement des Lucernaires. Arch. Zool. Exp. et Gén. 5e ser., t. 10, p. 1–95, pl. 1–3.