Species of Stauromedusae from Hokkaido, with Notes on Their Metamorphosis

By

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(With 12 Text-figures)

Of seven species of Stauromedusae ever reported from Japan, the following six species are known from Hokkaido: *Haliclystus auricula* (Rathke 1806), *H. borealis* Uchida 1933, *H. steinegeri* Kishinouye 1899, *Stenoscyphus inabai* (Kishinouye 1893), *Sasakiella cruciformis* Okubo 1917, and *Thaumatoscyphus distinctus* Kishinouye 1910. Remaining one species, *Kishinouyea nagatensis* is distributed in the warm-temperate region of Japanese waters, but has not been recorded from Hokkaido. In adjacent waters of Hokkaido, an additional species, *Octomanus monstrosus* was reported by Naumov (1961). Naumov established a new species, *Thaumatoscyphus uchidai* from Bering Strait, Kurile Islands and Hokkaido, for the species *T. distinctus* described by Uchida (1929) and Uchida and Hanaoka (1933). As accurate discrimination between these species could not be made in the present study, the species name *T. distinctus* by Uchida was followed below. In this paper the author describes six species found in Hokkaido and gives some notes on their early metamorphosis.

A seaweed, *Sargassum confusum* Agardh, on which Stauromedusae tightly attached was collected and preserved in 5% formalin solution after anesthetization for medusae with 1% $MgCl_2$ for about five minutes. In the solution each plant was shaken enough to release the animals from it. Many specimens of various stages and sizes were collected from the solution, and detailed observations were made on those preserved specimens. Many observations of successive developmental stages made the identification of the specimens of even very small size possible. Some developmental stages of each species were shown up to the stage which reveals the discriminative characters of the species.

Descriptions were mainly based on the specimens collected from Oshoro (for *Haliclystus auricula*, *Stenoscyphus inabai* and *Sasakiella cruciformis*) and those from Muroran (for *H. borealis*, *H. steinegeri* and *Thaumatoscyphus distinctus*).

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Discussions on the distribution of the species in Hokkaido will be treated in another paper.

Haliclystus auricula (Rathke 1806)

(Fig. 1, A-C)

Lucernaria auricula Rathke, 1806, p. 35.
Lucernaria octoradiata Lamarck, 1816, p. 474
Haliclystus auricula Clark, 1863, p. 559. — Mayer, 1910, p. 532, text-fig. 339. — Uchida, 1929, p. 113, Pl. 3, figs. 4, 6, text-figs, 9-27. — Kramp, 1961, p. 292.
Haliclystus octoradiatus Clark, 1863, p. 565. — Mayer, 1910, p. 534. — Ranson, 1945, p. 313.
Haliclystus tenuis Kishinouye, 1910, p. 4. Pl. 1, fig. 3.
Haliclystus sanjuanensis Hyman, 1940, p. 292, fig. 8.

Calyx conical to pyramidal, about as high as wide or somewhat lower. Exumbrella finely granulated with nematocysts. Margin of the bell produced into eight adradial arms, each with a tentacle cluster at the tip. The four perradial clefts between the arms are deeper than the four interradial ones. Each tentacle cluster consisting of about 20-40 tentacles with globular head. The base of each tentacle cluster provided with one U-shaped projection in the radial

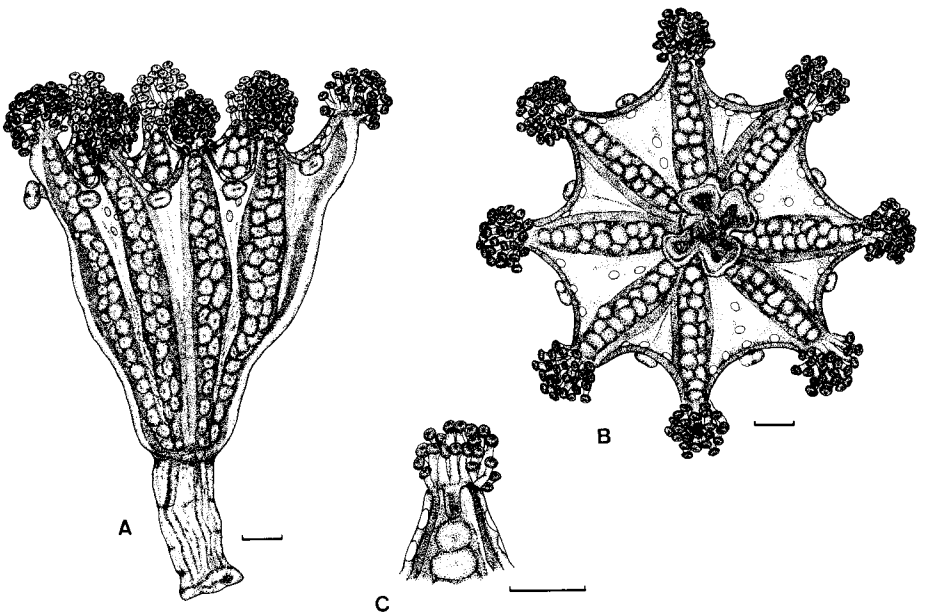

Fig. 1. *Haliclystus auricula*. (A), side view; (B), oral view; (C), the tip of arm. Bars represent 1 mm.

pocket (Fig. 1, C). The eight marginal anchors, perradial and interradial, kidney-shaped, the perradial ones being situated at a lower level than the interradial. Subumbrella generally smooth. Manubrium short, four-sided. Numerous gastric filaments along the wall of medial opening of radial pockets from the base of interradial mesogloeal partitions. White spots involving nematocysts prominent along the margin of the calyx, more numerous in the perradii than in the interradii. A few white spots also in the inner subumbrella of the perradii. Gonads in four interradial pairs, extending from the pyloric end of the umbrella to the end of the arms, each consisting of about 30-50 vesicles. Coronal muscles eight, separated in the adradii. Interradial muscles extending from the peduncle upwards to the calyx, bifurcating at the middle of the length of the calyx, and extending to the tip of the arms. Peduncle four-chambered.
Locality: Oshoro, Obira, Wakkanai, Esashi (Kitami), Abashiri.
Distribution: Europe, Greenland, North America, China, Japan.

Early metamorphosis (Fig. 2, A-C)

The youngest stage observed was about 0.5 mm in length of the calyx, with eight primary tentacles and eight secondary tentacles (Fig. 2, A). The adradial arms were not present. Metamorphosis of anchors occurred in both perradial and interradial primary tentacles. The interradial anchors were so small that these were barely observed. Peduncle was single-chambered.

In the next stage, with the calyx about 0.7 mm long, the second or the third adradial tentacles appeared (Fig. 2, B). The interradial anchors became rather prominent but was still much smaller than the perradial. Four white spots of nematocysts appeared, one in each perradius. The cavity of the peduncle was divided into four chambers near the base.

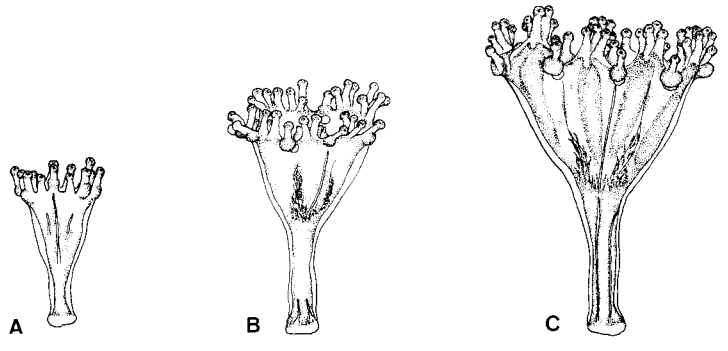

Fig. 2. *Haliclystus auricula*. Early metamorphosis. (A), juvenile with a secondary tentacle in each adradius ; (B), ditto with two or three secondary tentacles in each adradius ; (C), ditto with four or five secondary tentacles in each adradius. Bar represents 0.5 mm.

When the calyx attained about 1.3 mm long, eight arms were formed (Fig. 2, C). Secondary tentacles increased in number to four or five in each adradius. The anchors were larger in the perradii than in the interradii. Four white spots newly appeared, one in each interradius. U-shaped projections in the radial pockets were observed at the base of tentacle clusters. Until this stage, eight rudiments of gonads appeared in adradii. The cavity of the peduncle was completely divided into four chambers.

Remarks

Since Mayer (1910) regarded *Haliclystus tenuis* Kishinouye 1910, as a form of *H. auricula*, this species have been recorded from various localities of Japanese waters and described by Uchida (1927, 1929, 1954). On its morphology of adult, the author has nothing to add to what is already known to date, except for the U-shaped projection at the base of tentacle cluster. This characteristic can be recognized even in rather small specimens and are very useful for discrimination.

Japanese form of *H. auricula* is peculiar in the gonad structure; each gonad consists of several tens of vesicles arranged in only two rows. While each gonad consists of more than one hundred of vesicles in six to eight rows in *H. auricula* originally described (Rathke, 1806; Clark, 1863). Japanese form of *H. auricula* resembles *Haliclystus octoradiatus* (Montagu, 1808) in gonad structure and the number of tentacles, but differs in the proportion of the calyx, situation of eight arms and the shape of anchor. *H. octoradiatus* was regarded as a synonym of *H. auricula* by Kramp (1961). It is thus considered that there are wide variations of morphology in *H. auricula* which is widely distributed in northern hemisphere.

The present observation of metamorphosis of *H. auricula* is on the whole similar to that of *H. octoradiatus* (=*H. auricula*) reported by Wietrzykowski (1912). But the pattern of white spots' appearance is different. According to Wietrzykowski, eight spots appeared at the same time, one in each adradius. The pattern of white spots' appearance resembles that described by Uchida (1929), but differs in the number of spots. The present author mainly gives attention to the increase of adradial tentacles, metamorphosis of primary tentacles and appearance of white spots.

Haliclystus borealis Uchida 1933

(Fig. 3)

Haliclystus borealis Uchida, 1933, pp. 450-452, fig. 1. — Kramp, 1961, p. 293. — Naumov, 1961, p. 81 figs. 32, 57.

Calyx quadropyramidal, somewhat higher than wide. Exumbrella finely granulated with nematocysts. Margin of the bell produced into eight adradial arms, each with a tentacle cluster at the tip. The four perradial clefts between

the arms slightly wider than the four interradial ones. Each tentacle cluster consists of about 20-30 tentacles with globular head. The base of each tentacle cluster provided with one U-shaped projection in the radial pocket. The eight marginal anchors, perradial and interradial, provided each with a round cushion-like disc, each of which is provided with a longitudinal furrow in the central portion. Subumbrella smooth. Manubrium four-sided. Gastric filaments numerous and in eight rows on the medial opening of radial pockets. White spots arranged on the margin, not on the inner subumbrella. Gonads in four interradial pairs, extending from just below the bell margin barely to the point of the junction of the calyx with the peduncle, consisting of about 30-100 vesicles. Four interradial white stripes or white flecks of various shapes and sizes generally prominent. These stripes or flecks composed of filamentous structures of unknown function. Some individuals with neither white stripes nor white flecks. Peduncle four-chambered.

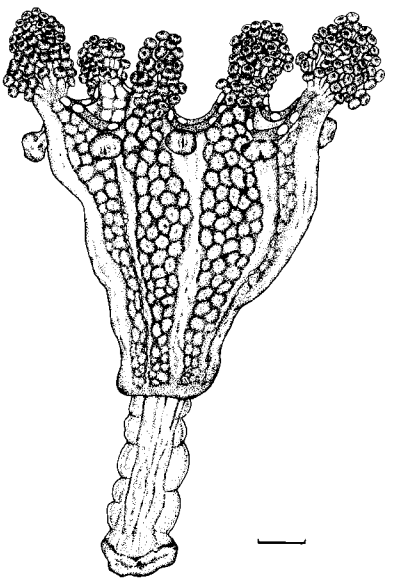

Fig. 3. *Haliclystus borealis*. Side view. Bar represents 1 mm.

Locality: Wakkanai, Esashi (Kitami), Abashiri, Kushiro, Erimo, Muroran.
Distribution: Japan, Kurile Islands.

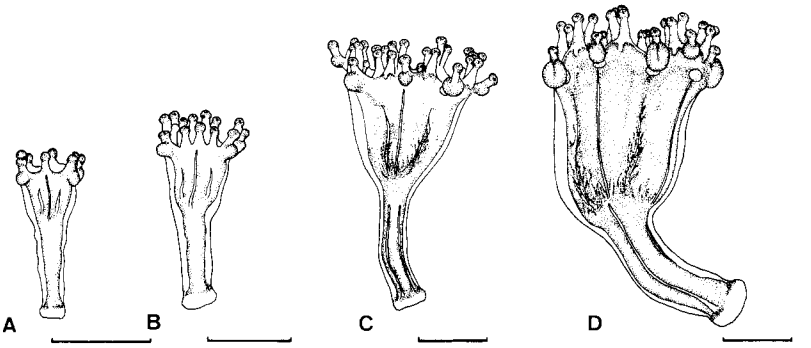

Fig. 4. *Haliclystus borealis*. Early metamorphosis. (A), juvenile with only eight primary tentacles; (B), ditto with one secondary tentacle in each adradius; (C), ditto with two or three secondary tentacles in each adradius; (D), ditto with four or five secondary tentacles in each adradius. Bars represent 0.5 mm.

Early metamorphosis (Fig. 4, A-D)

The youngest stage observed was about 0.3 mm in the length of the calyx and had eight primary tentacles only (Fig. 4, A). The four perradial tentacles were undergoing metamorphosis and had an anchor on the dorsal side near the base, while the interradial four tentacles did not show any change.

In the next stage, with the calyx about 0.5 mm long, the first adradial tentacles appeared (Fig. 4, B). Anchors were rather large and prominent in the perradii, while they were not yet found in the interradii. Peduncle contained still only one chamber.

When the calyx was about 1.0 mm long, eight adradial arms, each with two or three secondary tentacles, were formed (Fig. 4, C). Four anchors newly developed on interradial tentacles, which were much smaller than the perradial. Four white spots appeared, one in each perradius. The cavity of the peduncle was almost divided into four.

When the calyx was about 1.4 mm long, white spots appeared in four interradii (Fig. 4, D). The secondary tentacles were four or five in each adradius. Perradial anchors slightly shifted downwards so that they lay at a lower level than the interradial. U-shaped projections in radial pockets were conspicuous at the base of each tentacle cluster. Peduncle was four-chambered.

Remarks

The species also possesses a U-shaped projection at the base of each tentacle cluster like *H. auricula*. *H. borealis* and *H. auricula* are similar to each other not only in this character but also in other aspects, such as the shape of calyx and the appearance of gonad. Previously *H. borealis* was thought to be distinguished from *H. auricula* by the usual occurrence of the four interradial white stripes. But present study with many samplings at various localities revealed that many individuals of *H. borealis* did not have four interradial white stripes and that these stripes were sometimes deformed to white flecks which were radially arranged as four interradial rows or scattered here and there. Then the white stripes can not be an effective discriminative character of *H. borealis*. Living individuals of *H. borealis* can be distinguished by the shape of anchor, but identification is somewhat difficult in preserved specimens, for the shape of anchor is more or less deformed. The number of white spots which are packed with nematocysts is smaller in *H. borealis* than in *H. auricula*. The larger number of white spots in *H. auricula* occurs conspicuously in the perradii, where white spots are found not only at the margin of the umbrella but also on the middle portion of the subumbrellar octant (Fig. 1, B). In *H. borealis*, white spots are found only in the marginal portion of the umbrella. Whether there are a few white spots on the middle portion of perradial octant or not would be crucial to distinguish *H. borealis* from *H. auricula*. This feature is useful for the medusae larger than 3 mm length in calyx, for white spots are prominent enough even in preserved

specimens.

The metamorphosis of *H. borealis* is also similar to that of *H. auricula*. The metamorphosing condition of primary tentacles was, however, slightly different between the two species. The difference of the size of anchors between the perradii and the interradii was more conspicuous in *H. borealis* than in *H. auricula*.

Haliclystus steinegeri Kishinouye 1899

(Fig. 5, A-B)

Haliclystus steinegeri Kishinouye, 1899, p. 126, figs. 1-3. — Mayer, 1910, p. 535, text-fig. 340. — Bigelow, 1920, p. 12, Pl. 2, fig. 4. — Uchida, 1929, p. 125, figs. 28-34. — Kramp, 1961, p. 294.

Calyx conical, rather wider than high. Exumbrella beset with sparsely scattered nematocyst clusters. Eight adradial arms 45° apart, with comparatively shallow notches as deep and broad in the interradii as in the perradii. Each arm

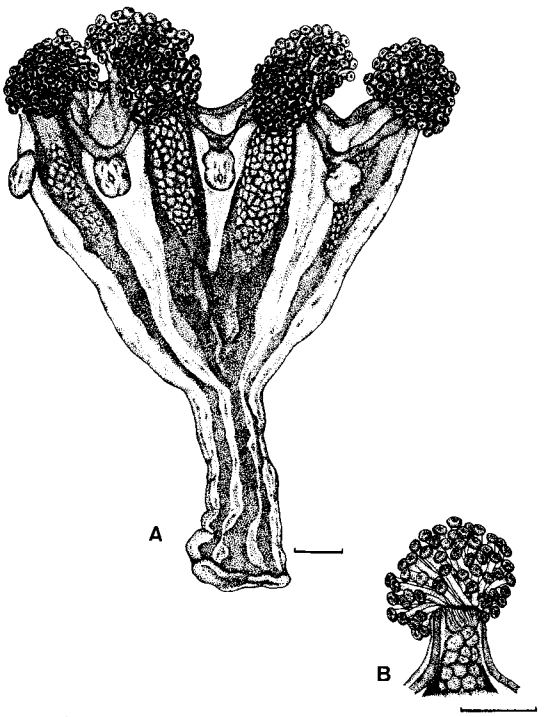

Fig. 5. *Haliclystus steinegeri*. (A), side view; (B), the tip of arm. Bars represent 1 mm.

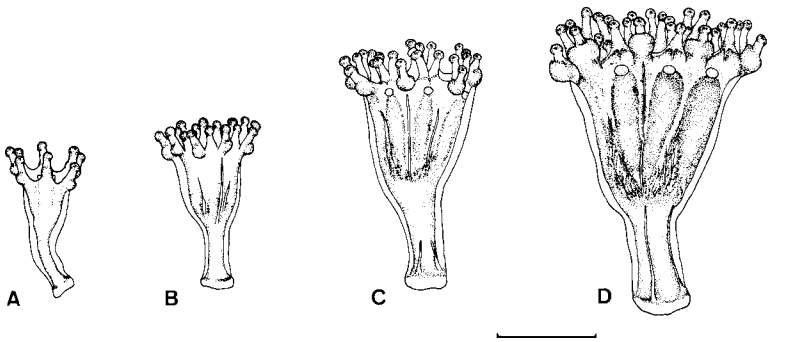

Fig. 6. *Haliclystus steinegeri*. Early metamorphosis. (A), juvenile with only eight primary tentacles; (B), ditto with one secondary tentacle in each adradius; (C), ditto with two or three secondary tentacles in each adradius; (D), ditto with three or four secondary tentacles in each adradius. Bar represents 0.5 mm.

with a terminal cluster of about 70-190 tentacles with a globular knob. The base of each tentacle cluster provided with several pleats in the radial pocket (Fig. 5, B). The eight marginal anchors in the perradii and interradii comparatively large and a little higher than wide, having a small protuberance at the upper portion. Subumbrella smooth. Manubrium four-sided. Gastric filaments numerous and arranged in eight rows on the wall of medial openings. White spots few, along the gonads near bell margin in the perradii. Generally no white spots in the interradii, rarely one in each interradius. Gonads eight in number, one in each adradius, extending from the arms to the base of the stomach, widened at the middle portion, connected two by two in the perradii along the proximal half of their length but completely separated in the interradii. Each gonad consisting of about 90-240, comparatively small vesicles. Peduncle four-chambered and the basal disc expanded and nearly quadrate, with four round edges and four perradial constrictions.

Locality: Oshoro, Obira, Wakkanai, Esashi (Kitami), Abashiri, Kushiro, Erimo, Muroran.

Distribution: Commander Islands, Alaska, Sakhalin, Japan.

Early metamorphosis (Fig. 6, A-D)

The youngest stage observed was about 0.3 mm in the length of the calyx and had eight primary tentacles only (Fig. 6, A). The eight adradial arms were absent and the outline was octagonal in oral view. Both perradial and interradial primary tentacles were undergoing metamorphosis. The interradial anchors were very small.

When the calyx was about 0.4 mm long (Fig. 6, B), the first adradial tentacles appeared. Peduncle was still single-chambered.

In the next stage, with the calyx about 0.7 mm long, the second or the third

adradial tentacles appeared (Fig. 6, C). The interradial anchors became larger but were a little smaller than the perradial. Until this stage, rudiments of gonads had already appeared in eight adradii. A white spot was found at the uppermost part of each rudiment. The lower portion of the peduncle contained four chambers.

When the calyx was about 1.0 mm long, eight arms appeared (Fig. 6, D). The secondary tentacles were three or four in each adradius. Eight anchors were almost the same in size. At the base of each tentacle cluster there was a pleat, which would increase in number with growth. Medusae with the calyx of 1.3 mm length had two pleats at each base. Peduncle was four-chambered.

Remarks

Among three species of *Haliclystus* reported from Japan, *H. steinegeri* can be easily distinguished from others in the shape of anchor which is oval and provided with a small protuberance at the upper portion. The funnel-shaped body and the appearance of gonad composed of numerous small vesicles are also characteristic of *H. steinegeri*. These chracteristics are less distinct in younger stage when metamorphosis of anchor from primary tentacle is undergoing. In such a case, the useful feature on the basal structure of tentacle cluster is given; *H. steinegeri* is provided with some pleats of exumbrella in the radial pocket. The number of the pleats becomes larger with growth.

H. steinegeri strongly shows octomerous in symmetry in the morphology of the calyx. Eight arms are 45° apart, the perradial and interradial notches are equally deep and broad. *Haliclystus salpinx*, *H. antarcticus*, *H. kerguelensis* also indicate octomerous in symmetry. These three species resemble *H. steinegeri* in the shape of anchor, but differ in the proportions of the body portions. The number of tentacles or that of vesicles in gonads are also different among the species.

The metamorphosis of *H. steinegeri* is somewhat different from that of *H. auricula* and *H. borealis*. The metamorphosis of primary tentacle almost equally progressed in perradii and interradii. Eight white spots appeared at the first time, one in each adradius, in contrast with four, one in each perradius in *H. auricula* and *H. borealis*.

Stenoscyphus inabai (Kishinouye 1893)

(Fig. 7, A-C)

Depastrum inabai Kishinouye, 1893, p. 416.

Stenoscyphus inabai Kishinouye, 1902, p. 2, Pl. 1, figs. 1-2. — Mayer, 1910, p. 525, text-fig. 334. — Uchida, 1929, p. 107, Pl. 3, figs. 1, 2, text-figs. 1-8. — Ling, 1939, p. 282, figs. 1-4. — Kramp, 1961, p. 296.

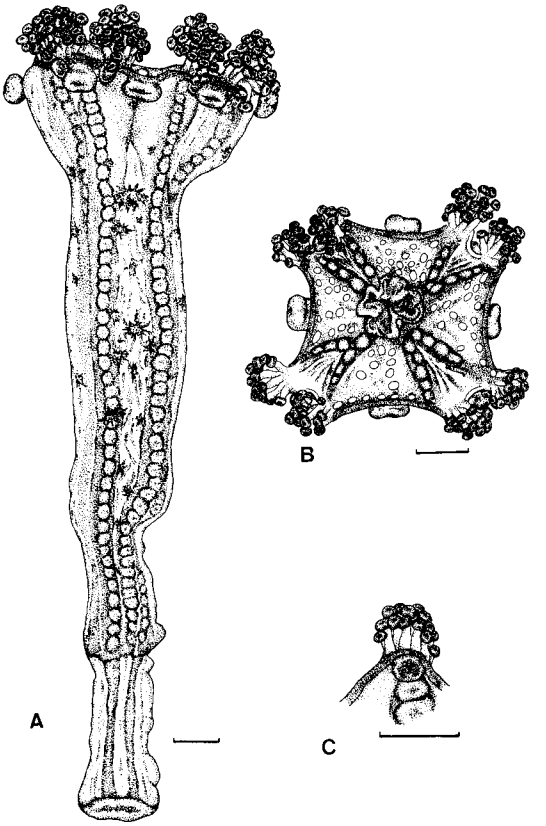

Fig. 7. *Stenoscyphus inabai*. (A), side view; (B), oral view; (C), the tip of arm. Bars represent 1 mm.

Calyx elongate and nearly quadropyramidal, gradually narrowing and terminating with a short peduncle. The margin nearly quadrate, with four wide perradial clefts and as many narrow interradial ones. Exumbrella granulated with nematocysts. Eight anchors, kidney-shaped, situated one in each perradius and interradius, the perradial ones lying at a lower level than the interradial. The secondary tentacles short, knobbed and grouped in eight adradial bunches close to the interradial anchors. The number of the tentacles about 10-20 in each bunch. The base of each bunch provided with a round projection in the radial pocket (Fig. 7, C). Subumbrella smooth, but bearing numerous white spots, only in the perradii. Numerous gastric filaments on the wall of medial openings, as two rows in each interradius. Gonads in four pairs of longitudinal rows, one in each interradius, extending from near bell margin to the base of the stomach cavity. The paired interradial rows united below but divided into two at the

junction point of the buccal and stomach cavity. Coronal muscle entire and well developed. Four interradial longitudinal muscles divided aborally into two from the junction point of the buccal and stomach cavity reaching to the root of the adradial tentacles. White flecks which are composed of filamentous structures distributed here and there on the exumbrella. These flecks variable in size and shape, some being small spots and others like melting snow-crystals. Some individuals without white flecks. Peduncle nearly rounded but somewhat quadrate in cross section, and four-chambered. The adhesive disc widened and almost round in outline.
Locality: Oshoro, Obira.
Distribution: Japan, China.

Early metamorphosis (Fig. 8, A-C)

The youngest stage observed was about 0.5 mm in the length of the calyx and had eight primary tentacles and eight secondary tentacles (Fig. 8, A). Metamorphosis of anchors occurred in both perradial and interradial tentacles. The interradial anchors were so small that were barely observed. Peduncle was single-chambered.

In the next stage, with the calyx about 0.8 mm long, the second or the third adradial tentacles appeared (Fig. 8, B). Of the eight metamorphosing tentacles, the four perradial ones were highly metamorphosed; the primary tentacle heads becoming smaller than the anchor newly developed. But in the four interradial tentacles the heads were comparatively large and newly developed anchors were not so advanced. Four white spots appeared, one in each perradius. The cavity of the peduncle was divided into four chambers in the lower portion.

When the calyx was about 1.1 mm long, primary tentacles completed their metamorphosis (Fig. 8, C). Four perradial anchors shifted downwards to lie at a lower level than the interradial. Eight tentacle bunches, each with four or five

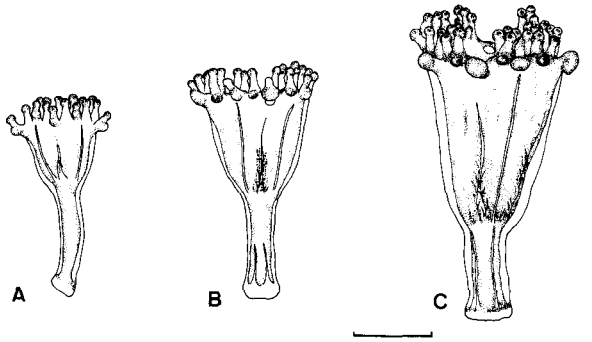

Fig. 8. *Stenoscyphus inabai*. Early metamorphosis. (A), juvenile with one secondary tentacle in each adradius; (B), ditto with two or three secondary tentacles in each adradius; (C), ditto with four or five secondary tentacles in each adradius. Bar represents 0.5 mm.

tentacles were arranged in four pairs in the interradii. The base of tentacle bunches appeared to be rounded in shape. The cavity of the peduncle was completely divided into four chambers.

Remarks

The species is the single representative of genus *Stenoscyphus*. Although the genus stands very close to genus *Haliclystus*, the character of the coronal muscle is mainly different; entire in the former and divided in the latter. *St. inabai* can be also distinguished from *Haliclystus* spp. in other characteristics, such as the conspicuously slender shape of calyx, the size difference of between perradial and interradial notches and the appearance of gonad of which vesicles are arranged in a row. Base of tentacle cluster is provided a round projection in the radial pocket (Fig. 7. C). Oval ring described by Ling (1939) is thought to be the round projection. This oval ring or round projection is remarkable characteristic of *St. inabai*.

The metamorphosis of *St. inabai* is similar to that of *H. auricula* in younger stages. But difference becomes gradually apparent in the metamorphosing primary tentacle. The metamorphosis of primary tentacle progressed rather rapidly in *St. inabai*. and was almost completed until the third secondary tentacle appeared at each adradial bunch. The earlier completion of metamorphosis of primary tentacle seems to be one of the most remarkable characteristics in *St. inabai*.

Sasakiella cruciformis Okubo 1917

(Fig. 9)

Sasakiella cruciformis Okubo, 1917, p. 317, figs. 1, 2. — Uchida, 1929, p. 140, Pl. 3, figs. 3, 5, Pls. 4, 5, text-figs. 46-58. — Ling, 1937, p. 16, figs. 8-19. — Kramp, 1961, p. 298.

Calyx with four interradial arms, each subdivided at the tip into two, bringing about a nearly cruciform shape. Exumbrella dotted with nematocyst clusters of various sizes. Eight primary tentacles, four in the perradii and four in the interradii, tapering each with a flat disc packed with nematocysts and a small white disc at the middle of its length. The four perradial tentacles longer than the interradial. The interradial arms divided each into two short arms with 10-20 secondary tentacles with globular knob. Subumbrella smooth with four interradial broad furrows extending from the base of the manubrium to the tip of the interradial ridges. Manubrium four-sided, its perradial ridges being continuous with those of the subumbrella. Gastric filaments forming groups in each interradius, close to the mouth, at the base of mesogloeal partitions. White spots numerous, especially abundant in the perradii and few on the marginal part of the interradii. Gonads in eight adradial rows of 9-12 vesicles, each extending from

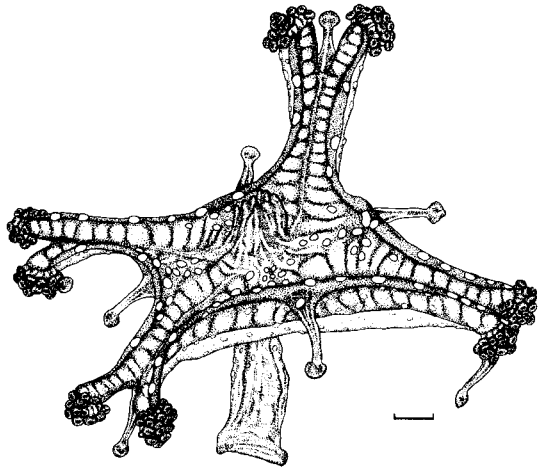

Fig. 9. *Sasakiella cruciformis*. Oblique side view. Bar represents 1 mm.

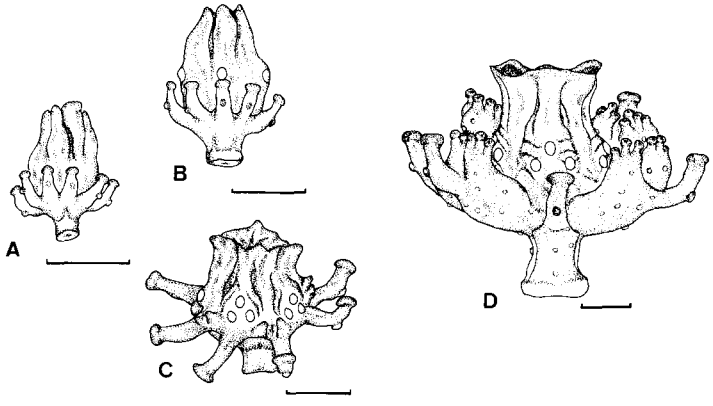

Fig. 10. *Sasakiella cruciformis*. Early metamorphosis. (A), juvenile with only eight primary tentacles ; (B), ditto with one white spot on the manubrium in each perradius ; (C), ditto with a pair of swellings at the base of manubrium ; (D), ditto with three secondary tentacles at the tip of each arm. Bars represent 0.5 mm.

the base of the manubrium to the tip of the arms. Coronal muscle divided into eight. Radial muscles four in number, bifurcated near the margin.
Locality; Oshoro, Obira, Muroran.
Distribution: Japan, China.

Early metamorphosis (Fig. 10, A-D)

The youngest stage observed was about 0.8 mm high (Fig. 10, A). The shape of the body was very particular and could be easily distinguished from other

species. The mouth was naked and very large. Around the mouth there were eight primary tentacles whose aboral side was provided with a small disc.

When the medusa was about 1.1 mm high, four white spots appeared on the manubrium, one in each perradius (Fig. 10, B).

In the next stage, with the body about 1.5 mm high, the formation of four interradial arms occurred (Fig. 10, C). The base of the manubrium exserted in the interradii, forming a pair of swellings, which had each one small disc at the tip. The perradial white spots increased to three in number.

When the medusa was about 2.5 mm high, formation of interradial pairs of arms advanced (Fig. 10, D). Calyx presented a cruciform shape. Each arm was provided with three secondary tentacles at the tip. Many nematocyst clusters were scattered on the exumbrella.

Remarks

The species can be easily distinguished from others in the unique shape of calyx and eight perradial and interradial primary tentacles which do not metamorphose into anchors. As to genus *Sasakiella*, two species, *Sa. cruciformis* and *Sa. tsingtaoensis* have been known. These two species are very similar to each other, only different in the number of remaining primary tentacles. *Sa. tsingtaoensis* has four perradial tentacles but no interradial tentacles or traces of them (Ling, 1937). Genus *Kishinouyea* is closely related to *Sasakiella*, but differs in lacking primary tentacles or anchors. *Sasakiella* and *Kishinouyea* indicate strikingly tetramerous symmetry in the flat and cruciform body shape which is not found in any other genera.

The metamorphosis of *Sa. cruciformis* is most peculiar among six species in the present paper. The youngest juvenile had large naked mouth and primary tentacles but no umbrella. Four arms were formed by exsertion of the base of manubrium. White spots appeared on the manubrium in younger stages. These are the most remarkable points in the metamorphosis of *Sa. cruciformis*.

Thaumatoscyphus distinctus Kishinouye 1910

(Fig. 11)

Thaumatoscyphus distinctus Kishinouye, 1910, p. 2, Pl. 1, figs. 1, 2. — Mayer, 1910, p. 727. — Uchida & Hanaoka, 1933, pp. 135-153, figs. 1-20. — Kramp, 1961, p. 302. — Naumov, 1961, p. 94 figs. 32, 67, 72.

Thaumatoscyphus uchidai Naumov, 1961, p. 91, figs. 32, 67-70

Body goblet-shaped. Calyx higher than wide, almost quadrate in cross section, narrowing towards the proximal portion. Exumbrella beset with sparsely scattered nematocyst clusters. The umbrella margin divided into eight short adradial arms, making four pairs with respect to the perradii, separated by

exceedingly shallow marginal clefts. Each arm with a terminal cluster of about 20-30 tentacles, the outer three tentacles accompanied by a shield-like covering. The primary tentacles considerably modified and similar to the outermost secondary tentacles just mentioned, with a globular head and around a shield-like covering. The axial base of each primary tentacle provided with a black spot. An undivided band of coronal muscle just outside the tentacle clusters and the primary tentacles along the bell margin, causing a high ridge. Subumbrella smooth. Manubrium four-sided. The gastric cavity divided into four radial and four mesogonial pockets. The openings to the mesogonial pockets rather large but these to radial pockets very small passages. The gastric filaments numerous, arranged in four pairs of perradial rows on the wall of medial openings. Each perradius with a bag-like swelling sprinkled with numerous white spots of nematocysts. The gonads contained in these swellings, laterally folded about 15-25 times, making

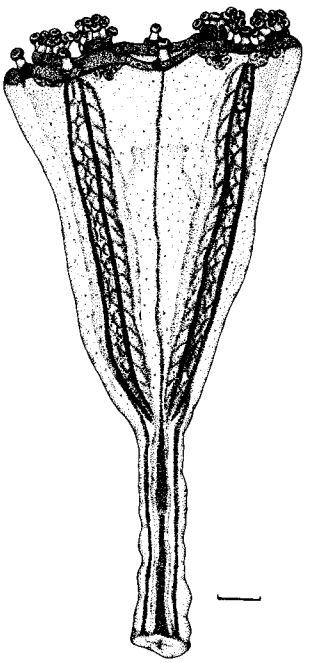

Fig. 11. *Thaumatoscyphus distinctus* Side view. Bar represents 1 mm.

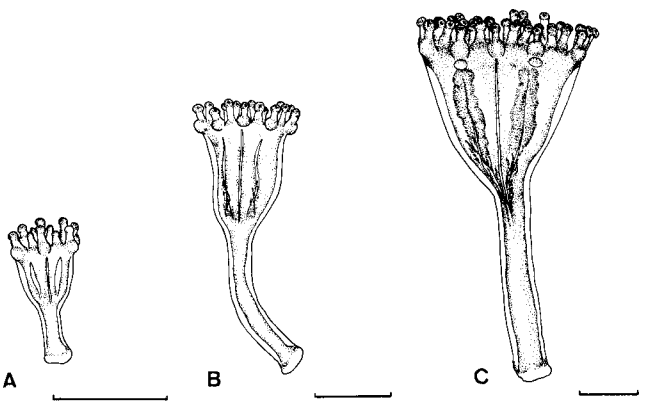

Fig. 12. *Thaumatoscyphus distinctus*. Early metamorphosis. (A), juvenile with one secondary tentacle in each adradius; (B), ditto with two or three secondary tentacles in each adradius; (C), ditto with four or five secondary tentacles in each adradius. Bars represent 0.5 mm.

four paired rows, extending from the perradial portions of the bell margin to the base of the bell cavity. Four perradial pairs of pigment stripes running corresponding to the rows of the gonads. The cavity of the peduncle divided near the calyx into the four perradial chambers.
Locality: Wakkanai, Abashiri, Akkeshi, Samani, Muroran.
Distribution: Japan, Sakhalin, Kurile Islands.

Early metamorphosis (Fig. 12, A-C)

The youngest stage observed was about 0.3 mm in the length of the calyx and had eight primary tentacles and eight secondary tentacles (Fig. 12, A). Eight primary tentacles were undergoing metamorphosis in almost equal degree in both perradial and interradial tentacles.

In the next stage, with the calyx about 0.7 mm long, the second or the third adradial tentacles appeared (Fig. 12, B). Eight anchors were almost the same in size.

When the calyx was about 1.1 mm long, four white spots appeared, one in each perradius (Fig. 12, C). Secondary tentacles increased to four or five in each tentacle cluster. The outermost tentacle of each cluster had a shield-like covering at the base. Eight rudimentary gonads were wavy and arranged in four paired perradial rows. Four chambers appeared only near the calyx.

Remarks

Naumov (1961) established a new species, *Thaumatoscyphus uchidai*, and he regarded that *T. distinctus* (Uchida, 1929; Uchida & Hanaoka, 1933) was as a synonym of *T. uchidai*. Naumov distinguished these *T. uchidai* from *T. distinctus* described by Kishinouye (1910) in some respects, such as arrangement of arms, relative length of peduncle and the size of primary tentacles. These characters, however, easily differ with condition of preservation or growth stages. Further, description of Uchida (1929) was agreed with that of Kishinouye (1910) in some of respects noticed by Naumov. Accurate discrimination should be held till more observations of specimens of various sizes will be conducted.

The metamorphosis of *T. distinctus* is externally similar to *Haliclystus* spp. Few differences are noticed in rather equally progressing metamorphosis of primary tentacle and the peduncle remaining to be single-chambered till rather older stages. The process of formation of mesogonial pockets could not be elucidated in the present study.

Discussion

Clark (1863) divided the order Stauromedusae into two families, Cleistocarpidae and Eleutherocarpidae, laying stress on the presence or absence of four perradial mesogonial pockets. After that some families were proposed, two of which being concerned for Japanese species. In consideration of the shape of

calyx margin, either cleft or uncleft, Kishinouye (1902) erected Stenoscyphidae for *Stenoscyphus inabai*. Later his family was abandoned by Uchida (1929), who mentioned that *Stenoscyphus* was similar to *Haliclystus* and differed only in the number of symmetry planes. Instead he separated *Kishinouyea* and *Sasakiella* from the rest of Eleutherocarpidae and proposed a new family, Kishinouyeidae for them. This proposal was revised by Carlgren (1935) who reduced the family to the subfamily, Kishinouyeinea, and included the genus *Lucernariopsis* in this subfamily. Although a disagreement was given by Thiele (1936), the classification proposed by Carlgren has been customarily used. The present author discusses here two respects on the taxonomy of the species treated in this study; one concerns the closer relationship between *Haliclystus* and *Stenoscyphus* and the other concerns the systematic position of *Sa. cruciformis*.

Comparison of successive changes in metamorphosis often gives some useful suggestions to assess the phylogenetic relationships among species. Among three species of *Haliclystus*, *H. steinegeri* is remarkably characteristic in metamorphosis. In *H. steinegeri*, the subsequent development of the interradial anchors progressed rapidly, which became almost the same size as the perradial until the third or fourth secondary tentacle appeared at each adradius. On the other hand, in *H. auricula* and *H. borealis*, the difference in the size of anchors between the perradii and the interradii was observed till more advanced stages. The difference was much more conspicuous in *H. borealis* than in *H. auricula*. Besides the metamorphosing condition of primary tentacles, the pattern of white spots' appearance makes *H. steinegeri* distinguishable from the other two *Haliclystus* species. In *H. steinegeri* eight spots appeared, each one in each adradius at the same time, while in *H. auricula* and *H. borealis*, the first four appeared in perradii and the next four in interradii. Thus a close relationship between *H. auricula* and *H. borealis* was suggested by the comparison of early metamorphosis.

In the present study some juveniles with only four primary tentacles were obtained. They were about 0.5 mm in height and 0.2 mm in width and were too young for accurate identification. These small juveniles were collected from July to August at Oshoro and from April to June at Muroran. Considering the seasonal abundance of each species in these localities (Hirano, unpubl.), they were undoubtedly referable to juveniles of *Stenoscyphus inabai* at Oshoro and those of *Haliclystus steinegeri* or *H. borealis* at Muroran. They were very similar to the juveniles of *Haliclystus octoradiatus* (= *H. auricula*) reported by Wietrzykowski (1912). Thus the very young stage of *St. inabai* is similar to that of the *Haliclystus* species. This fact favors the view that the genera of *Stenoscyphus* and *Haliclystus* are closely related to each other. Similarities were also shown in more advanced stages, especially between *St. inabai* and *H. auricula*. It is considered that *H. auricula* is most closely related to *St. inabai* among the three *Haliclystus* species.

The youngest stage of *Thaumatoscyphus distinctus* provided with only eight primary tentacles was not available in the present study. By comparing more

advanced stages between species, however, the youngest stage in *T. distinctus* was inferred to be essentially similar to that of the genera, *Haliclystus* and *Stenoscyphus*. The distinctive mark of *T. distinctus* was revealed at first in the condition of metamorphosing primary tentacles which progressed almost equally in perradii and interradii. The four chambers were subsequently found at the upper portion of the peduncle after the fourth or fifth adradial tentacles appeared. In *St. inabai* and *Haliclystus* species, the division of the chamber in the peduncle started from the base.

Since how and when the perradial mesogonial pockets were formed could not be clarified from the present study, it is impossible to discuss on the relationships between *T. distinctus* and other species in detail. But, besides the formation of mesogonial pockets, as the characteristic of family Cleistocarpidae, there are few minor differences in metamorphosis between *T. distinctus* and the species of *Stenoscyphus* and *Haliclystus*. *Sa. cruciformis* is rather distinct from others than *T. distinctus*, particularly in the young stages. *Sa. cruciformis* can be easily distinguished by the peculiar body shape. Four interradial arms were formed by exsertion of the base of the manubrium. White spots appeared on the manubrium in young stages. Judging from some characteristics in metamorphosis, it is inferred that the genus *Sasakiella* holds a special position among the species observed in the present study.

Some other features were found, which make *Sa. cruciformis* distinguishable from others. First, this species has the characteristic shape of primary tentacles with a flat discoidal head. These tentacles are conspicuously different from the primary tentacles of other species, whose heads are globular. Secondary tentacles provided with globular heads are similar among all the six species studied in the present study.

Second, the discoidal heads of primary tentacles in *Sa. cruciformis* are also characteristic in the nematocyst composition. These heads were thickly packed with one kind of ellipsoidal nematocysts. Detailed observations revealed them to be basitrichous isorhizes (Hirano unpubl.), which had never been reported in the Stauromedusae. These nematocysts were also found in the globular heads of secondary tentacles, but there were much more rod-shaped nematocysts of a different kind, atrichous isorhizes. In other species, including *T. distinctus* of the different family, the heads of primary tentacles and secondary tentacles were the same in nematocyst composition, which consists of numerous rod-shaped nematocysts, atrichous isorhizes and a few ellipsoidal nematocysts, microbasic euryteles. Basitrichous isorhizes were not found in other species than *Sa. cruciformis*.

Furthermore, the nematocyst composition was different in other body portions between *Sa. cruciformis* and the others. The nematocyst composition within gastric filaments and white spots was the same in all six species observed, which consists of only one kind of oval nematocysts, microbasic euryteles. Manubrium was the same in nematocyst composition as gastric filaments and

white spots in five species, excluding *Sa. cruciformis*. Instead of the oval nematocysts, ellipsoidal ones, basitrichous isorhizes, which were the same in kind as those of primary and secondary tentacles were found in manubrium of *Sa. cruciformis*. In consideration of characteristic shape of primary tentacles, presence of a special kind of nematocyst, distinct nematocyst composition in some body portions and characteristic changes in metamorphosis, it could be said that *Sa. cruciformis* is unique not only in the family Eleutherocarpidae but also in the order Stauromedusae. The phylogenetic position of *Sasakiella* will be elucidated after detailed comparisons on the metamorphosis and nematocyst composition are made between it and its closely related genera.

Summary

Redescriptions of the six species of Stauromedusae from Hokkaido, *Haliclystus auricula*, *H. borealis*, *H. steinegeri*, *Stenoscyphus inabai*, *Sasakiella cruciformis* and *Thaumatoscyphus distinctus* were given with some notes on their discriminative key characters newly revealed.

Small juveniles of various sizes were observed, by which developmental changes in early metamorphosis were reconstructed. With the knowledge of developmental changes, the relationships between closely related species, *H. auricula*, *H. borealis*, *H. steinegeri* and *St. inabai* were discussed. The systematic position of *Sa. cruciformis* was also discussed and the necessity of future revision of its position in higher taxa was proposed.

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