The Life-history of a Japanese Hydroid, *Hydrocoryne miurensis* Stechow[1)]

By

Tohru Uchida and **Zen Nagao**

Biological Laboratory, Imperial Palace, Tokyo

Akkeshi Marine Biological Station, Hokkaido University

(*With 11 Text-figures*)

The hydroid genus *Hydrocoryne* was instituted in the Corynidae by Stechow (1907, 1909) basing on preserved polyp specimens obtained by Doflein (1904–1905) in Sagami Bay. In 1932 Uchida reported the young medusa liberated from a polyp of the species collected by Dr. H. Sato from Mutsu Bay. Rees (1957) who published the review of capitate hydroids proposed a new family Hydrocorynidae for this hydroid. Recently we reared the hydroids of two different localities: those collected from Akkeshi in Northern Japan and those from Manazuru in Middle Japan, could reveal the life-history of the hydroid and made out that the adult medusa has specially high differentiated characters in the Corynoidea, such as four-sided lips and interradial gonads as will be described later on.

Colony (Fig. 1). The hydroid is at present found only in Japan and is rather common in tide pools or on rocks in low tide on coasts of Japan from Akkeshi to the Izu Peninsula from early spring in southern parts to summer in northern portions.

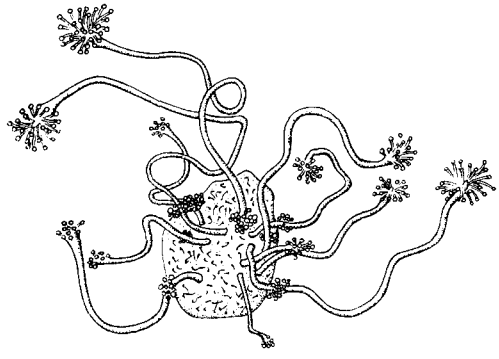

Fig. 1. A hydroid colony of *Hydrocoryne miurensis*.

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The colony of the hydroid is found attached to rocks, coral algae or barnacles and is formed of generally several to dozen polyps which are connected with each other by their stolons. Mingled with stolons are developed two or three layers of chitinous skeleton, which form an irregular network supported with props distributed here and there. Upper ends of these props have a tendency to be located in one direction and are arranged to form a circlet of 0.5–1.0 mm diameter around a polyp in specimens obtained in Akkeshi and Asamushi, but the circlet is not distinct in those from Manazuru. Young polyps are destitute of the skeleton.

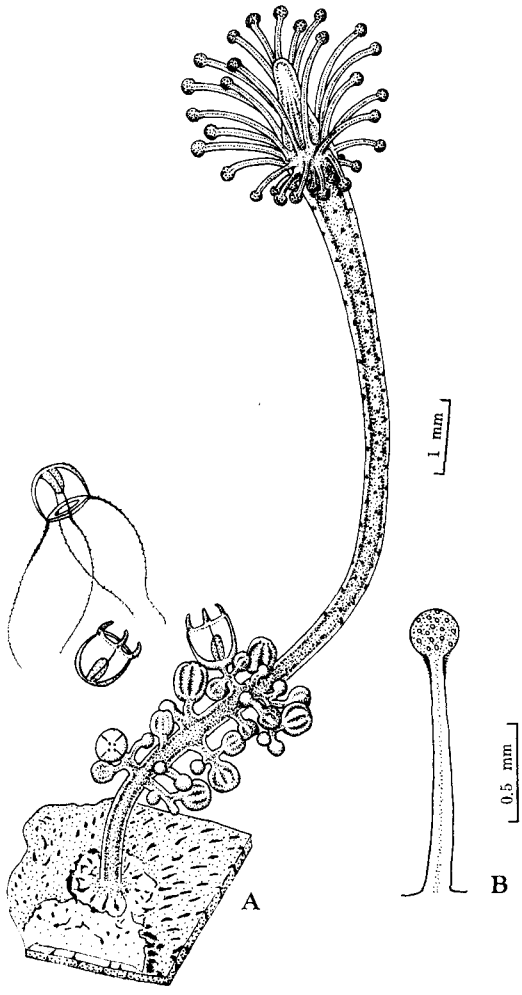

Fig. 2. A: A polyp with medusa-buds and young medusae newly liberated. B: A capped tentacle.

Coenosarcs of the colony are connected with each other and form an irregular network. The hydrorhiza is generally 0.1 mm thick and yellow brown in colour. As to the structure of skeleton Stechow (1909) described in detail. The colour of skeleton is dark brown or blackish brown.

Polyp (Fig. 2). The polyp is extensile and reaches 60 mm in well developed specimens but shrinks 1/5 the length in contraction. There is no remarkable demarcation between the hydranth and hydrocaulus. The hydranth of well-developed polyps is 3 mm or less in length, consisting of a blunt conical hypostome and a slightly broader tentacular region which bears often 60–70 capitate tentacles arranged generally alternative in position. These tentacles are disposed of 5–6 circlets, usually with younger tentacles in more proximal part. In living state they extend high above the hypostome, generally 0.5-1.6 mm in length, having a nematocyst knob at their terminal end. The nematocyst knobs are spherical, smooth in surface and contain 10-20 large nematocysts separately distributed. These nematocysts could not be so remarkably seen to be elevated as in those of *Coryne* and *Sarsia*. Capitate tentacles have each a canal in their peduncle, which leads to the gastric cavity of the hydranth. The hydrocaulus is cylindrical, widened near the hydranth and provided with numerous transversal foldings in contration. It is very extensile; when well-extended the whole shaft is nearly of the same width, but in contracted state the distal part is wider than the middle part, and the proximal part is slightly broader than the middle. The colour of polyps is in general brown but slightly variable in parts: nematocyst knobs pale brownish white, their peduncle slightly greenish, hydranth brown, distal part of hydrocaulus is provided with dark grey stripes, its middle part white and opaque. The ectoderm of hydrocaulus is tinted yellowish green, the endoderm of proximal part is brownish and slightly hyalin. The surface of hydrocaulus is sprinkled with white nematocyst clusters.

On July 19, 1963, Nagao observed a young polyp just budded off from hydrorhiza (Fig. 3, A). The polyp was 0.7 mm long and had 5 young knob-like tentacles which formed a whorl at the distal end. It developed rapidly; on the next day it reached 2 mm long, a blunt conical hypostome was differentiated and 5 young tentacles changed into capitate tentacles of 0.3 mm length. Just proximal to these tentacles 5 young tentacles of the second circlet more developed alternative in position to the first circlet (Fig. 3, B). Uchida examined a young polyp of 2 mm length and found that it had 8 short-pedunculated tentacles and its epistome is elevated but has no mouth.

Close to the base of hydrocaulus, 5–8 mm (in 1/5-1/6 the whole length) from the base, are grown numerous medusa-buds which surround the hydrocaulus, illustrating a complicated mass. At first the basal part of hydrocaulus gives rise to several (mostly 4) radial branches which are arranged perpendicularly to the hydrocaulus. These branches gradually swell out at their tip each to form a medusa-bud which enlarges and develops to a young medusa. The primary branches

elongate and give rise to further branches from the more proximal part, and these younger branches become to bear each a medusa-bud. Thus repeating, there will be arranged a series of radial branches, each bearing several medusa-buds, which shows a complicated mass of medusa-buds. The medusa-buds are universally brownish at first, but gradually become deeply tinted with reddish brown especially in radial canals and tentacle bases. Meanwhile, the exumbrellar ocelli become coloured carmine. Along with the development of medusa, brown colour of radial canals becomes faded out, leaving only the endoderm of tentacle bulbs and ocelli such coloured at liberation of medusa. Young medusae just liberated have thin jelly, a manubrium with a simple round mouth, 4 narrow radial canals and 4 hollow tentacles, each with an ocellus on the abaxial surface of tentacle bases.

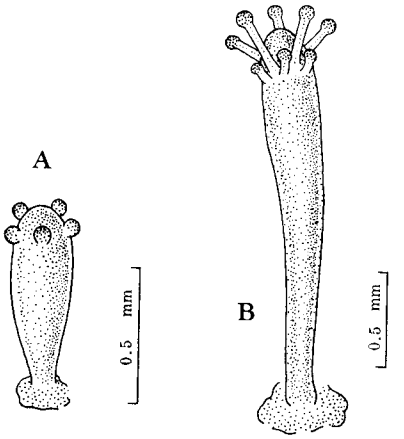

Fig. 3. Young polyps newly developed from hydrorhiza. A: Young polyps with 5 rudiments of tentacles. B: The polyps one day old of the former.

Histological observations on the polyp (Fig. 4, A,B,C,D). As to histological observations of polyps Stechow (1909) already described and the results were in general confirmed by Uchida (1932). Here will be stated some points more in detail. The tentacles are hollow and their axial canal conveys to the stomach cavity and extends to 1/4 the length of nematocyst knob. On the surface of nematocyst knobs one can find two kinds of nematocysts which are closely set. Most of them are small stenoteles which correspond to Stechow's „kleiner Nesselzellen", among them some microbasic euryteles are separately distributed. The epiderm of tentacle stalk is generally composed of cubical or flat cells, and the cells become gradually higher towards the nematocyst knob. The endoderm cells of the stalk are cuboidal and very small at the tip of tentacles. The mesolamella is very thick at the tip of tentacles but very thin elsewhere, indicating no sign of centrifugal

branches. Between the epidermis and the mesolamella there is observable to intervene well-developed longitudinal muscle fibres.

The epidermis and gastrodermis of polyps are characteristic in feature according to localities. The epidermis is the thinnest in the hypostome, composed of short columnar cells (Fig. 4, A) and is in the tentacular region made of high and large

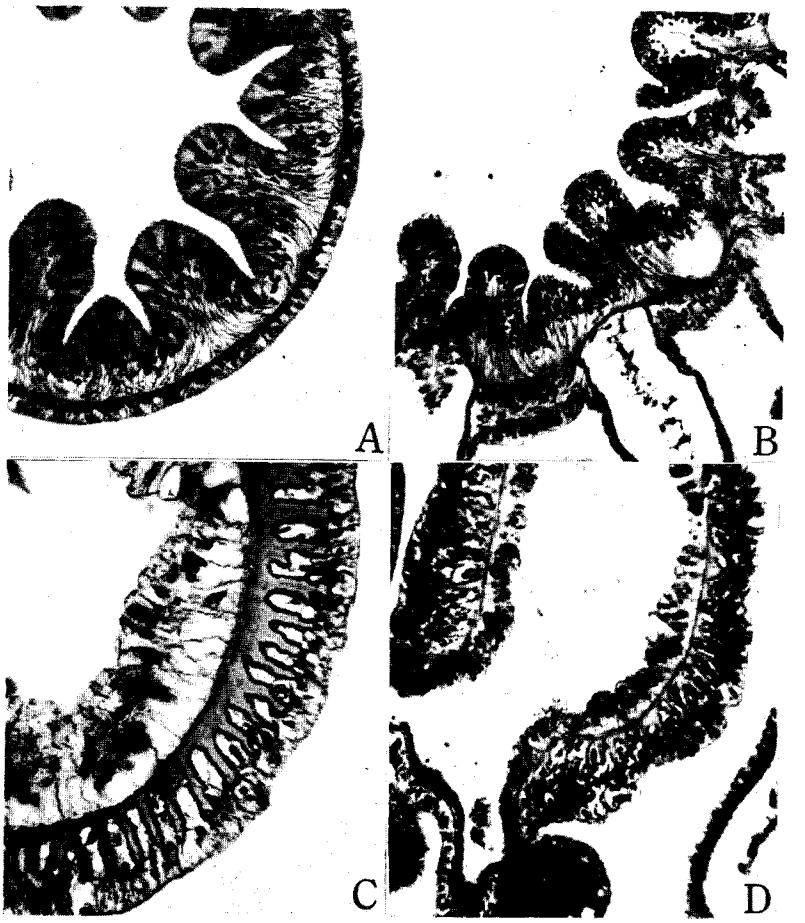

Fig. 4. Cross sections of polyps through different levels. A: Hypostome ×240. B: Tentacular region ×150. C: Hydrocaulus between tentacular region and medusa-buds region ×240. D: Medusa-buds region ×150.

cells, containing cnidoblasts, interstitial cells and fibrous elements near the mesolamella (Fig. 4, B). The epiderm cells of hydrocaulus are mostly high in its contraction and low in its extension. There are separately distributed nematocyst

clusters on the surface of epidermis. In the region of medusa-buds there are so numerous cnidoblasts and nematocysts between the epidermis and mesolamella that epitherial cells therein are extremely deformed and therefore boundaries of these cells are not distinct (Fig. 4, D). The hydrocaulus between the region of medusa-buds and hydrorhiza is almost of similar appearance to the region of medusa-buds.

The gastrodermis is composed of columnar cells, that of hydranth showing 10–15 remarkable foldings in cross section (Fig. 4, A, B). The gastrodermis of hypostome is mostly constituted of gland cells of mucous type, containing here and there gland cells of a different type. In the tentacular region the gland cells of mucous type decrease in number and digested granules are situated in the outer half (Fig. 4, B). In most part of hydrocaulus nutritive cells are obviously represented as luciferous columnar cells (Fig. 4, C). The inner side of hydrocaulus shows gentle foldings. Digestive gland cells are separately situated and especially crowded in the part just below the tentacle region. In the region from medusa-buds to hydrorhiza nutritive cells are low and provided with compact cytoplasm, containing many gland cells (Fig. 4, D).

The mesolamella is very thin, showing a simple lamella in the hypostome (Fig. 4, A) but gives rise to many characteristic centrifugal branches which are especially developed from proximal part of the tentacular region to medusa-buds regions (Fig. 4, C). The centrifugal branches are counted about 150 in cross sections through the part just proximal to the tentacle region and 50–60 of the rest. They are 1/2–2/3 the length of epidermis and sometimes repeat branching two or three times. Along with the outer side of centrifugal branches there are running longitudinal muscle fibres which are well-developed especially in the middle part of hydrocaulus. Circular muscle fibres are feebly developed in polyps.

The gastric cavity is the most spacious in the portion just proximal to the hydranth. Hydrorhiza, composed of chitinous skeleton, coenosarc and canals which lead to the gastric cavity, are irregularly running within coenosarc. The coenosarc consists of ectoderm, endoderm and very thin mesolamella. Endoderm cells forming the inner wall of canals are composed of short columnar cells which contain compact cytoplasm and a large quantity of assimilated materials. The ectoderm cells forming the outer wall of hydrorhiza and outer wall of canals, are columnar in form, and contain so numerous cnidoblasts and assimilated granules that boundaries of cells are obscure except the surface of hydrorhiza. They form cell masses which full up spaces between canals and skeleton.

Metamorphosis of medusa (Fig. 5–9). The metamorphosis of medusa is rather simple, but peculiar in the Capitata. The bell of young medusa just liberated is spherical or round in shape, slightly higher than wide, 1.0–1.25 mm high and 0.95–1.2 mm wide (Fig. 5, A). Jelly thin and exumbrella sprinkled with nematocyst clusters, each containing 1–6 nematocysts. Manubrium 1/3–2/5 the height of subumbrella, composed of a widened stomach and a narrowed mouth part which is tubular. The mouthpart is furnished with a round mouth of which the

lip is armed with nematocyst clusters. Radial canals four, straight and rather broad, connected with narrowed edges of stomach in the upper portion and conveying with tentacular canals downwards. Ring canal narrow and straight. Just below the junctionpoints of radial canals and stomach there can be seen endodermal

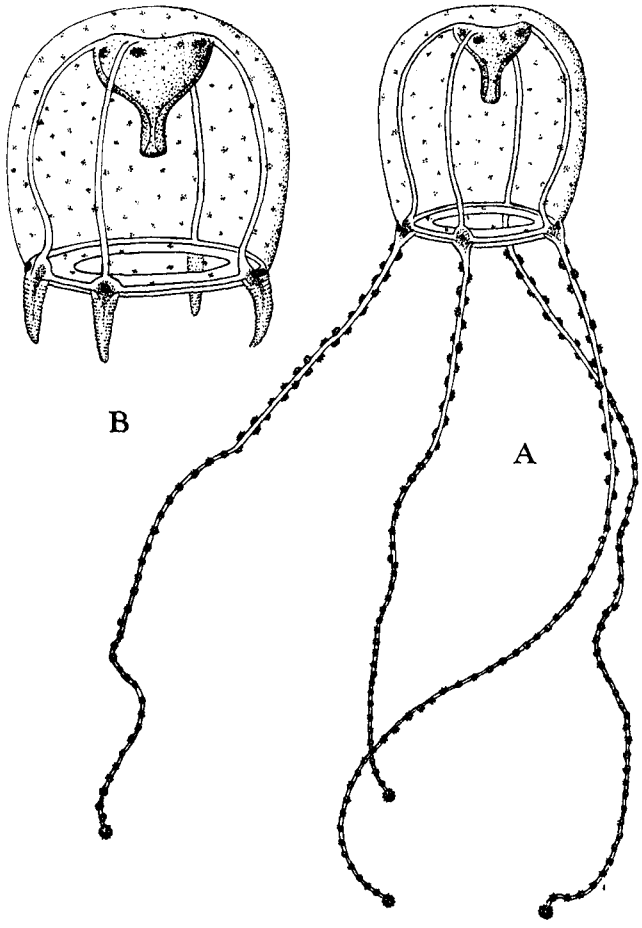

Fig. 5. Young medusae newly liberated. A: Medusa 2 days old. B: Medusa 3 days old.

flecks which are somewhat triangular in shape and brownish-orange or vermilion in colour. Tentacle-bulbs, broadly triangular in form, are well-developed, the endoderm being tinted brownish-red. On the abaxial side of tentacle-bulbs there are located carmine or dark reddish brown ocelli which are oblong-round in shape and concave on the surface. Tentacles four in number, arising from tentacle bulbs,

provided with 40–50 nematocyst clusters which are distributed on the whole shaft. The nematocyst clusters are arranged alternative in position on both sides of the shaft in the proximal part but disposed in a row in the distal portion. The terminal cluster is the largest and prominent (Fig. 6). The tentacles are usually rather short (Fig. 5, B) but are very extensile and extend over 3 times the bell-height (Fig. 5, A). Velum well-developed and with a rather small opening. Gonads not at all developed in specimens from Manazuru but their trace was perceived in specimens from Akkeshi.

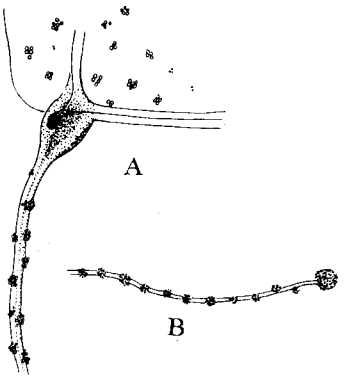

Fig. 6. Tentacle bulb and tentacle, showing arrangement of nematocyst clusters.
A: Basal part of tentacle. B: Distal part of tentacle.

On July 1st, 1962, Nagao collected two colonies of *Hydrocoryne* attached to a stone on the tidal line of Akkeshi Bay. The colonies gave rise to about 10 medusae of which gonads began to develop in one or two days at water temperature 15–18°C. These medusae were all females. He reared the medusae for a month. The medusae, one to two weeks after liberation, became bell-like in shape, 1.8–2.0 mm high and 1.6–1.8 mm wide (Fig. 7), Stomach having 1/3 the length of bell cavity, with four-sided tubular mouth part with a simple mouth. In the perradial portion of manubrium just below the junctionpoint a pigement patch is present. Interradial gonads have each 1–3 large ova, 0.15–0.2 mm in diameter. The number of ova is mostly different in each interradius and is 1–8 in one individual. These ova are formed in a day and are laid successively, and the egg-laying occurs 4-5 times in a month. According to Kakinuma's observations (1961) medusae in Asamushi attain the maturity about 2 weeks after liberation.

In the middle of March, 1966, several colonies were collected at Manazuru by the writers and were reared together with liberated medusae from them in the Imperial Laboratory and observed by Uchida. Young medusae just liberated had no sign of gonads. Three days afterwards these medusae became 1.5–2.0 mm high and 1.4–1.7 mm wide. In some of them rudimental gonads were perceived, perradial

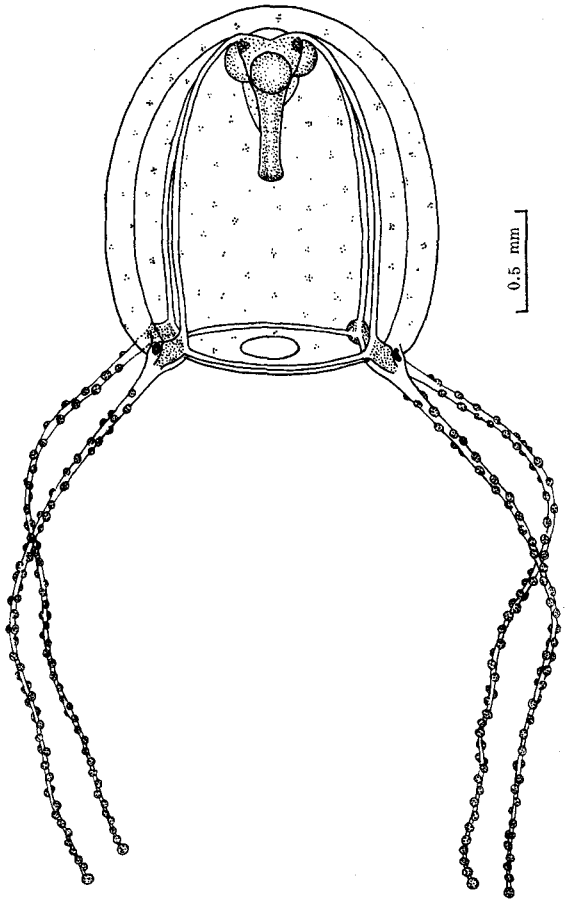

Fig. 7. Mature female medusa from Akkeshi, 12 days after liberation.

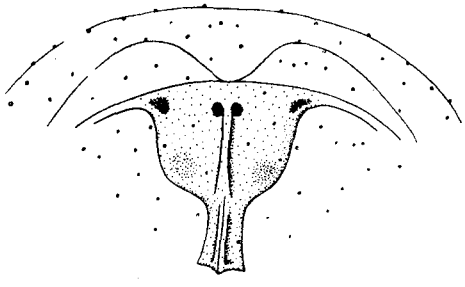

Fig. 8. Manubrium of male medusa from Manazuru, 12 days old, showing division of pigment patches and four-sided lips.

ridges of mouth part appeared and perradial pigment patches began to be divided into two. When these medusae became 12 days of age, opaque testes were clearly observed and perradial pigment patches were divided into two, forming a pair of patches in each perradius (Fig. 8). In these medusae the manubrium is four-sided and provided with, though not well-developed, 4 distinct lips.

In the same year Nagao collected about 20 medusae in Akkeshi Bay at the end of August. He reared them to the middle of September and got some well-developed males. Well-developed testes are spherical in form, milky white in colour and surround 2/3 the basal part of manubrium (Fig. 9).

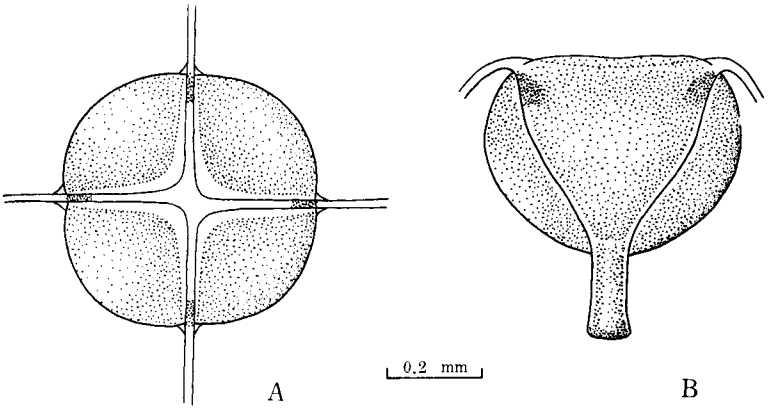

Fig. 9. Male gonad. A: Aboral view. B: Side view.

Judging from the facts, the medusae in Akkeshi Bay are more premature than those in and Asamushi Manazuru. The principal points of metamorphosis of the medusa lie in formation of four-sided manubrium, division of perradial pigment patches and appearance of interradial gonads. Here will be given the description of well-developed medusae.

Bell spherical, without any apical projection and with smoothly rounded exumbrella, upper half of the exumbrella being wider than the lower half. Well-developed medusae over 2 mm high and 2 mm wide. Exumbrella surface finely granulated with nematocyst clusters, containing generally 3–6 nematocysts. Four radial canals straight and moderate in width, somewhat becoming wider at the upper portion. Tentacle bulbs remarkably swollen, with oblong-rounded, concave abaxial ocelli. Tentacles hollow, generally short but very extensile. Nematocyst clusters distributed alternative in position on both sides in proximal part but arranged in a row in the distal part, with the terminal largest one. Velum wide. Manubrium about half as long as the depth of bell cavity, very wide at base, rapidly narrowed distally, four-sided, and with somewhat cruciform lips, four ridges on each perradius and four pairs of perradial endodermal pigment patches just below

the junctionpoints with the radial canals. Gonads developed in interradii of manubrium, surrounding nearly the whole manubrium.

Development of polyps from eggs (Fig. 10, A, B, C). Nagao reared 4 well-developed females and 2 well-developed males which were obtained on 30-31th, August, 1966 in Akkeshi Bay and got several swimming planulae. They were milky white in colour, oblong-ellipsoidal in shape, about 0.25 mm long, widened anteriorly and narrowed posteriorly (Fig. 10, A). They were observed to swim, rotating spirally and anti-clockwise. They were put in a bowl together with small pieces of the sea-alga, *Cystophyllum hakodatense* and got 5 young polyps 2-4 days afterwards. Young ployps, attaching to the substratum with the basal end, were long and tubular in form and were provided with 4-5 young tentacles which indicated blunt cone-like processes (Fig. 10, B). The polyps became to have capped ten-

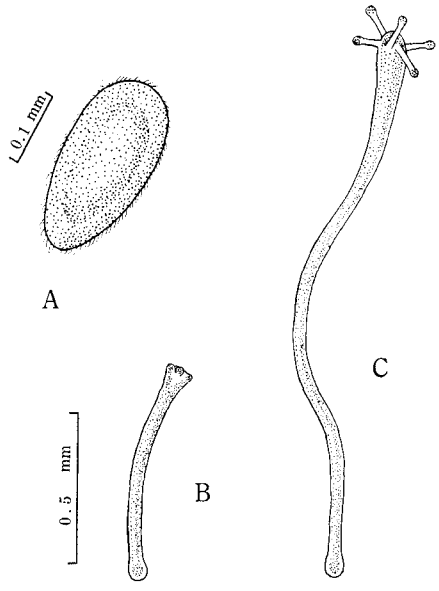

Fig. 10. A: Planula. B: Developing polyp. C: Young polyp.

tacles in a day (Fig. 10, C). They were milky white and very extensile. When well-extended they measured 1.5–2.0 mm long and 0.05 mm in diameter, the tentacular region being the widest and 0.08–0.1 mm. The hydranth was furnished with a blunt-conical hypostome and with 4–5 tentacles, 0.15–0.2 mm in length, which were arranged in a circlet. Besides these tentacles, 1–2 tentacle-buds were seen just proximal to the primary tentacle circlet. Nematocyst-knobs were not so remarkable as in those of well-developed polyps.

Nematocysts (Fig. 11, A-N). In regard to nematocysts the following facts were

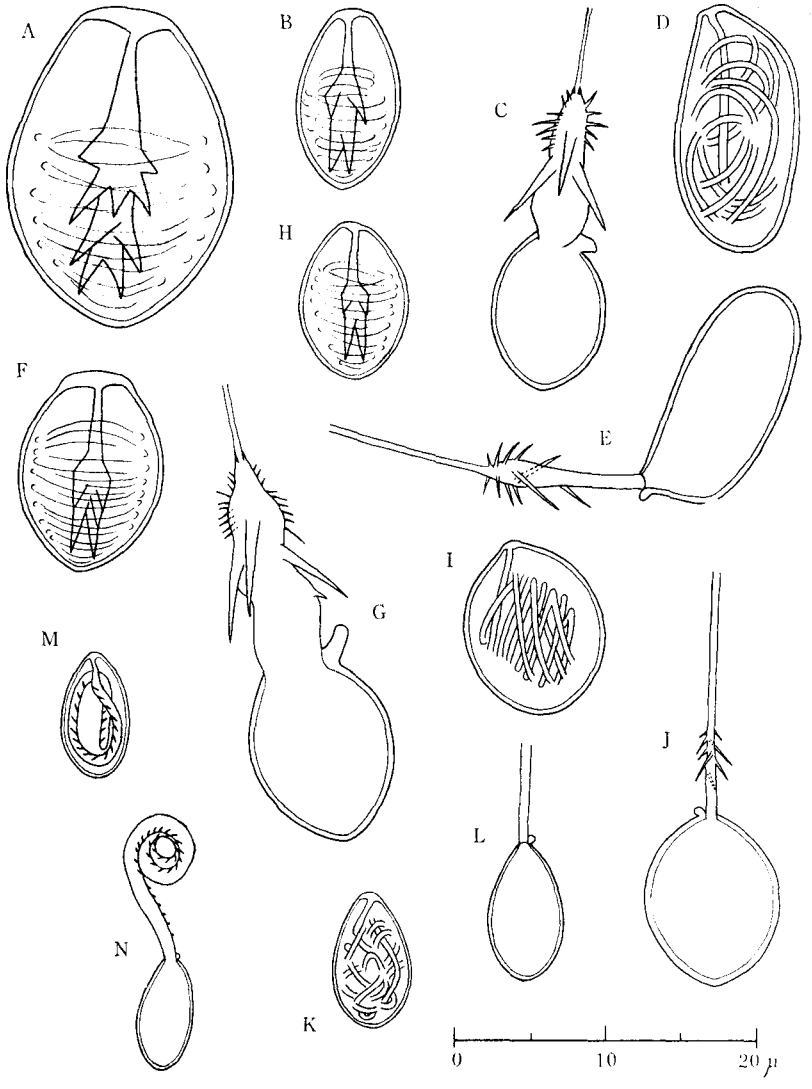

Fig. 11. Nematocysts. A-E: polyp. F-N: Medusa. A-C: stenoteles. D,E: microbasic euryteles. F-H: stenoteles. I, J: basitrichous haplonemes. K,L: atrichous isorhizes. M, N: desmonemes.

revealed. Polyps without medusa-buds have 2 kinds of nematocysts: stenoteles and microbasic euryteles. Polyps with medusa-buds have 5 kinds of nematocysts: stenoteles, microbasic euryteles, basitrichous haplonemes, atrichous isorhizes and

desmonemes. Medusae have 4 kinds of nematocysts: stenoteles, basitrichous haplonemes, atrichous isorhizes and desmonemes. Stenoteles are divided into two groups, one large and another small.

The nematocysts of polyps and medusae will be summarized as follows:

Polyps:
- Stenoteles
  - Large type: 19–24 × 13.5–18μ (undischarged)
  - Small type: 7–13 × 4.5–9.5μ (undischarged)
- Microbasic euryteles: 15–20 × 7–10.5μ (undischarged)

Medusa-buds region of polyps:
- Basitrichous haplonemes: 9.5–11.5×7–9μ (undischarged)
- Atrichous isorhizes: 8–9.5×4.5–5.5μ (undischarged)
- Desmonemes: 7–9×4μ (undischarged)

Medusae:
- Stenoteles
  - Large type: 12–13.5×8–11μ (undischarged)
  - Small type: 8–10.5×6–8μ (undischarged)
- Basitrichous haplonemes: 10–13×7–10μ (undischarged)
- Atrichous isorhizes: 8–10×4.5–6μ (undischarged)
- Desmonemes: 7–8×4–4.5μ (undischarged)

As is clear, the nematocysts of medusae are created in the medusa-buds region of polyps. Several investigators such as Weill (1934), Russell (1938), Rees (1957), Itô and Inoue (1962) and Werner (1965) pointed out that nematocysts are of some use in separating species and genera closely related. So far as we are aware, *Hydrocoryne* stands separate from Corynidae and rather closely allied to Tubulariidae from the viewpoint of nematocysts.

Remarks. In 1909 Bigelow described *Sarsia resplendens* as a new species from the Pacific coast of Mexico. Mayer (1910) cited his description in his monograph, retaining the specific name, but is doubtful if the species is synonymous with *Sarsia eximia* in the Atlantic. Uchida (1927) recorded *Sarsia resplendens* on two specimens collected at Misaki on March 24, 1924. These specimens exactly accorded with the figures and descriptions of Bigelow except the disparity in the number of pigment patches of the manubrium. While studying the metamorphosis of medusa of *Hydrocoryne miurensis*, the senior writer made out that the young medusae gradually developed to medusae quite similar to *Sarsia resplendens* as is described above. The young medusa of simple manubrium became to have equipped with four-sided manubrium with 4 lips. The gonads which were described as "surrounding the whole manubrium" by Bigelow (1909) and Uchida (1927) appeared first in the interradii of the manubrium and eventually developed as if they encircle the manubrium. But on closer examination on living materials they were observed to be demarcated each other by perradial lines. The disparity of the number of pigment patches seems to be due to difference of stages; Bigelow (1909) observed on

a well-developed specimen, 2.2 mm high and 2 mm wide, and Uchida (1927) described on a still younger specimen. Such being the case, *Sarsia resplendens* is, in all probabilities, synonymous with *Hydrocoryne miurensis*, though the polyps have not yet been recorded from the coast of Mexico. The hydroid polyp of *Sarsia eximia* is quite different from that of *Hydrocoryne miurensis*.

In 1957 Rees separated the genus *Hydrocoryne* from the Corynidae and correctly established the family mainly basing on the polyp-stage. The polyp seems to have differentiated from Corynidae in the hydranth, position of gonophore and skeleton formation. The medusa is more highly organized from Corynidae in four-sided manubrium and interradial gonads as seen in medusae belonging to the Filifera.

In conclusion, the following diagnosis of the family will be proposed.

Family Hydrocorynidae Rees (1957) emend

Corynoidea with thick encrusting base. Colonial and connected by stolons. Hydranth columnar, with only an oral whorl of capitate tentacles around a conical hypostome, with thick chitinous mesogloea. Gonophores borne in clusters near the base of hydrocaulus.

Newly liberated medusa of *Sarsia*-type. Adult medusa with deep bell shape, four straight radial canals and four tentacles each with swollen bulb and abaxial ocellus. Manubrium divided into a wide stomach part, and a narrow four-sided mouthpart ending in four-sided mouth. Gonads develop in the interradial part of manubrium.

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