Taxonomic Study on *Hydrocoryne miurensis* (Hydrozoa: Hydrocorynidae) in Japan

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With Text-figures 1–4 and Tables 1–2

Abstract The life cycle, nematocyst equipment, and the chromosomes of *Hydrocoryne* in Japan were studied from the taxonomic point of view. The morphology of *Hydrocoryne* was described and illustrated in the following developmental stages: the well-developed polyp with or without medusa buds, the regenerated polyp, the primary polyp, the newly liberated medusa, the earliest mature medusa, the aged mature and spent medusae, and the young and aged planulae. The morphology of gametes was also described and illustrated. It is highly probable that only one species, referable to *H. miurensis* Stechow, 1907, occurs in Japanese waters.

Hydrocoryne is one of the metagenetic hydrozoans that has a large polyp and a small medusa. The colonial polyps are common on pebbles and rocks in shallow waters of rather open coasts in the North Pacific. Rees (1957) erected the monotypic family Hydrocorynidae in order to accomodate this genus and his diagnosis of the family was slightly emended by Uchida & Nagao (1967). The genus *Hydrocoryne* Stechow, 1907 is composed of two species. Since Stechow (1907, 1909, 1923) described the type species from Japan, hydrocorynid polyps and medusae have been reported from Japanese coasts as given below.

The original description of *Hydrocoryne miurensis* Stechow, 1907, was based on some preserved polyps with medusa buds collected by Doflein in 1904–1905 at some localities nearby Misaki, Kanagawa Prefecture, central Japan. Since then, several polyps attached to buoys of a fishing net were found at Misaki (Yoshii, 1931). Polyps collected in Mutsu Bay, northern Japan, and their newly liberated medusae were described by Uchida (1932, 1938a) and mature medusae in this area were obtained by culture by Kakinuma (1961). Toyomasu (1938) observed the pattern of regeneration of *H. miurensis* polyps from Shimoda, Shizuoka Prefecture, central Japan. Four polyps without medusa buds in Onagawa Bay, Miyagi Prefecture (Uchida, 1938b), polyps at Akkeshi, Hokkaido (Uchida, 1940; Uchida *et al.*, 1963), and polyps attached to rocks at Sado Island, Niigata Prefecture (Uchida, 1958) were also recorded. The life cycle and the nematocyst equipment were described by Uchida & Nagao (1967), using the specimens collected from Akkeshi, Hokkaido, northern Japan, and Manazuru, Kanagawa Prefecture, central Japan. *H. miurensis* was reported in the faunal list of the hydroids in Japan (Yamada, 1959), and as one of

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the marine invertebrates distributed in Oshoro Bay and its neighbouring area (Okada *et al.*, 1971). Besides the above-enumerated specimens identified as *H. miurensis*, two mature medusae from Misaki were described by Uchida (1927) under the name of *Sarsia respledens* Bigelow, 1909. As is often the case in hydrozoan taxonomy, connection of the hydrocorynid polyp and its medusa was unknown at that time (cf. Uchida & Nagao, 1967). As is mentioned later, the taxonomic position of *S. respledens* is problematical.

Hydrocoryne bodegensis Rees, Hand et Mills, 1976, the other species of the present genus, was described based on both polypoid and medusan specimens from California, United States of America, by Rees *et al.*, (1976) after clarifying the life cycle and the nematocyst equipment. The occurrence of this species was subsequently reported in Petra Velikogo (Peter the Great Bay), Soviet Union, by Margulis & Karlsen (1980). This constituted a new record for *H. bodegensis* in the Sea of Japan as well as in the West Pacific.

In 1981, the author collected a hydrocorynid polyp at Oshoro, Hokkaido, facing the Sea of Japan. Examination of the nematocyst equipment of this polyp indicated that it was *H. bodegensis*. This was the second sighting of this species in the Sea of Japan after that of Margulis & Karlsen (1980). However, the characteristics of its mature medusa reared in the laboratory accorded well with those of *H. miurensis* described by Uchida & Nagao (1967). Therefore, this hydrozoan appeared to be an undescribed species in which the polyp was similar to *H. bodegensis* but the medusa was similar to *H. miurensis*. It was possible that three species of *Hydrocoryne,* i.e., *H. miurensis, H. bodegensis* and this species, all occurred in Japanese waters. In order to determine this possibility, a detailed study based upon the examination of the nematocysts of this animal as well as rearing experiments of the polyp and medusa has been carried out since 1981. The present paper deals with the results of this study.

Most polyps were collected from intertidal rocks and pebbles. The others were collected from subtidal rocks by dredging. They were reared in the laboratory to obtain their medusae. The medusae were reared normally at both 20°C and 12°C; furthermore they were reared in a refrigerator at 10°C in constant dark to test for additional variability and sexual differences. The morphology of gametes, the morphology and nematocyst equipment of the planula and the primary polyp were also examined. Measurements in the text are given as mean±SD, with range in parentheses, followed by the number of specimens examined. The dimensions of nematocysts, length and maximum width of undischarged capsules, in μm, are described in the same way. Figures 2, 3–B, and 4 were drawn with the aid of a drawing apparatus (Olympus BH-DA).

Many embryos were kept in 0.005–0.01% colchicine seawater for up to several hours, after which chromosome preparations were made by an ordinary air-drying method and stained by Giemsa solution. These embryos were obtained by crossing mature medusae reared in the laboratory at 21±1 °C. The polyps which liberated these medusae were collected at Kikonai, Hokkaido on June 14, 1987. Also in a laboratory-reared male medusa of 6 days old from Kikonai, the chromosome was examined after treating colchicine for about a day. The polyp of this medusa was collected on August 7, 1986.

Results

1. Polyp.

The external morphology of the polyp was examined in a total of 61 zooids with or without medusa buds that were removed from 35 colonies collected from a single place at Oshoro, Hokkaido on August 25, 1983, September 16, 1983, June 22, 1984, July 6 and 25, 1984, September 2, 1984, and July 9 and 27, 1986. These colonies were attached to a vertical surface of a rock and the zooids were usually washed by waves since they occurred just below the surface of the sea. Each colony is usually composed of several to six unbranched zooids, while occasional larger colonies composed of a dozen or more zooids are found at the site. A network of black chitinous skeleton is found on the basal mat of each colony. Zooids removed from the substratum were up to 40 mm long, with the tentacular region of the hydranth up to 0.8 mm wide in a well-extended condition. Zooids had up to 74 tentacles arranged in more than four whorls (Fig. 1, closed circles). (In one case, a tentacle was extraordinarily produced on the hydranth below the cluster of tentacles.) The capitate tentacles were up to 3.4 mm in length, with a terminal nematocyst knob up to 0.31 mm in diameter. (In one case two nematocyst knobs were found side by side in one tentacle.) The pedicels of medusa buds are born on the lower portion of the hydrocaulus. There were up to 15 pedicels arranged in more than four rows, surrounding the cylindrical hydrocaulus (Fig. 1, triangles). (In one

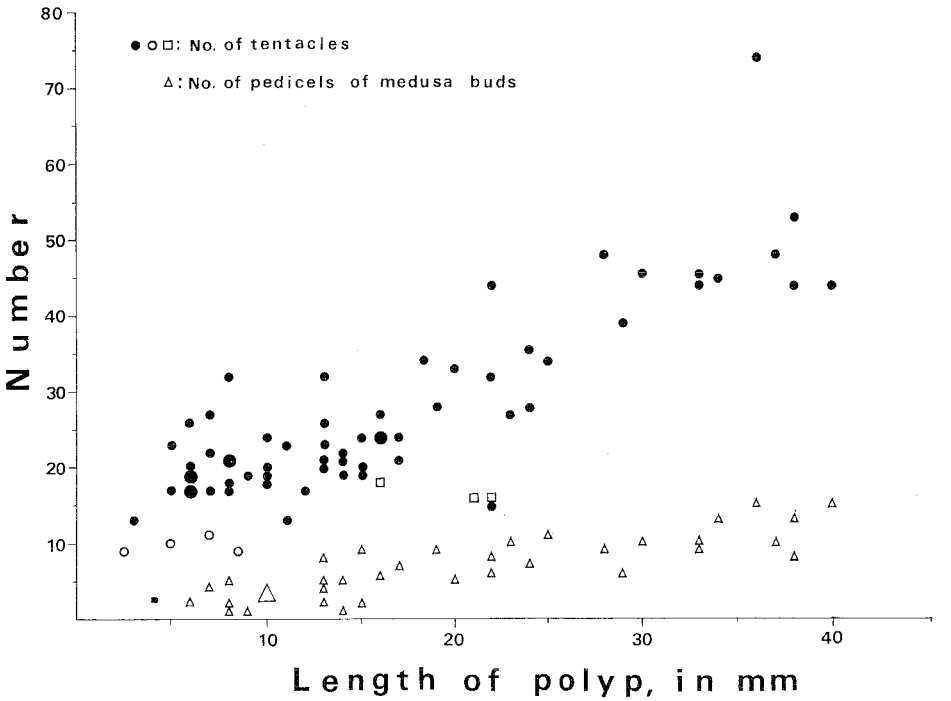

Fig. 1. The relationship between the length of polyp and the number of tentacles (circles and squares) and the number of pedicels of medusa buds (triangles: only for more than 1) in *Hydrocoryne* collected from Oshoro. Larger symbols show the overlap of values (circles: 2; triangles: 3). Open circles and squares show the number of tentacles of four polyps regenerated in the laboratory and the increase of tentacles in three of them, respectively.

specimen, one pedicel was produced at the middle of the hydrocaulus separated from the cluster of pedicels.) Each pedicel gives rise to branches, and up to 14 medusa buds were produced on each. Up to 89 medusa buds were present per zooid. At Oshoro, medusa buds were produced in warm seasons, at least from June to September.

After releasing medusae, some zooids collected on September 25, 1981 degenerated into small masses on the basal mat. They were kept in a refrigerator at about 2°C for about one and a half months. Then they were kept at 12°C in an incubator. About ten days later the formation of hydranths quickly took place and four zooids regenerated. They were 2.5–8.5 mm long, 0.2–0.3 mm wide, and had 9–11 capitate tentacles including young knob-like ones (Fig. 1, open circles). The larger zooids were transparent, the smallest one was orange in color. Three of the zooids continued to grow; after 10 days they were 16–22 mm long and had 16–18 tentacles arranged in two or three whorls (Fig. 1, squares).

In addition to the zooids from Oshoro described above, many zooids removed from six colonies collected at Kikonai on May 24, 1982, April 28, 1983, August 7, 1986 and June 14, 1987 were observed. They were attached to rocks and pebbles just the lowest level of the intertidal zone. Among them, one exceptional zooid was bifurcated at the lowest portion of hydrocaulus. The largest of these zooids was 25 mm in length and had 42 tentacles arranged in four or more whorls. It had nine pedicels on the hydrocaulus, but medusa buds were not yet produced. This zooid was reared in the laboratory, and fed with *Artemia* nauplii, until medusae were liberated. It became 45 mm long on the 12th day and just a month later one medusa was liberated. During this period, 14 medusa buds were produced on these nine pedicels, each of which bore up to three medusa buds.

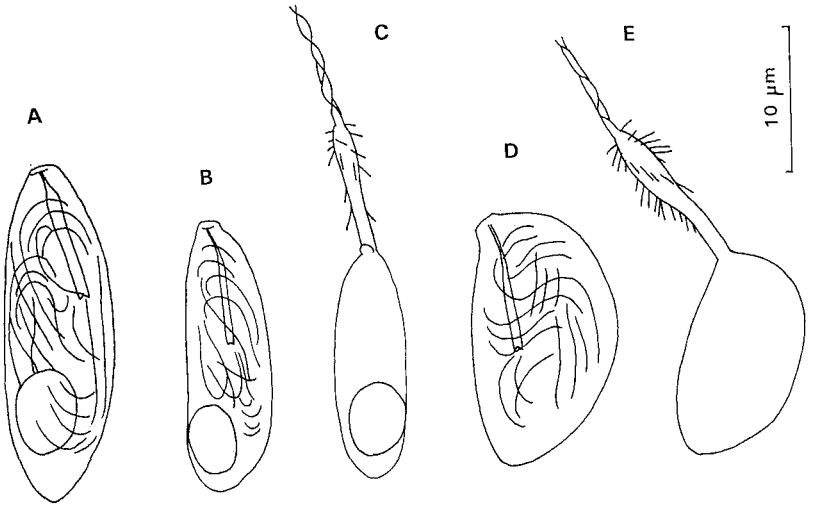

Fig. 2. Two types of microbasic euryteles found in the hydrocorynid polyp from Oshoro. Both discharged and undischarged states are shown.

A colony attached to a rock at about 5 m in depth was collected at Nakanose, Akkeshi Bay, Hokkaido by dredging on August 24, 1984 by Dr. K. Konishi. The largest zooid had 29 tentacles arranged in four whorls. In this specimen one exceptional tentacle with two nematocyst knobs was found.

Nematocyst equipment of the polyp was examined in 16 fresh zooids from different localities in Hokkaido within 11 days of collection and also in two specimens that had regenerated in the laboratory (Table 1). All of them had stenoteles and microbasic euryteles on the tentacles; the former are divided into four types by the

Table 1. Nematocysts on tentacles of *Hydrocoryne* polyps in Hokkaido and the size (length × width) of undischarged capsules in μm. Measurements are mean ± SD, range, and number of nematocysts examined.

Locality		Oshoro	Oshoro
No. of zooids examined		6	2*
Stenoteles	large type	26.5±2.3 (21.6–30.0) ×	22.0±0.6 (21.6–22.4) ×
		19.4±1.4 (17.0–21.6) 36	16.5±0.5 (16.2–16.8) 2
	medium type	17.2±1.9 (13.6–20.2) ×	19.8±1.4 (17.6–22.8) ×
		10.5±0.9 (8.8–12.8) 29	11.8±0.6 (10.8–13.0) 17
	smallt type I	13.6±1.1 (12.0–15.2) ×	13.2±1.1 (12.0–15.8) ×
		9.8±0.6 (8.8–10.8) 19	9.0±0.5 (8.2– 9.6) 15
	small type II	11.2±0.6 (10.2–12.4) ×	11.8±0.5 (11.2–12.8) ×
		6.4±0.2 (5.8– 6.8) 37	6.8±0.4 (6.4– 7.6) 10
Microbasic euryteles		19.8±1.8 (16.4–22.4) ×	18.7±1.0 (16.6–20.0) ×
		9.6±0.6 (8.8–10.8) 23	9.5±0.8 (8.2–10.6) 20
Microbasic euryteles		19.1±0.9 (17.6–21.2) ×	19.0±1.3 (16.8–23.0) ×
with inclusion		7.0±0.5 (5.6– 7.8) 26	6.5±0.3 (5.8– 7.2) 20
diameter of inclusion		4.9±0.2 (4.8– 5.2) 12	4.4±0.5 (3.4– 5.6) 18

Locality		Kikonai	Akkeshi
No. of zooids examined		8	2
Stenoteles	large type	26.6±2.2 (22.4–30.0) ×	28.4±1.2 (25.6–30.8) ×
		19.1±1.7 (15.2–21.6) 19	20.4±0.9 (18.8–22.0) 17
	medium type	17.6±2.2 (13.6–20.4) ×	19.4±0.6 (19.2–20.4) ×
		10.7±1.0 (9.0–12.4) 24	11.7±0.6 (10.4–12.2) 14
	small type I	12.4±0.5 (11.4–13.4) ×	14.4±0.4 (14.0–15.2) ×
		8.9±0.4 (8.2– 9.6) 19	10.6±0.8 (8.8–11.6) 9
	small type II	11.4±0.7 (10.4–12.8) ×	11.5±0.5 (10.4–12.0) ×
		6.5±0.3 (5.8– 7.0) 22	6.5±0.2 (6.4– 6.8) 12
Microbasic euryteles		19.4±0.7 (18.4–20.8) ×	19.0±0.6 (18.0–20.0) ×
		9.4±0.5 (8.2–10.4) 20	10.7±0.4 (10.0–11.2) 11
Microbasic euryteles		19.4±1.4 (17.2–21.4) ×	17.8±1.4 (15.6–19.4) ×
with inclusion		7.0±0.5 (6.4– 8.0) 20	6.9±0.4 (6.4– 7.6) 10
diameter of inclusion		4.9±0.3 (4.4– 5.6) 20	4.6±0.3 (4.0– 5.0) 10

* Examined in the polyp regenerated in the laboratory.

size and the shape of capsules, and the latter sorted into two types by the presence or absence of a spherical inclusion within the capsule and by the shape of the capsule (Fig. 2). The complement and the dimensions of nematocysts of the regenerated polyps are the same as those of polyps collected from the sea, except that the large type of stenoteles tends to be smaller in the former (Table 1). The complement and the dimensions of nematocysts of polyps from three localities in Hokkaido are nearly identical, except that the microbasic euryteles without inclusion tend to be stubbier in polyps from Akkeshi than other locations. The inclusion, of which the diameter shows little variation, is always contained at the side opposite to the opening of each capsule. This spherical inclusion cracked when the capsule was pressured.

The complement of nematocysts was checked in many other specimens of different developmental stages, which were collected from Oshoro and Kikonai on various occasions. The nematocysts were also examined in the other specimens collected from such localities as Kushimoto, Wakayama Prefecture, on March 20, 1988, and Sozu, Shimane Prefecture, on March 21, 1983. The latter was collected by Dr. Y. M. Hirano and Dr. Y. J. Hirano. All of these specimens invariably possessed the microbasic euryteles with the inclusion together with the other kinds and types of nematocysts on their tentacles.

The complement of nematocysts of the hydrocaulus differed slightly from that of the tentacles: stenoteles of the medium type were absent, stenoteles of the large type were few in number, and microbasic euryteles with the inclusion were very rare. The dimensions of nematocysts on the hydrocaulus were examined in three zooids from Oshoro: microbasic euryteles were 19.2–22.4×9.2–10.0, n=12; microbasic euryteles with the inclusion were 18.4–20.0×7.0–7.8, n=4; stenoteles of the large type were 26.4–28.8×18.4–20.2, n=5; stenoteles of the small type I were 13.6–17.0 ×9.2–10.2, n=5; stenoteles of the small type II were 12.0×6.6–7.2, n=5. It should be noted that no nematocysts were found on the conical hypostome of four zooids from Oshoro.

Three preserved colonies were examined by the author through the courtesy of Mr. H. Noda and Mr. H. Tanase. They obtained the polyps from intertidal rocks near the Seto Marine Biological Laboratory, i.e. Engetsu-to on March 19, 1980, Shisou-jima Is. on March 27, 1982, and Mezuzaki on February 19, 1984. All these polyps seem to be the same species as the polyps described above, though their nematocysts were not examined.

The morphology of the present polyps is summarized as follows: colony composed of up to a dozen or more zooids on a chitinous basal mat; each zooid up to 45 mm long, with up to 74 capitate tentacles arranged in four or more whorls around the conical hypostome, up to 15 branched pedicels bearing up to 89 medusa buds were produced on the lower portion of the cylindrical hydrocaulus of the zooid; two kinds of nematocysts, microbasic euryteles and stenoteles, are found on the tentacles and hydrocaulus.

Remarks. The microbasic euryteles with the inclusion were invariably present

in all of the present specimens examined, also in the regenerated ones in the laboratory. However, the presence of such a peculiar type of nematocyst has not previously been described in Japanese hydrocorynid polyps. Furthermore, two additional types of stenoteles have been found in the present material (cf. Uchida & Nagao, 1967). On the other hand, previously described polyps were more developed than the present largest one: these include a polyp that attained 70 mm long (Kakinuma, 1961); a polyp with 70 tentacles arranged in six whorls (Uchida & Nagao, 1967); a polyp with 80 tentacles arranged in five whorls (Stechow, 1909; Uchida, 1932); and a polyp having up to 15 medusa buds per pedicel, with a total of up to 150 medusa buds (Stechow, 1907, 1909).

2. Newly liberated medusa.

After a thin envelope of the medusa bud is ruptured, the medusa detaches from the pedicel of the polyp by means of pulsation. The umbrella of the newly liberated medusa within several minutes after release is slightly wider than high. Twelve such medusae were measured. They originated from several zooids removed from three colonies collected at Oshoro on July 9, 1986, and were liberated within two days after collection of the colonies. The umbrella was 1.07 ± 0.08 mm (1.00–1.19 mm) in width and 0.98 ± 0.13 mm (0.75–1.19 mm) in height. The manubrium with a round mouth was 0.42 ± 0.09 mm (0.25–0.50 mm) in length. The manubrium was nearly tubular, but with a slightly widened stomach portion. The radial canal and the tentacular bulbs were dark brown in color. The manubrium was usually also dark brown in color, but sometimes was tinted only on the upper half. In either case, pigmentation was strongest at the perradial corners of the manubrium. There were four tentacles of which the length was 2.6–3.8 mm when well-extended. Along the whole shaft of the tentacles were found 40–55 nematocyst knobs; this includes the large terminal knob.

The umbrella quickly became higher than wide. Within one day of liberation the umbrella was 1.24 ± 0.15 mm (1.00–1.50 mm) in height and 1.12 ± 0.12 mm (0.94–1.34 mm) in width in 19 specimens. These medusae were liberated from five zooids collected from Oshoro on September 25, 1981, July 6, 1984, and July 25, 1984, and they were obtained within five days after the collection of polyps. In these medusae as well as in many others obtained on different occasions, the color had faded out except for the junction points between the manubrium and the radial canals. The manubrium was 0.49 ± 0.05 mm (0.38–0.56 mm) in length, and stenoteles measuring 12.2 ± 0.5 (11.2–12.8) $\times 8.6\pm0.3$ (8.0–9.0), n=24 were found on the mouth. The stomach was small, measuring 0.22–0.31 mm in breadth. The four tentacular bulbs were dark brown or orange in color, and on each abaxial side was found an ovoid eye-spot, dark brown or crimson in color. The medusa was phototactic, quickly swimming toward a light. Three kinds of nematocysts were found on the tentacles — one of these is divided into two types. The dimensions of these nematocysts were as follows: desmonemes were 8.7 ± 1.0 (6.6–10.4) $\times 4.6\pm0.4$ (3.6–5.6), n=27; atrichous isorhizas were 10.2 ± 0.6 (9.2–11.2) $\times 5.4\pm0.5$ (4.8–6.4), n=

16; stenoteles of the large type were 16.0±0.7 (14.8–17.4)×11.9±0.6 (10.8–13.4), n=21; stenoteles of the small type were 11.5±0.6 (10.4–12.4)×7.6±0.5 (6.4–8.4), n=21. Many nematocysts were found on the exumbrella, forming clusters. There were 7±2 (3–13) nematocysts in each cluster, which were composed of 4±2 (1–10) atrichous isorhizas, 2±1 (0–4) basitrichous isorhizas, and 1±1 (0–3) stenoteles (examined in 53 nematocyst clusters of six medusae from Oshoro). The atrichous isorhizas were usually the most abundant type in each cluster. The dimensions of these nematocysts are as follows (examined in four medusae originating from four zooids removed from four colonies collected from Oshoro): atrichous isorhizas were 10.4±0.6 (9.4–11.2)×5.6±0.4 (4.8–6.4), n=21; basitrichous isorhizas were 12.8±0.5 (12.0–13.6)×9.4±0.4 (8.8–10.2), n=25; and stenoteles were 13.9±1.2 (12.0–16.0)×9.8±0.7 (8.8–10.8), n=20. Scattered nematocysts not forming a cluster were sometimes also found on the exumbrella. Among these, the microbasic euryteles without the inclusion were rarely found with almost all of those seen degenerating, and a single discharged microbasic eurytele with the inclusion was found. The subumbrella was pale green in color. The mesoglea was thin, measuring 0.06–0.08 mm in thickness at the apex of umbrella. Conforming to the cuboid-shaped umbrella, the ring canal was quadrate in shape.

Besides the 31 medusae from Oshoro described above, 17 medusae from Kikonai were also examined. Among the latter, one medusa specimen, originating from the laboratory-reared polyp collected on May 24, 1982, was liberated on the 30th day after the collection of the colony (see the preceding section). At liberation it was 1.5 mm high, 1.3 mm wide, 0.6 mm in length of manubrium, and 0.3 mm in breadth of stomach. It differed from the above-described specimens from Oshoro in two points: (1) the perradial pigment patches were absent; (2) the abaxial eye-spots were black in color. The pigment patches, however, appeared on the 3rd day. This specimen survived for 12 days, but died before attaining sexual maturity. Sixteen other medusae originating from five zooids removed from three colonies collected on August 7, 1986 were liberated within two days of collection of the colonies. The measurements, in mm, of these medusae of less than one day old were as follows: 1.06±0.07 (0.94–1.16) in width; 1.15±0.08 (1.00–1.25) in height; 0.44±0.04 (0.38–0.50) in length of manubrium; 0.31±0.04 (0.25–0.38) in breadth of stomach; 0.14±0.02 (0.13–0.19) in breadth of velum; 0.06 in thickness of mesoglea at the umbrellar apex. There were 32–45 nematocyst patches on their tentacles. The complement of nematocysts in the medusae from Kikonai was the same as that of the medusae from Oshoro except that no microbasic euryteles were found on the exumbrella.

The morphology of the present medusae within 24 hours of liberation from polyps is summarized as follows: the umbrella is 0.75–1.5 mm in height and 0.94–1.34 mm in width; the manubrium is 0.25–0.60 mm in length; the stomach is 0.22–0.38 mm in breadth; four pigment patches are present at the junction points of the stomach and the four radial canals; there are four tentacles with 32–55 nematocyst patches and an eye-spot is found on the abaxial side of each tentacular bulb; four kinds of nematocysts, desmonemes, atrichous isorhizas, basitrichous isorhizas, and

stenoteles, are found.

One immature medusa was collected from Oshoro by Dr. K. Konishi in a plankton sample of July 7, 1977. It was 1.0 mm wide, with black eye-spots and four red pigment patches on the manubrium. The mesoglea at the apex of the umbrella was 0.13 mm in thickness, the stomach was 0.31 mm in breadth, and the manubrium was 0.81 mm in length. In one tentacle 86 nematocyst clusters were present. The dimensions of nematocysts were as follows: desmonemes on the tentacles were 9.2 ± 0.6 (8.0–10.0) $\times 5.0\pm0.2$ (4.6–5.6), n=20; atrichous isorhizas on the tentacles were 10.8 ± 0.6 (9.8–12.0) $\times 5.8\pm0.3$ (5.2–6.4), n=20; stenoteles of the large type on the tentacles were 16.9 ± 0.4 (16.0–17.6) $\times 12.6\pm0.4$ (11.4–13.0), n=20; stenoteles of the small type on the tentacles were 11.9 ± 0.4 (11.2–12.8) $\times 8.2\pm0.2$ (7.8–8.6), n=20; and stenoteles on the oral lips were 12.9 ± 0.5 (12.0–13.6) $\times 9.0\pm0.4$ (8.2–9.6), n=20. Most of the features of this specimen accorded well with those of the above described specimens obtained in the laboratory, except that the manubrium was longer and there were more nematocyst clusters on the tentacles. More than two days might have passed since this specimen was liberated from a polyp.

Remarks. The morphology of the present newly liberated medusa agrees well with that of the specimens described in the earlier works. It is newly described in the present material that atrichous isorhizas occur on the tentacles and that stenoteles are found on the exumbrella (cf. Rees *et al.*, 1976, Table 1).

3. Mature medusa.

Medusae were reared in artificial seawater at 20°C and fed with *Artemia* nauplii. A rather quick maturation was observed. Measurements of the earliest mature medusae from Oshoro were as follows. In ten females of 3–4 days old, each produced 2 ± 2 (1–6) eggs on the manubrium (up to three eggs were produced in each quadrant), the umbrella was 1.55 ± 0.06 mm (1.40–1.60 mm) in width and 1.72 ± 0.08 mm (1.60–1.80 mm) in height, the mesoglea at the umbrellar apex was 0.12–0.15 mm in thickness, and the manubrium was 0.60–0.72 mm in length. These females originated from several zooids removed from two colonies collected on July 9, 1986. On the other hand, in five males of 3–4 days old, which were more globular than the females and had a shorter manubrium, the umbrella was 1.53 ± 0.09 mm (1.40–1.65 mm) in width and 1.58 ± 0.13 mm (1.50–1.80 mm) in height, the mesoglea at the umbrellar apex was 0.12–0.15 mm in thickness, and the manubrium was 0.50–0.60 mm in length. These males originated from several zooids removed from one colony collected on July 9, 1986. In both sexes of these medusae, the four orange or red perradial pigment patches were distinct and the interradial portion of the subumbrella was slightly projected beneath the umbrellar apex.

Two out of the five male specimens described above were reared at about 20°C for two months in artificial seawater (Fig. 3, A). From the 9th to 16th days they were kept in natural sea water supplied from Akkeshi Bay. By the 19th or the 20th day they had grown larger, measuring 2.1–2.3 mm in height and 2.1–2.2 mm in width, 0.8–0.9 mm in length of the manubrium, 0.3 mm in thickness of the mesoglea,

1.0–1.1 mm in breadth of the stomach, and 0.25–0.30 mm in breadth of the velum. The manubrium, on which the gonads developed interradially, was funnel-shaped in side view. The stomach was cruciform in shape in the aboral view (cf. Fig. 3, B). The gonads did not swell roundly as in the earliest mature medusae (Fig. 3, B). The four perradial pigment patches, orange in color, and the subumbrellar projections at the interradii had become distinct. When viewed from the aboral side, eight adradial ridges were found on the surface of the subumbrella, and the exumbrella had become octagonal. At about one month old, the apex of the umbrella was concave and the elongation of the perradial portion of the stomach along the radial canal was distinct. Growth continued until the medusae measured 2.3–2.4 mm in height and width and the mesoglea was 0.4 mm in thickness at the umbrellar apex.

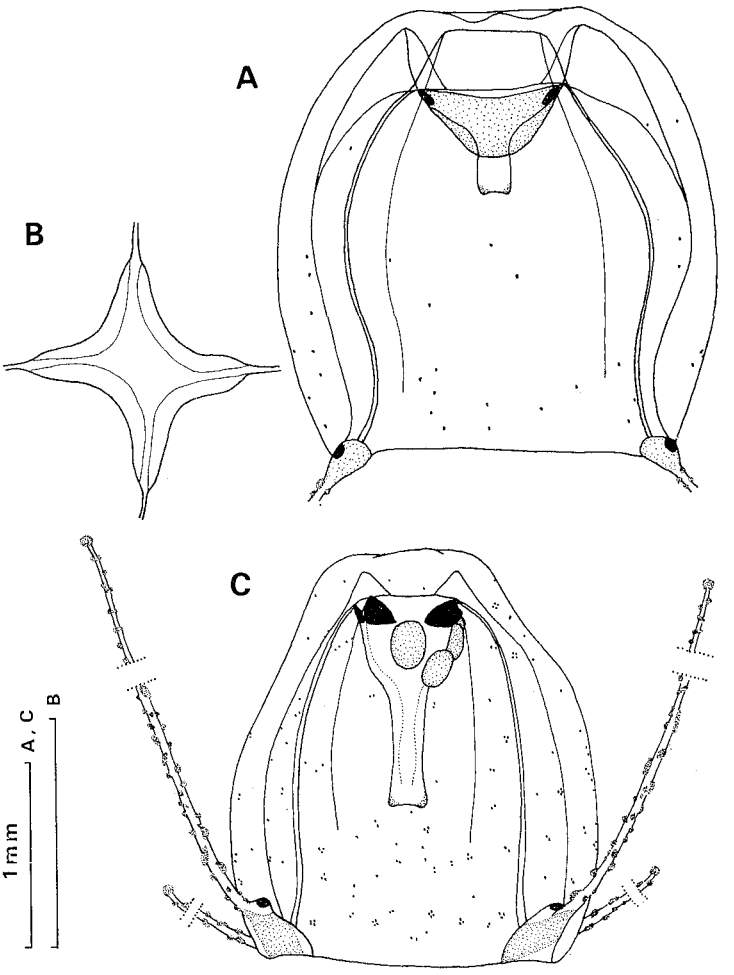

Fig. 3. A: a laboratory-reared male medusa of 34 days old from Oshoro. B: a cruciform stomach with gonads of the same specimen as A. C: a laboratory-reared female medusa of 22 days old from Oshoro. Note the formation of subumbrellar projection and adradial ridges in both sexes.

Three laboratory-reared female medusae were also examined in detail. They originated from several zooids collected from Oshoro on September 25, 1981. Two of them were reared at 20°C until eggs appeared on the 4th day, then they were kept at 12°C in filtered sea water supplied from Oshoro. The other female was reared at 12°C for 70 days, which was the maximum life span observed in the present material. This specimen was inactive on the 17th day and on the 35th to 42nd days. The former two females matured fully on the 7th day, while the latter matured on the 22nd day (Fig. 3, C). They were 1.8–2.2 mm high, 1.7–2.0 mm wide, 0.6–0.7 mm in breadth of the stomach, 0.2–0.3 mm in thickness of the mesoglea at the apex of umbrella, 0.7–1.1 mm in length of the manubrium, and up to 0.3 mm in breadth of the velum. Up to five eggs were produced in each quadrant on the upper half of the manubrium. The unfertilized eggs on the manubrium were about 0.19 mm in diameter. As the medusae developed, the oral lips became swollen by packing with nematocysts, and the interradial subumbrellar projections became distinct. The tentacular bulbs were red and the eye-spots were brownish-crimson in color. No distinct morphological changes had taken place in the life span of these medusae except that the umbrella attained 2.8 mm in height and width on the 49th day.

Six other medusae from Oshoro reared at 10°C in constant darkness were examined when they were one month old. Comparing these medusae with the above-described medusae reared at 12–20°C under natural conditions for light, it was noted that their eye-spots did not develop well and were sometimes absent.

Besides the above-described 18 medusae from Oshoro, the morphology of the earliest mature medusae from Kikonai was examined in two females of 5 days old and ten males of 6 days old. These originated from three colonies collected in 1986. The two females produced six and nine eggs, respectively, and their eye-spots were dark brown in color. The color of the eye-spots of the males was also dark brown. The morphology of the mature medusae from Kikonai was the same as that of the mature medusae from Oshoro described above. The measurements, in mm, of the Kikonai medusae were as follows: 1.6 ± 0.1 (1.5–1.7) in width; 1.7 ± 0.1 (1.6–1.8) in height; 0.59 ± 0.03 (0.55–0.65) in length of the manubrium; 0.15–0.20 in thickness of the mesoglea at the umbrellar apex; 0.5–0.6 in breadth of the stomach.

The nematocyst equipment of mature to spent medusae was examined in five specimens from Oshoro — three males of 26, 34, and 70 days old and two females of 28 and 36 days old. The nematocyst complement was also checked in four other specimens of 24–25 days old from Oshoro and two males of 17 and 19 days old from Kikonai. The nematocysts decreased in number on the exumbrella of aged medusae. On the oral lips stenoteles were found with dimensions 11.8 ± 1.0 (9.6–13.2) $\times$ 8.2 ± 0.8 (6.4–9.8), n=32. On the tentacles three kinds of nematocysts with the following dimensions were found: desmonemes were 8.9 ± 0.5 (7.6–9.6) $\times$ 4.6 ± 0.2 (4.2–4.8), n=34; basitrichous isorhizas were 13.0 ± 0.8 (11.2–15.4) $\times$ 9.5 ± 0.5 (8.8–10.4), n=20; stenoteles of the large type were 16.6 ± 0.7 (15.2–17.6) $\times$ 12.2 ± 0.7 (10.8–13.2), n=20; stenoteles of the small type were 11.7 ± 0.7 (10.4–13.0) $\times$ 7.8 ± 0.6 (7.2–8.8),

n=30. These nematocysts were nearly the same sizes as those found in the newly liberated medusae obtained in the laboratory and those found in the immature medusa collected from the sea. However, on the tentacles of these aged medusae, atrichous isorhizas were absent whereas basitrichous isorhizas, though small in number, were newly found.

The morphology of the mature and spent medusa is summarized as follows: the umbrella is 1.4–2.8 mm in width and 1.6–2.8 mm in height; the manubrium with four pigment patches is 0.5–1.1 mm in length; the mesoglea at the umbrellar apex is 0.12–0.4 mm in thickness and in this region the subumbrellar projection is formed interradially; three kinds of nematocysts, desmonemes, basitrichous isorhizas, and stenoteles, are found. The shape of the stomach is different in the two sexes, becoming cruciform in the male due to elongation of the perradial portion.

Remarks. The present medusae from Oshoro and Kikonai which were reared at 20°C matured more quickly than the specimens from Mutsu Bay reared at 17–20°C by Kakinuma (1961) and the specimens from Akkeshi reared at 15–18°C by Uchida & Nagao (1967). The present earliest mature medusa appeared on the 3rd day, when the size was very small, measuring 1.5 mm in umbrellar width. However, the present specimens reared at 10–12°C took much more time to mature. Comparing the present medusae with those described by Kakinuma (1961) and Uchida & Nagao (1967), the former grew larger, up to 2.8 mm in umbrellar height and width, and had more ova, up to five in a quadrant of the manubrium at one time. The pigment patches of the present specimens were variable in shape, ranging from triangular to rod-like in appearance (Fig. 3, A, C). Division of each of the four pigment patches was observed in the present medusae from Hokkaido, northern Japan, just as that described by Uchida & Nagao (1967) in the specimens from Manazuru, central Japan. This division is due to swelling of the stomach after the ingestion of food. The subumbrellar projections observed in the present well-grown medusa from Oshoro and Kikonai were previously noticed by Uchida & Nagao (1967) in the specimens from Manazuru. The umbrella of the present aged medusa in both sexes was not smoothly rounded as were the specimens from Akkeshi and Manazuru described by Uchida & Nagao (1967), but was truncated, sometimes forming a depression at the apex (Fig. 3).

4. Gametes and Larvae.

Many mature medusae less than a week old, which originated from two colonies collected from Oshoro on July 9, 1986, discharged eggs. Up to six eggs were released per specimen per day. The unfertilized eggs were mostly spherical in shape and milky white in color (Fig. 4, A), although some were ovoid in shape. Unfertilized eggs within one day of release were $174\pm13\,\mu m$ (152–200 μm), n=46 in diameter. Smaller eggs than these typical ones were sometimes found and these were $113\pm16\,\mu m$ (92–132 μm), n=8 in diameter. Egg-laying took place more than several times in the life span of medusa. No eggs developed parthenogenetically in the present medusae (see Kubota, 1987, p. 13).

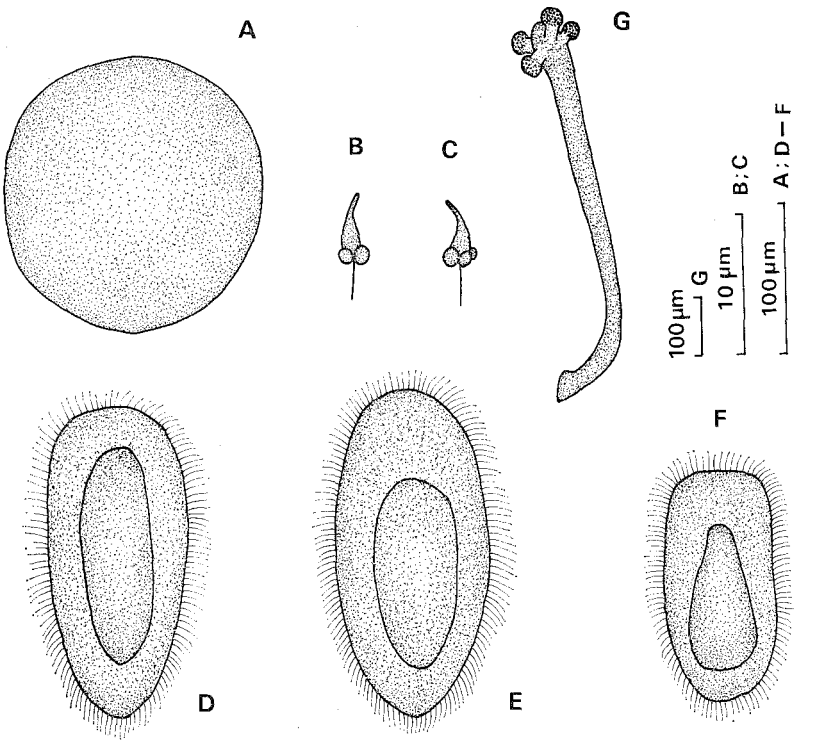

Fig. 4. A: an unfertilized egg. B,C: two spermatozoa. D: a well-developed half-day old larva without nematocysts. E: a 1.5 day old planula. F: a 16 day old planula, slightly contracted. G: a primary polyp.

The head of the spermatozoon was pointed and several, at least four, mitocondria were found. The length of the head and middle piece was about 4.8 μm, of which one-third was a thin process (Fig. 4, B, C). The maximum width was 2.0–2.4 μm. The tail was 54–58 μm in length.

Larvae were obtained by several crosses carried out in the laboratory at 20°C in artificial seawater, using many males and females originating from a total of six colonies collected at Oshoro on July 9 and 27, 1986. From a single pair, up to 11 larvae were produced per day. The half-day old larvae were oblong-ellipsoidal in shape with widened anterior portion, measuring 218 ± 30 μm (168–248 μm) in length and 105 ± 14 μm (88–124 μm) in width (n=6). They swam by means of cilia which were about 16 μm in length, rotating clockwise when viewed from the direction of movement (Fig. 4, D). Five of these larvae were squashed but no nematocysts had been produced yet. The 1.5–5 day old larvae (Fig. 4, E) possessed stenoteles and microbasic euryteles without the inclusion. The dimensions of these nematocysts in four planulae of 1.5–5 days old were as follows: microbasic euryteles were $8.2\pm$ 1.1 (6.4–10.4) $\times 4.2\pm0.6$ (3.4–5.6), n=21; stenoteles were 9.4 ± 1.4 (7.2–12.8) $\times 6.2\pm$ 0.8 (5.2–8.4), n=18. Planulae more than 6 days old also possessed the type of microbasic euyrtele with the inclusion. The dimensions of nematocysts in three planulae

of 6–12 days old were as follows: microbasic euryteles without inclusion were 9.2±1.5 (6.6–11.2)×5.0±1.1 (3.6–6.4), n=18; microbasic euryteles with the inclusion of which the diameter was 2.7±0.2 (2.6–3.2), n=5 were 9.7±0.4 (9.2–10.4)×4.4±0.2 (4.2–4.8), n=5; stenoteles were 12.6±2.3 (9.2–16.0)×8.9±1.8 (6.4–12.0), n=19. The sizes of nematocysts tended to be larger as the planulae grew.

Another successful conspecific cross test was carried out in 1986 in four cases in which females from Oshoro and males from Kikonai were used. In a single pair, up to 11 larvae were produced for one day. The nematocyst equipment of three planulae of 10–16 days old (Fig. 4, F) was the same as that of the above-described planula that were more than 6 days old. The measurements of nematocysts in these planulae were as follows: microbasic euryteles without the inclusion were 9.8±1.0 (8.0–11.4)× 5.2±0.6 (4.2–6.0), n=12; microbasic euryteles with the inclusoin of which diameter was 2.9±0.4 (2.4–3.2), n=4 were 9.8±0.5 (9.2–10.4)×2.9±0.4 (2.4–3.2), n=4; stenoteles were 11.5±2.2 (8.8–15.2)×7.8±1.6 (5.8–10.4), n=16. Regardless of the ages of the larvae, no nematocysts were found at the widened anterior body portion.

Remarks. The observed direction of rotation of swimming of the larvae was opposite to that described for the larvae obtained by Uchida & Nagao (1967).

5. Primary Polyp.

Two planulae metamorphosed into primary polyps on the bottom of a polystyrene vessel. This occurred about a month after crossing medusae which originated from polyps collected at Oshoro on July 27, 1986. One primary polyp (Fig. 4, G) was 0.94 mm in total length and had four capitate tentacles, while the other seemed to be degenerating and was 0.31 mm long with three tentacles. They had no chitinous skeleton on the pedal disk. The nematocyst equipment was examined in the former. Two kinds of nematocysts were found on the tentacles and on the hydrocaulus, but were absent on the hypostome. The dimensions of these nematocysts were as follows: stenoteles of the large type on the tentacles were 12.8–14.6×9.0–10.4, n=2; stenoteles of the small type on the tentacles were 9.0–10.0×5.6–6.4, n=5; microbasic euryteles without the inclusion were 10.4–11.0×5.8–6.0, n=3; stenoteles on the hydrocaulus were 8.0–9.0×4.8–6.4, n=4; microbasic euryteles without the inclusion on the hydrocaulus were 10.4–11.0×5.6–6.0, n=3. The microbasic euryteles with the inclusion were absent in this primary polyp, and the complement of nematocysts was the same as that of the young planula of 1.5–5 days old.

Remarks. The external morphology of the present primary polyp agreed well with that of the primary polyp metamorphosed on a sea-alga by Uchida & Nagao (1967).

6. Nematocysts.

The difference in nematocyst complement in seven developmental stages of the Japanese *Hydrocoryne* is summarized in Table 2. The Japanese hydrozoan material discussed in this paper possesses a total of five kinds of nematocysts in its life. Among these nematocysts, stenoteles are always present in every developmental stage.

Table 2. Difference in nematocyst complement in seven developmental stages of *Hydrocoryne miurensis* in Japan.

	Desmonemes	Atrichous isorhizas	Basitrichous isorhizas	Microbasic euryteles without inclusion	Microbasic euryteles with inclusion	Stenoteles
Well-developed polyp				+	+	+
Regenerated polyp				+	+	+
Primary polyp				+		+
Newly liberated medusa	+	+	+			+
Aged mature and spent medusa	+		+			+
Planula 1.5–5 days old				+		+
Planula 6–16 days old				+	+	+

Except for stenoteles, the other kinds of nematocysts found in the polyp are totally different from those of the medusa. The two types of microbasic euryteles found in the polyp (see Fig. 2) and the planula are separately shown in the Table 2, since the microbasic euryteles with the inclusion, previously considered to be a specific character of the American *Hydrocoryne bodegensis*, are newly found in the present Japanese polyp. This type of nematocysts will be found in the primary polyp of the Japanese *Hydrocoryne* if more specimens were examined.

7. Chromosomes.

The chromosome number could be counted in 73 cells of 15 embryos. Thirty chromosomes were found in 60 of these cells, although 26–29, 31, and 34 chromosomes were found in other cells. Additionally, 30 chromosomes per cell were counted in five gonadal cells of two laboratory-reared male medusae, the paternal medusae of the above embryos. In the other one male medusa, 30 chromosomes were found in 22 gonadal cells, 28 in 8 ones, and 29 in 4 ones.

Thus, there is probably no sexual difference in the number of chromosomes and it is concluded that the number is $2n=30$.

Discussion

The characteristics of the present *Hydrocoryne* specimens agree well with those of the previously described materials in Japan, except that microbasic euryteles with a spherical inclusion have invariably been found in every new polypoid specimen, regardless of the collecting season, developmental stage, and locality. Hydrocorynid polyps lacking this peculiar type of nematocyst, as were described by Uchida &

Nagao (1967), were not discovered in the present study.

Comparison of the polyp, the newly liberated medusa, and the mature medusa of *Hydrocoryne* in Japan with those of *H. bodegensis* from America (Rees *et al.*, 1976), shows no distinct morphological differences between the polyps of the two except that two more types of stenoteles are found in the present polyps and the diameter of the solid inclusion of the microbasic eurytele tends to be larger in the Japanese polyp. The morphology of the newly liberated medusa does not differ between the Japanese specimens and *H. bodegensis*, either, even in the dimensions of nematocysts except that stenoteles have been newly found on the exumbrella of the present Japanese material (cf. Rees *et al.*, 1976, Table 1). Since few stenoteles are contained in each nematocyst cluster on the exumbrella, the presence of this kind of nematocyst in this developmental stage may have been overlooked previously. The rare presence of either of the two types of microbasic euryteles on the exumbrella of *H. bodegensis* and the present Japanese *Hydrocoryne* may accidentally take place. The pattern of pigmentation on the manubrium differs between the two medusae, but this distinction is difficult especially when the medusa has been just liberated from the polyp. No distinct morphological differences were detected when the present medusae were reared in different temperatures and/or light conditions. Sexual differences are subtle, only in the shape of stomach and gonads. The Japanese and the American *Hydrocoryne* are separable by the following characteristics of the mature and the spent medusa: (1) A broad and conical peduncle is formed in *H. bodegensis*, but it is absent in the Japanese *Hydrocoryne*; (2) Distinct subumbrellar projections are formed interradially in the Japanese *Hydrocoryne*, but are only weakly indicated in *H. bodegensis*; (3) Four perradial pigment patches are present in the Japanese *Hydrocoryne*, but these are indistinct or absent in *H. bodegensis*; (4) The oral lips do not reach the umbrellar aperture in the Japanese *Hydrocoryne*, but do so in *H. bodegensis*. The above differences were confirmed when the type specimens (holotype and paratypes) of *H. bodegensis* were examined by the author.

In summary, the American and the Japanese *Hydrocoryne* are possibly two distinct species, with all Japanese specimens being referable to *H. miurensis* Stechow, 1907, with the addition of the various above-described characteristics newly found in both the polyp and the medusa. Further study must be done in order to confirm the species status of *Hydrocoryne* from the Soviet Union — a check of the morphology of its mature medusa is required.

Remaining to be considered is *Sarsia respledens*, which was described by Bigelow (1909) as a new species from six nearly mature medusae (probably male) collected from Acapulco Harbor, Mexico. Among the characteristics of this medusan species, he stressed the possession of short tentacles with only six to ten nematocyst clusters. Although the number of nematocyst clusters on the tentacles of *S. respledens* is smaller in number than those of any medusa of *Hydrocoryne*, *S. respledens* and the mature medusa of *H. miurensis* closely resemble with each other, as was pointed out by Uchida (1927) and Uchida & Nagao (1967). Reexamination of the Mexican species, particularly to reveal its polyp, is needed to conclude the identity of the two. It is

possible either that two hydrocorynid species are distributed in the east Pacific or that the polyp of *S. respledens* will indeed turn out to be of the so-called *Sarsia*-type.

Summary

1. The life cycle, nematocyst equipment, and the chromosomes of *Hydrocoryne* in Japan were studied from the taxonomic point of view, using specimens collected from 1977 to 1988.

2. Polyps regenerated in the laboratory and well-developed polyps collected from the sea possessed four types of stenoteles and two types of microbasic euryteles regardless of season or locality. Among these nematocysts, the microbasic eurytele with a spherical inclusion was newly found in Japanese specimens.

3. In newly liberated medusae, stenoteles on the exumbrella and atrichous isorhizas on the tentacles were newly found.

4. In aged mature and spent medusae, stenoteles were still present on exumbrella, while on the tentacles atrichous isorhizas had disappeared but basitrichous isorhizas were newly found. During the life span of the medusa, a maximum of about two and a half months, the umbrella reached 2.8 mm in height and width, the apex of umbrella became truncated, sometimes with a depression, and interradial subumbrellar projections were formed. The stomach of the male medusa became cruciform in shape, appearing to be the only sexual morphological difference. The constant presence of pigment patches just below the junction points of the stomach and the radial canals was confirmed.

5. The external morphology of the gametes and some early developmental stages were described. The head of the spermatozoon was pointed. From a single pair up to 11 larvae were produced per day. The planula swam by means of cilia, rotating clockwise when viewed from the direction of movement. The planula and the primary polyp possessed microbasic euryteles and stenoteles. The microbasic euryteles with the inclusion were present in aged planulae 6–16 days old.

6. The chromosome number was determined as $2n=30$.

7. Comparing these results with previous descriptions, it is highly probable that only one species, referable to *Hydrocoryne miurensis* Stechow, 1907, occurs in Japanese waters, and this species is distinguishable from *H. bodegensis* Rees, Hand, et Mills, 1976 from America in having the above-described characteristics of the mature and spent medusa.

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