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Life-History and Taxonomy of an *Obelia* Species (Hydrozoa; Campanulariidae) in Hokkaido, Japan

By

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(With 7 Text-figures and 4 Tables)

The taxonomy of the hydroids belonging to the genus *Obelia*, a notorious genus in the Campanulariidae, was in an unsatisfactory state until the appearance of the revisory work by Cornelius (1975). His elaborate work was, however, carried out mainly based on the morphology of the polyp, and the connection of the medusa with its associated polyp still remains unclear. For a further development of the taxonomy in this genus, therefore, the present study was performed to give a full description of one of the *Obelia*-species found in Japanese waters, a large colonial hydroid which has been treated as *Obelia plana* (M. Sars) in Japan.

In this paper, using the material collected from Oshoro, Hokkaido, northern Japan, the description on the morphology of the polyp and medusa including the nematocyst equipment, the developmental process from the newly liberated medusa to the mature one, and the seasonal occurrence of both polyp and medusa as well as some biological observations are given. Besides these, the morphological variation of the polyp and the newly liberated medusa from other localities than Oshoro in Hokkaido is described, and the taxonomic treatment of the present hydroid is discussed.

Before going further, the author expresses his sincere appreciation to Prof. Mayumi Yamada, Hokkaido University, for his kind directions, giving the author the privilege of studying his many specimens of the present species which were collected and gathered during the last few decades, and for the critical reading of the manuscript. Thanks are also due to the staff of the Akkeshi and Oshoro Marine Biological Stations, Hokkaido University, for the use of the facilities and helping him in collecting material.

Materials and Method

A number of polypoid colonies of the present species were collected from Oshoro Bay near Otaru, facing the Japan Sea in Hokkaido, northern Japan by

skin diving, and out of which eight colonies with gonangia (abbreviation: C1–C8) were chosen as the material for the observation of the development of medusa. They were over 30 cm in hieght (up to 43 cm in C5) and were found on April 26, 1976 (C1–C3), May 21, 1976 (C4–C6), and May 24, 1976 (C7–C8), respectively, when the water temperature was 7.0–11.9°C.

Several parts of each of these colonies bearing many trophozooids and gonangia were cut off and were kept in glass-vessel in laboratory. Within a few days a large number of medusae were liberated, and they were reared in covered glass-vessels filled with filtered and boiled sea water supplied from Oshoro Bay at about 12°C in an incubator until they matured and degenerated (for about a month). They were fed with newly hatched *Artemia* nauplii, once a day to satiety. For the youngest and very young medusae, the food was torn into pieces and was given by hands with the aid of needles under the dissecting microscope. The medium and vessels were changed every day after feeding.

Many polypoid specimens collected from other localities than Oshoro in Hokkaido during 1933–1973, attaching to various substrata, which are the parts of the collections of Professor Yamada and preserved in alcohol, were also examined in order to reveal the variation range in the present hydroid. Most of the polypoid specimens including the specimens found recently (1976–1979) from Akkeshi Bay (near the mouth of Akkeshi Lake), facing the Pacific Ocean were collected by dredging within about 5 m in depth. They were usually attached to the oyster and some other pelecypod shells luxuriantly together with other hydroids or bryozoans. And the youngest medusa, which were liberated from the polyps at Akkeshi *in situ* or from several portions of some colonies taken back to the laboratory in Sapporo, were also examined to compare their morphology of the medusa with that of the medusa from Oshoro.

Almost all the measurements of the medusa were taken on the living specimens after relaxation by 8% $MgCl_2$ solution, while the measurements of the polyp were on the preserved ones except for the number of the tentacles. All the measurements, taking in the specimens in the well-extended condition, are shown in the order: minimum-mean-maximum value, standard deviation, and the number of specimens examined. The drawings of Figs. 2, 3, and 7 were made with the aid of a drawing apparatus.

Description of Polyp from Oshoro

In Oshoro Bay, the colonial polyp was found growing on the following various substrata which were found within several meters in depth: fishermen's fishing-net, rope, and float as well as some algae and mussel shells. The colony (Fig. 1) which consists of a number of upright growths from hydrorhiza showing various developmental degrees often grows well and attains a considerable length owing to the plentiful ramification, up to 43 cm in height, showing an appearance of a large alga.

The main stem is thick and stout, up to 0.44 mm in width, and the periderm is brown in color. Many branches are given off alternately from the main stem, and

they are divided into a large number of branchlets which further branch several times. The periderm becomes progressively thinner and lighter towards the younger portions of colony, showing milky white in color. On the portions just above the junctions of main stem, branch, and of branchlets, 2–16 (mean 6) annulations are present, and their number on the main stem is more than that on the branches or brachlets; the former is 5–8.3–16, 2.1, 62 while the latter is 2–3.9–6, 0.9, 74.

The hydrotheca (Fig. 2, B-D, J) is campanulate in shape, without teeth on the margin, and a trophozooid with a trumpet-shaped hypostome and single verticil of filiform tentacles, 20–26.5–30, 3.18, 13 in number, is contained within it. The measurements of 35 hydrothecae of several colonies are as follows: 0.38–0.51–0.63 mm, 0.06 in length and 0.28–0.34–0.41 mm, 0.03 in width, and the ratio of length/width is 1.2–1.5–1.7, 0.1. When the tentacles are extended, they are arranged alternately elevated and depressed. Just below the hydrotheca several (3–6) annulations are present. The polyp proper is milky white in color.

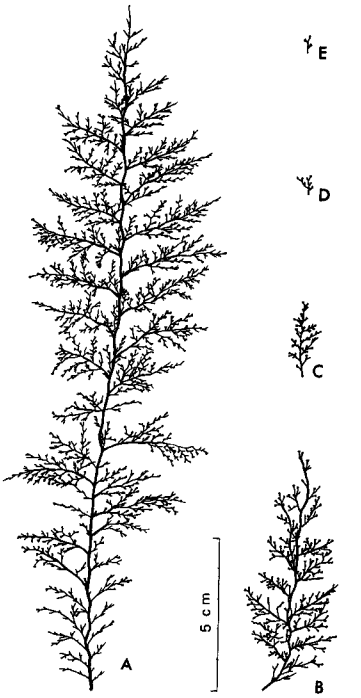

Fig. 1. A-E: Several upright growths from hydrorhiza of different growths (without gonangia) in a colony collected from Oshoro Bay (1/VII/1976).

The gonangium, in which many medusa-buds are produced, is borne on the axils of the branches or branchlets, usually one on each axil, rarely two (Fig. 2, A, B). The fully-developed gonangium (Fig. 2, B, G-I) is elongated obconical in shape, with a small collar at the distal end, which is indistinct in undeveloped one (Fig. 2, A, E, F). The proximal part of the gonangium becomes gradually slender, continuing into a short annulated stalk; and the gonotheca is nearly smooth. The size of 45 fully-developed gonangia of several colonies excluding collar and stalk is 0.84–1.15–1.44 mm, 0.16 in length and 0.36–0.45–0.56 mm, 0.06 in width, and the ratio of length/width is 2.1–2.6–3.0, 0.2.

The development of gonangium from a tiny bud (cf. Fig. 2, A) to the fully-developed form was completed within about a week at 12±2°C in laboratory, and it was observed that from the orifice of the collar at least 11 medusae, up to 16 ones, were liberated. It was observed that the gonangium produced in laboratory is to some extent smaller than that produced in the sea.

In Oshoro Bay, on the other hand, the well-grown colony bearing gonangia was found in April and May, and the colony without gonangia was in June and July.

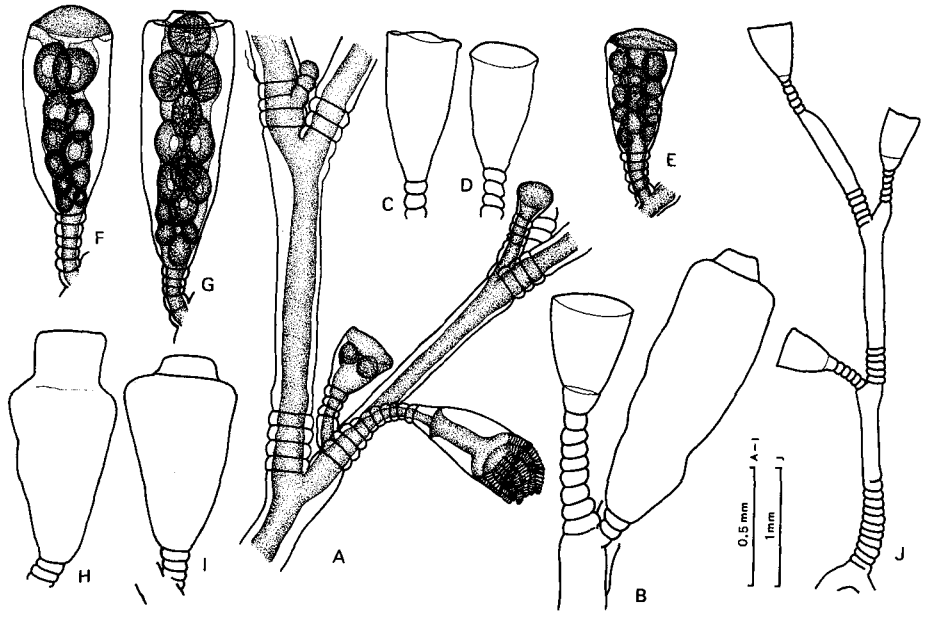

Fig. 2. Portions of polypoid colonies collected from Oshoro Bay. A: a portion of branch with a tiny bud of gonangium (C1). B: a portion of branch with a fully-developed gonangium which already produced in the sea when collected (C3). C, D: two hydrothecae (C2), note no teeth on the margin. E, F: two developing gonangia (E: C3, F: C1), note the medusa-bud without tentacles. G: a fully-developed gonangium produced in laboratory at 12°C (C1), note the medusa-buds with tentacles near the collar. H, I: two gonothecae already produced in the sea when collected (C3). J: magnified drawing of a very small upright growth from hydrorhiza which is shown in Fig. 1, E.

After that time the trophozooid begins to degenerate.

Description of Medusa from Oshoro

The umbrella of newly liberated medusa within a day after liberation (Fig. 3, A) is disk-shaped, and it is about 0.4 mm in diameter. The youngest medusa has four smooth radial canals, a ring canal, a reduced velum, a short manubrium with four simple oral lips, usually 24 marginal tentacles, and eight statocysts. On nearly middle of the radial canal (slightly toward the umbrellar margin) the rudiment of gonad, oval in shape, is present. However, it was observed that in the youngest medusa liberated from a portion of a colony (C3) which was cut off and reared for eight days in laboratory without feeding the number of tentacles was fewer than 24 and 16–17.5–20, 1.41, 15 in number. These medusae had also

four gonads and their umbrellar diameter was 0.38–0.43–0.44 mm, 0.02, 15 which was the equal size of the medusa to the above-described medusa with 24 tentacles.

During the life-span of the medusa, for about a month, the development of medusa was observed using a number of reared specimens liberated from eight different polypoid colonies (C1–C8), examining the same specimens during the observation period or examining several specimens picked up from the mass culture on each observation (Tables 1, 2; Figs. 3–5). It was found that the rate of the development of medusa is not much different between the colonies, so the mean value and range of the measurements of every colony are caliculated and the growth curve is plotted, while the mean value of each colony is shown (Fig. 5). The rapid growth is observed for about three weeks after liberation (Fig. 5, T, W; Table 1). The umbrellar diameter becomes nearly twice as large as that of the

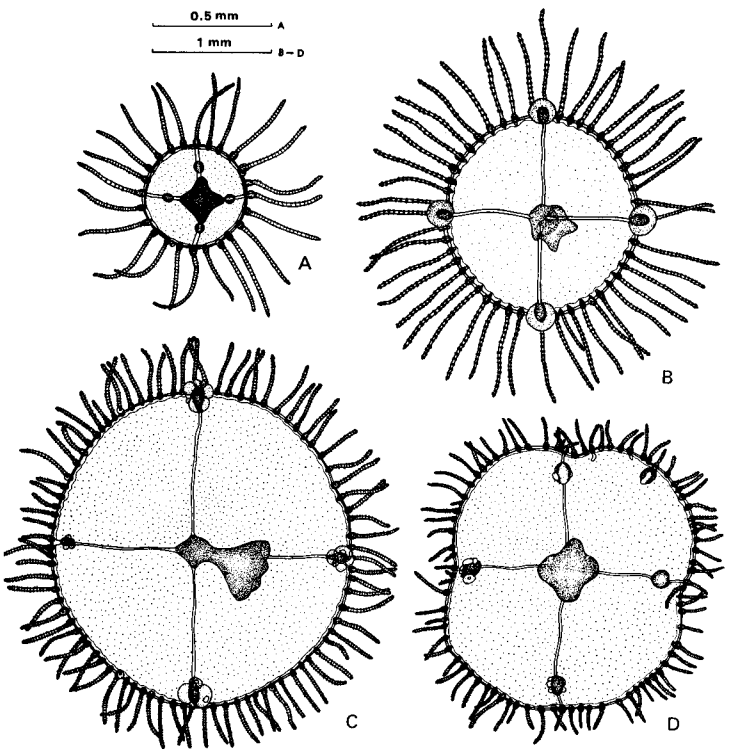

Fig. 3. Some laboratory-reared medusae on various developmental stages, oral view, in living state. A: a youngest medusa within several hours after liberation (C6), note a statocyst containing two statoliths and the mouth is opened. B: a male mature medusa 16 days old (C1), note seven statocysts. C: a female mature medusa 22 days old (C4). D: a spent female medusa [24 days old (C4), note the fifth gonad and the protrusion of endodermal canal in two tentacular bulbs in a quadrant.

Table 1. Measurements of various body portions

Age (days)	C[1)]	Umbrellar diameter	Number of tentacle	Number of statocyst
1	8	0.31-0.43-0.58 0.08, 95	21-23.9-25 0.48, 95	8-8.0-8 -, 95
2	3	0.59-0.72-0.81 0.05, 45	23-26.5-32 2.86, 45	4-7.7-8 -, 45
5	3	0.66-0.86-1.09 0.10, 71	24-33.7-45 5.25, 71	-
7	5	1.00-1.17-1.38 0.11, 27	43-47.4-50 1.31, 27	7-7.9-8 -, 27
14-16	8	1.30-1.89-2.40 0.22, 70	48-60.2-81 7.71, 70	7-7.6-8 -, 70
21-30	6	2.00-2.44-3.10 0.24, 62	66-81.8-95 5.24, 62	5-7.7-8 -, 61

1): total number of colonies from which the medusae come
2): length from center of stomach to middle portion of gonad/radius of umbrella.

youngest medusa on the second day, when some tentacles (up to nine tentacles in a medusa), are newly produced, though they are still short. About a week after liberation the umbrellar diameter becomes nearly three times as large as that of the newly liberated medusa, and the number of tentacles becomes nearly twice as many as that. When two weeks passed, the medusa matures (Fig. 3, B) and the discharge of sexual gametes is observed in many specimens of both sexes. Accompaning with the maturity and discharge of sexual gametes the umbrellar diameter and the number of tentacles of medusa still increase for about a week after that time, but on and after three weeks from liberation most of the gonads were degenerated and the medusan form became nearly fixed (Fig. 3, C; Figs. 4 and 5). The tentacles do not increase more in number, so 66–95 ones, three to four times as many as the number of tentacles of the youngest medusa, are present (Fig. 5, T); and the increase of umbrellar diameter also nearly stops, so the medusa is 2–3 mm in diameter, about six times as large as the diameter of the youngest medusa (Fig. 5, W). With the development of medusa, on the other hand, the position of gonad on the radial canal changes as shown in Fig. 5, R. The position shifts rapidly from the middle portion of the radial canal to the distal portion of it in a week after liberation, and thenceforce it does not change further. The mature male gonad is round in shape (Fig. 3, B). The core of the gonad of both sexes is orange (due to the carotin of *Artemia*) and the peripheral portion is green in color. Then, several tentacles begin to reduce on the 24th or the 25th day after liberation, and almost all of the medusae degenerate within a month. It was observed that in a 28 days old specimen some endodermal canals of tentacles extended into the jelly and one of which bore a gonad, so five gonads were present as an unusual case (Fig. 3, D).

of medusa on various developmental stages (in mm).*

Number of statolith	Length of gonad	Width of gonad	Position of gonad[2)]
8-8.2-10	0.04-0.05-0.07	0.03-0.04-0.05	0.51-0.61-0.75
-, 95	0.01, 50	0.01, 50	0.05, 50
4-7.7-9	-	-	-
-, 45			
-	-	-	-
7-8.3-11	0.11-0.14-0.18	0.09-0.14-0.19	0.72-0.93-1.00
-, 27	0.02, 27	0.03, 27	0.07, 27
7-8.3-10	0.20-0.25-0.30	0.20-0.23-0.28	0.93-0.98-1.00
-, 25	0.03, 25	0.03, 25	0.02, 25
5-7.7-10	0.22-0.28-0.35	0.20-0.28-0.40	0.87-0.96-1.00
-, 37	0.04, 25	0.04, 25	0.03, 31

* Measurements are shown in the order, minimum-mean-maximum value, standard deviation, and the number of specimens examined.

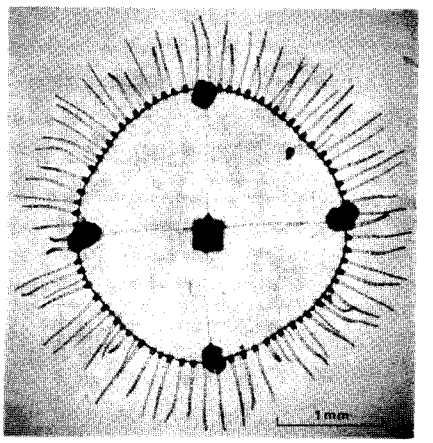

Fig. 4. A female mature medusa 21 days old with 86 tentacles and eight statocysts (C6), in living state.

In the development of medusa, the number of statocysts or that of statoliths in a statocyst does not change, namely usually eight statocysts, two in a quadrant, are present, but rarely less than eight; and a statocyst usually contains a statolith, rarely two or none (Table 1).

One of the important characteristics of medusa, the number of tentacles, is counted in every quadrant at various developmental stages (Table 3). In the young medusa as the newly liberated one or the seven and less days old one, the varia-

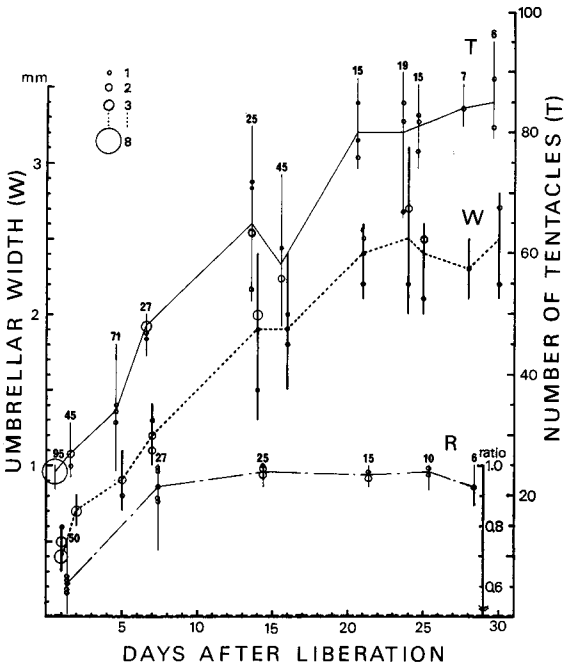

Fig. 5. Successive change of the umbrellar width (W), the number of tentacles including developing ones (T), and of the position of gonad on radial canal (R: length from center of stomach to the middle point of gonad/radius of umbrella) in the development of medusa. Note when W,T, and R are drawn they are slightly moved each other prevent from overlapping, and the mean value of the medusa liberated from the every different colony is shown by the size of circle (overlapping of these values is shown by the size of circle) on the bar (range), and the line is drawn by connecting the mean value of whole colonies.

tion range is narrow, six tentacles are present in almost all of the quadrants of the former and 12 tentacles in most of the quadrants of the latter, while in the grown medusa, the variation range is quite wide due to the difference of the development of each individual medusa, 12–17 tentacles are frequently found in the 14 or 16 days old medusa and 19–22 ones are in the 21–30 days old medusa.

On the other hand, the nematocyst equipment of the present species in the polyp and the newly liberated medusa was already reported by the author (Kubota, 1975) based on the specimens collected from the same habitat (Oshoro Bay). In the present study the nematocysts were examined in the grown or mature medusa as well as the youngest medusa. There were no nematocysts on manubrium and exumbrella, and only one kind of nematocysts, basitrichous isorhizes, is found on tentacles. The measurements (length $\times$ width of undischarged capsules) are as follows: in the youngest medusa within a day after liberation (three specimens examined), 6.3–6.9–7.4, 0.29$\times$1.9–2.0–2.2 μ, 0.08, 30; in the grown medusa 7 days

old (five specimens examined), 5.9–7.0–7.6, 0.41×1.8–2.0–2.2 μ, 0.10, 60; in the female medusa 21 days old (two specimens examined), 6.7–7.4–7.6, 0.23×1.9–2.0–2.3 μ, 0.10, 30. As a result, the constitution and size of nematocysts are same in all the developmental stages of medusa, though microbasic mastigophores which were found in some of the specimens of the youngest medusa in the previous examination were not found. It was observed that in the previous examination the measurements of 50 youngest medusae within one day old liberated from some polyps collected on May 9, 1975 were 0.28-0.45–0.60 mm, 0.06 in umbrellar diameter and 18–23.0–25, 1.18 in the number of tentacles, which are well in accord with the present measurements.

According to the medusan survey carried out for consecutive five years (1976–1980) in Oshoro Bay, a number of medusae which probably belong to the present species were captured from April to June, in that period the mature medusa appeared together with the newly liberated medusa. It was observed that (1) Most of the newly liberated medusa had 24 tentacles, while some had 20–23 ones, (2) Almost all of the specimens of different growths have eight statocysts and eight statoliths (one statolith in a statocyst), although there were some rare cases in which six or seven statocysts were found or two statoliths were contained in a statocyst, (3) The mature medusa found in the sea grows larger than the reared one in laboratory and the umbrellar diameter attains over 3.0 mm (up to 5.3 mm) and most of these specimens have 96±10 tentacles, with an exception of a female specimen of 4.9 mm in diameter with 127 tentacles (Table 4), (4) The well-developed gonad of both sexes is round and large, measuring 0.6 mm in diameter, and the core is light orange and the peripheral part is green in color, (5) In two male and one female specimens collected from the sea which are larger than the laboratory-reared ones (over 3.5 mm in diameter) the nematocyst equipment was examined. The constitution and size are not different between female and male medusa, and basitrichous isorhizes of 7.2–7.8–8.8, 0.36×2.0–2.3–2.4 μ, 0.14, 50 nematocysts were found, which are slightly larger than the nematocysts of reared specimens.

Notes on Some Early Developmental Stages

By rearing of a number of (about 60) mature medusae collected from Oshoro Bay at 6.5–10°C, some early developmental stages and their nematocyst equipment were observed.

The shape of a spermatozoon is similar to that of *Phialidium haemisphaericum* from Oshoro (see Kubota, 1978), and the length of head and middle piece together is 2.6–2.8 μ and the width of middle piece is 1.8–2.0 μ in 21 spermatozoa from two specimens. A discharged egg is spherical in shape, and the diameter is 180–194–230 μ, 13.6 in 26 unfertilized or fertilized eggs.

It took about several days to become a free-swimming planula from the discharged egg through a typical coeloblastula. All the planulae actively rotated clockwise when they were observed from the direction of proceeding. The length of

Table 2. Number of tentacles of a medusa

Age (days)	M(C)*	21-23	24	25-28	29-32	33-36	37-40	41-44	45-48
1	95(8)	10	83	2					
2	45(3)	4	14	17	8	2			
5	71(3)		3	12	16	13	22	3	2
7	27(5)							1	25
14-16	70(8)								2
21-30	62(6)								

* M(C): number of medusae

Table 3. Relative abundance of the number of tentacles in a quadrant

Age (days)	Q*	4	5	6	7 ····· 10	11	12	13
1	380	0.3	3.7	94.7	1.3			
7	108				4.6	7.4	86.1	1.9
14-16	280					1.8	12.1	15.4
21-30	248						0.4	0.0

* Q: number of

Table 4. Size and number of tentacles of mature medusa collected from Oshoro Bay.

Male mature medusa			Female mature medusa		
No. of specimens exmained	Umbrellar diameter	Number of tentacles	No. of specimens exmained	Umbrellar diameter	Number of tentacles
7	2.0-2.3-2.9mm, 0.31	69-79.3-94, 10.3	4	2.6-2.7-2.8mm, 0.10	63-86.8-96, 15.9
6	3.0-3.4-3.7mm, 0.32	79-85.3-96, 6.6	14	3.0-3.5-3.8mm, 0.30	80-92.9-112, 8.6
18	4.0-4.3-4.9mm, 0.29	86-94.0-109, 6.8	24	4.0-4.4-4.9mm, 0.27	85-97.3-127, 9.2
1	5.3	103	-	-	-

Measurements are shown in the order: minimum-mean-maximum value, and standard deviation.

a planula is 220–284–340 μ, 34 and the greatest width is 90–136–170 μ, 22 in 20 planulae. One kind of nematocyst, basitrichous isorhizes, is present in a planula and the size (length $\times$ greatest width of undischarged capsules) is 5.6–7.1–10.4, 1.1 $\times$1.6–2.1–2.6 μ, 0.31 in 95 nematocysts of seven planulae; the size is variable and somewhat different among the specimens. It was observed that the embryo just before a typical planula has neither cilia nor nematocysts. In this stage the length is 220–306–400 μ, 42 and the greatest width is 100–144–190 μ, 20 in 53 embryos.

on various developmental stages.

49-52	53-56	57-60	61-64	65-68	69-72	73-76	77-80	81-84	85-88	89-92	93-96
1											
13	14	8	10	12	9	1	0	1			
				2	0	5	17	19	16	2	1

(colonies) examined

of a medusa on various developmental stages, represented by %.

14	15	16	17	18	19	20	21	22	23	24
16.8	11.8	15.8	11.8	6.4	5.0	1.4	1.4	0.4		
1.2	1.6	0.8	4.8	7.7	12.1	18.5	20.2	19.0	8.5	5.2

quadrants examined

Morphological Comparison between the Materials from Oshoro and Those from Other Localities in Hokkaido

From various coasts of Hokkaido, besides from Oshoro, a number of specimens referable to the present species (Figs. 6, 7) were available to examine as summarized below.

	Locality	Collected date	Colony height (cm)	Presence of gonad
a)	Yagishiri Island	3/VIII/'79	12	−
b)	Lake Saroma	10/VIII/'75	11	−
c)	Rausu	9/VIII/'75	11.5	−
d)	Akkeshi	'32*	5.5	+
		11/VII/ '33*	3	+
		3/VIII/'33*	7.5	+
		VIII/'44	10	+
		27/VI/'53	6.5	+
		9/VII/'71	22	−
		10/VII/'76	24.5	−
		11/VII/'79*	32	+
e)	Kushiro	'47	23	+
f)	Hiroo	28/VIII/'44	18	−
g)	Muroran	8/VIII/'34	28.5	−
		V/'45*	18	+
		20/V/'71*	3.5	+

a)-g): each locality facing a) Sea of Japan, b)-c) Sea of Okhotsk, d)-g) Pacific Ocean

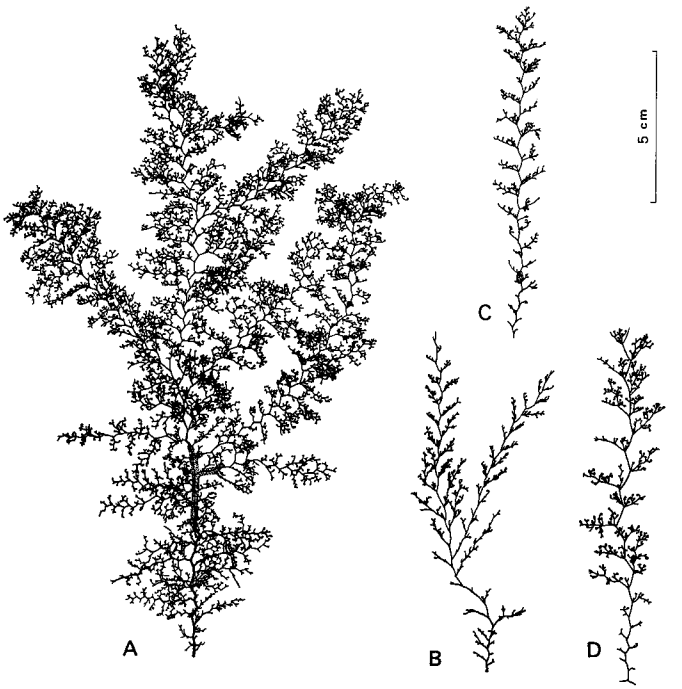

Fig. 6. Four polypoid colonies collected from various localities in Hokkaido, A: from Akkeshi Bay (11/VII/'79), B: from Yagishiri Island (3/VIII/'79), C: from Lake Saroma (10/VIII/'75), D: from Rausu (9/VIII/'75). The largest or larger upright growth from hydrorhiza is drawn for each locality. Note bryozoan colonies attached in A and C.

Among these specimens many hydrothecae and gonothecae of several colonies from both Muroran and Akkeshi (asterisked in above-description) were examined and the measurements (length excluding collar and stalk × greatest width, in mm and the ratio of length/width) are as follows: In the specimens from Muroran (V/'45), hydrotheca 0.46–0.53–0.64, 0.05×0.36–0.39–0.48, 0.04, 1.3–1.4–1.6, 0.1, 15 (Fig. 7, G), gonotheca 1.19–1.43–1.75, 0.13×0.44–0.49–0.56, 0.03, 2.5–2.9–3.5, 0.2, 30 (Fig. 7, H); ditto (V/'71) hydrotheca 0.44–0.54–0.64, 0.06×0.32–0.38–0.44, 0.04, 1.3–1.5–2.0, 0.2, 16 (Fig. 7, C), gonotheca 0.96–1.02–1.12, 0.08×0.32–0.37–0.42, 0.04, 2.5–2.8–3.1, 0.3, 6 (Fig. 7, D); in the specimens from Akkeshi in 1932–1979, hydrotheca 0.38–0.44–0.52, 0.05 × 0.28–0.31–0.36, 0.03 1.3–1.4–1.6, 0.1, 27 (Fig. 7, A), gonotheca 0.56–0.87–1.32, 0.19×0.28–0.36–0.44, 1.9–2.4–3.1, 0.3, 47 (Fig. 7, B).

As a result, the shape and the size of hydrotheca and gonotheca of the polyp from both the localities facing the Pacific Ocean are the same as those of the polyp from Oshoro facing the Sea of Japan excluding the gonotheca of the polyp

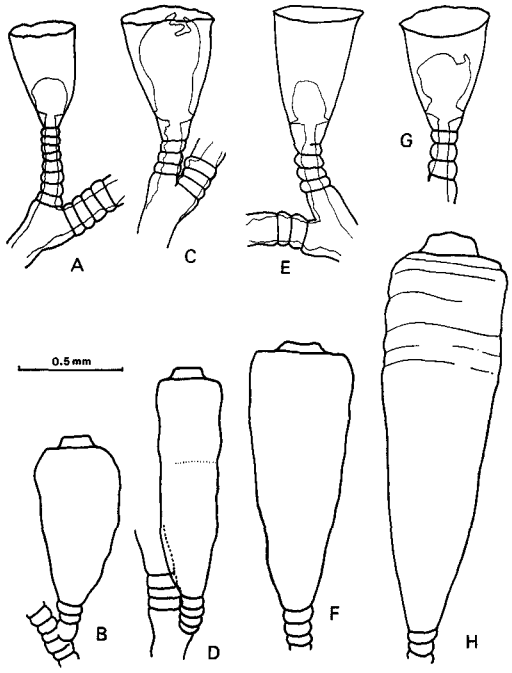

Fig. 7. Some hydrothecae and gonothecae of the polyps collected from Akkeshi (A, B: 11/VII/'79), Muroran (C, D: 20/V/'71; G, H: V/'45), and Oshoro (E, F: 11/V/'76), showing the morphological variation, note the even or slightly sinuous margin of the hydrothecae (A, C, E, G) and smooth but somewhat undulated or corrugated gonothecae (B, D, F, H).

from Muroran collected on May 5, 1945, which is remarkably long (Fig. 7, H). It is noticeable that (1) The number of tentacles of the polyp from Akkeshi collected on July 11, 1979 is 24–25.9–28, 1.45, 18, which is the same number as the polyp from Oshoro, (2) The main stem of the well-grown polyp only from Akkeshi Bay is dark brown or black in color, while light brown in others; and the whole body of some colonies collected from Akkeshi (August, 1954) and from Muroran (May, 1945) is brown in color conspicuously, (3) Other animals such as pycnogonids, small bivalves, bryozoans, and other hydroids were attached to the main stem or branch of the polyp from such localities as Akkeshi, Lake Saroma, and Muroran, while on the colony from Oshoro sea slugs were found eating the hydroid.

On the other hand, a large number of the newly liberated medusae from Akkeshi were obtained in laboratory (from six colonies collected on July 11, 1979), and the description of the important characteristics are as follows: the umbrellar diameter is 0.32–0.35–0.38 mm, 0.02 in 30 living specimens and 0.35–0.38–0.42 mm, 0.02 in 10 preserved specimens in formalin. In a quadrant of medusa, 4–6 marginal tentacles are present, and among 892 quadrants of 223 medusae four

tentacles were born in 8.6% of these quadrants, five tentacles in 42.8%, and six tentacles in 48.5%. The number of tentacles in a medusa, however, is much variable due to the presence of different number in each quadrant, and 17–24 tentacles are present. The number of medusae possessing various number of tentacles and its relative abundance (shown in percentage ratio) are as follows:

No. of tentacles	17	18	19	20	21	22	23	24
No. of individuals	1	5	18	31	34	69	46	19
%	0.4	2.2	8.1	13.9	15.2	30.9	20.6	8.5

Almost all the medusae (81 specimens out of 87 ones examined) possess eight statocysts, though in only six specimens seven statocysts are present; and in almost all the statocysts a statolith is contained (684 statocysts out of 690 ones of 87 medusae), while a statocyst contains three statoliths, four statocysts two ones, and a statocyst none. And one kind of nematocyst, basitrichous isorhizes, is found in three specimens of the newly liberated medusa within one day old, and the size (length × width) of undischarged capsules is 6.4–6.6–7.4, 0.26×1.8–2.1–2.4 μ, 0.13, 40.

As a result, in the specimens from Akkeshi the medusa with 20–23 tentacles is frequently observed and the most of the specimens had fewer tentacles than those from Oshoro, though the characteristics such as the umbrellar diameter, the number of statocysts and statoliths, and the nematocyst equipment are same between two localities. It was noticeable that the gonad was present near the stomach rather than the middle portion of the radial canal. And an aberrant newly liberated medusa was found, which was 0.36 mm in umbrellar diameter and had only three radial canals, and in each trisection there were 6, 6, 4 tentacles and 2, 2, 2 statocysts, respectively. In this medusa a statolith was contained in five statocysts, while two statoliths were in a statocyst.

On the other hand, two small medusae still contained in the gonangium of the polyp from Muroran (collected on May, 1945) were found, and the number of tentacle is 21 or 23.

Summary of the Morphology of the Present Hydroid in Hokkaido

The morphology of the present hydroid, which is commonly found around the coasts of Hokkaido, attaching to the various substrata, is summarized below in both polyp and medusa.

1) Polyp

Large colonial polyp with abundant ramification, attaining 43 cm in height. Main stem monosiphonic, thick and stout, and brown or black in color. A large number of branches or branchlets brown or milky white in color. 2–16 annulations on junctions of coenosarc with symmetrically thicked periderm. Campanulate hydrotheca without teeth, but sometimes with undulated margin, 0.38–0.51–0.64 mm in length and 0.28–0.36–0.48 mm in greatest width, the ratio of length/width 1.2–

1.5–2.0. 20–26–30 tentacles on hydranth. On axil of branch or branchlet elongated obconical gonangium containing many medusa-buds with short (0.1–0.3 mm in length and 0.1 mm in width) annulated (3–7, mostly 3 or 4) stalk and distinct collar (0.04–0.08 mm in height and 0.12–0.20 mm in width), gonotheca smooth but sometimes slightly undulated, and gonothecal size excluding collar and stalk 0.56–1.12–1.75 mm in length and 0.28–0.42–0.56 mm in greatest width, the ratio of length/width 1.9–2.7–3.5. Two kinds of nematocysts in trophozooid, basitrichous isorhizes on tentacle 6.5–7.3–7.6 μ in length and 1.9–1.9–2.1 μ in greatest width (undischarged state), while microbasic mastigophores on hydranth 8.4–9.1–9.5 μ in length and 1.9–2.1–2.4 μ in width (ditto).

2) Medusa

The youngest medusa within a day after liberation 0.28–0.41–0.60 mm in umbrellar diameter, with 16–25 (mostly 22–24) tentacles, 8 (rarely 7) statocysts containing a statolith per statocyst (rarely 0, 2, and 3), and immature small oval gonad on middle portion of radial canal or sometimes near stomach. 4–7 (mostly 5 or 6) tentacles and 2 statocysts in a quadrant. Laboratory-reared mature medusa 2.0–2.4–3.1 mm in diameter, with 66–82–95 tentacles, 8 (rarely 4–7) statocysts containing a statolith per statocyst (rarely 0 or 2), and gonads on each distal portion of four radial canals near umbrellar margin. 12–24 (mostly 19–22) tentacles and 2 statocysts in a quadrant. Mature medusa collected from the sea larger than the loboratory-reared one, attaining 5.3 mm in diameter and 127 tentacles (up to 33 tentacles in a quadrant). Two kinds of nematocysts on tentacle, constantly basitrichous isorhizes 5.6–7.0–8.8 μ in length and 1.4–2.1–2.4 μ in greatest width (undischarged state), while occasionally microbasic mastigophores 7.6–8.3–9.1 μ in length and 1.9–2.0–2.0 μ in width (ditto), and no nematocysts on exumbrella and manubrium.

Discussion

1) *Remarks on the present hydroid in Japanese and its adjacent waters*

Four *Obelia*-species, *O. dichotoma* (L.), *O. geniculata* (L.), *O. plana* (M. Sars), and *O. oxydentata* Stechow, have been recorded from Japan, and the present hydroid in Hokkaido, which forms the largest colonial polyp among these species in Japanese waters, has been treated as *Obelia plana* (Yamada, 1950 and 1959; Uchida et al, 1963; Hirohito, His Majesty the Emperor of Japan, 1969; Kubota, 1976), but its medusa has been poorly described until the present work reveals it in detail as described above. On the other hand, among the plankton samples at Oshoro in July probably of 1920 a large mature *Obelia* medusa which is 4 mm in diameter and with 120 or more tentacles, eight statocysts, and with gonads on radial canals near the bell margin was described under the name of *O. geniculata* by Uchida (1925).

Judging from the present study, the gonangia of the polypoid specimens from Akkeshi of the present species described by Yamada (1950) is a little shorter than

those of the present specimens despite of the well accordance of the shape and size of the hydrothecae as well as other characteristics between these two, and the mature medusa described by Uchida (1925) is referable to the present species (no polyp of *O. geniculata* has been recorded at Oshoro). It is noticeable that the smallest medusa (1 mm in diameter) which was also described at the same time by Uchida in 1925 had only 12 tentacles; this number is considerably fewer than that of the present youngest medusa in spite of its larger size. It is also noticeable that according to the plankton calender of Oshoro Bay compiled by Motoda (1971) *Obelia* medusae appeared in February and March (spring) and also in September (autumn); some of the medusae at least found in spring are possibly referable to the present species.

On the other hand, some hydroids probably referable to the same species as the present hydroid have been so far recorded from the following regions near Japan: It was recorded at first from Vladivostok by Marenzeller (1902) under the name of *O. flabellata* (Hincks), and successively recorded from Vladivostok, Sachalin, in Sea of Japan, and in Sea of Ochotsk by Linko (1911) under the name of *O. longissima* (Pallas), and furthermore from Vladivostok by Yamada (1957) under the name of *O. plana* (M. Sars) (see Stechow, 1923a; Yamada, 1957). Naumov (1969), in the hydroid fauna in USSR, described the large colonial hydroid in detail including its newly liberated medusa and mature medusa under the name of *O. longissima* (cf. discussions 2) and 3) described below). Stechow (1921, 1923a and b), who recorded *O. flabellata* from the Mediterranean and also studied Japanese hydroids formerly, considered that *O. flabellata* (Hincks, 1866) is synonymous with *O. plana* (M. Sars, 1835) and the latter has priority in its nomenclature. It should be mentioned here that this species name was originally assigned to the medusa by Sars under the name of *Thaumantias plana*, on the other hand *O. flabellata* and *O. longissima* were to the colonial polyp (see Mayer, 1910; Cornelius, 1975).

O. plana (=? *O. flabellata*) is widely distributed in the North and South Atlantic and also in the North Pacific, while *O. longissima* (Pallas, 1766) is also a world-widely distributed species (see Mayer, 1910; Nutting, 1915, Fraser, 1944; Yamada, 1959). But until the appearance of the revision by Cornelius (1975) (cf. discussion 3)) no particular or due taxonomic considerations on these two related hydroids seems to have been paid and they have been treated as the different species in spite of the subtle morphological difference between them. It is notable that Cornelius (1975) considered that *O. chinensis* Marktanner-Turneretscher, which was recorded from Yellow Sea, the coast of China and resembles *O. plana* (see Mayer, 1910), is synonymous with *O. dichotoma* (L.).

2) *Morphological comparison of the present hydroid with some other related hydroids*

Comparing the present polyp with some other related polyps recorded from various localities in the world, particularly with reference to the revision by Cornelius (1975), most of the characteristics, mainly the shape and the size of the

hydrotheca and the gonotheca, of the present polyp in Hokkaido are well in accord with those of the following polyps (they are *O. dichotoma* sensu Cornelius, 1975) designated as *O. dichotoma* (L.) in Europe (Cornelius, 1975) and in South Africa (Millard, 1975) and *O. longissima* (Pallas) in USA (Calder, 1975), in USSR (Naumov, 1969), and in New Zealand (Ralph, 1957), etc.

On the other hand, the newly liberated medusa of *O. dichotoma* sensu Cornelius, 1975 from various localities was described as follows, though somewhat fragmentarily: the number of tentacles is 16 (as *O. dichotoma* (L.) by Hincks, 1868; as *O. dichotoma* (L.) by Mayer, 1910, but occasionally 24; as *O. dichotoma* (L.) and *O. commissuralis* McCrady by Nutting, 1915; as *O. hyalina* Clarke = *O. griffini* Calkins by Vannucci, 1955), 24 (as *O. pyriformis* Verrill by Mayer, 1910; as *O. dichotoma* (L.), *O. longissima* (Pallas), *O. flabellata* (Hincks), *O. griffini* Calkins, and *O. surcularis* Calkins by Nutting, 1915; as *O. longissima* (Pallas) by Hincks, 1868, but 20–24; as *O. longissima* (Pallas) by Naumov, 1969, but 20–24), and 28 (as *O. gracilis* Calkins by Nutting, 1915), etc. In these hydroids, though the presence of gonad and its position are not fully described, this characteristic is quite variable, as is the same case in the number of tentacles described above. It is noticeable that the newly liberated medusa of *O. plana* (=? *O. flabellata*) is 0.4–0.5 mm in diameter and has 24 tentacles and oval gonads on near the middle of the radial canal (see Mayer, 1910); these characteristics are entirely in accord with those of the present hydroid.

Besides these, according to the monograph on the British medusae by Russell (1953), (1) Hartlaub (1894) reported the number of tentacles of the newly liberated medusa of *O. longissima* (a larger colony of *O. dichotoma* sensu Cornelius, 1975) as 24, and (2) Brown (1903) reared the medusa liberated from the polyp of a smaller colony of so-called *O. dichotoma*, obtaining a result in which the newly liberated medusa had 16 tentacles and no gonads, while its mature medusa 23 days old (2.0–2.5 mm in diameter) had up to 84 tentacles and the gonad on nearly middle point of the radial canal. Together with the medusan specimens found among the plankton samples, Russell (1953) recognized the two morphologically different mature medusae of *Obelia* with gonads on the middle of the radial canals, and allocated them to their associated polyps provisionally as follows: the mature medusa of a smaller colony of *O. dichotoma* (L.) is up to 2.5 mm in diameter and has less than 100 tentacles, while that of a larger colony of *O. dichotoma* (=*O. longissima*) is up to 6 mm in diameter and has 150–200 tentacles. Cornelius (1975) considered that the different morphology of their medusae is possibly due to the different environment (water mass or feeding opportunity) where they grow up. Furthermore Naumov (1969) reported both the newly liberated medusa and the mature medusa of *O. longissima* (*O. dichotoma* sensu Cornelius, 1975) from USSR, and the former is about 0.5 mm in diameter with 20–24 tentacles and the gonad on nearly middle of the radial canal, while the latter is up to 4 mm in diameter and has up to 100 tentacles and the gonad on distal part of the radial canal near umbrellar margin.

Consequently, the important characteristics of both polyp and medusa of *O.*

longissima from USSR described by Naumov (1969) are entirely in accord with those of the present hydroid in Japan. The newly liberated medusa of *O. longissima* ('*O. dichotoma*') in Britain, on the other hand, seems to resemble the present medusa in Japan, but its mature medusa is different, particularly in the position of gonads, even if the above-mentioned Russell's allocation (1953) is not right; while both the newly liberated medusa and mature medusa of so-called *O. dichotoma* in Britain are different from those of the present hydroid, namely the Japanese youngest medusa has already gonad at liberation and has also more tentacles, and the position of the gonad of the Japanese mature medusa is far more distal on the radial canal despite of the equal umbrellar diameter and the equal number of tentacles between them, hence the morphology of both the polyp and medusa of so-called *O. dichotoma* in Britain is clearly different from that of the present hydroid in Japan. The characteristics of the youngst medusa such as umbrellar diameter, the number of tentacles, and the position of gonad, however, may be variable and changable according to some conditions of the mother polyp and/or the environment as is observed in the present materials, while the position of gonad in the mature medusa is possibly an important character.

It should be mentioned here that the nematocyst equipment of *O. longissima* or *O. plana* has been scarcely examined, and only one type of one kind of namatocyst (probably microbasic b-mastigophores) is found in the former (Cornelius, 1975; Östman, 1979), while two types of one or two kinds of nematocysts in the latter, though it is occasionally two types as is described above. More examinations on the nematocyst equipment in both polyp and medusa of different growing stages are needful for further taxonomic discussion.

3) *Systematic considerations*

As is often declared, the classification of the hydroids belonging to the genus *Obelia* has been confused and remains unsettled. Recently this notorious genus *Obelia* was elaborately revised by Cornelius (1975) and he recognized only three valid species, *O. bidentata* Clarke, *O. dichotoma* (L.), and *O. geniculata* (L.) based on the morphology of polyp. According to his system, one of the recorded Japanese *Obelia*-species *O. oxydentata* Stechow above-mentioned is synonymous with *O. bidentata*, but he did not mention about the systematic treatment of the present larger colonial polyp from northern Japan. The present polyp, however, is assignable to *O. dichotoma* sensu Cornelius because he lumped various *Obelia*-species from a small colonial polyp to a large one under a single species *O. dichotoma* (L.).

I agree with his attitude to reduce the number of species in this genus, because almost all of the useful and important characteristics such as colony size, branching mode, minute morphology of various body-parts (hydrotheca, gonotheca, pedicel, etc.) of polyp are considerably variable among the different colonies as well as among the upright growths from hydrorhiza of each colony (cf. assessement of characteristics in the genus *Obelia* made by Cornelius, 1975). Moreover the

number of characteristics of both polyp and medusa is very few, which I experienced previously in the systematic investigations on *Cytia* (=*Phialidium*)-species in Japanese waters (Kubota, 1978 a and b) belonging to the same Campanulariidae. Therefore in morphology the accurate and apparent limitation of *Obelia*-species is very difficult and so many species cannot be recognized. I also consider that a large number of *Obelia*-species described in former times are possibly ascribed to the mere phenotypic variations caused by the different environmental conditions such as substratum, water temperature, salinity, water pressure, light, food, etc. or by the morphological difference due to the different life-stages as is alredy stated by Mayer (1910) and Cornelius (1975), though it is possible that a certain genetic difference which displays a trifle morphological distinction is present among them despite of the similar external morphology.

As is mentioned in discussion 2), Cornelius (1975) concluded that many larger colonial polyps previously designated as *O. longissima* (Pallas, 1766), *O. commissuralis* McCrady, 1857, *O. flabellata* (Hincks, 1866), and *O. australis* von Ledenfeld, 1884, etc. from various localities in the world are synonymous with the very small colonial polyp *O. dichotoma* (Linnaeus, 1758), particularly for the existence of morphologically intermediate forms and the similarity of isolated second-order hydrocauli among them. Although the morphology of the polyp of the present hydroid closely resembles the larger colony of *O. dichotoma* sensu Cornelius, that of the medusa is different, particularly in the position of gonad. Therefore the assignment of the reasonable systematic position of the present hydroid which has been so far treated under the name of *O. plana* in Japan is a problem. According to the observation by the author in Oshoro Bay, Akkeshi Bay, and Muroran in Hokkaido, besides the large colonial present hydroid described here, numerous small colonial polyps referable to the so-called *O. dichotoma* were commonly found, attaching to the various substarata such as algae, rock, stone, barnacle shell, crab carapace, mussel shell, etc., though its medusa, especially the mature medusa, has been poorly known. And among the plankton samples in Oshoro Bay two kinds of mature medusae are discriminated in the character of the position of gonad, one is the form with gonad on distal part of radial canal (belonging to the present species) and another is the form with gonad on nearly middle of radial canal, though the latter was rarely found. Furthermore it is noteworthy that the large colonial present polyp has been recorded exclusively in Hokkaido, northern Japan while the small colonial polyp, so-called *O. dichotoma*, has been recorded from various localities from northern to southern Japan. Hence so-called *O. dichotoma* and the present hydroid in Japanese waters are treated here separately.

Considering these facts as well as the above-mentioned discussion it can be concluded in two ways: (1) The present hydroid and the British one (type-species) are the same species and they are referable to *O. dichotoma* based on the classification of polyp in spite of their difference of the morphology of medusae, though there is a suspiction that *O. dichotoma* and *O. longissima* are not the same species; (2) The present hydroid and the British one are the different species in spite of their

resemblance of polypoid morphology, so their morphology of medusae are different.

The author has been studying the life-history of a smaller Japanese hydroid, so-called *O. dichotoma*. Its systematic relationship to the present hydroid will be revealed in the near future, when the taxonomic status of these two Japanese hydroids will be apparent. Furthermore the life-history of the other two *Obelia*-species, *O. geniculata* (L.) and *O. bidentata* Clarke, which also found in Japanese waters should be clarified in order to discuss the taxonomy and systematics of *Obelia*-species, because their medusan stages have been scarcely known in Japan as well as in the world.

Summary

The life-history, particularly the development of medusa reared in laboratory, of a large colonial hydroid from Hokkaido which has been treated as *Obelia plana* (M. Sars) in Japan, is described and illustrated in detail, using mainly the specimens collected from Oshoro. The polypoid colony attains 43 cm in height, and the small youngest medusa (0.3–0.6 mm in diameter) with usually 22–24 tentacles and eight statocysts is liberated from the orifice of collar of the elongated obconical gonangium (0.56–1.75 mm in length and 0.28–0.56 mm in greatest width excluding collar and stalk) produced on axils of branches and branchlets. In the life-span of medusa, about a month, the rapid growth is observed for three weeks after liberation, and the maturation and the discharge of sexual gametes occur between two and three weeks after liberation, preceeded by the stability of medusan form. The laboratory-reared mature medusa is 2–3 mm in diameter, with 66–95 tentacles, usually 8 statocysts, and gonads on the umbrellar margin. The mature medusa collected from the sea, however, grows larger, attaining 5.3 mm in diameter and 127 in the number of tentacles.

The morphology of the mature medusa of the present hydroid from northern Japan is different from that of *O. dichotoma* sensu Cornelius from British waters (type-species), particularly in the position of gonad, though their morphology of polyp closely resembles each other. The taxonomic problem on the treatment of the present hydroid as well as the similar hydroid already reported from USSR is discussed.

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