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The Life Cycle of the Hydromedusa, *Nemopsis dofleini* Maas,
with a Supplementary Note on the Life-History of
Bougainvillia superciliaris (L. Agassiz)¹⁾

With 13 Text-figures

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(Communicated by T. UCHIDA)

Although the medusa of *Nemopsis dofleini* has frequently been reported from the Kurile Islands, Saghalien, and central and northern Japan (Maas, 1909; Kishinouye, 1910; Uchida, 1925, 1927; etc.), the hydroid remains unknown. Moreover, little is known of the medusan development except from a fragmental record by Uchida (1927).

On July 2nd, 1962, the author obtained many well-developed medusae bearing many eggs and planulae from Akkeshi Bay. Swimming planulae freed from the medusae were reared in petri dishes. These planulae metamorphosed to hydroids. About seven months later, medusa buds began to develop on the hydroids and many young medusae were set free from March to July in 1963, and were reared up to the adult stage.

The hydroids and medusae were kept at room temperature and were usually fed with *Artemia* larvae, and occasionally with visceral pieces of *Patinopecten yessoensis* or *Mytilus edulis*. At the beginning of the culture, water temperature was 15°–20°C and gradually fell to between 1°–4°C in February, 1963. After that, it gradually rose again to 18°C in June when the young medusae were actively growing.

Development of Hydroids from Planulae

After one or two days, the planulae were detached from the gonadal wall of the adult medusae and began active swimming in the bowl. The planulae were ellipsoidal in shape, about 0.2mm in length, tapering toward the posterior end (Fig. 1). After two to six days, they began to sink to the bottom and assumed

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spherical forms (Fig. 2). Following this the planulae began to settle to substratum such as small pieces of stone and the bottom of the dish; then they flattened and assumed a disc-like form, 0.1-0.2 mm in diameter, and were covered with a thin transparent membrane (Figs. 3, 4). About one day after they settled, a small bud appeared in the center of the disc (Fig. 5). In one to two days the bud gradually elongated and 2-4 conical tentacular rudiments arranged in a single circlet were formed near the tip (Figs. 6, 7). Next the tentacular rudiments, increasing to 3-4 in number, gradually became slender and filamentous with several nematocyst clusters on their shafts.

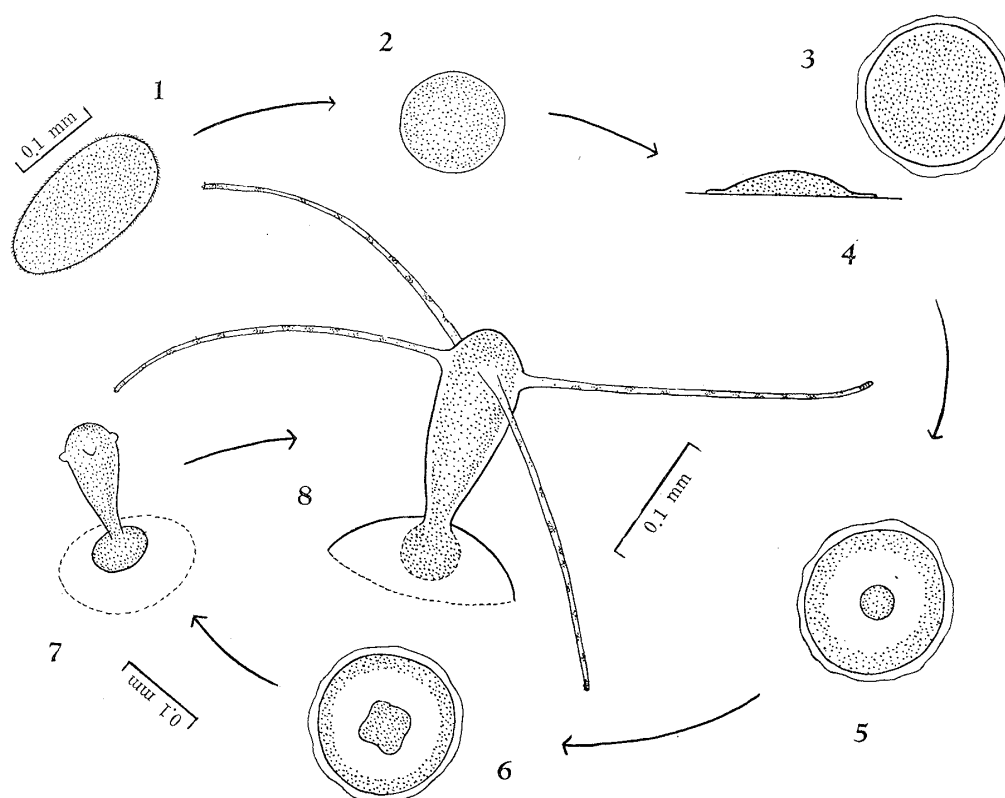


Fig. 1. Planula. Fig. 2. Planula sinking to the bottom. Figs. 3-7. Successive changes during metamorphosis to hydroid. Detailed explanation in text. Fig. 8. Young hydroid.

About two weeks after settling to the substratum, the young hydroid was bluntly club-shaped, 0.15-0.2 mm high, 0.06-0.1 mm wide at the tentacle circlet, tapering toward the base where it was connected with the pedal membranous disc (Fig. 8). It was colorless or translucent. The hydranth, not distinctly demarcated from the hydrocaulus, was hemispherical or bluntly conical in shape with a terminal mouth and had 3-5, usually 4, filiform tentacles at its base. The tentacles, 0.3-0.6 mm long, had 6-8 nematocyst clusters on their shafts.

Hydroid

For more than one year following this, the hydroids grew and increased in

size without forming any colonies or without any branching of their stems. The number of tentacles increased to 4-6 after one to two months and to 5-9 in three months.

The fully grown hydroid was solitary, arising from the thin membranous pedal capsule (Fig. 9). The stem was bluntly club-shaped, tapering from the

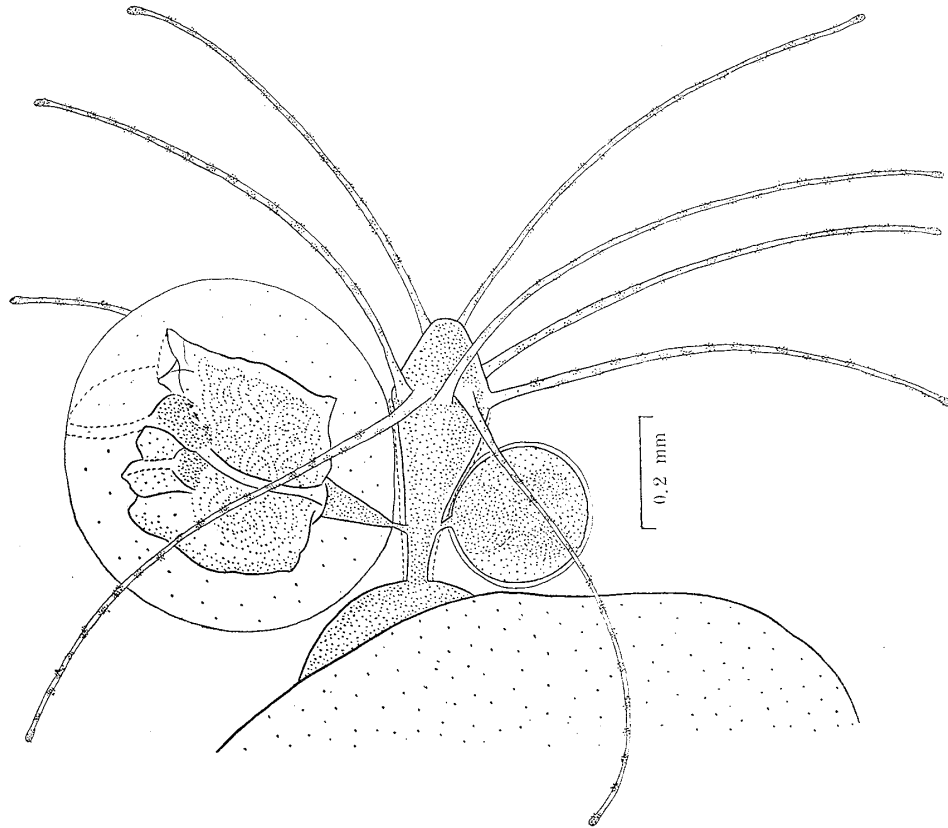


Fig. 9. Hydroid with two medusa buds.

tentacle circling to the base and very small in size, 0.4-0.6 mm high, 0.15-0.2 mm wide at the tentacle circling and about 0.05 mm wide at the base. Below the tentacle circling it was covered with a thin, soft mucous envelope which was often thickly encrusted with small particles or diatoms. The endoderm region of the stem was pale yellow or yellowish grey in color. The hydranth was bluntly conical in shape with a terminal mouth and was not distinctly demarcated from the hydrocaulus. The filiform tentacles were arranged in a circling at the base of the hydranth, alternately up and down, 5-17, usually 7-11 in number, with many nematocyst clusters on their shafts in a moniliform arrangement. They were very contractile, attaining several times the length of the stem when well extended. The pedal capsule was of the flat helmet shape, 0.05-0.1 mm thick, 0.2-0.5 mm in diameter, covered with a thin membranous periderm which was filled with a pale orange or pale yellowish coenosarc. When the stem was artificially cut off or a part of the capsule was damaged, a new hydroid was formed from the capsule at that point. These regenerated hydroids were similar

in form to the normal primary hydroid but had more tentacles, usually 4-8.

From late January to early July in 1963 many medusa buds were observed on the hydroids. They were borne on a slightly lower portion of the stems with short peduncles which were almost embedded in the mucous envelope surrounding the stem. Usually one to three buds in various developmental stages were found on one hydroid at the same time. New buds were located on opposite portions of the stem, somewhat higher than the old ones. The buds first appeared as ellipsoidal bodies and gradually increased in size along with development of manubria, tentacle bulbs and tentacles. Just before liberation, the buds were nearly spherical, about 0.5 mm in diameter (Fig. 9, left side). Twenty to forty days, usually about 30 days, after the appearance of the buds, the young medusae were liberated from the hydroids. About 30 young medusae were liberated from the hydroids from March to July, 1963. Half of them were set free in April and May.

Medusa

Young medusae newly liberated (Fig. 10). When newly liberated from the hydroid the medusae have a nearly spherical umbrella, 0.8-1.2 mm high, 0.8-1.1 mm wide. The jelly is moderately thick, with nematocysts sparsely scattered over the exumbrella. The stomach is a tubular widening toward the apical end, about one-fourth the height of the subumbrellar cavity, and pale brownish orange in color. Usually a small conical apical knob is present. The four perradial oral tentacles, about 0.1 mm long, have an unbranched bar-like form inserted just above the simple mouth opening. They terminate in a nematocyst cluster composed

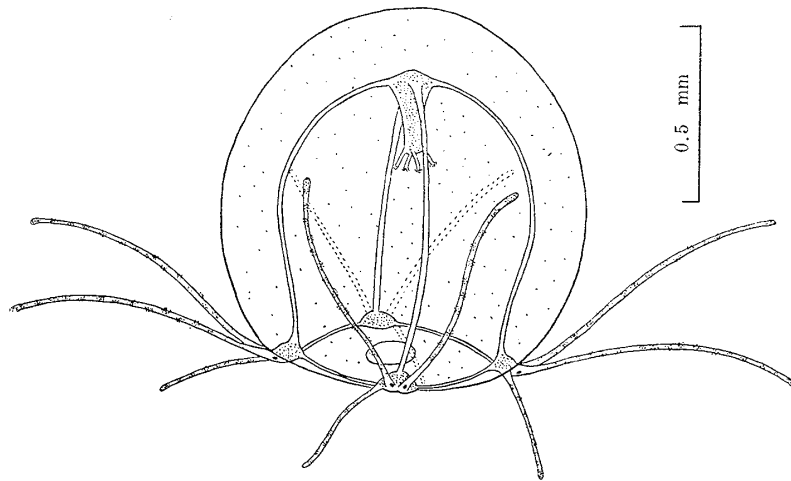


Fig. 10. Newly liberated young medusa.

of many fine peduncled nematocysts. The radial canal is rather broad and smooth. The ring canal is narrow. The marginal tentacle bulbs are trapezoidal in shape, mounted on the ring canal, and covered with milky colored nematocyst tissue; the central region of the bulb is pale or brownish orange. Each tentacle bulb gives rise to usually three, rarely four, tentacles on which many nematocyst

clusters are arranged at almost equal intervals. The first tentacle develops on the perradial line or close to it. Successive tentacles develop alternately, one by one, on each side of the first. The first and second tentacles are well developed and extend to more than twice the length of the third one, running more upwards than the others. One or two weeks after liberation, development of these tentacles ceases and the third and other successive tentacles grow longer than the two median ones. On the adaxial base of the first and second marginal tentacles, and rarely on the third one, there is one dark red ocellus. The vellum is well developed.

Medusae with first branching of oral tentacles (Fig. 11). Thirteen to twenty-three days after the medusae are liberated, the terminal ends of their oral tentacles become dichotomously divided into two, 0.2-0.3 mm in total length. The umbrella becomes bell-shaped, 1.5-2.1 mm high, 1.4-2.2 mm in diameter. The exumbrellar nematocysts gradually disperse. The basal portion of the stomach is slightly extended along the radial canals, and formation of the basal pouch begins. The marginal tentacles in each cluster now increase in number to 5-8,

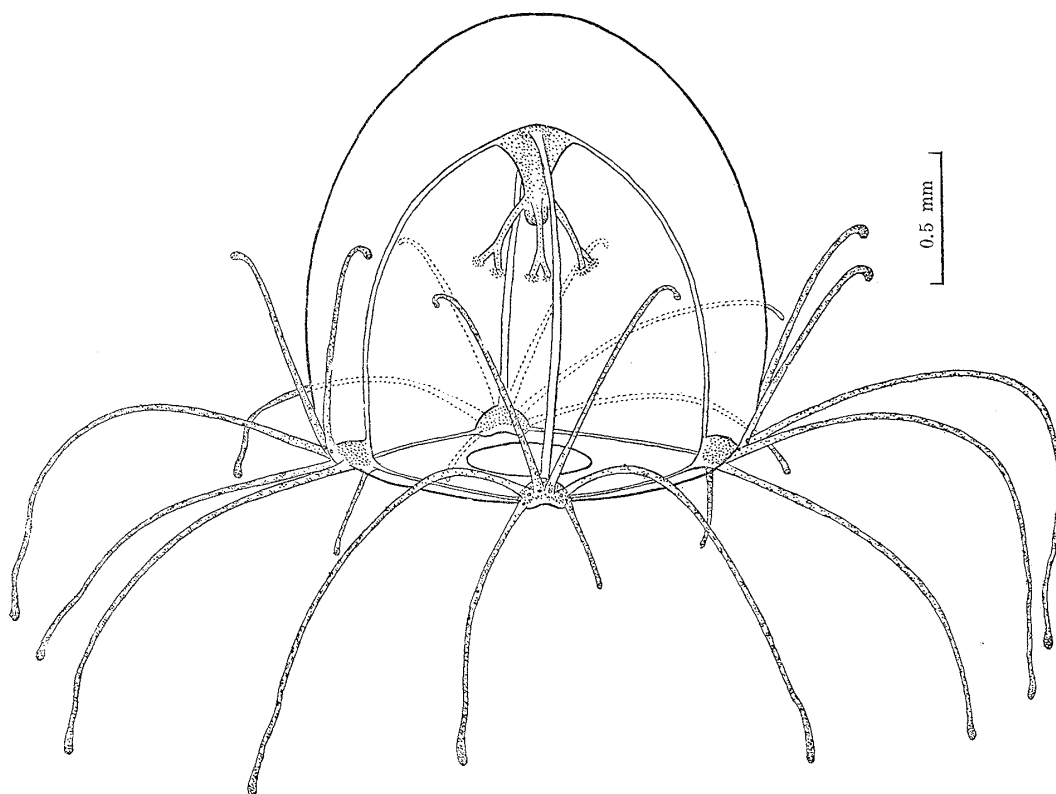


Fig. 11. Medusa with oral tentacles bifurcated once.

alternately adding one on each side of the older tentacles. By this time growth of the two median tentacles has already ceased. Ocelli follow the marginal tentacles in development, so that 4-7 ocelli are found on each bulb in this stage.

Medusae with second branching of oral tentacles. Medusae, twenty-four to thirty-five days old, are 2.0-2.3 mm high, 1.8-2.3 mm in diameter. The jelly has

become thicker, especially in the apical portion. The second dichotomous branching of the oral tentacles takes place in the terminal portion, but all of the terminals are not always synchronously divided. The basal part of the stomach gradually extends to the radial canals, forming four stomach pouches. At the same time, the portion below the oral tentacles becomes moderately elongated. Now there are 7-10 marginal tentacles and 6-8 ocelli at each perradial tentacle epaulet. The two median ocelli are rather distally located and have a tendency to fuse with each other.

Medusae with third branching of oral tentacles (Fig. 12). Medusae 27-50 days old are up to 2.4-2.6 mm both in height and diameter. The stomach attains about one-third the height of the subumbrellar cavity. The proximal part of the

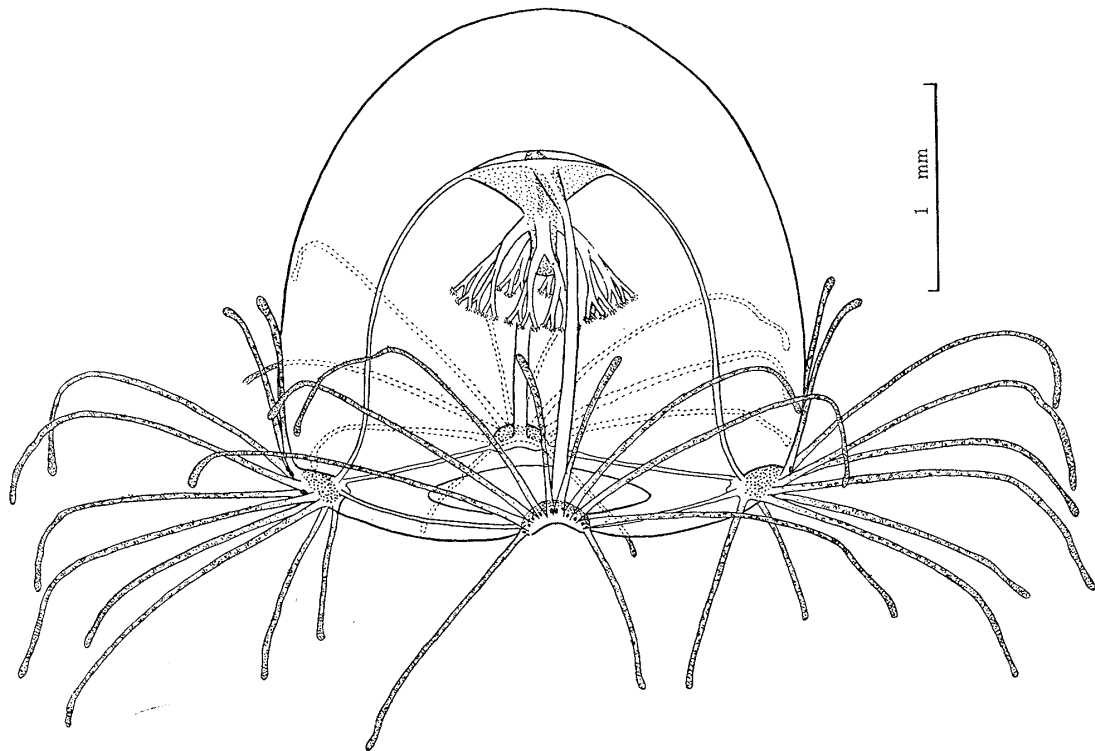


Fig. 12. Medusa with third branching of oral tentacles.

stomach, above the oral tentacles, increasingly widens toward the radial canal, forming a triangular pouch. On the other hand, the portion of the stomach below the base of the oral tentacles is more elongated, forming a four-sided tube. The oral tentacles branch three times, first in the portion slightly above the middle, second somewhat below the middle, and third near the end. The branches have a tendency to cross perpendicularly. The radial canal becomes broad and slightly jagged. There are 8-12 marginal tentacles and 7-10 ocelli at each tentacle epaulet.

Medusae with fifth branching of oral tentacles. In medusae, 40-65 days old, the umbrella becomes slightly wider than high, 3.5-4.0 mm high, 3.8-4.3 mm wide. The gonad now begins to develop on the lateral wall of the basal pouch of the stomach extending to the dorsal corner of the radial canal. The mouth is of

relatively wide quadratic form with four lips. The oral tentacles have now divided five times; their proximal stems are short and thick. The first two branchings begin in the basal portion of the tentacles; the fourth and the fifth branchings begin near the terminal portion. In each cluster there are 12-19 marginal tentacles, the median pair of which now become fairly rigid and club-shaped and extend upwards along the exumbrellar surface. There are 11-17 ocelli on each epaulet. The radial canal becomes more jagged and slightly wider toward the marginal end.

A medusa with five branched oral tentacles was obtained by a surface tow in the bay on July 26th, 1963. The specimen closely resembled the medusae described above although it was larger, 5.2 mm high and 5.3 mm wide, and had more prominent ocelli and well extended stomach pouches which extended slightly down along the radial canals. On the other hand, a medusa in the same stage from Oshoro, Hokkaido, reported by Uchida (1925), had 26 marginal tentacles and a gonad extending outwards about half the length of the radial canal.

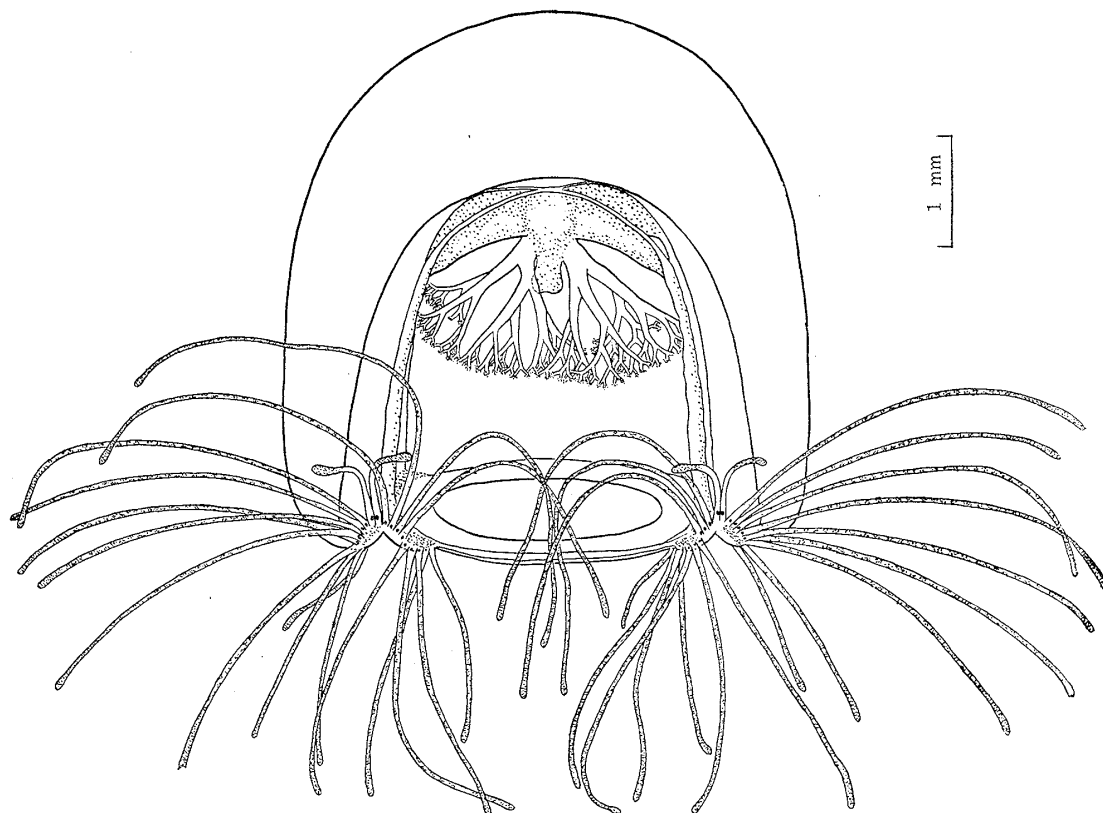


Fig. 13. Medusa with sixth branching of oral tentacles.

Medusae with sixth branching of oral tentacles (Fig. 13). Sixty to eighty days after liberation medusae have sixth branched oral tentacles and attain 4.0-5.0 mm high, 4.1-5.8 mm in diameter. The stomach pouch begins to extend down along the radial canal and to fold, and is covered by the gonad growing on its wall. The gonad and the stomach wall are pale yellow or yellowish grey in color. The endoderm area of the marginal tentacle bulb is dark or reddish orange and the

ocelli are dark reddish brown or dark red.

The oral tentacles then undergo a seventh branching and the umbrella grows to 6.0–6.5 mm in height, 5.7–6.4 mm in diameter and the medusae assume nearly adult form.

A Supplementary Note on the Life-History of *Bougainvillia superciliaris* (L. Agassiz)

Recently, by dredging in Akkeshi Bay, Uchida and Nagao (1960) found a hydroid colony attached to a shell of *Neptunea* sp. The colony was probably referable to *Bougainvillia superciliaris*, and several medusa buds were observed on the hydroids, but these medusa buds were unfortunately absorbed just prior to liberation.

Later, in December of 1962, several colonies identical with the hydroid above mentioned were obtained again and reared in the laboratory. In late January, 1963, about 20 medusa buds began to appear on the stolons and gradually developed. From the end of February to early March several young medusae were liberated. During this season, the water temperature in the culture dish rose gradually from 3° to 13°C.

The newly liberated young medusae had 7–9 marginal tentacles in each perradial cluster and oral tentacles which were bifurcated 3–4 times. These medusae were definitely referable to *Bougainvillia superciliaris*. The general features of these medusae closely agreed with those of the youngest specimens obtained from Akkeshi Bay by Uchida and Nagao in March, 1960, and were in a slightly more advanced stage than those reared by Werner (1961) at Helgoland.

DISCUSSION

Up to the present, four species belonging to the genus *Nemopsis* have been recorded: *N. bachei* L. Agassiz, *N. crucifera* (Forbes and Goodsir), *N. dofleini* Maas and *N. heteronema* Haeckel. According to Hartlaub (1911), however, *N. crucifera* is probably identical with *N. bachei*. Moreover, Mayer (1910) and Kramp (1959) pointed out that *N. heteronema* may be referable to *N. bachei*. Therefore there remain two good species, *N. bachei* in the Atlantic and *N. dofleini* in the Pacific.

The hydroid and the young medusa of *N. bachei* were recorded from Beaufort, N. C. by Brooks (1883). According to Brooks' description, the hydroid was about an inch high and each main stem gave rise to three or four short alternating branches ending in hydranths, which were very extensively funnel-shaped, with 24 long slender tentacles. The stem was covered with a transparent, horny ectosarc with 2–3 irregular annulations near the base of the branches. Therefore, it is clear that the hydroid of *N. dofleini* is distinctly different from that of *N. bachei* in spite of the rather close resemblance of the medusae.

The present hydroid observed by the author exhibits the general characters of the so-called genus *Perigonimus* and resembles superficially the hydroid of *Leuckartiara octona* or that of *L. abyssi* described by Rees (1938). However, as Rees (1956) pointed out, the genus *Perigonimus*, which includes many heterogeneous

species, is not valid. Recently Vannucci and Rees (1961) revised the genus *Bougainvillia* and gave the generic characters of the hydroid. The present hydroid agrees generally with the character described by them, but the solitary life is a peculiar character of *N. dofleini*. Furthermore, the pedal disc of the present species is relatively similar to the podocyst of the hydroid, *Ostromovia* belonging to the Limnomedusae, observed by Kramp and Paspaleff (1938), Uchida and Nagao (1959) and others.

In *N. bachei* the medusa buds develop between the proximal end of hydranth and the tentacle whorl (Brooks, 1883). On the other hand, in *N. dofleini*, the medusa buds are found in the middle or lower part of the stem. According to Brooks, the young medusae of *N. bachei* were liberated from the hydroid in a much earlier stage than was in the case of the present species; namely, he said, "The proboscis is short and simple, without oral tentacles, Most of the specimens had four perradial tentacles—one at the end of each radiating tube." On the other hand, Agassiz (1862) reported that there were four tentacles in each cluster in the first set of marginal tentacles of the young medusa of *N. bachei* and that successive tentacles developed in pairs on each side of the first. The order of appearance of the tentacles in Brooks' specimens showed considerable variation. In *N. dofleini* the marginal tentacles are developed alternately, one by one, on each side of the two median tentacles.

It is generally known that the medusa of *Nemopsis* is distinguishable from that of *Bougainvillia* by the presence of the median pair of club-shaped marginal tentacles and that the stomach pouch extends outwards along the radial canal (Hartlaub, 1911; Uchida, 1927). Concerning these points, Mayer (1910) pointed out that the wide extension of the radial pouch of the stomach also occurs to a greater or less degree in *Bougainvillia*, so that it is of no conclusive generic value in *Nemopsis*; however, the presence of two kinds of marginal tentacles is the sole distinctive generic feature. He concluded that the genus *Nemopsis* is derived from the more generalized genus *Bougainvillia*.

The medusa of *N. dofleini* was first described from Tokyo Bay, central Japan, by Maas who examined 9 specimens but he did not describe the characteristic club-shaped tentacles (Maas, 1909). Later, Uchida (1930) re-examined Maas' specimens and confirmed the presence of the club-shaped tentacles. He also pointed out that the tentacles are characteristic of the genus.

The observations reported by the author show that all of the marginal tentacles of *N. dofleini* are filiform when first developed as are those of *Bougainvillia*. Later, however, development of the two median tentacles ceases and then they assume the typical club-shape. It is probable that the marginal tentacles of *Bougainvillia* become specialized into the two types seen in *Nemopsis* as pointed out by Mayer (1910). Judging from the developmental morphology of *N. dofleini*, it may be concluded that the genus *Nemopsis* is a rather specialized form derived from the genus *Bougainvillia*.

SUMMARY

- 1) The planulae of the Bougainvillid medusa, *Nemopsis dofleini*, were reared

to the stage of adult medusae. The hydroid of this species is described for the first time.

2) The hydroid arising from a helmet-shaped pedal capsule is solitary, with an unbranched stem covered by a thin mucous envelope. It has a blunt conical hypostome usually with 7-11 filiform tentacles in a circlet. One to three medusa buds are borne in the middle or lower part of the stem.

3) The newly liberated young medusae have tubular stomachs with unbranched oral tentacles and 3-4 perradial, filiform, marginal tentacles in a cluster. Later, successive marginal tentacles arise alternately one by one, on each side of the first. The median two finally become club-shaped in the stage of the fifth branched oral tentacles.

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