NOTES ON BRITISH AND NORWEGIAN HYDROIDS AND MEDUSAE

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(Text-figs. 1-7)

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The notes collected in this paper are a continuation of earlier observations on British and Norwegian hydroids and their medusae. The observations were made at the Biological Stations of Herdla (Bergen), Millport and Plymouth.

Two of the hydroids described below, *Dipurena ophiogaster* Haeckel and *Tiaropsis multicirrata* (M. Sars), were previously unknown, although their medusae have been known for a long time. The earlier description of the medusa of the hydroid *Trichydra pudica* by Wright (1863) is confirmed and asexual budding in the hydroid *Coryne tubulosa* (M. Sars) is described. Miss Maude J. Delap has kindly allowed me to publish her sketches of the rare hydroid *Tricyclusa singularis* (Schulze).

I am much indebted to Dr Stanley Kemp, F.R.S., for many facilities and much encouragement. I also wish to thank Prof. August Brinkmann and Mr Richard Elmhirst for facilities at Bergen and Millport respectively. The work at Millport was carried out while I was holding a grant from the Royal Society.

ASEXUAL BUDDING IN THE HYDROID CORYNE TUBULOSA (M. SARS, 1835)

A large colony of *Coryne tubulosa* (M. Sars, 1835), better known as *Syn-coryne sarsi* (Loven, 1836), was found growing in a plunger jar kept by Amanuensis D. Rustad at the Biological Station, Herdla, in September 1937. Mr Rustad kindly allowed me to examine the hydroid, which was creeping over the greater part of the bottom of a plunger jar. The colony was of the creeping form (Fig. 1*a*), the stems usually bearing single hydranths, many with medusa buds. Some medusae had been liberated and were

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identified as young specimens of *Coryne tubulosa*. The most interesting feature of the contents of the jar, however, were "free hydranths" carrying two whorls of tentacles and sometimes also one or two medusa buds (Fig. 1 b, c).

A close examination of the hydroid on the bottom of the jar showed that many of these "free hydranths" were developing from the body of the fixed hydranths below the most proximal tentacles. These hydranth buds when liberated showed a striking similarity to the pelagic hydranths of *Margelopsis* (Fig. 1c).



Fig. I. Coryne tubulosa. a, Single hydranth from the colony brought back alive to Plymouth from Herdla; drawn 22. iv. 38. b, Single hydranth with fully developed bud, drawn from material fixed in formalin. c, Newly liberated hydranth bud with a young medusa bud, Herdla, 6. ix. 37.

There was never more than one bud on any hydranth and several buds became free from the parent hydranths during the time they were being examined. Some buds also carried medusa buds. The hydranth buds at liberation were 0.25-0.35 mm. long and 0.15 mm. in diameter. They carried two whorls of four capitate tentacles each, and in some there were one or two medusa buds borne on very short stalks immediately posterior to the proximal whorl of tentacles. The tentacles of the buds were about 0.2 mm. long with capitate terminal knobs 0.05 mm. in diameter.

Budding from the hydranth in this species has been observed by Hartlaub (1916). He figures a bud (p. 103, Fig. 22) similar to those found at Herdla.

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Hartlaub also gives many other figures of budding in the same colony but these do not seem to be figures of normal polyps and I am inclined to regard many of them as abnormalities. During the first week of September at Herdla I found one of these "free hydranths" in a plankton haul taken close to the Biological Station. This method of budding "free hydranths" is probably a common feature in the life history of this hydroid when there is an abundant food supply available. A portion of this colony was brought back alive to Plymouth from Herdla, and although it was kept for many months, no further budding of daughter polyps was observed. A few medusae were, however, developed and liberated in May 1938.

THE HYDROID OF DIPURENA OPHIOGASTER HAECKEL

The hydroid of the medusa *Dipurena ophiogaster* Haeckel was found on the stipe of *Himanthallia loreata* by Miss M. J. Delap at Valentia Island in May 1904. Miss Delap sent the hydroid and the medusae reared from it to the late Mr E. T. Browne. This hydroid, of which there is no published description, is described here from a re-examination of the original colony found by Miss Delap.

The colony was small, consisting of upright stems arising from a creeping stolon and with a total height of about 4 mm. The stems bearing the hydranths arise from creeping stolons, $0 \cdot 1 - 0 \cdot 12$ mm. in diameter. Both stems and stolons were covered by a thin perisarc without annulations. In welldeveloped stems the hydrocaulus reached a height of 2 mm., while in young polyp stems no perisarc was visible. The stems each carried a single hydranth, but short stolons were frequently given off a little distance from the point of origin of the upright stems (Fig. 2*a*). The production of these stolons on the stems was a characteristic feature of the colony.

Mature hydranths with medusa buds were 1-2 mm. long with a diameter of 0.2-0.35 mm. (Fig. 2b,c). There were two kinds of tentacles, capitate and filiform, present in most hydranths. The capitate tentacles, 10-18 in number, were scattered over the anterior two-thirds of the body; they had a tendency to be arranged in whorls. There was always an oral whorl of four tentacles around the mouth, the remainder being scattered. The capitate heads of the tentacles were 0.07-0.12 mm. in diameter and frequently decreased in size posteriorly.

The filiform tentacles were situated posterior to the capitate tentacles and varied in number in different polyps. There were never more than four on any hydranth (Fig. 2b), and frequently only one or two were present. In some hydranths they were absent and in others they formed part of a proximal whorl of capitate tentacles. A closer examination showed that these filiform tentacles always carried a number of nematocysts at the tip, and that transitional stages between capitate and filiform tentacles could be found in one whorl. In this species at least they may be regarded as reduced capitate tentacles (Fig. 2c).

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Medusa buds were borne singly or in a cluster of two to four buds on the body of the hydranth a little anterior to the posterior whorl of "filiform" tentacles (Fig. 2b, c). Usually there was only one cluster but sometimes there were two. The young buds were sessile, but as they developed to full size they became stalked with a thin stalk up to 0.2 mm. in length. The largest medusa bud was 0.5 mm. long with a diameter of 0.45 mm. In the largest buds the manubrium, and the four tentacles with their ocelli, could be clearly seen through the thin perisarc covering the bud.



Fig. 2. Dipurena ophiogaster. a, General appearance of a portion of the colony, drawn from material preserved in formalin. b, Single polyp with medusa buds, redrawn from a pencil sketch of a living polyp by Miss M. J. Delap. c, Single hydranth, from material preserved in formalin.

The medusae reared from this colony by Miss Delap have been identified by Mr F. S. Russell as *Dipurena ophiogaster* Haeckel. This hydroid bears a superficial resemblance to *Stauridiosarsia* [= *Stauridium*] producta (Wright), but in the present hydroid the capitate tentacles are more scattered, there are only four oral tentacles, and the so-called filiform tentacles are really imperfectly developed capitate tentacles. The hydroid of *Dipurena ophiogaster* is also distinct from that of *D. halterata* (Forbes), which has more capitate tentacles, no filiform tentacles, and develops medusa buds singly (Rees, 1939b). Although the two hydroids which give rise to *Dipurena* medusae are well marked, the differences do not justify the allocation of the species to separate genera.

THE HYDROID AND FREE HYDRANTH OF *TRICYCLUSA SINGULARIS* (SCHULZE, 1876)

The following account of a rare and little known hydroid is based on figures and notes made by Miss Maud J. Delap. Miss Delap has kindly permitted me to publish an account of this hydroid, which I have identified with *Tricyclusa singularis* (Schulze, 1876) (= *Margelopsis stylostoma* Hartlaub, 1903, *syn.nov*.).

The Hydroid. Six specimens with buds were found on a piece of Zostera at Reenagiveen Point, Valentia Island, Co. Kerry, on July 19, 1909, and these were kept under observation by Miss Delap until July 30, 1909. The hydroid was attached to the Zostera by a short cylindrical stalk. The hydranth itself was more or less flask-shaped, with three whorls of capitate tentacles. Between the middle and oral whorl the body narrows to form a slender neck. The oral tentacles, which are terminal, are four in number, each with a terminal knob of nematocysts. There were six tentacles in the middle whorl. These and the proximal whorl carried two groups of nematocysts on their distal half in addition to the terminal knob. The proximal whorl, situated near the posterior end of the body, had twelve tentacles, disposed in two closely approximated whorls of six tentacles pointing upwards and six tentacles pointing downwards.

In one polyp the hydranth was cut off and the stem grew a new one. Some of the hydranths carried pink or pinkish yellow buds at the posterior end of the body (Fig. 3a). These developed into young hydranths which were budded off (Fig. 3b).

The young hydranths budded off in this way were identical, and may be regarded as synonymous, with *Margelopsis stylostoma* Hartlaub, 1903. Miss Delap states that "the young when liberated have fewer nematocysts and the tentacles appear longer than in the adult: they use their tentacles to crawl about with." A young specimen after liberation was I mm. long and the tentacles were 1.5 mm. long; in another specimen the tentacles were 0.5 mm. long.

The fixed hydroid differs in one respect from the description given by Schulze. There are fewer tentacles in the proximal whorl of the specimen figured by Schulze than in the present species, but their number probably varies with age and I have therefore referred this hydroid to *Tricyclusa* singularis.

SYSTEMATIC DISCUSSION ON THE MARGELOPSIDAE

The peculiar hydroid described above was first described by Schulze (1876) as *Tiarella singularis*. The name *Tiarella*, however, was preoccupied and Stechow (1919) has given it the new generic name *Tricyclusa*. The hydroid is of an unusual type, which is intermediate between the Tubulariidae and the Corynidae. Its remarkable power of budding young hydranths from the

body, just behind the most proximal whorl of tentacles, was noticed by Schulze. He also observed gonophores developing between the middle and lower whorl of tentacles.

In 1903 Hartlaub published a description of a "schwimmender" hydroid, Margelopsis stylostoma, which he referred to his genus Margelopsis, of which M. haeckeli is the genotype. This latter species is a planktonic hydroid which superficially resembles M. stylostoma. Hartlaub drew attention to the marked similarity between his M. stylostoma and the hydranth of Tricyclusa singularis, and expressed the opinion that they might prove to be the same. species. Hartlaub also indicated that the medusa Margelopsis hartlaubi Browne, 1903, might be the medusa of Tricyclusa singularis. The observations



Fig. 3. *Tricyclusa singularis. a*, Fixed hydroid. *b*, Free hydranth. From tracings of original pencil drawings by Miss M. J. Delap.

made by Miss Delap show that *Margelopsis stylostoma* comes from the fixed hydroid, *Tricyclusa singularis*.

Mayer (1910) erected a new subfamily of the Codonidae, the Margelopsinae, to take Margelopsis and Pelagohydra Dendy, 1902. The free hydroids of Margelopsis haeckeli and Tricyclusa singularis differ in several respects. There are only two whorls of tentacles in Margelopsis haeckeli, whereas Tricyclusa singularis has a third oral whorl; in the latter all the tentacles are capitate, but they are filiform in the former. These differences have evidently been considered by Stechow (1923), who, in his tables (pp. 37, 49), separates Margelopsis (i.e. M. haeckeli) from Tricyclusa in different families. He places Margelopsis haeckeli and M. gibbesi (McCrady) in the Tubulariidae in the subfamily Pelagohydrinae, of which Pelagohydra is the type; Tricyclusa he

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refers to the Corynidae. The separation of *Tricyclusa* from *Margelopsis* and the removal of the former to the Corvnidae appears justifiable.

Uchida (1927) does not appear to have been aware of Stechow's suggestion and placed *Margelopsis*, *Hypolytus* Murbach, 1899, *Pelagohydra* and *Climacocodon* Uchida, 1924, in his family Margelopsidae. This arrangement appears to be satisfactory if we exclude *Tricyclusa* and *Hypolytus*. I have already indicated (Rees, 1938, p. 29) that *Hypolytus* clearly belongs to the Corymorphinae, if not to the genus *Corymorpha* itself. This species, according to Murbach, is capable of a certain amount of movement, but so are other species of *Corymorpha* (unpublished observations on *C. aurata* and *C. nutans*).

The medusae of *Margelopsis*, *Pelagohydra* and *Climacocodon* are all of the same type and are quite distinct from those of the Tubulariidae and Corynidae and justify the erection of a separate family. As Uchida (1924) has indicated, *Pelagohydra* is probably the only one of these genera that may be regarded as truly pelagic, and it has yet to be shown that the other forms have no fixed hydroid stage in addition to their free hydranths. Dendy has shown that in *Pelogohydra mirabilis* the proximal portion of the hydranth is modified to form a float, whereas a float is either poorly developed* or absent in *Margelopsis* and *Climacocodon*. There are other differences, such as the number and disposition of the tentacles, which indicate that *Pelagohydra* is not so closely related to the other two genera as they are to each other. On the other hand, the structure of the medusa in *Pelagohydra*, which is of the *Margelopsis* type, is proof that these forms are related.

I propose therefore to recognize two subfamilies, the Margelopsinae and the Pelagohydrinae, within the Margelopsidae.

The Margelopsinae may be distinguished by the possession of whorls of tentacles and by the absence of a distinct float. It contains the genera *Margelopsis* and *Climacocodon*.

The Pelagohydrinae may be distinguished by the scattered position of the tentacles all over the body of the hydranth, and by the modification of the proximal portion of the body to form a float. Sole genus: *Pelagohydra* Dendy, 1902.

THE MEDUSA OF TRICHYDRA PUDICA WRIGHT

Two well-developed colonies of the hydroid *Trichydra pudica* Wright, 1858, were found on two clinkers trawled off Fairlie Buoy in the Clyde Sea Area on April 11, 1940. This is the first record of the hydroid from this area. Previously it has been reported from the Firth of Forth by Wright (1858), from the English Channel (*Plymouth Marine Fauna*, 1931) and from Valentia Harbour, Co. Kerry (personal communication from Miss M. J. Delap). The hydroid which van Beneden (1866) described as *Eudendrium pudicum* is certainly not the present species (Rees, 1938).

 \star Leloup (1929) has shown that in *M. haeckeli* the endodermal cells are vacuolated and that the structure of the short stalk of the hydranth resembles early stages in the formation of the float in siphonophores.

Wright (1863) described a medusa which he found in a vessel containing *Trichydra* and which he thought might be its medusa, but he could detect no trace of gonophores on his hydroid colony. On two clinkers from Fairlie there was a heavy growth of this hydroid and no other species were present. Two days later two medusae were liberated. Although a careful daily examination until April 19 revealed no trace of developing or fully developed medusa buds, six more medusae appeared in the bowl during this period. These clinkers with their numerous tiny pockets afford an excellent hiding-place for such buds, which must have been very small. I do not doubt that these tiny medusae came from the *Trichydra*; they agree in structure with those described by Wright except for the presence in Wright's specimens of two or three rudiments of interradial bulbs. Their presence or absence may vary from colony to colony.

A brief redescription of both hydroid and medusa is given below.

The polyps are connected by a creeping filiform stolon which is covered by a thin perisarc and from this stolon the polyps arise at short intervals. At the base of the hydranth there is a collar-like perisarc into which the hydranth can partially contract. This collar varies in length from 0.15 to 0.35 mm. and has a diameter of 0.1-0.14 mm. When disturbed the hydranth can contract so that only the tips of the tentacles show beyond the edge of the perisarc. When expanded, however, the hydranth may reach a height of 1 mm. beyond the edge of the perisarc, and in this state the stem supporting the hypostome and the tentacles is very thin with a diameter of about 0.03 mm. (Fig. 4). Distally the stem broadens to give rise to a whorl of tentacles, and beyond the latter there is a distinct conical hypostome. The tentacles when expanded may reach a length of 1.2 mm.; they carry numerous irregularly disposed nematocysts.

The first medusae were liberated in the laboratory on April 13 and others on succeeding days.

The newly liberated medusae were very small, having a length of 0.4 mm. and a diameter of 0.3 mm. They were of a deep bell shape, higher than wide (Fig. 5). The jelly was uniformly thin and all over the bell there were numerous nematocysts. The velum was well developed. The stomach was short, tubular, 0.14-0.17 mm. in length, and was distinctly broadened at its base. It was difficult to distinguish the stomach proper from the beginnings of the radial canals. The four radial canals were distinct and moderately broad. There were four perradial tentacle bulbs each about 0.05 mm. in diameter. The four perradial tentacles were not observed expanded, but when contracted they had a length of 0.15 mm. The base of the stomach and the tentacle bulbs were yellowish brown or brownish in colour. The medusae did not grow appreciably and did not grow more tentacles during the time I was able to keep them.

This young medusa cannot be identified with certainty with any known medusa because of the lack of any distinctive characters. It is probably a



Fig. 4. Trichydra pudica. Four polyps from a colony; Millport, 12. iv. 40.





very early stage of a known medusa, and the form and colour of the tentacle bulbs suggest that it might possibly be an early stage of *Lizzia blondina* Forbes. The absence of mouth tentacles, however, does not support this view although their absence in such an early stage does not rule out the possibility that it might be this species.

THE HYDROID OF THE MEDUSA TIAROPSIS MULTICIRRATA (M. SARS, 1835)

The medusa *Tiaropsis multicirrata* was first described by Michael Sars (1835) as *Thaumantias multicirrata* and later by Louis Agassiz as *Tiaropsis diademata*. Agassiz mentions that the hydroid of this species is a *Campanularia* and that he had traced the whole life history. A. Agassiz (1865), however, stated that the hydroid had not been observed, so it appears that he was in some doubt about the earlier observation of his father. L. Agassiz (1849) definitely states that he had observed the planulae, "recently hatched from eggs, I have seen move slowly, then attach themselves to the solid bodies in the jars in which they were kept, and grow into a Campanularioid polypidom...".

Recent work on an operculate hydroid of the "*Campanulina*" type, which liberated a young specimen of *Tiaropsis multicirrata*, appears at first sight to contradict Agassiz's observations, but it must be remembered that at this time (1849) the genus *Campanularia* consisted of a heterogeneous group of hydroids including operculate and non-operculate forms. Apart from the vague record of the hydroid by Agassiz there is no description of the hydroid or of the newly liberated medusa and they are therefore described below.

The hydroid colony was found on an old *Buccinum* shell dredged off Keppel Pier, Millport, from a depth of about 5 fm. on April 18, 1940. No expanded hydranths were seen and of the few gonothecae present only one contained a medusa. This was liberated in the laboratory and was identified as *Tiaropsis multicirrata*.

Description of the Hydroid. The colony consisted of a large number of hydranths connected by creeping stolons running in all directions over the apical half of the shell. The stolons were 0.05 mm. in diameter and were not annulated. The hydranths were borne singly at short intervals on the creeping stolon and were supported on short imperfectly ringed stalks, which varied in length from 0.06 to 0.10 mm. The total height of the hydranths from the stolon to the tip of the operculum was never more than 1 mm. The hydrotheca itself varied from 0.38 to 0.80 mm. in length and in breadth from 0.1 to 0.13 mm. The perisarc of the hydrotheca was thin but firm and at its distal end became folded to form a distinct conical operculum with seven to eleven outer segments (Fig. 6). The operculum varied in height from 0.16 to 0.25 mm. When the operculum was closed the segments formed a somewhat blunt apex.

When found the colony was dying down after producing medusae and no hydrotheca contained a living polyp. Several gonothecae were present but all except one were empty. One gonotheca contained a single medusa which

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Fig. 6. *Tiaropsis multicirrata. a*, Two hydrothecae. *b*, One hydrotheca and a gonotheca; Millport, 19. iv. 40.



Fig. 7. Tiaropsis multicirrata. Newly liberated medusa; Millport, 19. iv. 40.

completely filled it. The gonothecae, like the hydrothecae, were supported on short imperfectly ringed stalks, and were large, elongate oval in shape, with a smooth surface. The mouth of the theca was circular, with a diameter much less than the maximum diameter of the theca itself (Fig. 6b).

Description of the Medusa. The newly liberated medusa had a deep bellshaped umbrella with a thin jelly which was slightly thicker at the apex (Fig. 7). The surface of the umbrella was thickly covered by a large number of small nematocysts. There was a well-developed velum. There was a short quadrangular stomach extending to about half the height of the subumbrellar cavity. The mouth consisted of four well-developed perradial lobes, armed along their free margin by a single row of nematocysts. There were four moderately broad radial canals connecting with the ring canal. The marginal tentacles were many, twenty-three in number, and these were in different stages of development. The four perradial and the four interradial tentacles were equally well developed and when extended reached a length of 1.5 mm. There were also smaller tentacles, one on each side of the interradial tentacles and one on each side of the perradial tentacles. In one quadrant of this medusa (see Fig. 7) one tentacle, immediately adjacent to a perradial tentacle, was missing. Situated adradially and between these younger tentacles were eight prominent black ocelli and eight large oval marginal vesicles. The marginal vesicles measured 0.04 by 0.05 mm. and were adaxial in position on the umbrella margin. The vesicles contained from three to five spherical concretions.

The newly liberated medusa was $1 \cdot 1$ mm. high by $1 \cdot 1$ mm. in diameter. The larger tentacle bulbs were $0 \cdot 1$ mm. in diameter. They were pale brown in colour. The stomach was also faintly brownish in colour with the pigment concentrated more towards its base.

From its characters, especially the adradial position of the eight black ocelli and the eight marginal vesicles, there can be no doubt as to the identity of this young medusa, which can be referred to *Tiaropsis multicirrata*.

The hydroid described above is of the so-called "*Campanulina*" type, and when the shape of the gonotheca and the hydrotheca are taken into consideration, it appears morphologically to stand nearest to *Phialella quadrata* (Forbes, 1848). It has been shown by Rees (1939*a*) that a number of distinct medusa genera belonging to different families all possess "*Campanulina*" hydroids and thus the apparent morphological similarity between this hydroid and *Phialella quadrata* does not indicate that the species are related.

There are distinct differences between this hydroid and P. quadrata; the hydranths are all subsessile, the hydrothecae are longer and the gonothecae firmer than in P. quadrata.

Young specimens of *Tiaropsis multicirrata* with 25–35 tentacles appeared in plankton caught off Keppel Pier on March 5, 1940.

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