

ON THE NEMATOCYSTS OF HYDRO- MEDUSAE. II

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(Text-figs. 1-4)

In a previous publication (Russell, 1938) I described the nematocysts in twenty species of Hydromedusae. The present report gives observations on five more species among which are three species of *Aequorea*. Among the medusae there is perhaps no genus in which the identity of the different species has been so confused as that of *Aequorea*. This genus is characterized by a large number of radial canals, and the specific distinctions are chiefly based on the number of these canals and the ratio that this number bears to the number of marginal tentacles. But in any one species neither are constant in number, and indeed both may show considerable variation in either direction. This is perhaps only to be expected since the character is of a meristic nature and must be dependent upon the rate of growth of the individual and the size to which it grows under different conditions. The type of the genus as selected by Haeckel (1879) is *A. forskalea* Péron & Lesueur. This name was given by Péron & Lesueur (1809) to a medusa described and figured by Forskål (1775, p. 110 and 1776, pl. xxxii) as *Medusa aequorea*. Some authors (e.g. Bigelow, 1913, p. 38) have retained the specific name *aequorea*, but this name cannot be kept since it had been used previously both by Linnaeus* and by Löffling (1858) for species which were inadequately described. Forskål's drawing is excellent and leaves no doubt as to which species he had. The usual number of radial canals is about 60-80 (cf. Claus, 1883; and Fraser, 1916). In his description, however, Forskål says that there are 129 canals, but he also states that these are paired, and we are probably right in assuming, as Claus (1883) did, that he was referring to the lamellae of the gonads and that the radial canals were really half this number. The medusa figured by Forskål has 104 radial canals and 105 tentacles. This is slightly more than is usual, but occasional large specimens may be found with 90-100 or slightly more canals. The species was excellently described in full detail and in all its stages by Claus (1883) as *A. forskalea*, and this is an additional argument for keeping that name.

A. forskalea forms an excellent type for the genus, for its characters can be

* The description given by Linnaeus in *Systema naturae*, 10th edition, 1758, p. 659, refers to Loeffling's medusa. It may be questioned whether this medusa belongs to the same genus. I have not seen Loeffling's original description, but Péron & Lesueur (1809) give for it "point de bras", i.e. "no mouth lips"; this probably fits the genus *Aequorea* better than any other.

regarded as forming a central point from which other species depart in different directions. Ideally it is a species in which the numbers of radial canals, mouth lips, and marginal tentacles are equal. But owing to slightly different rates of growth and development of the three characters this degree of perfection is rarely exactly attained. Thus the tentacles may be fewer or more than the radial canals, but they are hardly ever less than half or more than twice the number of canals. The tentacles also do not always appear on the umbrella margin opposite the radial canals, probably because, if the tentacle happens to be the first of the two to develop, the corresponding radial canal does not always grow along the exact line necessary to reach the ring canal opposite the tentacle.

Bearing these facts in mind the identification of this species becomes much easier, and I have as a result found little difficulty in distinguishing it from two other species which occur off Plymouth. These are *A. vitrina* Gosse, whose number of tentacles far exceeds that of the radial canals, and *A. pensilis* (Modeer), whose number of radial canals far exceeds that of the tentacles.

An examination of the nematocysts of these three species has confirmed their separation.

The other two species whose nematocysts are described in this paper are the siphonophores *Agalma elegans* (M. Sars) and *Velella velella* (L.). The nematocysts of *Aequorea forskalea* and *A. vitrina* were examined on medusae preserved in formalin and sea water. For the other three species observations were made on fresh material.

LEPTOMEDUSAE

Aequorea forskalea Péron & Lesueur

I am indebted to Mr P. G. Corbin for a collection of many *A. forskalea* taken in the mouth of the English Channel in July 1937. These specimens were between 45 and 100 mm. in diameter; they had 64-99 radial canals and 51-79 tentacles. The ratio of the diameter of the stomach to that of the umbrella varied approximately from 1 : 1.8 to 1 : 2.4.

The nematocysts, both in the marginal tentacles and the mouth lips were of two kinds: basitrichous haplonemes* and atrichous haplonemes (Fig. 1 a-c).

Basitriches: 12-18 × 2.5-4 μ undischarged.

Atriches: 17-34 × 7-17 μ undischarged.

Both types of nematocyst showed considerable variation in size from one specimen to another. This was especially noticeable in the large oval atriches, which tended to fall into two size groups 17-22 and 26-34 μ long, both sizes being present in a single specimen, but only the smaller size occurring in the mouth lips.

My results thus differ from those of Weill (1934, p. 458) who states that

* I cannot be sure whether these nematocysts, in this and the next two species of *Aequorea*, are basitrichous haplonemes or microbasic mastigophores (see Russell, 1938, p. 146).

basitriches are not present in the mouth lips. He gives the size of the basitriches as 15μ long and that of the atriches as $15-20\mu$.

Now that I have seen so many specimens of *A. forskalea* I think there can be little doubt that *A. forbesiana* of Gosse (1853) is the same species.

Aequorea vitrina Gosse

I have seen four specimens of *A. vitrina*, whose characters were as follows:

Diameter of umbrella mm.	Diameter of stomach mm.	No. of radial canals	No. of tentacles	No. of mouth lips
55	25	76	ca. 304	..
75	37	68	ca. 275	..
80	40	68	> 300	ca. 39
90	40	90	ca. 600	ca. 40

The nematocysts both in the marginal tentacles and in the mouth lips were of two kinds: basitrichous haplonemes and atrichous haplonemes (Fig. 1 *d, e*).

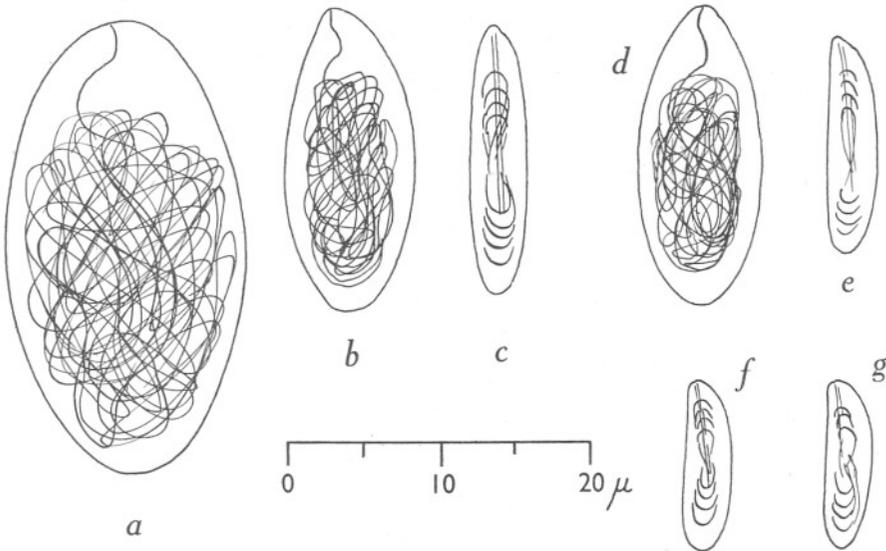


Fig. 1. *a-c*, *Aequorea forskalea*; *a, b*, atrichous haplonemes; *c*, basitrichous haplonemes; *d, e*, *A. vitrina*; *d*, atrichous haploneme; *e*, basitrichous haploneme; *f*, *A. pensilis*, basitrichous haploneme; *g*, ? *A. pensilis*, basitrichous haploneme. \times ca. 2000.

Basitriches: $10-15 \times 2.5-3\mu$ undischarged.

Atriches: $19-22 \times 7.5-8.5\mu$ undischarged.

The very large atrichous haplonemes, characteristic of *A. forskalea* were absent.

The number of mouth lips, estimated on the basis of the number of transparent lines of large endodermal cells running down the stomach wall, appears to be usually in the neighbourhood of half or less than half the number of

radial canals in *A. vitrina*, whereas in *A. forskalea* they are of more nearly the same number as the radial canals.

The specimens described by Hartlaub (1894) as *A. forskalea* are clearly *A. vitrina*.

Evans & Ashworth (1909) recorded a number of medusae from the Firth of Forth, which were identified by E. T. Browne as *A. norvegica* Browne. I have found one of these specimens in Mr Browne's collection. Its nematocysts were of the same types and approximately the same size as those of *A. vitrina*.

Basitriches: 12-13 × 3 μ undischarged.

Atriches: 18-20 × 7.5-8 μ undischarged.

The numbers of mouth lips both in the medusae described by Evans & Ashworth and in the type specimen of *A. norvegica* described by Browne (1903) also agree with those of *A. vitrina*. I am therefore inclined to agree with the suggestion made by Kramp (1933) that *A. norvegica* and *A. vitrina* are the same species. There is, however, an indication that the medusa does not grow to so large a size in these waters as it does farther north.

A. vitrina evidently comes very close to *A. coerulescens* (Brandt) as described by Bigelow (1909). In fact if it were not for the deep bluish black pigmentation in the tentacle bulbs, which appears to be so characteristic of *A. coerulescens*, there does not seem to be any character by which they can be distinguished. Bigelow's photograph of that species (1909, pl. 4, fig. 4) might well be a typical *A. vitrina*. An examination of the nematocysts of *A. coerulescens* might be helpful.

On the American side of the Atlantic *A. vitrina* appears to be represented by *A. albida* A. Agassiz.

Both *A. forskalea* and *A. pensilis* are present in the Atlantic and the Pacific, and it seems reasonable to suppose that eventually *A. vitrina* may be shown to have a similar distribution by regarding *A. coerulescens* and *A. albida* as geographical races. We need, however, more detailed observations on the numerical characters of these species.

Aequorea pensilis (Modeer)

In September 1938 a number of medusae were collected off Plymouth which are undoubtedly *A. pensilis*. The nematocysts, both in the marginal tentacles and in the mouth lips, were only of one kind, basitrichous haplonemes (Fig. 1f).

Basitriches: 9-13 × 2.5-3 μ undischarged.

The medusae were thus immediately distinguishable from the two preceding species of *Aequorea* by the absence of large oval atrichous haplonemes.

The occurrence of *A. pensilis* off Plymouth was somewhat unexpected and it is necessary to discuss these specimens in some detail. Full details of the numerical characters are given in Table I. It will be seen that these characters agree well with those in the table drawn up by Bigelow (1919, p. 312).

Bigelow gives the ratio of radial canals to tentacles as between 10 : 1 and 12 : 1 for specimens of 60 mm. diameter and less. The Plymouth specimens, over a much larger range of numbers, show a ratio of 3.5 : 1 to 13 : 1. It is, however, to be observed that this ratio changes with the size of the medusa. In specimens under 40 mm. in diameter it varies between 8 : 1 and 13 : 1. Above this size the number of tentacles increases owing to the development of tentacles on some of the marginal bulbs. The ratio of the stomach diameter to that of the umbrella varies between 1 : 1.3 and 1 : 2.0, thus agreeing closely with the corresponding ratios of 1 : 1.4 to 1 : 2.0 derived from Bigelow's table. In all specimens the central mass of jelly was very thick, and in the form of a plano-convex lens, and anastomosis of the radial canals was frequent. The gonads were yellowish green overlain by bluish grey pigment: the green colouration disappeared after preservation.

TABLE I. *AEQUOREA PENSILIS* CAUGHT OFF PLYMOUTH, SEPTEMBER 1938

Diameter of umbrella mm.	No. of radial canals	No. of tentacles	Ratio of radial canals : tentacles	Diameter of stomach mm.	Ratio of diameter of stomach : umbrella
16	129	11	13 : 1	10	1 : 1.6
18	124	10	12 : 1	10	1 : 1.8
20	> 117	13	..	15	1 : 1.3
20	128	16	8 : 1	15	1 : 1.3
20	122	11	11 : 1	13	1 : 1.5
22	137	12	11 : 1	14	1 : 1.6
22	121	12	10 : 1	15	1 : 1.5
25	127	12	11 : 1	17	1 : 1.5
27	> 111	15	..	16	1 : 1.7
29	> 126	16	..	18	1 : 1.6
30	> 118	> 16	..	18	1 : 1.7
30	146	13	11 : 1	16	1 : 1.9
30	139	15	9 : 1	17	1 : 1.8
30	130	12	11 : 1	15	1 : 2.0
32	125	15	8 : 1	18	1 : 1.8
35	127	16	8 : 1	19	1 : 1.8
35	148	15	10 : 1	25	1 : 1.4
37	146	11	13 : 1	19	1 : 1.9
37	123	> 14	..	20	1 : 1.9
40	151	16	9 : 1	20	1 : 2.0
45	140	24	1 : 1.9
45	166	17	10 : 1	27	1 : 1.7
45	154	22	7 : 1	30	1 : 1.5
50	138	24	6 : 1	28	1 : 1.8
55	127	22	6 : 1	30	1 : 1.8
60	126	> 21	..	30	1 : 2.0
60	140	34	4 : 1	38	1 : 1.6
60	144	41*	3.5 : 1	37	1 : 1.6
60	129	24	5 : 1
65	138	22	6 : 1	40	1 : 1.6
80	ca. 175†	55	1 : 1.5

* 18 large.

† 85-90 in half—remainder damaged.

While in the above characters the specimens agree with *A. pensilis*, the structure of the tentacle bases is exactly like that of *A. macrodactyla* (Brandt); they are conical and laterally expanded, and clasp the umbrella margin and

have a slight median spur (Fig. 2c, d). The median spur is prolonged downwards over the abaxial surface of the tentacle bulb as a median ridge. But the true condition of spur and ridge is only seen when the specimens are perfectly preserved. In many specimens the tentacle bulbs had become distorted and merely appeared as rather large laterally expanded swellings as has been described by various authors for *A. pensilis*. The tentacles are irregularly distributed round the umbrella margin. The number of marginal warts between adjacent tentacles is variable; usually there are about seven to

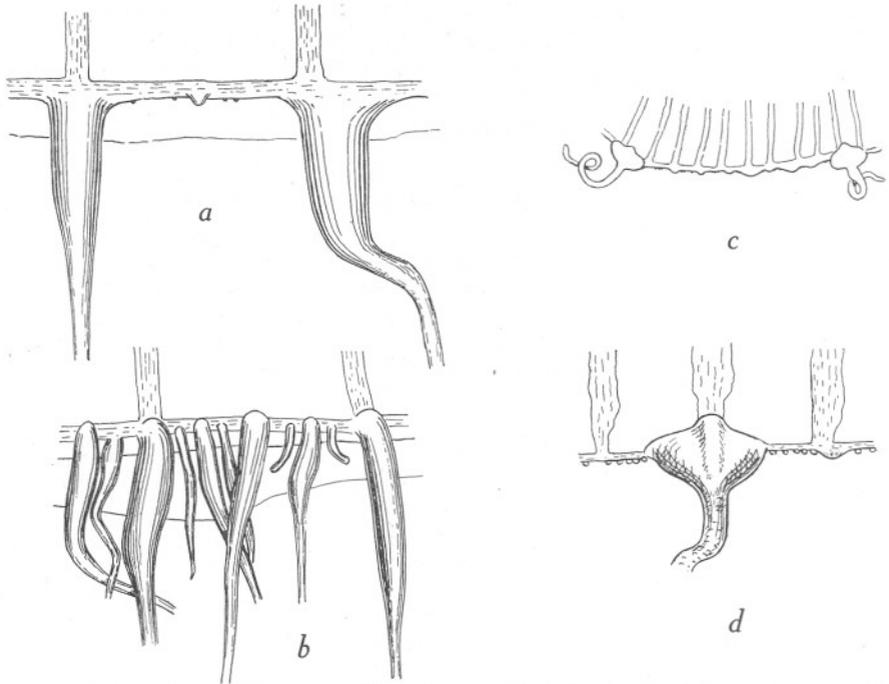


Fig. 2. Portions of umbrella margin of: a, *Aequorea forskalea*; b, *A. vitrina*; c, d, *A. pensilis*. (a, b, and d approximately to same scale; c, less enlarged.)

nine. The marginal vesicles are extremely numerous and may exceed forty between two adjacent tentacles; each contains 2-5 concretions.

In many specimens it was impossible to find any excretory pores or papillae; in some, small slits without papillae could be found, while in others the papillae were quite distinct. The above three conditions might be found in the same specimen.

The Plymouth specimens thus appear to combine the characters of the two species *A. pensilis* and *A. macrodactyla*, except in so far as the number of radial canals is concerned; for *A. macrodactyla* is generally considered to have far fewer radial canals. Among the Plymouth medusae there was, however, one specimen (not included in Table I) which had only 63 radial

canals. It was 27 mm. in diameter and had ten tentacles; the diameter of the stomach was 13 mm. In all other respects it was identical with the other specimens, and had the same single type of nematocyst. The occurrence of this one specimen among the others raises the question whether at times *A. pensilis* may have only half the normal number of radial canals and whether therefore *A. pensilis* and *A. macrodactyla* are really separate species. I will return to this later.

A. pensilis has not been recorded from the North Atlantic before. It is possible that the specimen so well figured by Forskål (1776) came from the Mediterranean, but he makes no mention of its origin and it may just as well have come from the Red Sea. But a search in the literature shows the occurrence of medusae which are probably *A. pensilis* recorded under other names.

The medusae referred to by Claus (1883, p. 80) as *A. discus* are most probably *A. pensilis*. Claus, who had seen so many typical *A. forskalea*, did not hesitate to regard this as a distinct species on account of its disproportionate number of radial canals. A summary of Claus's table for the characters of *A. discus* is given in Table II.

TABLE II

Diameter of umbrella mm.	No. of radial canals	No. of tentacles
7-8	59	8
12	95	8
15	112	8
20	94	16
30	93	16+

Browne (1897) describes six specimens from Valencia under the name of *forskalea*. While the largest of these is clearly *A. forskalea*, being 160 mm. in diameter and having 88 radial canals and 56 tentacles, the remaining five are just as clearly *A. pensilis*. Table III gives a summary of Browne's observation on these specimens.

TABLE III

Diameter of umbrella mm.	Diameter of stomach mm.	No. of radial canals	No. of tentacles
25	13	140	7
30	..	114	8
55	26	145	16
60	33	180	28
135	55	153	43

I have found a specimen in Mr Browne's collection taken on the same date as those mentioned above and it agrees with the Plymouth specimens in having only one type of nematocyst.

There can thus be little doubt that *A. pensilis* is a fairly common and widespread medusa, and as such it might be expected to show variation from place to place. We now have quite a number of observations for comparison and in Fig. 3 I have plotted the numbers of tentacles against the numbers of radial

canals for most of the specimens recorded in the literature. These include the following specimens: those listed by Bigelow (1919, pp. 312, 314) as *A. pensilis** and *A. macrodactyla*; those recorded by Vanhöffen (1911, p. 232) as *Mesonema coelum pensile*; the Plymouth specimens recorded in this paper; and those recorded as *Aequorea discus* by Claus (1883, p. 80) and as *Polycanna forskalea* by Browne (1897, p. 829). The figure shows that there is a tendency towards two distinct groupings into *Aequorea macrodactyla* and *A. pensilis*. Yet this distinction does not seem to be sufficiently clear cut to warrant their separation

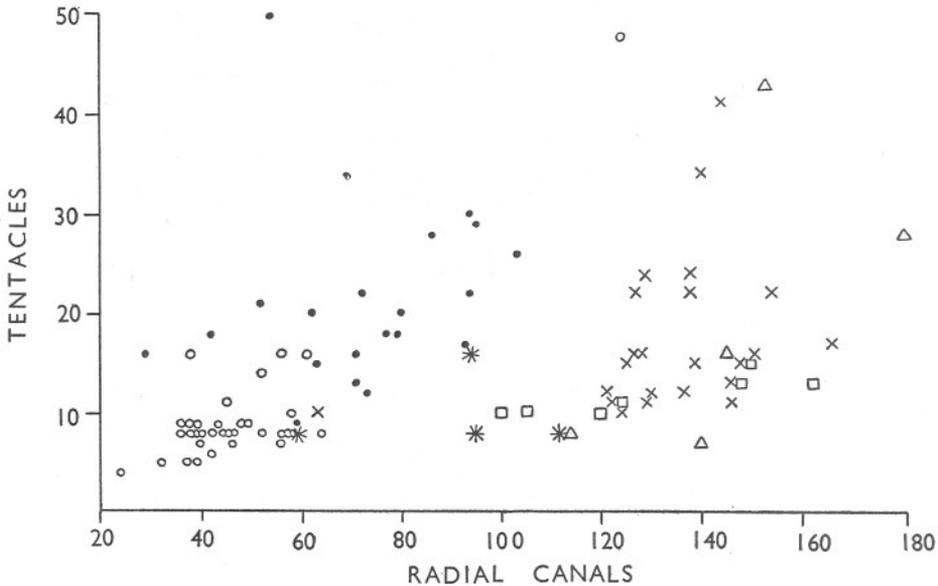


Fig. 3. Ratio of number of marginal tentacles to number of radial canals of *Aequorea pensilis* from the following sources. □, *A. pensilis*, and ●, *A. macrodactyla* from Bigelow (1919, pp. 312, 314); ○, *Mesonema coelum pensile* of Vanhöffen (1911, p. 232); ×, *A. pensilis* from Plymouth, recorded in this paper; *, *A. discus* of Claus (1883, p. 80); and △, *Polycanna forskalea* of Browne (1897, p. 829).

into two species. It is preferable to regard them all as belonging to one species, *A. pensilis*, with a variety, *macrodactyla*, in which only half the full number of radial canals is developed. The occurrence of only one specimen of the latter type among the many specimens caught off Plymouth would seem to favour this view. It is possible that in some localities one or the other variety might predominate. This splitting of the one species into two varieties is also more convenient, since, with increasing observations, specimens are sure to be found on

October 4 1932 the weekly oblique haul with the 2 m. ring trawl contained fragments of a large medusa. Fragments of about five-sixths of this specimen were present and it must have been about 180 mm. in diameter. There were 114 radial canals, making a probable total of about 140, and the tentacles were about two-thirds the number of radial canals and very irregularly distributed. The gonads were bluish grey in colour. The tentacle bulbs appeared more like those of *A. forskalea*, but they had become very much squashed in preservation. On examining the nematocysts, it was found that both in the tentacles and mouth lips only one type was present, namely basitrichous haplonemes.

Basitriches: 10-11 × 2.5-3 μ undischarged (Fig. 1g).

The large atrichous haplonemes so typical of *A. forskalea* were absent. I hesitate to identify this medusa for certain, but from the number of radial canals and the type of nematocyst it seems possible that it may have been a very fully developed *A. pensilis* in which the number of tentacles has increased considerably. The specimen appears to agree with that described by Forbes (1851) from the Minch as *A. forskalea*. His specimen, ca. 130 mm. (5 in.) in diameter, had 136 radial canals and ca. 68 large tentacles, with 68 small tentacles and 136 marginal bulbs.

ON THE IDENTIFICATION OF THE THREE PLYMOUTH SPECIES OF *AEQUOREA*

The distinguishing characters of the three species, *A. forskalea*, *A. vitrina*, and *A. pensilis* including var. *macroductyla*, in their adult stages, can now be defined as follows.

	<i>forskalea</i>	<i>vitrina</i>	<i>pensilis</i>
No. of radial canals	Usually 60-80 rarely exceeding 100	60-90	ca. 120-180 or half this number
No. of tentacles	ca. 40-85, usually approximating to number of radial canals, rarely less than half or more than twice	ca. 300 or more; always exceeding number of radial canals by more than three times	Usually less than, often much less than, one-third of the number of radial canals
Tentacle bases	Elongated and conical (Fig. 2a)	Elongated, and slightly laterally compressed (Fig. 2b)	Conical, laterally expanded, often with median spur (Fig. 2c, d)
Mouth lips	Approximating to number of radial canals*	Usually about half the number of radial canals	Approximating to number of radial canals†
<u>Umbrella diameter</u> <u>stomach diameter</u>	ca. 1.8-2.4	ca. 1.8-3.0	ca. 1.3-2.0
Nematocysts	Two kinds	Two kinds	One kind

* Fraser (1916) states that the mouth lips are never more than half the number of radial canals in specimens from Departure Bay in the Pacific. This may be a geographical variation.

† Maas (1905) gives figures in the neighbourhood of half the number of radial canals: his drawing (pl. viii, fig. 54), however, shows approximately equal numbers.

The ratio of the number of tentacles to the number of radial canals is also a sure guide for the identification of the young stages of the three species. Some difficulty may, however, arise in separating the young of the *macrodactyla* variety of *A. pensilis* from the young of *A. forskalea*. But herein lies the value of a study of the nematocysts, for it is only necessary to crush a tentacle under a cover glass, or take a piece of mouth lip, and examination under the microscope with a $\frac{1}{8}$ in. objective will disclose at once the presence or absence of the conspicuous atrichous haplonemes characteristic of *A. forskalea*. An additional diagnostic character for young stages appears to lie in the number of marginal vesicles. In *A. forskalea* there are only one or two marginal vesicles between adjacent marginal bulbs and tentacles, whereas in *A. pensilis* they are much more numerous.

Of the three species *A. vitrina* appears to be the most northerly in its distribution and *A. pensilis* is perhaps most confined to warm water.

It is not without interest to note here that, among the Leptomedusae that I have examined so far, I have only found one other species besides *A. pensilis* in which I could see no atrichous haplonemes. This was *Phialella cymbaloides*. It suggests the possibility that *Aequorea pensilis* and the other two species of *Aequorea* may have evolved separately.

SIPHONOPHORA

Agalma elegans (M. Sars)

Although the identity and synonymy of *A. elegans* (M. Sars) is well known it will be as well to state here that the species examined was that with the tricornuate tentillae, since Sars described two species under the one name.

There were four kinds of nematocysts. Large microbasic mastigophores and anisorhize homotrichous haplonemes, in the batteries of the tentillae; desmonemes in the two terminal filaments of a tentilla; and microbasic euryteles situated at the ends of the tentacles and in two small groups on either side of the velar openings of the nectophores (Fig. 4a-h).

Mastigophores: $185-205 \times 25-28 \mu$ undischarged.

The thread was beset along its whole length with three rows of stout barbs.

The barbs appear to be set in three parallel longitudinal rows and not spirally (cf. Schneider, 1900, p. 101).

Anisorhize: up to ca. $75 \times 6-7 \mu$ undischarged.

The smallest nematocysts of this type were ca. $22 \times 4 \mu$.

Desmonemes: $6-7 \times 6 \mu$ undischarged.

Euryteles: $90-105 \times 30-35 \mu$ undischarged; ca. $70-23 \mu$ discharged.

These large euryteles had three basal stylets similar to those of stenoteles.

In addition to the above nematocysts there were large numbers of "anacrophores" in the terminal filaments and distal ends of the spiral nematocyst bands. These ranged in size from 7×2 to $20 \times 5 \mu$ undischarged. In a previous publication (Russell, 1938) I suggested that these may be stages in the develop-

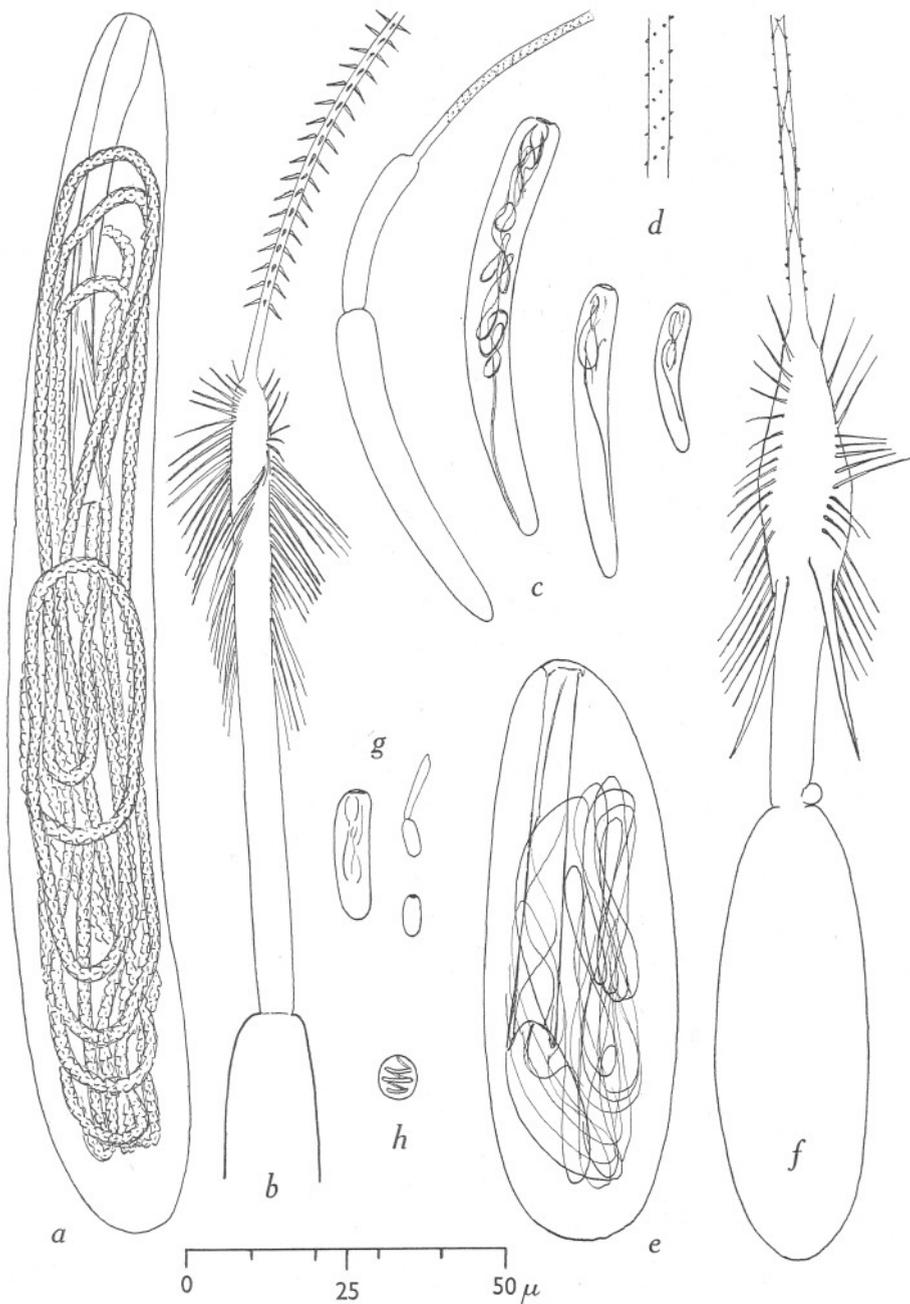


Fig. 4. *Agalma elegans*: a, b, microbasic mastigophore; c, anisorhize haplonemes of different sizes, with enlarged portion of thread, d; e, f, eurytele; g, "anacrophores"; h, desmoneme. \times ca. 850.

ment of the desmonemes and anisorhize haplonemes. After seeing the nematocysts of *Agalma elegans* I am inclined to modify this suggestion and say that they are anisorhize haplonemes in an arrested state of development. Among the anisorhize haplonemes a complete range in size may be found in any one battery from the smallest "anacrophore" upwards. The "anacrophores" up to a length of about 20μ are straight with rounded ends, while the smallest anisorhize haplonemes down to a length of about 27μ are tending towards this shape. It is also noticeable that the smaller the anisorhize the shorter is its thread. There does, however, usually appear to be a break in the series between about 20 and 27μ .

Velella velella (L.)

In October 1938 a small specimen of *Velella*, ca. 15 mm. long, was caught in the plankton. There were two kinds of nematocysts: stenoteles and atrichous haplonemes.

Stenoteles: these were of two sizes, $18-21 \times 14-16\mu$ and $13-15 \times 10-11\mu$ undischarged.

Atriches: $8-9 \times 4.5\mu$ undischarged.

The specimen when examined was in a very decomposed condition and the armature of the discharged stenoteles always broke away and could not be made out in detail.

These nematocysts agree fairly closely with the sizes given by Weill (1934, p. 516) for specimens from Samoa preserved in alcohol in the British Museum. This is additional evidence in favour of the conclusion of Bigelow & Sears (1937) that the Atlantic and Pacific *Velella* are the same species.

SUMMARY

The nematocysts of the three species of Leptomedusae, *Aequorea forskalea*, *A. vitrina*, and *A. pensilis*, and of the two siphonophores *Agalma elegans* and *Velella velella* are described.

The specific characters of the three species of *Aequorea* are discussed and it is shown that *A. pensilis* is probably the same species as *A. macrodactyla*.

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