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THE MEDUSAE OF THE BRITISH ISLES

THE MEDUSAE OF THE BRITISH ISLES

ANTHOMEDUSAE, LEPTOMEDUSAE, LIMNOMEDUSAE, TRACHYMEDUSAE AND NARCOMEDUSAE

BY

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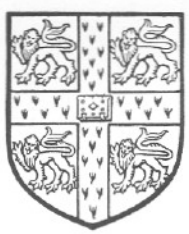
THE UNITED KINGDOM



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To

MY WIFE

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INTRODUCTION

It is now more than one hundred years since the publication of Edward Forbes's *Monograph of the British Naked-eyed Medusae* by the Ray Society in 1848. In that monograph Forbes stated: 'There are forty-three species of Gymnothalmatous Pulmograda known to the author as inhabiting the British Seas. The greater number of these are undescribed forms.' In fact, owing to his lack of knowledge of the appearance of medusae in their different stages of development, Forbes's list consisted only of twenty-four species as now known (plus five whose identity is obscure). Thus while he described for the first time many stages of medusae as different species, and others, already known, as new species, in reality the specific names of only eleven medusae now stand in his name.

To-day we can probably claim about ninety species as belonging to the British fauna; of these a dozen or so are deep-sea oceanic species which, although occurring rather far off shore, may come within reach of research vessels working on our western coasts.

The history of the literature on medusae was reviewed by Forbes in his annotated bibliography, the last title in which was Lesson's *Histoire Naturelle des Zoophytes; Acalèphes*, published in 1843. In his *Contributions to the Natural History of the United States of America*, in 1862, Louis Agassiz gave a tabular review of the species in the group. The historical sequence of the development of our knowledge on medusae was again reviewed at considerable length by G. J. Allman in 1871–2 in his Ray Society *Monograph of the Gymnoblastic or Tubularian Hydroids*. Allman's monograph was quickly followed by Ernst Haeckel's *System der Medusen* in 1879 in which all the medusae of the world were treated. The next monographic publication was not until 1910 when Alfred Goldsborough Mayer, at the earlier suggestion of Alexander Agassiz, produced his classical three-volumed *Medusae of the World*. This work incorporated the work of such leading authorities of the day as Ernst Vanhöffen, Otto Maas, Clemens Hartlaub, and Edward T. Browne. Around the same period Cl. Hartlaub's publications in the *Nordisches Plankton* were of outstanding importance in clarifying the relationships of the Anthomedusae; and Henry B. Bigelow had already produced his first great work on the medusae collected by the *Albatross* expedition in the tropical Pacific, which was to be followed by so many valuable contributions to the subject.

In 1913 there appeared the first of a series of publications from the hand of Paul L. Kramp, to whose very detailed researches especially we owe the greatest advances in knowledge since that time, and who is the leading exponent of the group in the world to-day. Like the present author, Kramp experienced the warm encouragement of E. T. Browne in his early days.

My own interest in medusae began some twenty years ago when I was realizing their value as indicators of the movement of water masses in the sea, as had already been so ably shown by Kramp (1927). At that time E. T. Browne fostered my interest and gave me much stimulating encouragement and friendly advice.

In 1935 he suggested that I might collaborate with him in writing a monograph on the British medusae, which he had himself contemplated doing for many years. He had in fact started to collect notes for the purpose at the end of last century; but, appreciating the preliminary need for a fuller knowledge of the group as a whole and judging that at that time a monograph would

be premature, he had abandoned the work by 1905 and devoted his time to research on collections from all parts of the world.

But even in 1935 there were still many gaps in our knowledge of the hydroid stages of British medusae. Accordingly, by generous grants Browne made it possible for Dr W. J. Rees to work at the Plymouth Laboratory and elsewhere on the rearing of hydroids, and in this way many of the gaps were closed.

When I actually started work on the monograph Browne was already unable to take an active share in the writing and it devolved on me to prepare and submit drafts for his criticism. Unfortunately, before the work was far advanced Browne died and I had to face the task alone without the help of his valued advice and encouragement. But before his death, this benefactor to science had bequeathed to the Marine Biological Association a sum of money then sufficient to ensure the publication of the monograph. This knowledge and the memories of E. T. Browne stimulated me to aim at completion of a work that I had at first doubted my ability to do alone. I had, however, as a background the benefits of Browne's great experience which I had gained through discussion with him, and the use of his earlier notes and of his fine collections of specimens.

By 1940 the manuscript was nearly complete and most of the paintings and drawings had been made. Then for five and a half years I served in the forces, to return to Plymouth as Director of the Laboratory when war was over. Many of the finer details of the work had by then slipped my memory and it was only with difficulty that I was able to pick up the threads again and set about the task of bringing the text up to date and seeing to the many editorial details made necessary by nearly a thousand illustrations.

Had there been no war, I had intended to devote some time to studying the histological structure of medusae, and to travel to different parts of the British coasts to see the few species I still had not seen alive. With the duties devolving on me as Director and the energies required to repair the damages of war these hopes were clearly impossible to fulfil and I had to abandon all ideas of further research. Therefore, when bringing the work to completion for printing, I became sadly conscious of the many deficiencies I can now never attempt to remedy. It is doubtful indeed whether the monograph would ever have reached the printers' hands, had it not been for the encouragement of my friend Paul Kramp, who so kindly read the manuscript in 1948 and stimulated me to make the final effort. The manuscript was sent to the printers in the autumn of 1949, to be further delayed by accumulations of printing created by the war.

The writing of a book of this nature is a long process and from many friends I have received much assistance and encouragement on the way. Especially I should like to recall the names of the late Directors under whom I served at Plymouth, E. J. Allen and Stanley W. Kemp, to both of whom I owed so much. I am glad also to record with gratitude the pleasant time of fruitful research and discussion I spent with W. J. Rees, when for several years we were colleagues in an attack on linking medusae to their hydroids. Lastly my debt is deepest to P. L. Kramp for his generous advice at all times and to the late E. T. Browne but for whom the work would never have been attempted.

With the lapse of time since Browne's death in 1937 it was inevitable that money then deemed sufficient for the purpose should no longer be so. I had feared that the production of the monograph might not have been on so fine a scale as his legacy had given hope. My fears were allayed by generous grants from the Council of the Royal Society from its E. T. Browne Research Fund and the Syndics of the Cambridge University Press. To the Press my thanks are also due for the very great care they have given to ensure that there should be no other errors than those of my own making.

I should like also to thank again Dr W. J. Rees and Dr P. L. Kramp for the additional assistance they have given me in the critical reading of the proofs, and Dr J. S. Alexandrowicz for devoting much time to a very careful check of the bibliography. I am also grateful to Dr D. P. Wilson for allowing me to reproduce the beautiful photographs shown in Plates XXXII–XXXV; to Mr C. V. Adams for making many of the outline tracings from published illustrations; to Dr P. L. Kramp for lending his original drawings for the reproduction of text-figures 138, 143, 162, 163, 215 and 227 B, C; to Mr G. L. Wilkins for making a drawing for text-figure 161.

My thanks are no less due to the President, Professor James Gray, C.B.E., F.R.S., and members of the Council of the Marine Biological Association for their continued encouragement; and to them and Her Majesty's Development Commissioners for allowing me to undertake this work as part of my official duties on the Scientific Staff of the Plymouth Laboratory.

Except where otherwise stated I have made all the drawings myself. I have made a point of providing illustrations of preserved specimens in the crumpled and contorted states in which they often appear in plankton collections. Earlier monographs have given only idealized drawings of perfect or living animals which often do not suffice for the identification of badly preserved specimens which those who work on plankton collections are so accustomed to see. Many of these drawings I have made from E. T. Browne's collection in which the specimens were forty to fifty years old.

The classification of hydroids and medusae has always been illogical, since, even when hydroid and medusa are known to be the same species, separate generic and specific names (and sometimes separate families) are used for the two stages of the one animal. At first it seemed to me that our knowledge might be now sufficiently advanced in some directions to enable an attempt to be made in this monograph to bring the hydroids and medusae into a rational single classification. I came to realize, however, that our knowledge of the hydroids as a whole is still too imperfect. It might have been possible in one or two instances to make a beginning in this direction, but in order to be consistent I have not done so. The names of most of our medusae are now well established. It seemed to me wiser to leave it so, than to introduce new names which might have to be soon changed again as knowledge of hydroids advanced. Until a satisfactory natural classification can be made, it is better that the classification and names adopted should at present serve the more useful needs of identification.

The classification here adopted at family level is in general well recognized; I have, however, attempted to help advance by breaking up the large group of medusae previously included in the Eucopidae into more rational units.

In a group of organisms with so few characters suitable for classificatory purposes the manufacture of an orthodox diagnostic key is very difficult and unsatisfactory. I hope that I have overcome this by supplying the pictorial keys given on pp. 42–45.

Finally, I should state that, while I have occasionally used the word Hydromedusae since its meaning is so familiar, I find it difficult to believe that the Limnomedusae, Trachymedusae and Narcomedusae are derived from the same stock as the Anthomedusae and Leptomedusae with their characteristic hydroids.

THE STRUCTURAL CHARACTERS OF MEDUSAE

The basic structure of the hydromedusa type may be summarized as follows, the terms in italics being those used in the descriptions of species in this monograph.

The main body of the medusa (Text-fig. 1) consists of a gelatinous swimming bell or *umbrella*. The outer convex surface of the umbrella is the *exumbrellar surface*, and the inner concave surface is the *subumbrellar surface*. The cavity bounded by the subumbrellar surface is the *subumbrellar cavity*. The marginal edge of the umbrella is the *umbrella margin*. From the centre of the subumbrellar surface hangs the hollow *stomach*, terminating distally in the *mouth*. Four hollow *radial canals* run from the stomach just beneath the subumbrellar surface to join a continuous hollow circular canal or *ring canal*, which runs round the umbrella margin. On the umbrella margin, at each of the four points where a radial canal joins the ring canal, is a contractile *marginal tentacle*. Finally, the opening of the subumbrellar cavity is partially closed by a continuous horizontal shelf, the *velum*, which is situated just inside the umbrella margin.

For purposes of descriptive orientation the umbrella is divided into radial planes (Text-fig. 2). The four planes meeting at right angles at the summit of the umbrella in which the four radial canals lie are *perradial*. Intermediate between these four perradial planes, or *perradii*, and bisecting the four equal sectors or *quadrants* are four similar planes meeting at right angles at the umbrella summit, the *interradial* planes or *interradii*. The four perradii and four interradii thus divide the umbrella into eight equal sectors or *octants*. These eight sectors may be again equally divided by eight *adradial* planes or *adradii*; each adradius is thus situated midway between a perradius and an interradius, and the umbrella is divided into sixteen sectors.

In common with other coelenterates there are only two cell layers, the *ectoderm* and the *endoderm*. The ectoderm covers the whole exumbrellar and subumbrellar surfaces of the umbrella, and the external surfaces of the stomach, mouth, and marginal tentacles. The velum is entirely ectodermal. The endoderm lines the cavities of the stomach, of the radial and ring canals, and of the marginal tentacles, and spreads out between the radial canals to form a double lamella near the subumbrellar surface. Between the exumbrellar and subumbrellar surfaces of the umbrella there is a thickened supporting lamella of a gelatinous nature, the *jelly* or *mesogloea*.

This is the essential plan of a hydromedusa, and the specific differences are based on the form, or numbers, of the chief structures mentioned above together with additional characters such as the presence or absence of sense organs or marginal cirri. These latter structures will be defined below, where each character of the medusa is considered independently.

THE UMBRELLA

The *umbrella*, or swimming bell, is typically bell-shaped, e.g. *Sarsia* (Text-fig. 3A). It shows, however, considerable variation in form from species to species. Its height may be increased until it is almost mitre-shaped, e.g. *Aglantha* (Text-fig. 3B). It may be almost spherical, e.g. *Bougainvillia ramosa* (Text-fig. 3C). Or it may be flattened in varying degrees to produce a shape that is hemispherical, e.g. *Phialella* (Text-fig. 3D), saucer-shaped, e.g. *Aequorea* (Text-fig. 3E), or even flat and disk-like, e.g. *Obelia* (Text-fig. 3F).

The umbrella also varies considerably in its degree of solidity. This solidity is imparted by the presence of the jelly or mesogloea. In some species the jelly may be extremely thin, e.g. *Obelia*,

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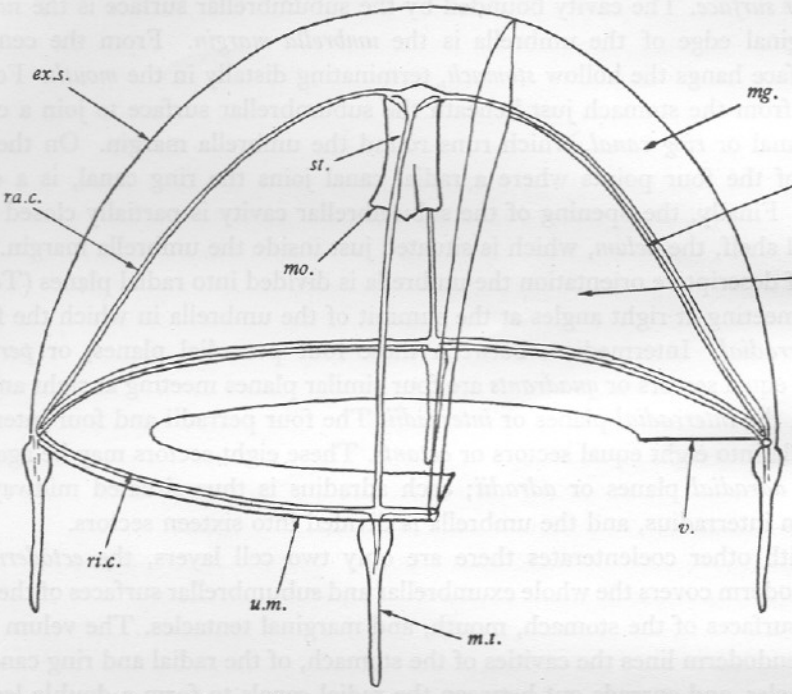
and the medusa is of a flimsy nature. It may be of moderate thickness, e.g. *Phialidium*, or very thick, e.g. *Bougainvillia*. The degree of development of the jelly in different regions of the umbrella also varies. In some species the jelly is much thickened at the summit or apex of the umbrella which may be drawn out into a rounded or pointed cone of varying size, e.g. *Leuckartiara* and *Amphinema* (Text-fig. 3G). Such a thickening at the summit of the umbrella is known as an *apical projection* or *process*. In one species at least the apical projection may have sensory papillae, e.g. *Steenstrupia nutans* (Text-fig. 37C). An unusual type of umbrella thickening is shown by *Halicreas minimum* in which there are lateral papillose prominences (Text-fig. 300B).



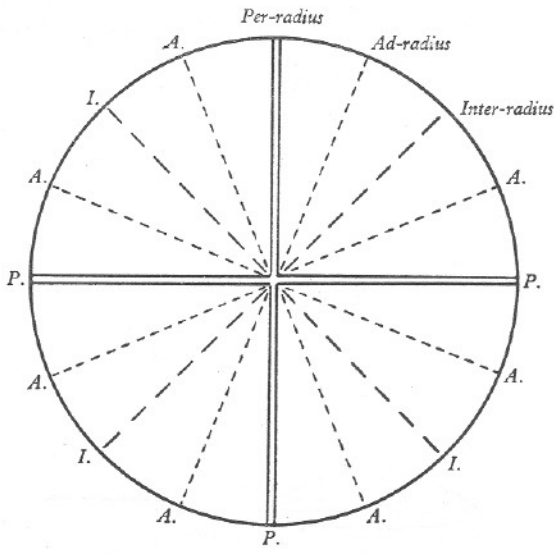
Text-fig. 1. Diagram of a medusa with one quadrant cut away. *ex.s.* exumbrellar surface; *mg.* mesogloea; *mo.* mouth; *m.t.* marginal tentacle; *ra.c.* radial canal; *ri.c.* ring canal; *st.* stomach; *sub.c.* subumbrellar cavity; *sub.s.* subumbrellar surface; *u.m.* umbrella margin; *v.* velum.

In most hydromedusae the margin of the umbrella is entire, but in the Narcomedusae (see p. 463) it may be incised or lobed (Text-fig. 3H); the cleft between the lobes has a strand of ectoderm cells running up to the base of the marginal tentacle called a *peronium*.

The size of the umbrella in adult medusae varies from a diameter of 1 or 2 mm. to as much as 20 cm. The size is to a certain extent related to the umbrella shape. In small medusae the umbrella is generally bell-shaped, *Obelia* being an exception; with increase in size the umbrella becomes progressively more flattened through a hemispherical shape to that of a saucer. As a general rule the Anthomedusae are bell-shaped and the Leptomedusae more flattened (see pp. 46 and 227). There are no British Anthomedusae with a bell height greater than about 20 mm., e.g. *Neoturris pileata*; among the Leptomedusae on the other hand, while the majority of British species are in the neighbourhood of 20–30 mm. or less in diameter, a few such as *Aequorea*, *Tima* and *Staurophora* grow to a considerable size and might at first glance be mistaken for Scyphomedusae. Among the Limnomedusae and Trachymedusae both bell-shaped and flattened medusae may be found (see pp. 385 and 418).

All medusae have stinging cells or nematocysts (see p. 14) scattered over the exumbrellar surface, especially in the region of the umbrella margin. These scattered nematocysts are especially noticeable in the youngest stages of the medusae in which the surface area of the exumbrella is small and the nematocysts consequently appear relatively large. In larger medusae the exumbrellar nematocysts are more widely scattered and less noticeable. But in some species there is a more precisely defined nematocyst armature on the exumbrella, the nematocysts being abundantly confined to certain zones. This armature may be in the form of diffuse tracks of nematocysts running in radial lines from the umbrella margin towards its summit, e.g. *Ectopleura* and *Hybocodon* (Pl. III, figs. 3–6). In one instance the nematocysts are arranged in a wide band round the middle of the umbrella, e.g. young *Aequorea* (Pl. XXI, fig. 3). In some medusae, however, the nematocysts are much more strictly confined to definite patches of tissue, e.g. *Zanclea* (Pl. IV, figs. 1–3) and *Proboscidactyla stellata* (Pl. XXIII, fig. 4).

In many young specimens of medusae the remnants of the attachment to the hydroid persist in the apical jelly of the umbrella as an *umbilical canal*, and sometimes even to the adult stage.



Text-fig. 2. Diagram to define the radii of a medusa. *P.* per-radii, these are the radii on which the four primary radial canals lie; *I.* inter-radii; *A.* ad-radii.

THE VELUM

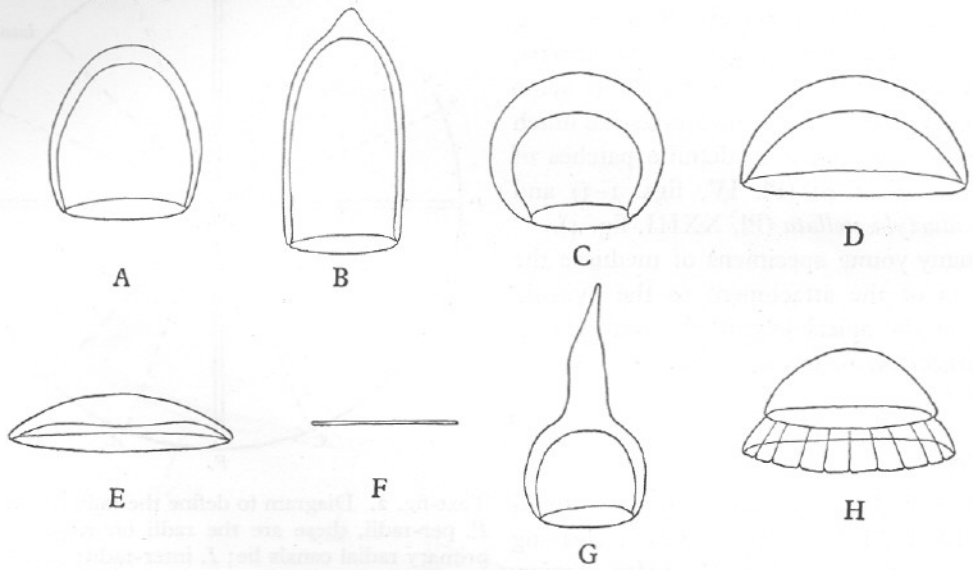
The *velum* forms a horizontal shelf round the aperture of the subumbrellar cavity, leaving a central circular aperture, the *velar opening*. The proportional size of this opening varies usually with the size of the medusa. In small specimens the ratio of the diameter of the opening to the diameter of the medusa itself is much less than in large specimens. This change in size of the velar opening is related to the swimming mechanism of the medusa.

In some medusae, especially in certain Trachymedusae and Limnomedusae, the velum is very strongly developed and it may hang downwards like a curtain round the umbrella margin. Rarely, as in *Obelia*, it is quite reduced.

THE STOMACH

The *stomach*, which hangs down from the centre of the subumbrellar surface, is essentially a simple sack. In most medusae when the stomach is not dilated with food it is somewhat cross-shaped in section, the arms of the cross being in line with the radial canals, i.e. perradial. At the distal end of the stomach is the mouth, which opens to the exterior. The stomach may be cylindrical or fusiform, and it may be large in proportion to the umbrella, especially is this so in the Anthomedusae. In some species it is very elongated or serpentine, e.g. *Sarsia tubulosa* (Pl. I, fig. 2). A similar serpentine appearance is produced in some Leptomedusae by quite another means. The jelly at the summit of the subumbrellar cavity has a cone-shaped thickening projecting downwards into the cavity, to the end of which the stomach is attached. This

thickening of the jelly is known as the *peduncle*. The peduncle may be very shallow and hardly noticeable, e.g. *Proboscidactyla stellata* (Text-fig. 250); it may be more pronounced and conical, e.g. *Lizzia* (Pl. VII, figs. 1, 2) and *Eirene* (Pl. XX, fig. 4); or it may form a very elongated cone resulting in the protrusion of the stomach beyond the umbrella margin, e.g. *Octorchis gegenbauri* (Pl. XXII, fig. 4). In extreme examples, e.g. *Eutima gracilis*, the peduncle is very long and narrow, and has a serpentine appearance (Pl. XXII, fig. 1); it terminates in the short stomach. The portion of the medusa which hangs down in the subumbrellar cavity like the clapper of a bell is commonly called the *manubrium*. Thus the manubrium of *Sarsia tubulosa* and that of *Eutima gracilis* are very similar in appearance, but in the former it consists of stomach only and in the latter mostly of gelatinous peduncle.



Text-fig. 3. Diagrams of umbrellas of different medusae. A, *Sarsia*; B, *Aglantha*; C, *Bougainvillia*; D, *Phialella*; E, *Aequorea*; F, *Obelia*; G, *Amphinema*; and H, a narcomedusa.

The area of attachment of the stomach to the subumbrella is its *base*. In some medusae the stomach is attached to the subumbrella by the whole of its basal surface, and if the stomach be large and wide the base is very broad, e.g. *Aequorea*. In others the base of the stomach is only attached along the four perradial lines which form a continuation of the radial canals to the centre of the subumbrella, i.e. the attachment is along the arms of a perradial cross. With this method of attachment, when the base of the stomach is broad, triangular pockets are formed between the subumbrellar surface and the dorsal wall of the stomach in the angles between the arms of the cross; these are most pronounced when the stomach is contracted with the mouth fully open, e.g. *Cosmetira* (Text-fig. 158A).

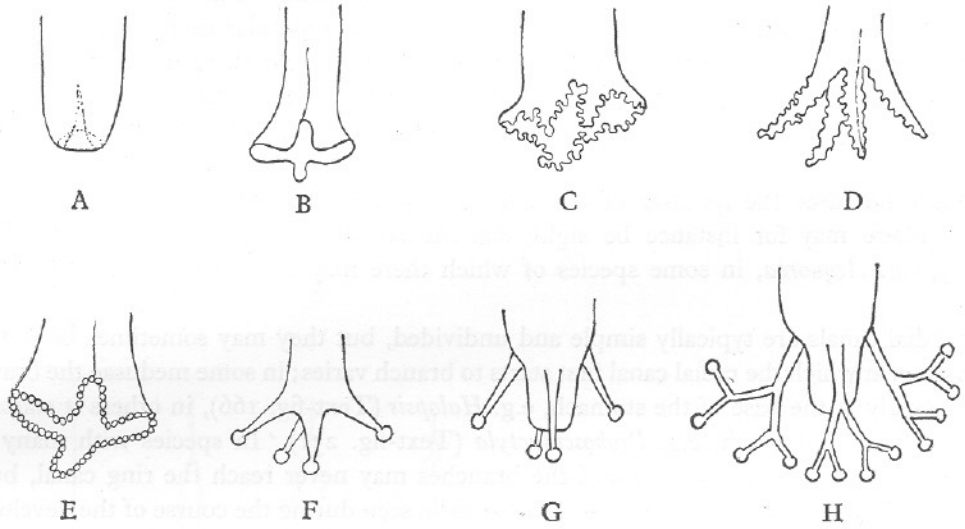
In some medusae, e.g. *Sarsia*, at the base of the stomach there is a small protrusion into the substance of the jelly known as an *apical knob* or *chamber*.

THE MOUTH

The *mouth* is the opening of the stomach to the exterior, the actual margin of this opening forming the mouth *lips*. The structure of the mouth and of its lips is a character of great importance in the classification of the Anthomedusae.

The mouth may be quite simple and *circular* (Text-fig. 4A), e.g. *Sarsia* and *Steenstrupia*. It may have four simple perradial lips, e.g. *Phialidium* (Text-fig. 4B). In other species the four lips may be folded or crenulated to varying degrees (Text-fig. 4C), e.g. *Cosmetira*, *Leuckartiara*. The four perradial lips may be quite short, e.g. *Phialidium*, or they may be drawn out and pointed, e.g. *Eirene* (Text-fig. 4D). In medusae with more than four radial canals the number of lips often corresponds with the number of radial canals, e.g. *Melicertum*.

In many species the mouth opening itself is circular, but arising from the outer surface of the stomach a short distance above the mouth there are four perradial *oral tentacles* each terminating in a cluster of nematocysts; these oral tentacles may be simple and undivided, e.g. *Lizzia* (Text-fig. 4G), or they may be dichotomously branched, e.g. *Bougainvillia* (Text-fig. 4H).



Text-fig. 4. Diagrams of mouths of different medusae. A, *Sarsia*; B, *Phialidium*; C, *Cosmetira*; D, *Eirene*; E, *Turritopsis*; F, *Podocoryne*; G, *Lizzia*; H, *Bougainvillia*.

The mouth is nearly always armed with nematocysts along its lips, and in some species this nematocyst armature may take a distinctive form. In *Turritopsis*, for instance, there are spherical clusters of nematocysts distributed uniformly along the lips (Text-fig. 4E); in other species, e.g. *Podocoryne* (Text-fig. 4F) and *Rathkea*, there may be only a few clusters and their distribution is of classificatory value.

A very unusual type of mouth is found in *Staurophora*; in this medusa the opening of the mouth is continued for a considerable length along the course of each of the four radial canals; it thus forms a large cross-shaped opening (Text-fig. 133).

THE RADIAL CANALS

The *radial canals* are tubes running from the perradial corners of the base of the stomach to the ring canal near the umbrella margin. Usually they are straight and narrow, and have smooth sides, e.g. *Phialidium*. They vary, however, in width among different species of medusae and may be so wide as to appear like smooth bands or ribbons, e.g. *Amphinema* (Pl. XI, fig. 3); the edges of such broad radial canals are often uneven, having jagged angular or rounded outgrowths, e.g. *Leuckartiara* (Pl. XII, fig. 3).

STRUCTURAL CHARACTERS

The radial canal generally enters the stomach by a small circular or slightly funnel-shaped orifice. In some species, e.g. *Laodicea*, the funnel is quite large and forms a vertical slit (Text-fig. 128). This is carried to an extreme degree in such medusae as *Leuckartiara* in which the form of the radial canal opening is influenced by the direction of growth of the stomach (Pl. XXX, fig. 1). In this medusa the base of the stomach is attached to the subumbrella along the four arms of a perradial cross. In young specimens the base of the stomach is quite small and the radial canals therefore enter the stomach high up at its base. As the medusa grows, however, the basal portion of the stomach grows quicker than the more distal portion. The openings of the radial canals thus become carried down the side of the stomach until in adult specimens the radial canals appear to enter the stomach only about half-way up its sides. But above the entrance of each canal the stomach is still attached to the subumbrella along the arms of a perradial cross, and as a result four distinct pouches are formed in the subumbrellar cavity above the level of the openings of the radial canals. The tissue separating these pouches has, in the past, been called 'mesentery'; it is in reality merely the line of attachment of the stomach to the subumbrella. Its degree of development depends entirely upon the differential growth in different regions of the stomach.

In many medusae the number of radial canals is greater than the typical number which is four. There may for instance be eight, e.g. *Melicertum*; twelve to sixteen, e.g. *Halopsis*; or many, e.g. *Aequorea*, in some species of which there may be more than a hundred radial canals.

The radial canals are typically simple and undivided, but they may sometimes be branched. The position at which the radial canal first starts to branch varies; in some medusae the branching begins actually at the base of the stomach, e.g. *Halopsis* (Text-fig. 166), in others it starts some distance from the stomach, e.g. *Proboscidactyla* (Text-fig. 251). In species with many radial canals produced by branching some of the branches may never reach the ring canal, but end blindly. Blindly ending canals are of course also to be seen during the course of the development of those species whose numbers of radial canals increase with the growth of the medusa. It is usual for the new canals to grow out from the base of the stomach towards the ring canal; they thus develop centrifugally. In a few species, however, e.g. *Melicertum*, the new canals arise from the ring canal and grow inwards towards the stomach, i.e. centripetally. A few medusae have such canals which never reach the stomach; in this condition they are known as *centripetal canals* (Pl. XIII).

Since radial canals normally issue from the stomach it follows that in those medusae with peduncles the radial canals themselves run down the peduncle to the stomach at its end.

In the Narcomedusae typical radial canals are absent. Their place may be taken by pouches which grow outwards over the subumbrellar surface from the large circular stomach.

THE RING CANAL

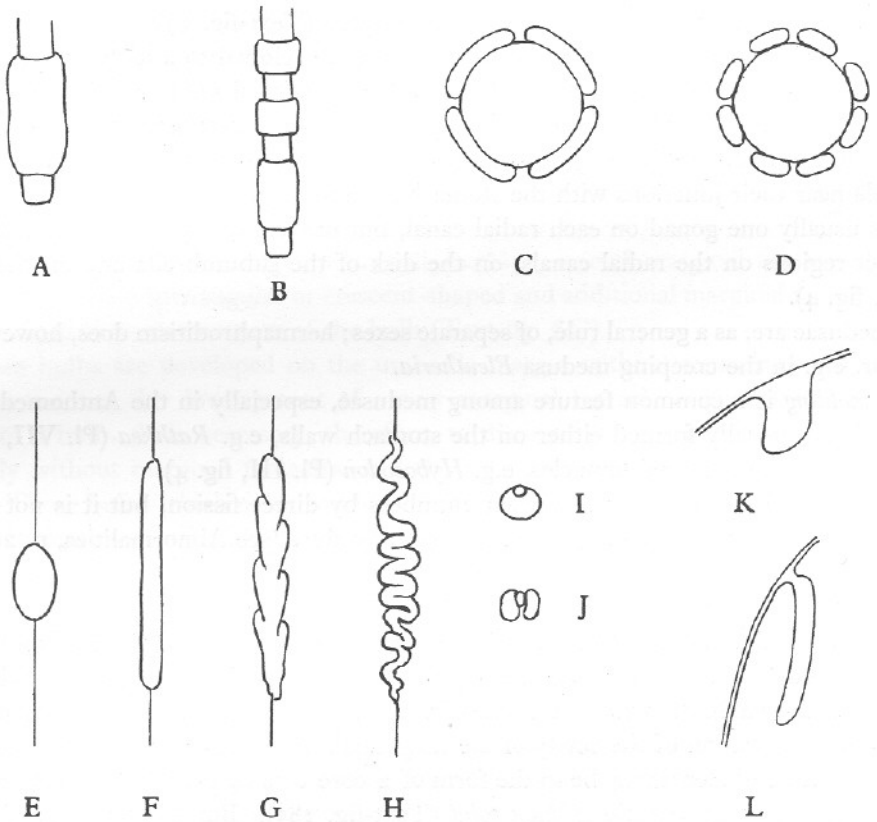
The *ring canal* is typically a simple circular canal running round the umbrella margin. Like the radial canals, it may sometimes be rather broad and have jagged edges. Occasionally, e.g. in *Proboscidactyla*, the ring canal is not hollow, but consists of a solid core of endoderm cells. In the Narcomedusae a ring canal may or may not be present. It is characteristic of the Narcomedusae that the umbrella margin is lobed. When the margin is deeply cleft the marginal canal is continued up each side of the cleft and thus runs in a vertical direction. These vertical canals are known as *peronial canals*.

THE GONADS

The *gonads* are of considerable value as classificatory characters. Their position, for instance, forms one of the principal distinguishing characters between the Anthomedusae and Leptomedusae.

The gonads may be situated on the walls of the stomach or on the radial canals.

When situated on the stomach the form of the gonad and its position are valuable characters for purposes of classification. The gonad may be cylindrical and completely surrounding the stomach, e.g. *Sarsia, Rathkea.* Such cylindrical gonads are usually continuous longitudinally, forming one complete mass of tissue (Text-fig. 5A); but they may sometimes be split to form a number of discontinuous gonadial bands, e.g. *Dipurena* (Text-fig. 5B).



Text-fig. 5. Diagrams of gonads of different medusae. A and B, lateral view of stomach; A, *Sarsia*; B, *Dipurena*. C and D, cross-section of stomach: C, *Bougainvillia ramosa*; D, *B. principis*. E–H, types of gonad on radial canals: E, oval; F, linear; G, folded; H, sinuous; I and J, cross-sections of gonad on radial canals: I, *Phialidium*; J, *Tiaropsis*. K and L, lateral view of gonad: K, *Craspedacusta*; L, *Aglantha*.

When the gonads are not cylindrical their situation on the stomach wall is of importance. They may be interradial, e.g. *Bougainvillia ramosa* (Text-fig. 5C), or adradial, e.g. *Bougainvillia principis* (Text-fig. 5D). They may form simple pad-like cushions, e.g. *Bougainvillia*, or be thrown into folds which form pockets or pits in the stomach wall, e.g. *Leuckartiara, Neoturris* (Pl. XII, figs. 1–4).

When situated on the radial canals the gonads are usually completely separated from the stomach. In a few medusae, however, e.g. *Laodicea* (Pl. XIV, fig. 1), their proximal ends are

contiguous with the stomach itself. Occasionally also the gonad is present both on the walls of the stomach and for a short distance along the radial canal, e.g. *Podocoryne hartlaubi* (Pl. VI, fig. 4).

When completely separated from the stomach the position of the gonad along the course of the radial canal is often a diagnostic character. The gonads on the radial canals may be *oval* in shape (Text-fig. 5E) or they may be elongated to varying degrees. When considerably elongated and consequently extending for some way along the course of the radial canal they are said to be *linear*. When the gonad is linear it may be straight, folded or sinuous (Text-fig. 5F–H). In some medusae the gonads may be flattened and leaf-shaped, e.g. *Liriope* (Text-figs. 280–1).

The gonadial tissue is developed on the lateral walls of the radial canal, but in some medusae it is continuous also over the ventral wall, e.g. *Phialidium hemisphaericum* (Text-fig. 5I). When the gonadial tissue is present only on the lateral walls of the canal the gonad is divided along its ventral or lower surface by a *median furrow*, e.g. *Tiaropsis* (Text-fig. 5J).

The gonadial tissue on the radial canals is sometimes developed to a high degree and covers an area considerably greater than that of the walls of the normal radial canal, the gonads then hang down into the subumbrellar cavity like pouches, e.g. *Craspedacusta* (Text-fig. 5K and Pl. XXIV, fig. 1). In *Aglantha* the gonads form sausage-shaped pouches hanging down from the radial canals near their junctions with the stomach (Text-fig. 5L and Pl. XXVI, fig. 9).

There is usually one gonad on each radial canal, but in *Octorchis gegenbauri* gonads occur in two distinct regions on the radial canals, on the disk of the subumbrella and on the peduncle (Pl. XXII, fig. 4).

Hydromedusae are, as a general rule, of separate sexes; hermaphroditism does, however, sometimes occur, e.g. in the creeping medusa *Eleutheria*.

Asexual budding is a common feature among medusae, especially in the Anthomedusae. The medusa buds are usually formed either on the stomach walls, e.g. *Rathkea* (Pl. VII, fig. 3), or from the bases of the marginal tentacles, e.g. *Hybocodon* (Pl. III, fig. 4).

Occasionally medusae may increase their numbers by direct fission, but it is not known to what extent this can be considered to be a normal procedure (see Abnormalities, p. 20).

MARGINAL TENTACLES

1. *Structure*. The marginal tentacles, whose main function is the capture of prey, show as might be expected great diversity of form. They have an outer covering of ectoderm and internally there is an endodermal lining which originates from the ring canal. This endodermal centre may grow out as a continuation of the cavity of the ring canal, in which event the marginal tentacles are *hollow*; or the endoderm may be in the form of a core of single cylindrical cells placed end to end and the marginal tentacle is then *solid* (Text-fig. 183). But the term 'solid' requires qualification. It is only used when the endoderm forms a core of single cells. Often marginal tentacles may be found whose central cavities are filled with endoderm cells; they are thus to all intents and purposes solid. But this endodermal core is composed of several peripheral rows of cells, and sections in the basal regions of such marginal tentacles often disclose central cavities. These cavities become so narrow as to be virtually non-existent in the distal portions of the marginal tentacles which become filled with a solid endodermal mass.

It is very usual for a marginal tentacle to be dilated at its base next to the umbrella margin; this dilated portion is called the *tentacle bulb*. In some medusae, however, there is no basal swelling and the marginal tentacle is of uniform thickness right up to the umbrella margin, e.g. *Gossea*, *Proboscidactyla* (Text-figs. 6E, I).

The marginal tentacle bulbs are of various shapes and sizes. They may be considerably swollen, e.g. *Sarsia*, in which there is a horseshoe-shaped ring of nematocyst tissue (Text-fig. 6B). Often the shape of the bulb is not of so definite a character and its shape depends very much on its degree of contraction. In preserved specimens, however, they may appear quite distinctly different, such as spherical, e.g. *Phialella*, or conical, e.g. *Phialidium* (Text-fig. 6H). Sometimes they are long drawn out and tapering and distinctly laterally compressed, e.g. *Leuckartiara* (Text-fig. 6A).

The marginal tentacle bulb may also grow upwards for a short distance and clasp the margin of the umbrella forming an *exumbrellar spur*, e.g. *Steenstrupia*, *Leuckartiara* (Text-fig. 6A).

When speaking of the marginal tentacle the outer surface, facing away from the umbrella, is known as the *abaxial* surface, while the inner surface is *adaxial*. The degree of thickening of the marginal tentacle bulb is not always the same all round the base of the marginal tentacle, thus in *Laodicea* it is more thickened on the adaxial side.

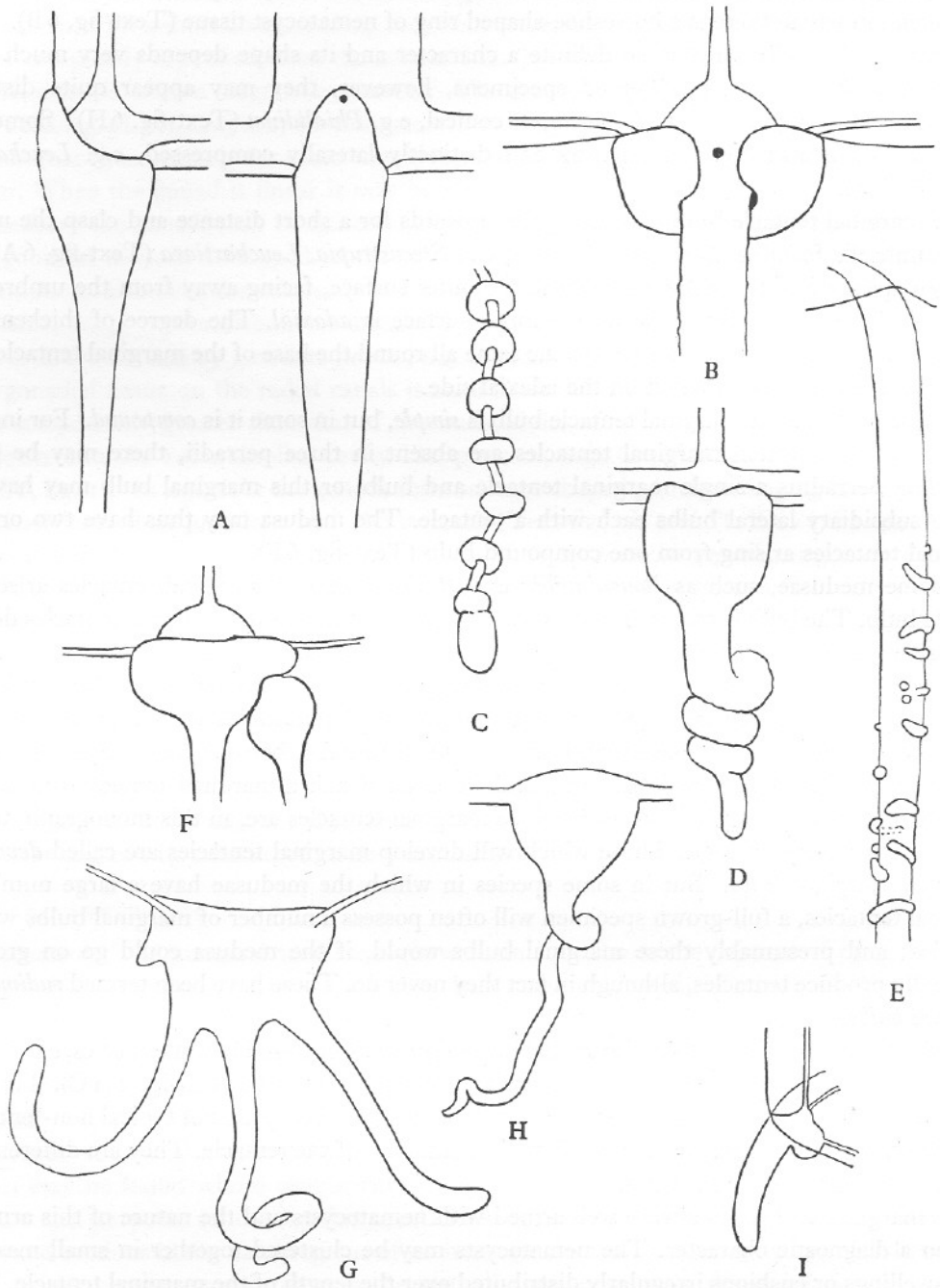
In most medusae the marginal tentacle bulb is *simple*, but in some it is *compound*. For instance in *Hybocodon*, in which marginal tentacles are absent in three perradii, there may be in the remaining perradius a single marginal tentacle and bulb, or this marginal bulb may have one or two subsidiary lateral bulbs each with a tentacle. The medusa may thus have two or three marginal tentacles arising from one compound bulb (Text-fig. 6F).

In some medusae, such as *Bougainvillia* and *Rathkea*, several marginal tentacles arise from a single bulb. The bulb is triangular or crescent-shaped and additional marginal tentacles develop successively from the outer corners of the bulb (Text-fig. 6G).

Sometimes bulbs are developed on the umbrella margin without tentacles. But during the growth of a medusa the development of a new marginal tentacle is always preceded by the formation of a bulb. It is necessary, therefore, to distinguish between those bulbs which are permanently without marginal tentacles, and those on which a marginal tentacle will later be developed. Those bulbs which never produce marginal tentacles are, in this monograph, termed *non-tentacular marginal bulbs*. Those which will develop marginal tentacles are called *developing tentacular marginal bulbs*. But in some species in which the medusae have a large number of marginal tentacles, a full-grown specimen will often possess a number of marginal bulbs without tentacles; and presumably these marginal bulbs would, if the medusa could go on growing, eventually produce tentacles, although in fact they never do. These have been termed *rudimentary marginal bulbs*.

In addition to the above types of marginal bulbs there may be found in some species, e.g. *Eutima*, a number of small wart-like swellings round the umbrella margin (Text-fig. 231C). These are quite obviously never destined to carry marginal tentacles, and they are not typical non-tentacular marginal bulbs which have been evolved by the reduction of the tentacle. They are differentiated here as *marginal swellings* or *warts*.

The marginal tentacle is always well armed with nematocysts and the nature of this armature is often a diagnostic character. The nematocysts may be clustered together in small masses to form swellings or cushions irregularly distributed over the length of the marginal tentacle. These are generally referred to as *nematocyst clusters*, and they may in some species have a more regular arrangement. In any event, when the marginal tentacle is fully extended they have a more regularly distributed appearance and make the marginal tentacle look moniliform. In some medusae the nematocysts are grouped together more compactly to form complete annulations surrounding the marginal tentacle; these are known as *nematocyst rings* (Text-fig. 6C).



Text-fig. 6. Diagrams of details of marginal tentacles of different medusae. A, *Leuckartiara octona* (lateral and abaxial views of base); B, *Sarsia tubulosa*; C, *Steenstrupia nutans*; D, *Cosmetira pilosella*; E, *Gossea corynetes*; F, *Hybocodon prolifer*; G, *Bougainvillia britannica*; H, *Phialidium hemisphaericum*; I, *Proboscidactyla stellata*.

A very specialized form of armature is found in *Zanclea*, in which the marginal tentacle carries numerous capsules filled with nematocysts; each capsule is attached to the marginal tentacle by a contractile stalk, and is known as a *cnidophore* (Text-fig. 47). In *Craspedacusta* the nematocysts are in papillae (Text-fig. 272).

In many medusae the nematocysts are not conspicuously grouped on the marginal tentacles, but are fairly evenly distributed over their surfaces. The marginal tentacles then appear to be *smooth*.

In most species the marginal tentacles are entire, but there are a few medusae in which the marginal tentacles are bifurcated or branched, e.g. *Cladonema*, *Eleutheria* (Text-figs. 50, 52; Pl. IV, figs. 4–6). These medusae also have organs of adhesion on their marginal tentacles, and somewhat similar organs are found in *Gonionemus* (Text-fig. 263 D).

Most marginal tentacles are very extensile and can be extended into long threads of gossamer-like fineness. They are shortened by contraction which may take place in one of two ways. In some medusae contraction of the marginal tentacles is brought about by direct shortening of the tissue like a concertina. But in many species, in addition to direct contraction, the virtual length of the marginal tentacle is greatly reduced by spiral coiling, the coils of the spiral being tightly wound.

2. *Arrangement*. In the above account of the fundamental structure of a medusa the typical number of marginal tentacles has been taken as four, perradially situated. They do, however, vary greatly in number in different species, or in the same species at different ages.

In some species the number is reduced to three, two, or one, or there may even be no marginal tentacles. Increase in number during growth generally follows a regular law until about twenty-four or thirty-two marginal tentacles are developed, by the addition successively of interradial and adradial marginal tentacles, i.e.

$$4 \text{ perradial} + 4 \text{ interradial} + 8 \text{ adradial} = 16,$$

and then one between every two = 32.

An alternative method is,

$$4 \text{ perradial} + 8 \text{ adradial} = 12,$$

and then one between every two = 24.

These alternative methods of increasing the numbers of marginal tentacles may be found in the developmental stages of medusae of the same species.

After a number of twenty-four or thirty-two marginal tentacles has been reached their distribution becomes more irregular. In some species the only limit set to the total number of marginal tentacles appears to be the space available round the margin of the umbrella.

Sometimes the marginal tentacles appear grouped at regular intervals round the umbrella margin. This may be due either to actual grouping, e.g. *Gossea* (Pl. XXIII, fig. 1); or, more usually, to the growth of a number of marginal tentacles from a common marginal bulb, e.g. *Rathkea*, *Bougainvillia* (Text-figs. 65, 79).

The position of the marginal tentacle is not always exactly on the margin of the umbrella. This is especially so in medusae whose marginal tentacles have no distinct basal bulb. The older marginal tentacles appear to arise some distance above the margin of the umbrella owing to the growth of the umbrella margin downwards immediately under the base of the marginal tentacle. This marginal growth takes place of course all round the margin and the last marginal tentacles to appear are directly on the margin. The disposition of the marginal tentacles with reference to the margin is thus a function of the age of the medusa, e.g. *Craspedacusta* (Text-fig. 271).

STRUCTURAL CHARACTERS

The marginal tentacles of any one medusa are usually always of one kind, differing only in size according to age. In a few species, however, there are two kinds of marginal tentacles, e.g. *Liriope* (Text-fig. 275).

In *Amphinema rugosum* there are a number of very small solid tentacles between the two hollow marginal tentacles; these I have called *marginal tentaculae* (Pl. XI, fig. 4).

CIRRI

Cirri are small tentacular-like organs situated on the umbrella margin between the true marginal tentacles. They are always much smaller than the marginal tentacles and never have swollen basal bulbs. They are solid, and have a core of a single row of endoderm cells. Two types are recognizable.

Spiral cirri (Text-fig. 154). These coil spirally and have a terminal nematocyst cluster usually slightly spiral in shape. They are the commoner kind.

Flexile cirri (Text-fig. 160) have so far only been described from *Cosmetira*. They have nematocysts arranged in rings along their whole length, and, at any rate in preserved material, are found straight and not coiled spirally.

As with the marginal tentacles, the older cirri may sometimes be found above the umbrella margin. This is especially so in *Cosmetira* (Text-fig. 159).

Cirri may be situated immediately adjacent to the basal bulbs of the marginal tentacles and are then known as *lateral cirri*. They may also occur all along the umbrella margin in the interspaces between the marginal tentacles, when they are called *marginal cirri*.

SENSE ORGANS

Two kinds of sense organs are found, *ocelli* and *statocysts*. There may perhaps be a third, the *cordylus*, but its function is not yet known.

Ocelli are organs for light reception. They are most common and best developed in the Anthomedusae. Exteriorly they appear as round or oblong spots of black, chocolate brown, or red pigment (Text-fig. 22). Their structure has been studied especially by Linko (1900*b*). The ocellus usually consists of a small mass of pigmented ectoderm cells lining a pit on a protuberance and associated with nerve cells. A lens may or may not be present. In *Tiaropsis* the pigment cells are endodermal.

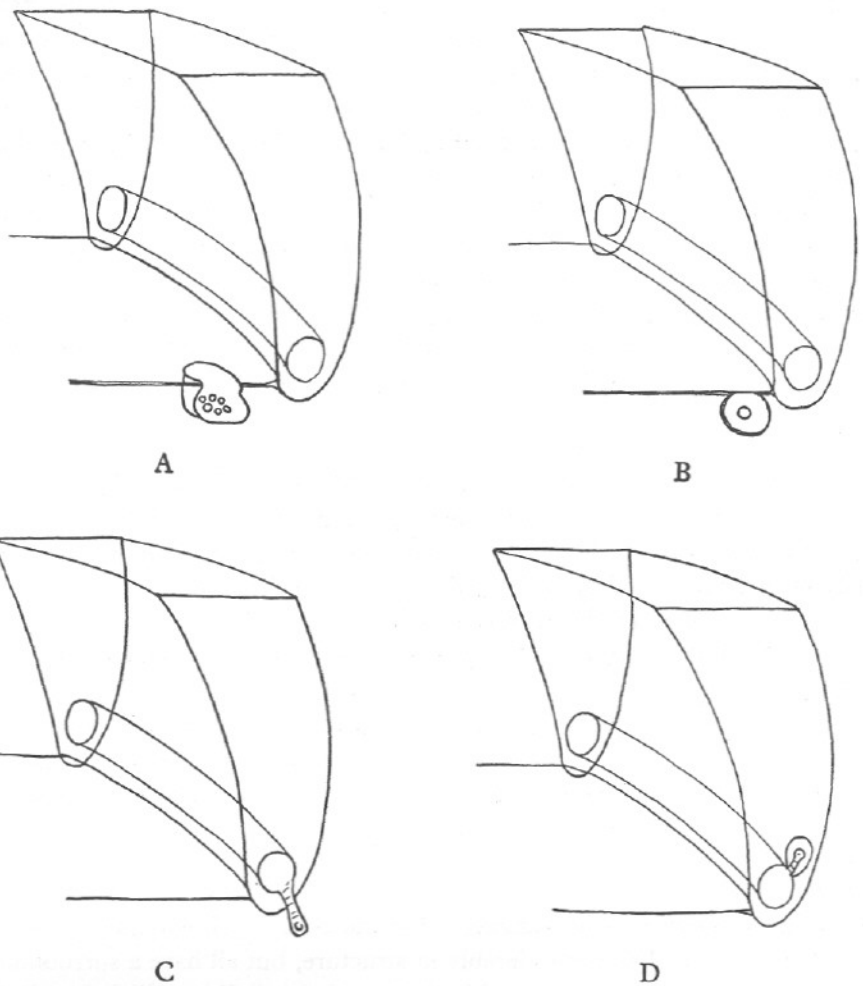
Ocelli are usually situated on the basal bulbs of the marginal tentacles. They may be on the outer side of the marginal tentacle bulb, i.e. *abaxial*, e.g. *Sarsia*, *Leuckartiara* (Text-fig. 93); or they may be on the inner side, i.e. *adaxial*, e.g. *Bougainvillia*, *Laodicea* (Text-fig. 129). Their situation under the marginal vesicles in *Tiaropsis* is unusual (Text-fig. 169).

The so-called *statocysts* are possibly organs of orientation. They are not found in the Anthomedusae, but occur in many Leptomedusae and Limnomedusae, and in all Trachymedusae and Narcomedusae. Their structure has been studied especially by O. & R. Hertwig (1878).

The statocysts are of two chief kinds which are of great value for classificatory purposes. They may be entirely ectodermal in origin, as in the Leptomedusae (Text-fig. 7A, B), or essentially of endodermal origin, as in the Limnomedusae, the Trachymedusae and the Narcomedusae (Text-fig. 7C, D).

Ectodermal statocysts. The ectodermal statocysts develop in the velum just where it joins the margin of the umbrella. Since the velum is composed entirely of ectoderm the statocysts are also formed only from ectoderm cells. In general structure they are small hollows or pits in the velum

which may remain open or be completely closed. The organ thus has a cavity and is in essence a small vesicle. They are therefore known as *marginal vesicles*. If they are in the form of depressions or pits in the velum still remaining open on their upper or subumbrellar sides they are called *open marginal vesicles* (Text-fig. 7A). If the velar tissue entirely seals off the upper opening so that complete spherical or oval capsules are formed hanging on the under side of the velum, the organ is known as a *closed marginal vesicle* (Text-fig. 7B). Owing to the fact that the organ is



Text-fig. 7. Types of statocysts: A, open marginal vesicle; B, closed marginal vesicle; C, free marginal sensory club; D, enclosed marginal sensory club.

formed as a depression in the velum the capsule is covered externally with ectoderm from the lower or exumbrellar surface of the velum and lined internally by ectoderm of the upper or subumbrellar surface.

The vesicles contain small spherical or polygonal *concretions*. There may be one, two, or many concretions in each vesicle. When there are many concretions they are often arranged in crescentic rows.

In closed marginal vesicles there is a basal cushion of cells with sensory hairs.

STRUCTURAL CHARACTERS

Endodermal statocysts. The structure of an endodermal statocyst is quite different from that of an ectodermal statocyst, although certain types may show a superficial resemblance to the latter. Essentially they are *sensory clubs*; that is, small tentacle-like structures growing out from the umbrella margin, each with an axis of endoderm cells originating from the ring canal. They thus form small club-like organs covered with ectoderm and having a central core of endoderm. In their distal portion there are one or more large endoderm cells each containing a solid concretion. In this form they are known as *free marginal sensory clubs* (Text-fig. 7C).

But in some medusae the ectoderm surrounds the club so that it is entirely enclosed and contained in a small vesicle. The organs are then *enclosed marginal sensory clubs* (Text-fig. 7D). The development of an enclosed from a free sensory club is shown in *Rhopalonema* in which the clubs are at first free and later become enclosed (Text-figs. 283, 284). In many medusae, notably in the Limnomedusae, the statocysts are embedded deeply in the mesogloea. While such organs may quite legitimately be called marginal vesicles I have used the term *enclosed marginal sensory clubs* in this monograph to distinguish them from the ectodermal marginal vesicles of the Leptomedusae, and to emphasize their difference. The sensory clubs are always free in the Narcomedusae, but in the Limnomedusae and in the Trachymedusae they may be either free or enclosed. In some Narcomedusae tracks of ectoderm cells with bristles run up over the exumbrella from the cushions from which the sensory clubs arise; these are known as *otoporpae*.

CORDYLI

Cordyli are marginal club-like structures occurring in Leptomedusae of the family Laodiceidae (Text-fig. 130D). Their function is not known, although it has been thought to be sensory. A typical cordylus is club-shaped, having a thick distal portion and a narrow peduncle. It has an internal layer of large endoderm cells and is covered externally by ectoderm. It is hollow, but may be completely filled by the endoderm cells in the narrow stalk region, the lumen being confined to the distal portion. As a rule it has no nematocysts, but they are present in *Ptychogena antarctica* and *P. crocea*.*

Structures somewhat similar in appearance to cordyli are found in certain Anthomedusae of the family Tiarannidae. They differ, however, in that they usually contain nematocysts, especially at the distal end. They are often not so typically club-shaped as a true cordylus. Their homology has been discussed by Kramp (1919, p. 4).

NEMATOCYSTS

All medusae have *nematocysts* or stinging cells; the cells which contain the nematocysts are *nematoblasts*. Nematocysts differ considerably in structure, but all have a surrounding envelope or *capsule* containing a refringent fluid; within the capsule is a hollow coiled *thread*, which can be everted by turning inside out. The act of everting the thread to the exterior is called the *discharge*; some authors have used the word 'explode', but the word 'discharge' is preferable in distinction to the explosion or complete disruption of the nematocyst in certain chemicals. When the nematocyst is in the undischarged state the end of the capsule at the base of the thread is closed by an *operculum*, which can be seen as a small button-like projection when the nematocyst is discharged.

While the shape of the capsule varies considerably in different kinds of nematocysts, the differences in the form and armature of the thread are more striking and of use in defining the

* These species have not been recorded in British waters.

different kinds of nematocysts. There have in the past been various attempts to group certain types of nematocysts roughly into separate categories. But the most detailed and useful classification is that of Weill (1934*a*).

The wall of the thread has three thickenings running along it in a dextral spiral. These thickenings often carry spinous processes, especially near the basal region of the thread. The thread itself may be of approximately uniform thickness throughout, or it may taper or have a basal dilatation. The length of the thread also varies up to many times the length of the capsule. As already stated, the thread is hollow, but it may or may not open to the exterior. It is on such characters that the following classification of Weill is based (Text-fig. 8).

ASTOMOCNIDES—thread without terminal opening (α-, without; στόμα, mouth; κνίδη, nettle).

A. *Rhopalonemes*—thread club-shaped (ῥόπαλον, club; νῆμα, thread).

I. Anacrophore—without apical lash (α-, without; ἄκρος, topmost; φορέω, to bear).

II. Acrophore—with apical lash.

B. *Desmonemes*—discharged thread spiral (δεσμός, mooring cable).

STOMOCNIDES—thread with terminal opening.

A. *Haplonemes*—without a basal swelling or hamp (ἁπλόος, simple).

I. Isorhize—thread of uniform diameter (ἴσος, equal; ῥίζα, root).

i. Holotriche—armed with spines along whole length (ὅλος, whole; θρίξ (τριχός), hair).

ii. Atriche—completely unarmed.

iii. Basitriche—armed only at base (βάσις, base).

II. Anisorhize—thread tapering.

i. Homotriche—spines all identical (ὁμός, one and the same).

ii. Heterotriche—spines more developed in basal region (ἕτερος, other).

B. *Heteronemes*—with well-defined basal hamp.

I. Rhabdoid—hamp of uniform diameter (ῥάβδος, rod).

i. Mastigophore—with terminal thread (μάστιξ, whip).

a. Microbasic—hamp at most three times as long as capsule.

b. Macrobasic—hamp at least four times as long as capsule.

ii. Amastigophore—without terminal thread.

a. Microbasic—(as above).

b. Macrobasic—(as above).

II. Rhopaloid—hamp not of uniform diameter.

i. Eurytele—hamp with terminal dilatation (εὐρύς, wide; τέλος, end).

a. Microbasic—at most three times as long as capsule.

Homotriche—spines all identical.

Heterotriche—spines more developed in basal region.

b. Macrobasic—at least four times as long as capsule.

Telotriche—armed throughout its distal part.

Merotriche—armed only in its middle portion (μέρος, part).

ii. Stenotele—hamp dilated at its base (στενός, narrow).

It can be realized that the terms used in this classification afford the possibility of clearly defining almost any combination of characters. The full title of any one kind of nematocyst is,

however, often of necessity somewhat cumbersome, and in practice it is possible to differentiate the nematocysts of many medusae under the abbreviated descriptions of desmonemes, haplonemes, mastigophores, euryteles and stenoteles. It is only necessary to qualify these terms further when nematocysts of one of these chief categories have to be compared with others in the same category.

While the desmonemes, euryteles, and stenoteles are almost always easy to distinguish, it is by no means always possible to be quite certain between haplonemes and mastigophores. The armature on the base of the thread in basitrichous haplonemes gives optically a slightly thickened appearance to this portion of the thread thus simulating a basitrichous mastigophore in which the hamp is slightly thicker than the remainder of the thread (see also Russell, 1938*b*). But apart from such difficulties it is on the whole fairly easy to place a nematocyst in its category when in the discharged state.

The nematocysts of medusae are mostly very small, the majority having a capsule under 20μ in length. In many species, therefore, the finer armature of the thread is difficult to determine even under the best conditions of illumination, with an oil immersion objective. The preparation of material for examination is very simple, but it should if possible be done with fresh, unpreserved material. All that is necessary is to place the required tissue, whether it be marginal tentacle, mouth lip, etc., on a slide and place a cover glass over it. The easiest method of obtaining discharged nematocysts is to remove the sea water with blotting paper and place a drop of distilled water on the slide before putting on the cover glass. The slides are then permanent without further treatment. They dry up, but can be re-examined by running in a drop of distilled water. Undischarged nematocysts will still discharge even after a period of several years (Weill, 1934*a*). While this will also happen with material preserved in alcohol, it should be noted that it is not possible to make the nematocysts discharge once they have been preserved with formalin.

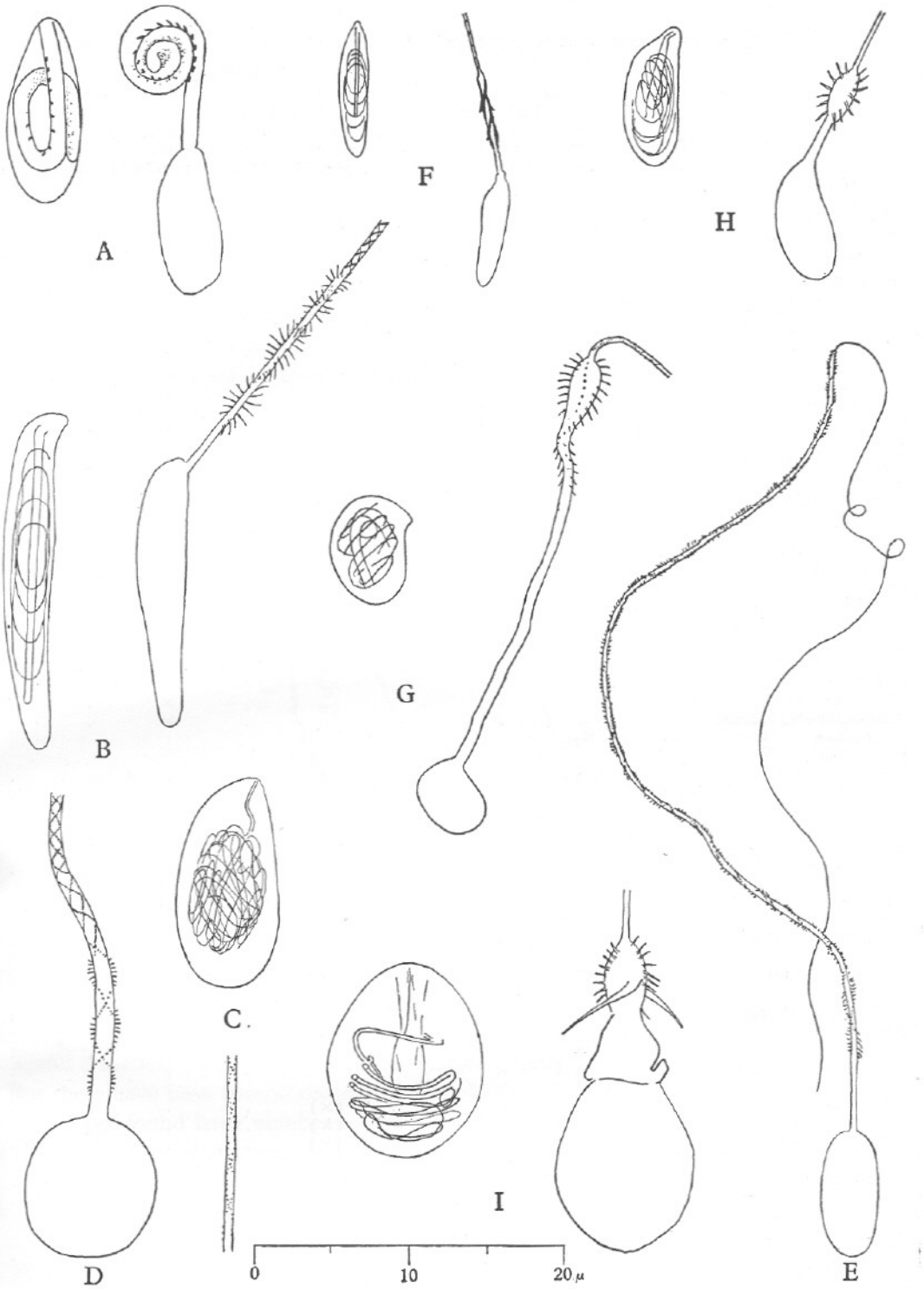
For detailed examination stains such as neutral red, methylene blue or magenta may be used. The use of the intravital stains shows at once the difference between desmonemes and other kinds of nematocysts, since desmonemes retain their coloration for some time after discharge as their threads have no opening to the exterior.

Examination of the nematocysts in a wide range of species of medusae has shown that to a certain extent the nematocysts may be used as supplementary characters for classification. This is especially so among the Anthomedusae in which several kinds of nematocysts are to be found. It has been shown (Weill, 1934*b*; Russell, 1938*b*) that the grouping of the different types of nematocysts among the different families of Anthomedusae supports the classification founded on other structural characters. The nematocysts may, therefore, sometimes prove to be characters throwing light on the phylogenetic relationships of aberrant species whose true systematic position is not clear from other structural characters. Unfortunately in the Leptomedusae, which have proved extremely difficult to classify on their general structural characters, the nematocysts give little help, being almost uniformly throughout of two similar types. They have, however, proved of value as additional specific characters, e.g. in the species of *Aequorea* (Russell, 1939*b*).

Table I shows the occurrence of the different types of nematocysts among those species of British medusae which have so far been examined.

ABNORMALITIES AND VARIATIONS

In almost all species of medusae, specimens are to be found showing variations from the normal. The most usual variation is of a meristic nature, being a departure from the normal number of



Text-fig. 8. Types of nematocysts: A, desmoneme, *Sarsia eximia*; B, basitrichous haploneme, *Eutima gracilis*; C, atrichous haploneme, *Eutima gracilis*; D, anisorhize, *Steenstrupia nutans*; E, macrobasic mastigophore, *Lar sabellarum* (hydroid of *Proboscidactyla stellata*); F, microbasic mastigophore, *Phialidium hemisphaericum*; G, macrobasic eurytele, *Zanclea costata*; H, microbasic eurytele, *Leuckartiara octona*; I, stenotele, *Steenstrupia nutans*. (After Russell, 1938*b*.)

TABLE I. Occurrence of different types of nematocysts in British medusae

		Haplonemes			Heteronemes				
	Desmonemes	Atrichous	Basitrichous	Anisorhize	Microbasic mastigophores	Macrobasic mastigophores	Microbasic euryteles	Macrobasic euryteles	Stenoteles
ANTHOMEDUSAE									
Corynidae									
Sarsia eximia	×	.	.	.	.	.	.	.	×
*Sarsia prolifera**	×	.	.	.	.	.	.	.	×
Sarsia gemmifera	×	.	.	.	.	.	.	.	×
Tubulariidae									
Steenstrupia nutans	×	.	.	×	(×)	.	(×)	.	×
*Ectopleura dumortieri**	×	.	.	×	×	.	.	.	×
Zancleidae									
Zanclea costata?	.	×	.	.	.	.	.	×	×
Cladonemidae									
Cladonema radiatum†	×	.	.	.	.	.	.	.	×
Eleutheriidae									
Eleutheria dichotoma†	×	.	.	.	.	.	.	.	×
Clavidae									
Turritopsis nutricula	×	.	.	.	.	.	×	.	.
Rathkeidae									
Rathkea octopunctata	×	.	.	.	.	.	×	.	.
Bougainvilliidae									
Lizzia blondina	×	.	.	.	.	.	×	.	.
Bougainvillia ramosa	×	.	.	.	.	.	×	.	.
Bougainvillia britannica	×	.	.	.	.	.	×	.	.
Pandeidae									
Amphinema dinema	‡	.	.	.	.	.	×	.	.
Amphinema rugosum	.	.	.	.	.	.	×	.	.
Leuckartiara octona	.	.	.	.	×	.	×	.	.
Bythotiara murrayi	×	.	.	.	.	.	(×)	.	.
Tiarannidae									
Tiaranna rotunda	.	.	.	.	.	.	×	.	.
Chromatonema rubrum	.	.	.	.	.	.	×	.	
LEPTOMEDUSAE									
Laodiceidae									
Laodicea undulata	.	×	.	.	×	.	.	.	.
Staurophora mertensi	.	.	.	.	×	.	.	.	.
Melicertidae									
Melicertum octocostatum	.	×	.	.	×	.	.	.	.
Dipleurosomidae									
Dipleurosoma typicum	.	.	.	.	(×)	.	(×)	.	.
Mitrocomidae									
Mitrocomella brownei	.	×	×	.	.	.	.	.	.
Campanulariidae									
Phialidium hemisphericum	.	×	(×)	.	(×)	.	.	.	.
Lovenellidae									
Lovenella clausa	.	×	(×)	.	(×)	.	.	.	.
Phialellidae									
Phialella quadrata	.	.	(×)	.	(×)	.	.	.	.
Eirenidae									
*Eirene viridula**	.	×	.	.	×	.	.	.	.
Helgicirrha schulzei	.	×	×	.	.	.	.	.	.
Aequoridae									
Aequorea forskalia	.	×	×	.	(×)	.	.	.	.
Aequorea vitrina	.	×	(×)	.	(×)	.	.	.	.
Aequorea pensilis	.	.	(×)	.	(×)	.	.	.	.
Eutimidae									
Eutima gracilis	.	×	×	.	.	.	.	.	.
Octorchis gegenbauri	.	×	×	.	.	.	.	.	.
LIMNOMEDUSAE									
Proboscidactylidae									
Proboscidactyla stellata (Hydroid)	×	.	.	.	.	×	×	.	.
TRACHYMEDUSAE									
Rhopalonematidae									
Aglantha digitale var. *rosea*	.	.	.	.	.	.	(×)	.	(×)

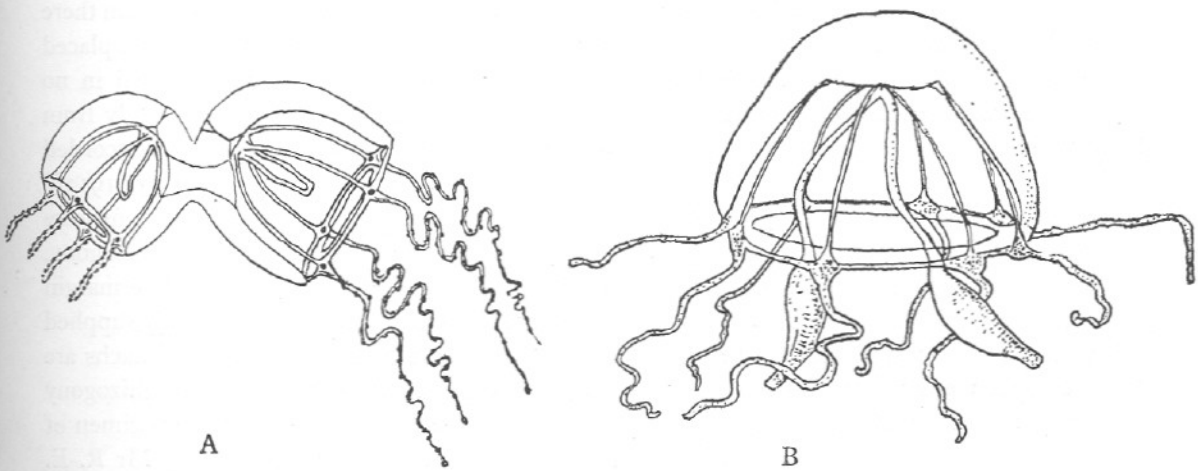
* Weill (1934*b*). † Weill (1936*b*). ‡ Present only in medusa just liberated from hydroid.

A cross in brackets (×) indicates that it is uncertain to which category the nematocyst should belong; both alternatives are given.

radii. For instance medusae which normally have four radial canals may be found with two, three, five, or even more, canals, and in such instances the numbers of gonads and marginal tentacles usually conform with the number of radial canals. Other abnormalities shown in the radial canals are abnormal branching or fusion, and uneven spacing. Similar variations may be shown in the stomach which may have an abnormal number of mouth-lips corresponding with the number of radial canals. Not infrequently, however, the stomach will maintain its normal symmetry although the number of radial canals is abnormal.

One of the most striking forms of abnormality is that known as polygastry (Text-fig. 10B) in which the medusa may have two or more separate stomachs (see below, p. 20).

Other abnormalities are fusion or branching of marginal tentacles, or even fusion of a marginal tentacle with the stomach. Medusae showing varying degrees of Siamese-twinning are also to



Text-fig. 9. A and B, twinning in *Sarsia medusae* (after Hartlaub, 1907).

be found (Text-fig. 9A, B). The two more important papers on the subject are Agassiz & Woodworth (1896) on *Obelia*, and C. W. Hargitt (1901) on several different species. The numbers of abnormalities recorded in the literature are very great; references to such observations on British medusae will be found in the subject index on pp. 517–21 of this monograph.

As a general rule the frequency of abnormality is low. Hargitt for instance did not find more than 2–5% abnormal among the species he examined. In fact among 200 specimens of *Hybocodon* he found a marked constancy and absence of abnormality.

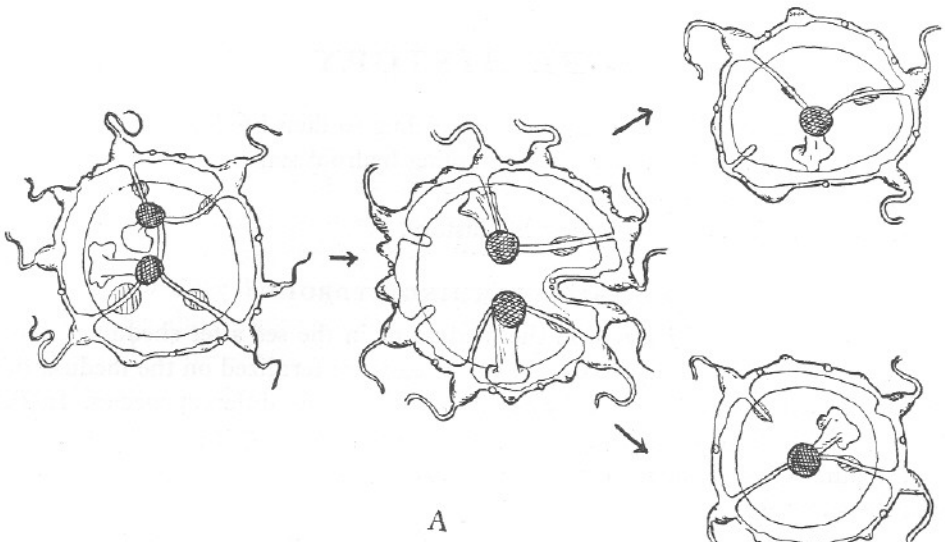
But there have been several records of remarkable abundance of abnormal specimens. Thus Neppi (1909) found large numbers of *Eirene* and *Helgichirra* in the Gulf of Trieste displaying all the above types of abnormality. In *Eirene* 37% were abnormal in 1907 and 19·3% in 1908; while in *Helgicirrha* the corresponding percentages were 27·1 and 16·8. The circumstances of the occurrence of these abnormalities would perhaps point to their being the result of unfavourable conditions, but evidence is not wanting that at times they may be due to mutation.

There are for instance two genera of Leptomedusae, *Phialidium* and *Phialucium*, each with four radial canals, but differing in that in the first all the bulbs on the umbrella margin develop tentacles, while in the second there are in addition to the marginal tentacles numerous permanently rudimentary marginal bulbs without tentacles. In 1897 Mayer found at Tortugas a medusa of the same form as *Phialidium* and indistinguishable from it except that it had five radial canals

and that the gonads were situated in a slightly different position on the radial canals. In 1899 Mayer found among 1000 specimens, 703 with five radial canals and five lips. The medusa was extremely abundant from 1897 to 1904, it was rare in 1906 and 1907, absent in 1908, and again numerous in 1909 (see Mayer, 1910, p. 279). Mayer regarded the medusa as a self-perpetuating mutant arising from *Clytia* (*Phialidium*) and raised for it a new genus *Pseudoclytia*. Observations were not made in subsequent years, but in 1929 a new search was made for the medusa by Burkenroad (1931) who again found five-rayed medusae, but this time the medusa had many permanently rudimentary marginal bulbs and had evidently arisen from *Phialucium*.

Another possible instance of mutation among medusae is to be found in polygastry. Keller (1883) recorded large numbers of medusae from the Red Sea in which the numbers of radial canals were highly variable and which had more than one stomach (Text-fig. 10B). The medusa was possibly related to *Aequorea* but Keller erected for it the genus *Gastroblasta*. Since then there have been several records of medusae with more than one stomach and they were at first placed in the genus *Gastroblasta*. Apart, however, from having more stomachs they differed in no way from *Phialidium*. Such specimens have been recorded from Tortugas and especially from the Mediterranean, where they have been caught in thousands. These medusae were recorded by Davidoff (1881) at Villefranche, by Lang (1886) at Naples, and by Neppi & Stiasny (1913*b*) in the Gulf of Trieste. Davidoff realized the significance of polygastry and his observations were confirmed by Neppi and Stiasny. Polygastry is in fact a prelude to asexual division, or schizogony. Normally, after the appearance of the second stomach, an indentation develops on the margin of the umbrella, which eventually divides into two medusae each of which is thus already supplied with a stomach (Text-fig. 10A). Presumably those medusae with more than two stomachs are abnormal specimens in which division has failed to take place. A similar form of schizogony has been recorded by Pasteels (1939) in *Cladonema*; and I have seen an abnormal specimen of *Eutima gracilis* which might have divided into two (Text-fig. 10C), sent to me by Mr R. E. Savage from Conway, North Wales.

In conclusion mention should be made of the medusa *Dipleurosoma typicum*. All recorded specimens of this species show so great variation that it is not possible to describe any one specimen as typical of the species (Text-fig. 145).



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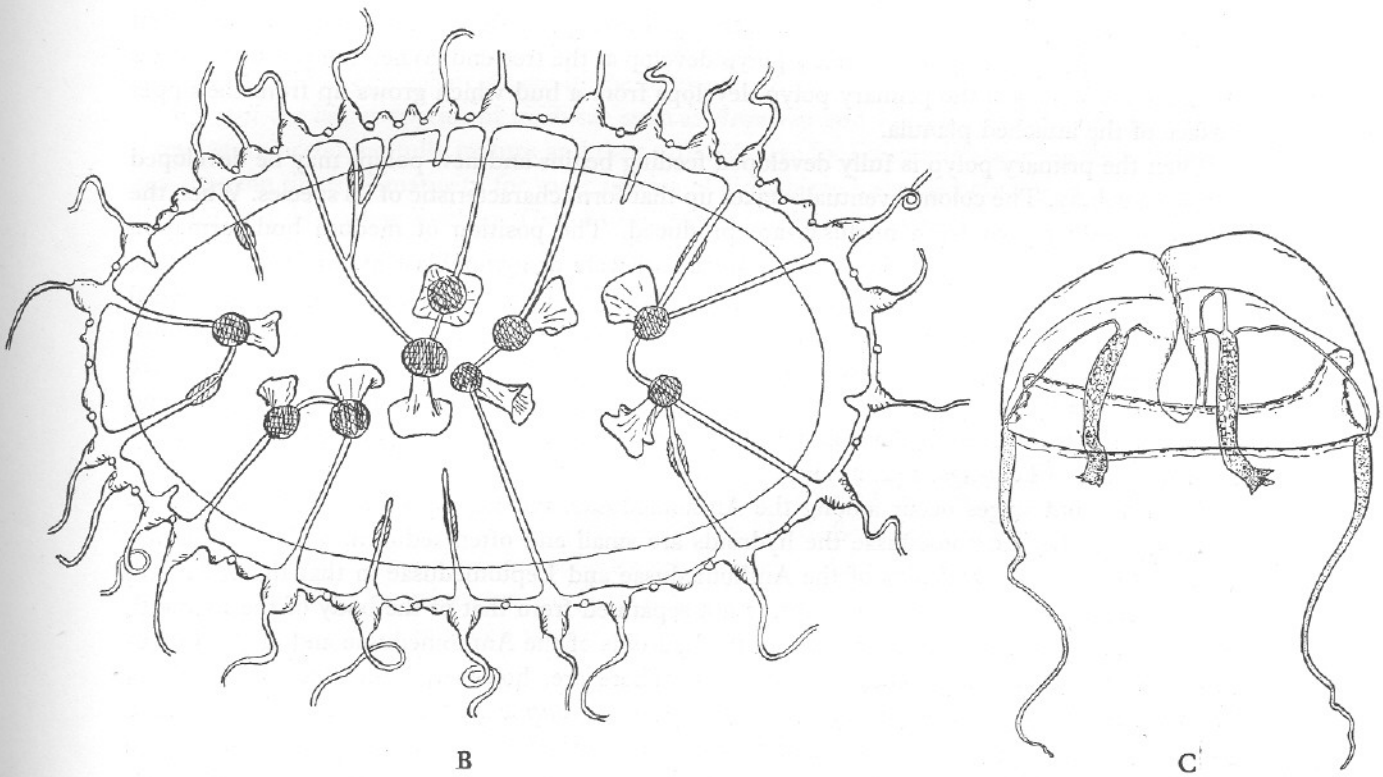


B C

Text-fig. 10. A, schizogony (after Neppi & Stiasny, 1913*b*); B, polygastry (after Keller, 1883); C, possible prelude to division in *Eutima gracilis*.

LIFE HISTORY

Medusae may be divided into three categories according to their life histories.

1. Those with a fixed hydroid or a free-swimming hydroid stage.
2. Those with direct development.
3. Those with a parasitic stage in their life history.

MEDUSAE WITH A FIXED OR A FREE-SWIMMING HYDROID

The eggs, which may be fertilized on the medusa or in the sea after shedding, develop into planulae which give rise to the hydroids. When the eggs are fertilized on the medusa the degree to which development proceeds before the parent is left varies for different species. In *Turritopsis nutricula*, for instance, the eggs develop only as far as the planula stage (Pl. V, fig. 1). In *Hybocodon prolifer* development goes much farther and specimens are often found with young actinula larvae clinging to the stomach.

When the egg is fertilized in the sea a free-swimming ciliated planula is developed. The planula settles to the bottom and attaches to a suitable substratum. It may do this either by one end, e.g. *Phialidium*, or along its whole length, e.g. *Turritopsis*. In the former type of attachment the mouth and tentacles of the primary polyp develop at the free end. When the planula attaches along its whole length the primary polyp develops from a bud which grows up from the upper surface of the attached planula.

When the primary polyp is fully developed feeding begins and new polyps may be developed to form a colony. The colony eventually takes up that form characteristic of its species. When the colony is fully grown fresh medusae are produced. The position of medusa bud formation naturally varies according to the species. In the athecate or gymnoblast hydroids the medusae are born unprotected, except for a thin enveloping skin, either on the hydranth itself, or on special polyps without tentacles known as blastostyles, or singly from the creeping stolon or hydrocaulus. In the thecate or calyptoblast hydroids, the medusae usually develop on blastostyles which are protected by a specialized perisarc capsule or gonotheca. Occasionally, as in *Melicertum* and *Aequorea*, the medusa buds develop singly, without well-marked gonothecae, from the stem or from the stolon (Text-figs. 142, 221).

Fixed hydroid stages occur among the Anthomedusae, the Leptomedusae, and the Limnomedusae. In the Limnomedusae the hydroids are small and often reduced, without tentacles. They differ from the hydroids of the Anthomedusae and Leptomedusae in that the endoderm of the tentacles, when these are present, is not separated from that of the body of the hydranth by a diaphragm of mesogloea. In general the hydroids of the Anthomedusae and of the Leptomedusae are athecate and thecate respectively. There are, however, a few exceptions among the Leptomedusae. The hydroids of *Melicertum octocostatum* and *Octorchis gegenbauri* have athecate or naked polyps in the sense that they cannot retract into the hydrotheca which may be so reduced as merely to be an extension of the hydrocaulus (Text-figs. 141, 238). This is, however, probably a secondary development from the thecate form, as intermediate types may be found among some of the thecate hydroids with fixed sporosacs. Similarly among the true athecate hydroids of the Anthomedusae such species as *Leuckartiara octona* and *Bougainvillia ramosa* have a partially developed and ill-defined hydrothecal cup into which the polyp can be partially withdrawn.

At the time of liberation from the parent hydroid the medusae are always very small, usually 1 mm. or less in height. Among the largest are those of *Aequorea*, but even these are only about 1·4 mm. in height. In those species in which the mature medusa has only four or fewer marginal tentacles the newly liberated medusa is usually a miniature of the adult, the only structural changes being due to the development of the gonads and sometimes a slight alteration in the shape of the umbrella or lengthening of the stomach. But in those medusae whose adults have many marginal tentacles the young individuals are quite unlike the adults, and the medusae pass through a number of developmental stages until the mature appearance is reached. This has given rise to much confusion in the past, the different stages having been described as separate species.

The lengths of life of the different species are very different. In the shortest-lived species, such as *Podocoryne carnea*, the gonads may already be fully developed as soon as the medusa is liberated from its hydroid. In some species, such as *Syncoryne lovéni*, the medusa, which is usually reduced in these species to a swimming bell and stomach without marginal tentacles, is never even liberated from the hydroid, the eggs and sperm maturing while the medusa is still attached (Pl. II, fig. 5). The average length of life of the majority of free-swimming medusae is probably in the neighbourhood of two months. Some species such as *Phialidium hemisphaericum* and *Obelia* may thus produce more than one successive generation in a year, each generation including the complete cycle from medusa to hydroid and back to medusa. More often, however, the hydroids have a single well-defined season during which they produce medusae. In such species the medusae, after their period of life in the plankton, give rise to hydroids which do not produce medusae until the equivalent season in the following year.

A few of the larger species of medusae such as *Aequorea* and *Tima bairdi* have long planktonic lives before becoming fully mature and they probably live for six months or longer. It is safe to say that the times of maturity for most species of British medusae lie between early spring and late autumn, but a few, such as *Tima bairdi*, become mature in winter. The composition of the medusa fauna shows a definite seasonal sequence and this is shown in Table II (from Russell, 1938*a*) which gives the months of occurrence of different species in the plankton at Plymouth.

When the medusa is mature the eggs are fertilized and planulae are developed which settle on the bottom and grow into hydroids, thus completing the cycle.

Very rarely, e.g. *Margelopsis haeckeli*, a free-living pelagic hydroid is produced which has no fixed stage in its life history. Hydroids of fixed habits are, however, sometimes found in plankton collections. These must have been torn from their substratum by rough weather or tidal action or by trawls. The hydroid of *Phialidium hemisphaericum* (= *Clytia johnstoni*) is thus quite commonly found in the plankton in some parts of the southern North Sea. It must remain drifting in the water for a considerable time, for colonies are frequently found which have regenerated into a spherical form. One may even catch such hydroids as *Corymorpha nutans* (medusa = *Steenstrupia*) in the plankton in rough weather.

MEDUSAE WITH DIRECT DEVELOPMENT

As far as is known, direct development, without the intervention of a true hydroid stage, only occurs in the Trachymedusae and the Narcomedusae. Such medusae are essentially oceanic in habitat.

As in other medusae a planula is developed. The planula does not attach to any substratum but itself develops tentacles, and becomes transformed directly into a free-swimming medusa (Text-fig. 282).

TABLE II. Seasonal distribution of medusae off Plymouth

× recorded as present; × months of greatest abundance.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ANTHOMEDUSAE												
Rathkea octopunctata	×	×	×	**×**	**×**	.	.	.	.	.	×	×
Hybocodon prolifer	.	×	×	×	**×**	×	.	.	.	.	.	.
Euphysa aurata	.	.	×	×	×	×	.	.	×	.	.	.
Steenstrupia nutans	.	.	.	×	**×**	**×**	×	×	×	.	.	.
Podocoryne borealis	×	.	.	.	.	×	.	×	×	.	.	.
Podocoryne carnea	.	×	×	.	.	.	×	×	.	.	.	.
Bougainvillia principis	.	.	.	×	×	.	.	.	.	.	.	.
Sarsia tubulosa	.	.	×	×	×	×	×	.	×	×	×	.
Sarsia eximia	.	.	.	×	×	×	×	.	×	.	.	.
Bougainvillia britannica	.	.	.	×	**×**	**×**	×	.	.	.	.	.
Ectopleura dumortieri	.	.	.	×	×	.	.	.	×	×	×	.
Lizzia blondina	.	.	×	**×**	**×**	**×**	**×**	×	**×**	.	×	.
Leuckartiara octona	.	×	×	×	**×**	**×**	**×**	**×**	**×**	×	×	×
Bougainvillia ramosa	.	.	.	×	×	.	.	×	×	×	×	.
Sarsia gemmifera	.	.	.	.	×	**×**	**×**	.	×	.	×	.
Amphinema rugosum	.	.	.	×	**×**	**×**	**×**	×	×	×	.	.
Zanclea costata	.	.	.	.	×	.	×	×	×	.	.	.
*Sarsia prolifera**	.	.	.	×	×	×	**×**	×	×	×	**×**	.
Dipurena halterata	.	.	.	×	×	×	×	×	×	.	.	.
Dipurena ophiogaster	.	.	.	.	.	×	×	.	.	.	.	.
Amphinema dinema	×	.	.	.	.	.	×	.	**×**	**×**	×	.
Turritopsis nutricula	×	.	.	.	.	.	.	×	×	**×**	×	×
Eucodonium brownei	.	.	.	.	.	.	.	.	×	.	.	.
Pochella polynema	.	.	.	.	×	×	.	.	.	.	.	.
LEPTOMEDUSAE												
Tiaropsis multicirrata	.	.	×	×	.	.	.	.	.	.	.	.
Phialidium hemisphericum	×	×	**×**	**×**	**×**	**×**	**×**	**×**	**×**	**×**	×	×
Obelia spp.	×	×	×	**×**	**×**	**×**	**×**	**×**	**×**	**×**	**×**	×
Phialella quadrata	.	.	×	×	**×**	×	×	.	×	×	.	.
Cosmetira pilosella	.	.	×	**×**	**×**	**×**	**×**	**×**	×	×	.	.
Mitrocomella brownei	.	.	.	×	×	.	.	×	×	.	.	.
Eutima gracilis	×	×	×	×	**×**	**×**	**×**	×	×	×	×	×
Aequorea forskalea	.	.	×	×	×	×	×	×	×	×	×	×
Aequorea vitrina	.	.	.	.	.	×	.	.	.	.	.	.
Laodicea undulata	.	×†	×	×	×	×	×	**×**	**×**	×	×	.
Lovenella clausa	×	.	.	×	.	×	×	.	×	**×**	×	×
Helgicirrha schulzei	.	.	.	.	.	×	×	×	×	×	.	×
Eirene viridula	.	.	.	.	.	.	×	×	**×**	**×**	×	×
Octorchis gegenbauri	×	.	.	.	.	.	×	**×**	×	×	.	.
Agastra mira	.	.	.	.	.	.	×	×	.	.	×	.
LIMNOMEDUSAE												
Proboscidactyla stellata	×	×‡	×§	×	×	×	**×**	×	**×**	×	×	×
Gossea corynetes	.	.	.	.	.	.	×	×	×	×	×	×
TRACHYMEDUSAE												
Aglantha digitale var. *rosea*	×	×	×	×	×	**×**	**×**	**×**	**×**	×	×	×
Liriope exigua	×	×	.	.	×	×	×	**×**	**×**	**×**	**×**	**×**
NARCOMEDUSA												
Solmaris corona	.	.	.	.	.	.	.	.	×	.	.	.

* Plymouth Marine Fauna gives Jan.–Oct.; this is possibly a misprint for June–Oct.
† 21 February 1938 one specimen.
‡ Hydroid with medusa ready for liberation. (E. T. Browne, MS. notes, 22 February 1899.)
§ Liberated from hydroid, 30 March 1936.

MEDUSAE WITH A PARASITIC STAGE IN THEIR LIFE HISTORY

While a number of hydroids may live epiphytically on other animals there are some which are apparently true parasites. As far as is known at present none of the British species of medusae has truly parasitic hydroids. For observations on such parasitic hydroids on fishes and other animals the reader may be referred to Kramp (1922) and Gudger (1928). Mention might also be made here of the *Mnestra parasites* in which the medusa itself is apparently parasitic on the

mollusc *Phyllirhoe* (see Günther, 1903*b*).* The most remarkable parasitism is that shown by some of the stages in the life histories of certain Narcomedusae. Such species are *Cunoctantha octonaria*, *C. parasitica*, *Pegantha clara*, and *Cunina proboscidalis*, but none of these is known to the British fauna. *Cunoctantha octonaria* produces planulae which attach themselves to the mouth of the Anthomedusa, *Turritopsis nutricula*; there they develop into four-tentacled actinula-like larvae which develop directly into medusae and can produce buds which do likewise. In *Cunina proboscidalis* a four-tentacled medusa develops from the egg and this medusa itself has eggs which give rise to stolon-like larvae parasitic on the Trachymedusa, *Geryonia proboscidalis*. The buds from these larvae develop once more into medusae like those of the first generation.

In *Cunoctantha parasitica* and *Pegantha clara* the life history is even more strange. They are represented by an amoeboid stage parasitic in the mesogloea of *Geryonia* and in the parent host respectively. These amoeboid cells, which are associated with a nurse cell, develop into tentacled larvae which may develop directly into free-swimming medusae or bud off similar larvae which also develop into medusae. Whether these medusae grow into adults like the original parent or are themselves only an intermediate stage is not known. The development and origin of the amoeboid cells themselves is not fully understood nor is it known whether those present in the parent host originated from it or from another species of Narcomedusa.†

Of special interest in this connexion are the observations that led Weill (1938*a*) to put forward the extremely interesting suggestion that the Cnidosporidia, the systematic position of which has always been a subject for discussion among protozoologists, may actually have been derived from Narcomedusae in which the free-swimming stage has been suppressed.

* But see Ankel, W. E. 1952. *Phyllirhoe bucephala* Pér. & Les. und die Meduse *Mnestra parasites* Krohn. *Pubbl. Staz. Zool. Napoli*, Bd. 23, pp. 91–140, 15 text-figs. and Rees, W. J. 1952. Note on *Phyllirhoe bucephala* Péron & Lesueur and *Mnestra parasites* Krohn. *Proc. Malac. Soc.* vol. XXIX, pt. 5 (in press).

† A detailed account of these life histories is out of place in this monograph, which is concerned only with British medusae. But for further information the reader may be referred to the following works among others: Metschnikoff (1886*a*), Brooks (1886*a*), Wilson (1887), Korotneff (1888), Maas (1892), Woltereck (1905), Bigelow (1909*a*), Mayer (1910), Hanitzsch (1911), Uchida (1928, p. 87), and Kramp (1947, p. 33).

DISTRIBUTION ROUND THE BRITISH ISLES

In order to understand the distribution of medusae round the British Isles we must know the geographical distribution of the species and the local influences of hydrographic conditions.

The British medusa fauna is composed of species which come under the following broad categories:

1. Arctic-boreal.
2. Boreal.
3. Mediterranean-boreal.
4. Mediterranean or warm water.
5. Cosmopolitan.

The species may be further subdivided into neritic or coastal and oceanic species which may be surface-living or deep-sea. The categories of geographical distribution do not imply limitation to clearly defined geographical areas. They are based on temperature conditions, and as a result the geographical distribution is dependent upon the disposition of the water masses at any one time. The temperature limits which define the above categories of distribution are those within which the successful reproduction and normal early development of a species can take place. Actually therefore the distribution of the adult of any species may exceed the temperature limits since it may be able to withstand conditions which are unfavourable for reproduction and early development. But the area of distribution of a species as a whole is conditioned by the capacity to reproduce successfully, and the extremes within which this may happen should be regarded as the true limits of distribution.

The temperature limits for the above categories are approximately as follows:

Arctic-boreal	1–11° C.
Boreal	4–16° C.
Mediterranean-boreal	8–23° C.
Mediterranean	13–26° C.

The cosmopolitan species are apparently able to withstand the full range of temperatures.

These figures are taken from Runnström (1928) who gives a valuable discussion on the subject. Runnström further gives the regions within which the above categories of species may occur as lying between the following temperatures:

Arctic region	2–6° C.
Boreal region	3–16° C.
Mediterranean	13–26° C.

The distribution of neritic medusae is thus largely conditioned by successful reproduction and early development of the hydroid which must naturally have conditions suitable to its own needs. But after liberation from the hydroid the medusae may be carried by water movements into areas far removed from that in which the hydroid lived. It is possible, therefore, that many medusae are carried into areas in which they are unable to reproduce the species. The composition of the British fauna is thus composed of species which may be carried into certain areas in which they are unable to maintain the species and of species which are indigenous to certain areas and

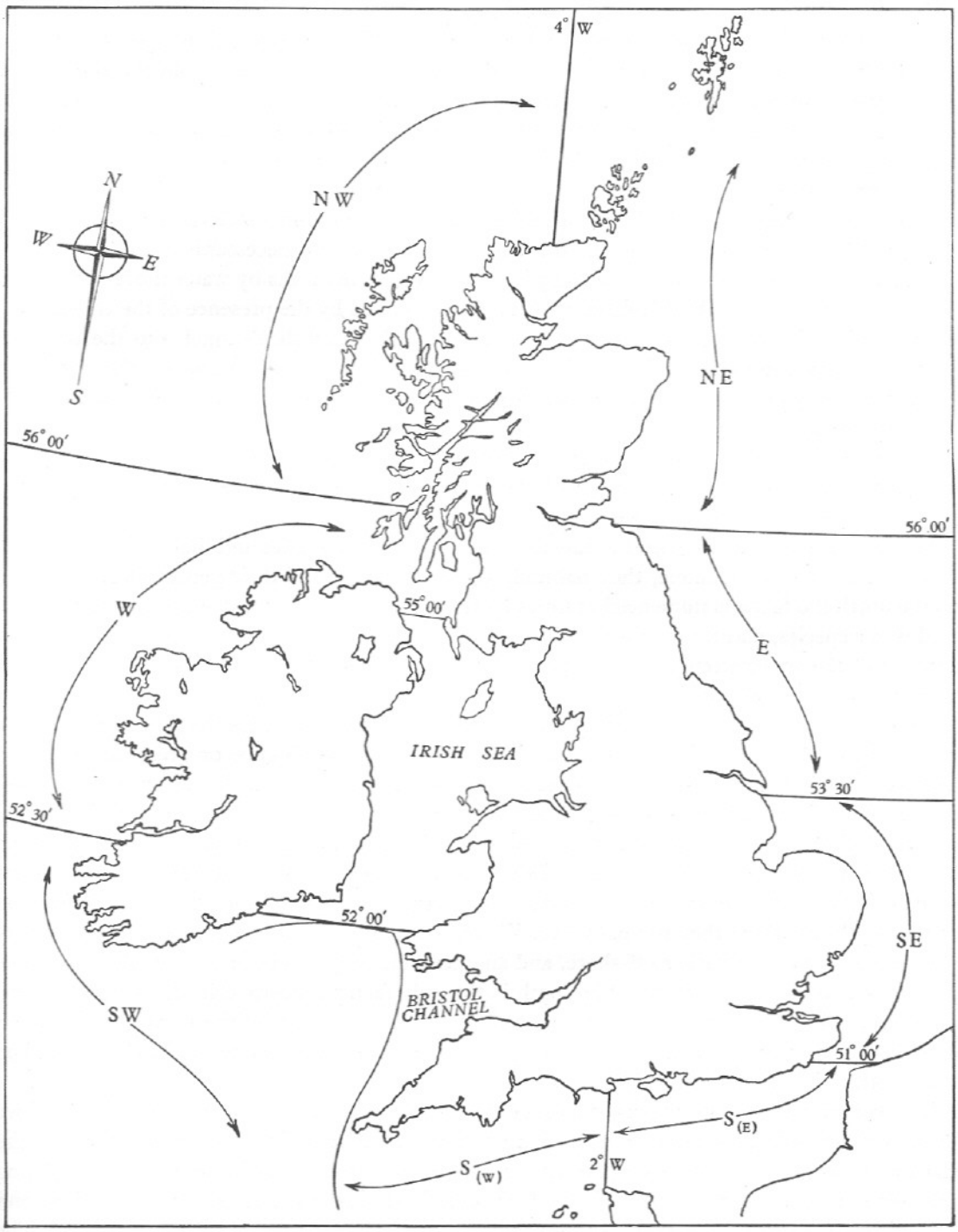


Chart. Distribution of medusae round the British Isles: faunistic areas.

able to maintain a local population. To understand the composition of the fauna then it is clearly necessary to know the hydrographical conditions round our coasts.

The essential feature is that there is a large bay, the North Sea, which is open to influx of Atlantic oceanic water from the north and through the Straits of Dover from the south-west. Where the inflowing oceanic water mixes with the coastal water, as for instance between the Orkneys and Shetlands and in the region off the mouth of the English Channel south of Ireland, a heavy production of plankton occurs. This is presumably due to the enrichment of the area with nutrient salts by upwelling. A similar rich plankton fauna is to be found along the outer western and northern coasts of the British Isles where the sea bottom is steep too. These rich areas are especially abundant in medusae. But this abundance is not necessarily confined to these limited areas, for the rich community may be carried into other areas by water movement. Thus the rich water to the south of Ireland, which is characterized by the presence of the chaetognath *Sagitta elegans*, may pass in an easterly direction up the English Channel into the southern North Sea and also northwards into the Irish Sea. Similarly the rich water off the north-east of Scotland may be carried down the east coast of Scotland and east England, even as far as the Thames Estuary.

The main body of water of the North Sea and English Channel is characterized by the chaetognath *Sagitta setosa* and on the whole it has a low plankton content and the majority of species of medusae in it are scarce.

While to a large extent the area to the north-east of the British Isles and that in the south-west carry the same medusa fauna, they naturally differ on account of their geographical localities. In the north the fauna is influenced at times by the east Iceland arctic current bringing northern cold water species, and the south-west receives additions from warmer waters. A more detailed account of the water circulation round the British Isles and its influence on the plankton has been given by Russell (1939*c*).

Before analysing the British medusa fauna it is necessary also to stress the difference between oceanic and neritic medusae. This division depends upon the absence or presence of a fixed hydroid stage in the life history. The oceanic medusae, such as the Trachymedusae, have direct development. The neritic medusae are limited to coastal areas by virtue of having a fixed stage which requires a bottom in comparatively shallow regions. But the composition of the population of neritic medusae does show certain changes as one goes farther from the shore. In some species the hydroids are limited to tidal regions, in others the hydroids seem to show differences in the depths at which they normally live. We may thus meet with one species of medusa very close inshore, another farther off-shore, and another well away from the coast in almost oceanic conditions. It is not certain whether depth is the only factor concerned in this latter instance, for the distribution of the hydroid may possibly also be governed by the purity of the water. The distance to which a medusa may be dispersed from the shore must naturally also depend on the length of its life in the plankton.

The composition of the medusa fauna of the British Isles can be shown very clearly if we divide the British coasts into a number of areas. The boundaries of these areas are shown in the chart on p. 27. The north-western area runs approximately between 4° W. and 56° N., including the western coast of Scotland and the Hebrides. The western area is between 56° N. and 52° 30′ N., including the western and northern coasts of Ireland and the Clyde Sea area. The Irish Sea is closed off as a separate area, as is that of the Bristol Channel; south-west of these boundaries and north to 52° 30′ N. on the west coast of Ireland is the south-western area. The

English Channel comprises the southern area, and this has been divided at 2° W. into a western half (S. (W.)) and an eastern half (S. (E.)). The south-eastern area runs between 51° N. and 53° 30′ N., i.e. from the Dover Straits to the Humber. The eastern area stretches between the Humber and North Berwick at 56° N. The north-eastern area runs from the Firth of Forth to 4° W. off the north of Scotland and includes the Orkneys and Shetlands. Finally we can insert the 100 fathom line as the approximate boundary beyond which the oceanic and deep-sea medusae live.

If now we arrange these areas in the order, N.E., E., N.W., W., Irish Sea and Bristol Channel, S.W., S. (W.), S. (E.), and S.E., we can combine them roughly into three faunistic zones. These are N.E. to E., containing a fauna with an arctic influence; N.W. to S. (W.), being influenced by the Atlantic; S. (E.) to S.E., of essentially coastal water. The oceanic medusae can also be differentiated into those living in the upper water layers and the deep-sea species.

In Table III the British coastal Anthomedusae and Leptomedusae are tabulated according to their occurrence in the above areas of distribution. The table shows clearly how the fauna changes between the north-east and the south-west and it has the added advantage of setting out the species in the order of their temperature requirements, the cold-water species being at the top of the list and the warm-water species at the bottom. The table also shows that there are a few blanks to be filled in between the known limits of distribution of some species. The reader can at once see which species he is likely to find in an area and he should include also any species not yet recorded in that area if its presence is shown on both sides of the blank.

These faunistic areas should also prove useful to the fishery naturalist, since they have approximately the same boundaries as most of the fishery statistical areas laid down by the International Council for the Exploration of the Sea.

The reader should be cautioned against supposing that because a species is recorded as occurring in a certain area it must necessarily always be abundant there, or even present at all in some years. As shown above, their presence must depend in some areas on hydrographic conditions. It is probably safe to say that the poorest areas are those of the English Channel and southern North Sea, since they are dependent upon the inflow of mixed oceanic and coastal water for an abundant fauna. For this reason it is, therefore, probable that the waters off the western, northern and north-eastern coasts of the British Isles would always prove the most reliable collecting grounds for all those species recorded in the area.

A list of literature dealing with the medusa fauna in each area is given below.

Faunistic Literature

North-eastern Area. Peterhead (Peach, 1868). St Andrews (M'Intosh, 1889, 1890*a*, *b*, *c*, 1893, 1926; Crawford, 1891, 1895; Holt, 1891). Firth of Forth (Leslie & Herdman, 1881, Fauna List; Evans & Ashworth, 1909; Evans, 1916; Gemmill, 1915).

Eastern Area. Berwick—Northumberland—Durham (Alder, 1857, 1862; Hodge, 1861; Robson, 1913, 1914*a*; Coy, 1924; Peacock, 1924; Watson, 1930; Sanderson, 1930; Bull, 1933, literature list).

North-western Area. Barra, Outer Hebrides (Cant & Crichton, 1936). North Uist (Nicol, 1936).

Western Area. Firth of Clyde (Browne, 1905*a*; Gemmill, 1921*a*; Marshall, 1925; Rees, 1941*a*, *b*).

Irish Sea. Isle of Man (Chadwick, 1899; Fauna List, 1937). L.M.B.C. district (Browne, 1895, 1897*b*). Tenby (Davis, 1841).

South-western Area. Valencia (Browne, 1896*b*, 1900; M. & C. Delap, 1905*a*, 1906). Dublin (Green, 1857). St Ives Bay (Vallentin, 1907).

Southern Area (west). Scilly Isles (Browne & Vallentin, 1904; Vallentin, 1909). Falmouth (Cocks, 1849, 1850; Peach, 1867; Vallentin, 1897, 1900). Plymouth (Garstang, 1894; Browne, 1898*b*; Lebour, 1917; Marine Biological Association, 1931, Fauna List; Russell, 1933, 1938*a*, 1940*b*; Rees, 1938).

South-eastern Area. Thames Estuary (Wells, 1938).
Britain generally. Forbes, 1846, 1848; Forbes & Goodsir, 1851; Hincks, 1868; Allman, 1871–2; Browne, 1896*a*, 1897*a*; Hartlaub, 1904.
Scotland. Dalyell, 1847–8.
Ireland. Stephens, 1905.

TABLE III. Distribution of British Anthomedusae and Leptomedusae in different areas

	N.E.	E.	N.W.	W.	I.S.	S.W.	S.(W.)	S.(E.)	S.E.	
ANTHOMEDUSAE										
Bougainvillia superciliaris	×	.	.	.	.	.	.	.	.	A.
Euphysa aurata	×	×	×	×	×	×	×	.	.	N.B.
Bougainvillia principis	×	.	×	.	×	×	×	.	.	N.B.
Podocoryne borealis		×	.	×	×	×	×	.	.	?N.B.
Hybocodon prolifer	×	×	×	×	×	×	×	×?	×?	N.B.
Steenstrupia nutans	×	×	×	×	×	×	×	?	?	N.B.
Sarsia eximia	×	×	×	×	×	×	×	×	×	?N.B.
Sarsia tubulosa	×	×	×	×	×	×	×	×	×	N.B.
Rathkea octopunctata	×	×	×	×	×	×	×	×	×	N.B.
Leuckartiara octona	×	×	×	×	×	×	×	×	×	S.B.
Lizzia blondina	×	×	×	×	×	×	×	.	×	S.B.
Podocoryne carnea	×	.	.	×	×	×	×	.	×	C.
Bougainvillia britannica	×	×	×	×	×	×	×	.	×	B.
Amphinema rugosum	×	.	.	.	.	×	×	.	.	?S.B.
Neoturris pileata	×	×	.	.	×	×	.	.	.	S.B.
Dipurena halterata	.	×	.	×	×	×	×	×	.	S.
Ectopleura dumortieri	.	.	.	×	.	×	×	.	×	?S.B.
Bougainvillia ramosa	.	×	.	.	×	×	.	.	.	S.B.
Sarsia prolifera	.	×	×	.	.	×	×	.	.	S.
Sarsia gemmifera	.	×	×	×	.	×	×	×	×	S.B.
Stauridiosarsia producta	.	×	.	.	.	×	.	.	.	?S.B.
Eleutheria dichotoma	.	×	×	.	×	×	×	.	.	?
Turritopsis nutricula	.	.	.	.	×	.	×	.	.	S.
Amphinema dinema	.	.	.	.	.	×	×	.	×	S.
Thamnostoma sp.	.	.	.	×	.	.	.	.	.	?
Bougainvillia pyramidata	.	.	×	×	×	×	.	.	.	S.B.
Podocoryne minima	.	.	.	.	.	.	×	.	.	?
Cladonema radiatum	.	.	.	.	.	×	×	.	×	?
Eucodonium brownei	.	.	.	.	.	.	×	.	.	?
Dipurena ophiogaster	.	.	.	.	.	×	×	.	.	S.
LEPTOMEDUSAE										
Phialidium islandicum	×	.	.	.	.	×	.	.	.	N.B.
Staurophora mertensi	×	.	.	.	.	.	.	.	.	N.B.
Tima bairdi	×	×	.	.	.	.	.	.	.	N.B.
Eutonina indicans	×	×	.	.	.	.	.	.	.	N.B.
Melicertum octocostatum	×	×	×	×	×	×	(×)	.	.	?N.B.
Mitrocomella polydiademata	×	×	×	×	×	.	.	.	.	?N.B.
Tiaropsis multicirrata	×	×	.	×	×	×	(×)	.	.	N.B.
Aequorea vitrina	×	×	.	.	.	×	×	.	.	?S.
Eutima gracilis	×	×	×	×	×	×	×	.	.	?S.
Phialella quadrata	×	.	×	×	×	×	×	.	.	?B.
Cosmetira pilosella	×	×	.	.	×	×	×	×	.	S.B.
Phialidium hemisphericum	×	×	×	×	×	×	×	×	×	B.
Laodicea undulata	×	.	×	×	×	×	×	×	×	S.
Octorchis gegenbauri	.	.	.	×	.	×	×	×	.	?S.B.
Eucheilota maculata	.	.	.	.	.	.	.	×	×	?S.B.
Lovenella clausa	.	.	.	.	.	×	×	.	.	?S.
Aequorea forskalea	.	.	.	.	.	×	×	.	.	S.
Dipleurosoma typicum	.	.	.	×	.	×	.	(×)	.	?
Aequorea pensilis	.	.	.	.	.	×	×	.	.	?S.
Agastra mira	.	.	.	.	.	×	×	.	.	?S.
Helgicirrha schulzei	.	.	.	.	.	×	×	.	×	S.
Eirene viridula	.	.	×	.	.	×	×	×	.	.

Note. A., arctic; B., boreal; N.B., northern boreal; S.B., southern boreal; S., southern; C., cosmopolitan.

REARING HYDROIDS AND MEDUSAE

The complete life cycle of a medusa may be watched in the laboratory. This entails rearing the hydroid from fertilized eggs of the adult medusa, keeping these hydroids until they liberate medusae, and then rearing these medusae to the adult stage. The whole operation is, however, difficult, requiring constant care and attention to feeding, and it is necessarily tedious since it may take many months to complete the full cycle. But it is a necessary method of research for discovering which are the hydroids of the different species of medusae.

It has been possible to describe the complete life histories of many of the commoner species without resort to laboratory culture. The many stages of the medusae in the plankton can be pieced together if there is a wealth of material. If the hydroids are large and conspicuous and easily obtainable it is always possible to find colonies at the time of year when they are liberating medusae. The young medusae can then be compared with the earliest stages caught in the plankton.

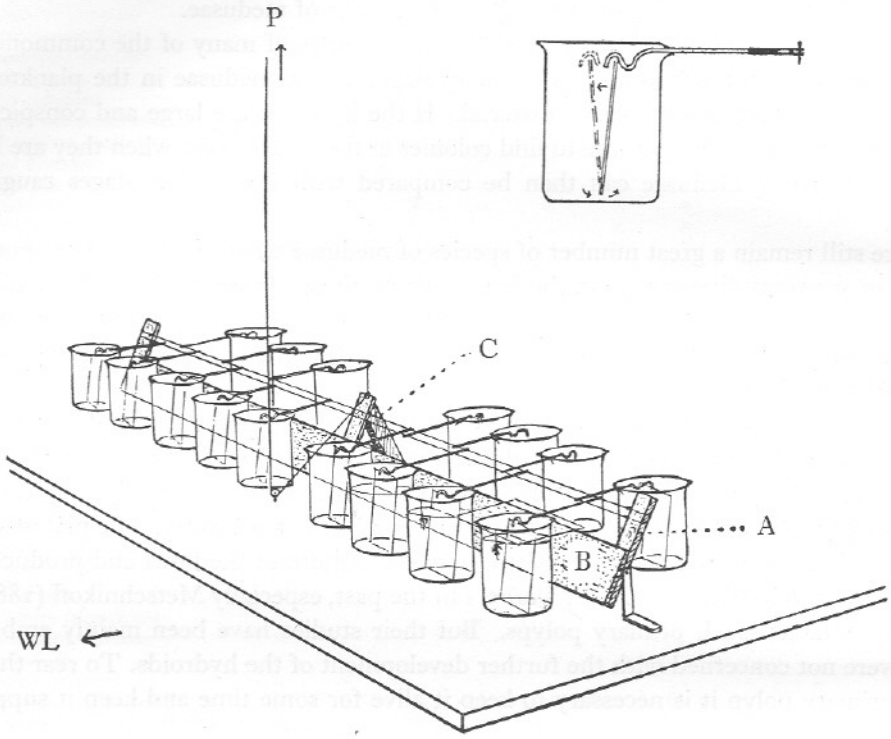
But there still remain a great number of species of medusae whose hydroids have not yet been identified, over twenty-five species in the British fauna alone. It seems almost certain that most of these unknown hydroids will be small and inconspicuous. Some of them, in fact, have probably already been described, but, owing to the difficulty of finding them, specimens have not yet been seen liberating medusae.

It was therefore soon realized that attention must be paid to methods of laboratory rearing if our knowledge of the life histories of medusae was to be completed. Given a supply of adult medusae it is not difficult to obtain fertilized eggs in the laboratory. It is only necessary to place one or two ripe male and female medusae together in a bowl of sea water. The planulae are soon developed and in many species these will settle to the bottom of the bowl and produce primary polyps without much difficulty. Many workers in the past, especially Metschnikoff (1886*a*), have successfully obtained such primary polyps. But their studies have been mainly embryological and they were not concerned with the further development of the hydroids. To rear the hydroid from the primary polyp it is necessary to keep it alive for some time and keep it supplied with sufficient food for normal growth.

The first great advance in this field was made by Browne (1898*a*) when he introduced the plunger-jar system for keeping sea-water in good condition over long periods of time. By this means it was possible to rear adult medusae from hydroid colonies. But the method rather left it to chance that the hydroid should have sufficient food brought to it either by the stirring of the water or by the movements of the food organisms themselves. Later Browne (1907*a*) described a method whereby a constant stream of water with its contained food was passed over the hydroid colony. In this way he obtained considerable growth in the hydroid. Success in elucidating a whole life history may be obtained at any time, by chance, by a combination of these methods. If a number of living medusae are introduced into the bell jar, and food continually added, in course of time it may be found that a colony of hydroids has developed, and these can be placed in the constant current tube. The method has, however, the great drawback that one can never be certain that planulae from some other species of medusa have not been introduced with food from the plankton. Even if the colony has been reared with success it is difficult to find such small objects as newly liberated medusae in so large a body of water as that contained in a bell jar, unless the

medusae be very numerous. But the method is always worth trying, and it should be remembered that our knowledge of the life histories of some medusae has been gained in the past by the sudden appearance of hydroid colonies which produced medusae in small well-balanced aquaria containing a variety of marine organisms or selected fragments of likely material.

But when I first started this type of research myself I soon realized that for really satisfactory results it was necessary that some more rigidly controlled method should be adopted, so that the identity of the hydroid and of the newly liberated medusa would be known for certain. Further, in order that a number of different species might be studied at the same time they had for convenience to be kept in smaller vessels. The solution was provided by the use of beakers with



Text-fig. 11. Diagram showing arrangement of beakers with rocking plates for keeping hydroids. For full description see text: A, wooden upright; B, horizontal wooden batten; C, stopper; P, to plunger jar wire; WL, direction of window light. In the top right-hand corner is shown an enlarged drawing of a beaker and method of attachment of rubber tube to wire. (Rees & Russell, 1937, fig. 12.)

rocking plates devised by Dr H. W. Harvey, F.R.S., for the culture of diatoms. I accordingly arranged for a battery of such beakers, placed in such a position that the hydroid could be hung near the surface on the side nearest the light, where most of the food organisms would congregate. The primary polyps, which settled on the bottom of the bowl, were at first hand-fed with small copepod nauplii or food organisms of suitable size. In this way a small colony of several polyps was obtained. The colony was then scraped from the glass and hung by a piece of silk in the beaker. A description of the rocking apparatus is given below from Rees & Russell (1937) (Text-fig. 11):

The essential principle is that a glass plate cut to a suitable size stands upright in a beaker so that it may be rocked backwards and forwards. Owing to the curvature at the bottom of the

beaker the lower edge of the glass plate remains slightly above the bottom, leaving a clearance through which a current of water passes when the upper edge of the plate is rocked backwards and forwards.

The beakers used are $5\frac{1}{2}$ in. in height with an internal diameter of 4 in. The glass plates are about $4\frac{3}{4}$ in. in length and cut just wide enough to fit the beaker without scraping its sides. The two bottom corners of a plate rest upon the incurved sides at the foot of the beaker and pivot there, while the upper edge of the plate has a backwards and forwards play of about 1 in. A glass rod, with a bent end, hooks over the top edge of the plate, the straight body of the rod projecting through the beaker spout. The free end of the glass rod is attached to a wire stretched between wooden uprights by a rubber tube whose end is split; the two ends of this split are fastened with a pin after the wire has been inserted between. The wooden uprights are fixed to a long horizontal wooden batten which is pivoted at either end in two angle-irons screwed to the bench. A string attached to the wire which works the main plunger-jar system of the laboratory passes under a pulley on the bench to the top of a central wooden upright on the batten. The wooden structure is set so that in the forward position of the glass plates in the beakers it is leaning slightly backwards; on the release of the tension on the plunger string, it then drops backwards about an inch under its own weight against a stopper. It is convenient to have two wires at slightly different levels on the wooden uprights to allow for inequalities in the heights of the beakers. The whole battery is set up on a bench about 14 ft. from a north window. Excessive plant growth is thus avoided.

While the use of the above method has been proved successful for growing healthy colonies of small sessile hydroids, it has not yet been shown that the larger branching hydroids will produce their typical natural form.

This will probably depend upon an abundant food supply and on the hydroid itself hanging free from the side of the beaker. A single polyp of *Bougainvillia muscus* soon sent stolons on to the beaker side, and a creeping colony as described by Browne (1907*a*) was quickly formed. In the centre of the colony, however, many of the polyps started to branch and grow upwards; these developed into quite typical growths of the *B. fruticosa* type.

In rearing primary polyps from medusae the substratum for the settling of the planulae may be of importance. We have reared first polyps from the following species of medusae: *Steenstrupia rubra**, *Bougainvillia britannica*, *Turritopsis nutricula*, *Rathkea octopunctata*, *Amphinema dinema*, *Laodicea undulata*, *Mitrocomella brownei*, *Phialidium hemisphericum*, *Phialella cymbaloides*,† and *Octorchis gegenbauri*. The planulae of all of these apparently settled without difficulty on glass except *Bougainvillia britannica* and *Rathkea octopunctata*, and possibly *Octorchis*. Of these, the planulae of the first settled on a piece of smooth shell, but the polyps did not develop far enough to become distinctive.

The *Rathkea* planulae settled in detrital masses and rough hollows in a piece of cleaned stem of *Eunicella*.

It seems possible that the best results on glass will be obtained if sea water has been allowed to stand in the bowl for some time so that a thin bacterial or diatomaceous film is formed on the surface of the glass.

* = *S. nutans*. † = *P. quadrata*.

COLLECTING AND PRESERVATION

The most usual method of collecting medusae is with the ordinary plankton tow-net, a conical net shaped rather like a butterfly net, which is towed through the water and filters off the plankton organisms. The net may be made of various materials, but it should be realized that the size of the organism retained depends upon the mesh of the material, or the pore spaces between the interwoven threads. The material in most general use is bolting silk, which is used by millers for grading flour. This material has the advantages that it can be obtained in a wide range of mesh sizes and that, owing to the way the threads are woven, the meshes keep a fairly constant size and the threads do not pull apart under strain. Bolting silk is supplied in a number of standard gauges corresponding to the number of strands of thread to the inch; a complete range can be obtained from the finest, which has 200 threads to the inch, to the coarsest with only fourteen to the inch. Silk nets are not, however, generally used coarser than twenty-five threads to the inch, since to capture the larger plankton animals it is necessary to filter a large body of water, and so the net itself must be large. It is, therefore, desirable to use a cheaper and stronger material such as cheesecloth or stramin.* Silk is not usually used for nets larger than 70 cm., or at most 1 m., in diameter at their mouths, while stramin is used for the large nets, such as the ring-trawl, which is 2 m. in diameter at the mouth.

Medusae are delicate organisms and in order to collect them with least damage it is always advisable to use a tow-net which has an enamelled or galvanized bucket, or even a glass jam-jar, tied at its end. The medusae are thus still in water while the net is being untied after its removal from the sea.

The condition of the medusae also depends on the quantity of other plankton organisms contained in the catch, and it is desirable to use a mesh which will allow the passage of all organisms below the size of the medusae required. Thus for the majority of adult medusae a coarse mesh should be used. In fact the author has used a silk net of fourteen strands to the inch and obtained catches in inshore waters consisting almost entirely of medusae, since nearly all other plankton organisms had passed through the meshes. This is especially convenient when it is necessary to separate out living medusae on board ship. Material such as stramin will retain all adult and young stages of medusae whose umbrellas have a diameter greater than 2–3 mm., that is, it will retain the larger specimens of *Rathkea*, but almost entirely miss such species as *Lizzia*. For the smaller medusae silk with a mesh of fifty threads to the inch is necessary, while for some of the very smallest newly liberated medusae an even finer silk may be needed.

While bolting silk and stramin are the materials most used for scientific purposes, this is not to say that other materials may not be employed with equal success for collecting specimens. In fact, a cone-shaped bag of almost any material drawn through the water will catch medusae; and it is interesting to recall that the most fundamental researches on Hydromedusae were done by T. H. Huxley with material collected in tow-nets made from ship's flag bunting. It is as well, however, to avoid materials which are liable to throw off much fluff or loose material, since it may get entangled in the tentacles of the medusae.

Collections are usually made at sea from large or small vessels. When using large nets, which can only be conveniently handled on a powered vessel, the best speed for towing is between 1 and

* A hempen material with *c.* sixteen strands to the inch, made in Denmark.

2 knots. Collections can be successfully made with small tow-nets from a vessel of any size which is just drifting with the tide or wind; the net should have a 7 or 14 lb. lead attached in front to sink it below the surface. From rowing boats the net may be fished at quite slow speed.

The composition of the catch will naturally depend on the distance it is made from the shore, since many species are only found well off-shore. But in many localities a number of species occur quite close in-shore, and in such places it is not even necessary to use a boat, if there is a convenient pier or jetty. Here the net can be merely streamed in the tide, and indeed much of our knowledge about medusae has been gleaned from collections made in this way from piers or harbours. It is best in such circumstances to fish on a rising tide since medusae are then being carried in from farther off-shore. The richest catches will probably be obtained on a rising tide in the dusk or dark, when many of the species which normally live deep down in the daytime will have migrated to the upper layers and been carried in-shore in the surface water.

Specimens may even be obtained with a dip-net or a glass vessel from rock pools in some localities, or in the sea itself by fishing from the rocks in sheltered coves with a net on the end of a long pole (see, e.g. Gosse, 1853, p. 349). When collecting in rock pools it is advisable to lie flat and peer into the water for some time to accustom the eyes to the conditions (see, e.g. Hincks, 1868, p. 298, n.). Small medusae may thus often be seen just after liberation from hydroids attached to the submerged rocks and weeds. Very young medusae may of course also be obtained by collecting the hydroids and allowing them to liberate medusae in small aquaria. In this way large supplies of young specimens can be obtained from a number of different hydroids.

When the net has been lifted, the contents of the catch should be poured immediately into large glass vessels and diluted with pure sea water. Sometimes it will be necessary to divide the catch among a number of jars. The living medusae should then be removed with a pipette or glass dipping tube into another vessel of pure sea-water. If the specimens are not required for examination on the spot it is essential that they should be shielded from direct sunlight when being taken to the laboratory, and that they should be kept as cool as possible. On board ship, if some hours may elapse before landing the material, it is customary to tie a piece of silk or canvas over the top of the jar, which is then placed under circulation if this is available. But I have found that this method is not desirable since the medusae become covered with many fine bubbles of air. The most satisfactory method is to place a few specimens in a breffit (a glass jar of about 2 l. capacity) filled only to one-quarter of its capacity with clean sea-water (to allow a large volume of air in proportion to that of water). The lid is then replaced and the breffit floated in a bath of water under the circulation system. In this way the medusae are prevented from lying on the bottom of the jar, which is continually rolling over with the motion of the ship, or through the play of the sea-water jets upon it. If only one specimen of a species that is rare, or particularly required, is caught, it should be isolated in a separate jar, for great disappointment may be caused on returning to the laboratory when it is found that the precious specimen is neatly packed away in the stomach of some other medusa.

Once in the laboratory the medusae may be placed in finger bowls of clean sea-water where they will live for several days without further attention. It is, however, essential that the water should be pure, and in the Plymouth Laboratory 'outside sea-water', water collected well clear of the land, is used in preference to the water circulating through the aquarium tanks. In laboratories in which the water circulation is directly from the sea this should not be necessary, provided that the water is not contaminated by the pumps or by the presence of too much life in the aquaria. The worker should not be misled by the appearance of the medusae when first

placed in the bowls in the laboratory; sometimes they appear somewhat unhappy and contracted, but usually after a few hours they will have completely recovered and will be actively swimming in the water.

Specimens brought into the laboratory alive are very suitable for making excellently preserved material. For specimens not required for detailed histological examination the best preservative is 5% formalin in sea-water. It is not usually* necessary to use any narcotizing reagents to preserve the specimens in a fully expanded condition. The medusae should be placed in a small vessel and left for a few minutes until swimming actively. Strong formalin may then be squirted in by a pipette, and it is essential to keep the water and the medusae moving and well stirred. This is best done by continually squirting, with the pipette under water, on the medusae themselves. This should be continued until a short time after the medusae show no spontaneous movements. It will be found that the action of the stream of water over the specimens has drawn the tentacles out until well expanded, and the umbrella is also kept from contracting by jets which strike occasionally on the subumbrellar surface.

When there are a large number of specimens to be preserved the majority will be found in excellent condition if strong formalin is poured into the jar and the water is kept gently stirred for a short time with a glass rod.

When satisfied that the medusae are dead and when there is no further sign of movement or contraction of the tentacles when the water is allowed to come to rest, the specimens may be bottled off in tubes of 5% formalin in sea-water. It is always advisable to keep the specimens in formalin in sea-water rather than in fresh water.

Always avoid the use of alcohol as a preservative (except for nematocysts, see p. 16), unless formalin is unobtainable, since it causes shrinkage and contraction of the specimens. When the umbrella is much shrunk the proportional sizes of stomach, marginal tentacles, etc., appear altogether different, and it becomes difficult to reconcile the appearance of such specimens with published drawings of well-preserved or living medusae (see Text-figs. 175, 176).

If whole plankton catches are to be preserved, it cannot be too strongly emphasized that the catch should be preserved immediately it has come on board. Crowded together as they are many of the animals quickly die, and delicate organisms are also liable to damage by the depredations of the more hardy or by contact with crustacean spines.

* If available a 7½% isotonic solution of magnesium chloride gives good results as a narcotic.

SUBJECT INDEX TO LITERATURE OF HYDROMEDUSAE

This subject index does not pretend to be complete; it does, however, include all the important papers and many others.

Histology

General. Kölliker, 1865; Krasińska, 1914.

Nervous system. Eimer, 1877; Hertwig, O. & H., 1878; Schäfer, 1878; Hyde, 1902 (see also Bozler, 1927, and Woollard & Harpmann, 1939, Scyphomedusae).

Sense organs. Müller, F., 1865; Hertwig, O. & H., 1878; Agassiz & Mayer, 1899, *Tiaropsis*; Linko, 1900*a*, *b*; Joseph, 1920; Kramp, 1932, Mitrocomidae.

Ciliation. Gemmill, 1920, *Melicertum.*

Nematocysts. For full literature see Weill, 1934*a*, *b*; Weill, 1936*b*; Russell, 1938*b*, 1939*b*, 1940*a*.

Embryology

General. Metschnikoff, 1870, 1874, 1886*a*; Fol, 1873; Claus, 1882, 1883; Hammann, 1883; Brooks, 1886*a*; Häcker, 1892; Gerd, 1892; Brooks & Rittenhouse, 1907; Rittenhouse, 1910.

Origin of germ cells and nuclear studies. Varenne, 1882; Mérejkowsky, 1883; Weismann, 1883, 1884; Hartlaub, 1884; Ishikawa, 1888; Bunting, 1894; Trinci 1905, 1906; Bigelow, 1907; Goette, 1907; Müller, H., 1908; Nekrasoff, 1911; Apstein, I., 1913; Hargitt, C. W., 1917; Faulkner, 1929; Kramp, 1932; Brien, 1942; Berrill & Liu, 1948.

Chromosome numbers. See Harvey, 1916; Hargitt, C. W., 1917; Faulkner, 1929.

Variations and Abnormalities

Romanes, 1876*a*, 1877*a*, Davidoff, 1881, *Phialidium*, schizogony; Keller, 1883, *Gastroblasta*, polygastry; Lang, 1886, *Phialidium*, polygastry; Agassiz & Woodworth, 1896, *Obelia*; Mayer, 1901, *Pseudoclytia*, review of literature to date; Hargitt, 1901; Neppi, 1909, *Helgicirrha* and *Eirene*; Nekrasoff, 1911; Boulenger, C. L., 1911*b*, *Moerisia*; Drzewina & Bohn, 1911, 1912*a*, *Eleutheria*; Neppi & Stiasny, 1913*b*, *Phialidium*, schizogony; Rugh, 1930, *Gonionemus*; Burkenroad, 1931, pentamerism; Pasteels, 1939, *Cladonema*, schizogony.

Occasional records. Gosse, 1853, *Cosmetira pilosella*; Allman, 1871, *Sarsia tubulosa*; Grobben, 1875, *Podocoryne*; Mereschkowsky, 1879, *Rathkea* (as *Bougainvillia*), Maas, 1893, *Phialidium*; Browne, 1895, *Rathkea*; Browne, 1896*a*, *Lizzia*; Hartlaub, 1896, *Sarsia* sp.; Hargitt, G. T., 1902, *Gonionemus*; Mayer, 1910, *Sarsia tubulosa*; Hartlaub, 1911, *Bougainvillia britannica* and *B. ramosa*; Maas, 1911, *Octocanna funeraria*; Neppi & Stiasny, 1913*a*, *Aequorea forskalea*; Hartlaub, 1914, *Leuckartiara*; Robson, 1914*a*, *Bougainvillia*; Kramp, 1919, *Chromatonema rubrum*, *Phialidium islandicum*, *Tima bairdi*; Kramp, 1924, *Bythotiara murrayi*, *Octocanna funeraria*; Kramp & Damas, 1925, *Halopsis ocellata*, *Octocanna funeraria*; Sanderson, 1930, *Mitrocomella polydiademata*; Ranson, 1936, *Tiaranna rotunda*, *Chromatonema rubrum*, *Octocanna funeraria*; Kramp, 1939*a*, *Sarsia tubulosa*; this monograph, p. 51, *Sarsia eximia*, p. 185, *Amphinema rugosum*, p. 236, *Laodicea undulata*, p. 318, *Phialella quadrata*, p. 357, *Aequorea pensilis*, pp. 20, 365, *Eutima gracilis*.

Habits and Biology

Feeding. Agassiz, L., 1849, *Staurophora*, *Tiaropsis*; Romanes, 1885, *Staurophora*; Linko, 1900*a*, *Sarsia tubulosa*; Drzewina & Bohn, 1911, 1912*b*, 1913, *Eleutheria*; Lebour, 1922, 1923; M'Intosh, 1926, *Hybocodon*; Henschel, 1935, *Sarsia tubulosa.*

Swimming. Agassiz, L., 1849, *Staurophora*, *Tiaropsis*; Gosse, 1853, *Aequorea*; Agassiz, A., 1865, *Gonionemus.*

Growth and length of life. Browne, 1898*a*, production of medusae from *Bougainvillia ramosa* hydroid; Orton, 1914, age of *B. ramosa* hydroid at medusa production; Orton, 1920, age of *Clytia* hydroid at medusa production; Elmhirst, 1925, lunar periodicity in *Obelia*; Kramp, 1930, stunting in *Laodicea* and *Leuckartiara octona*; Russell, 1938*a*, growth and length of life of *Bougainvillia britannica*, seasonal size in *Phialidium* and *Aglantha*, stunted growth in *Laodicea*; Vallentin, 1907, 1909, dead and dying *Cosmetira.*

Luminescence. Forbes, 1848, *Liriope, Tima bairdi*; Gosse, 1853, *Cosmetira, Aequorea*; Romanes, 1876*a*, *Mitrocomella polydiademata, Eutonina indicans*; Bles, 1892, *Obelia*; Evans & Ashworth, 1909, *Tima bairdi*; Hartlaub, 1914, *Leuckartiara octona*; M'Intosh, 1926, *Obelia.*

Parasitic and commensal habits. Gunther, 1903*b*, *Mnestra parasites* on *Phyllorhöe*; Kramp, 1922, hydroids on pteropods, Gudger, 1928, hydroids on fishes; Russell & Rees, 1936, *Zanclea* hydroid on *Cellepora*; Rees, 1939*a*, *Dipurena halterata* hydroid in a sponge; Hincks, 1868, and Uchida & Okuda, 1941, *Proboscidactyla* hydroid on *Sabellaria* and *Potamilla* tubes.

Vertical distribution and migrations. Russell, 1925, 1927, 1928, 1931.

Immigrants. Künne, 1933, *Bougainvillia macloviana* in North Sea; Kramp, 1937, *Gonionemus murbachi* in Oslo Harbour; Werner, 1950*a*, *b*, *G. murbachi* at Sylt; this monograph, p. 399, 402, *G. vertens* in Port Erin tanks, and *G. murbachi* in Cullercoats tanks.

Abundance. Vallentin, 1897, *Tiaropsis* in Falmouth Harbour; Russell, 1938*a*, yearly comparisons off Plymouth.

Enemies. Agassiz, L., 1849, *Tiaropsis* eaten by *Sarsia*; Delap, M. J., 1905, 1906, medusae eaten by young *Cyanea* and *Aurelia*; Littleford, 1939, *Rathkea* eaten by *Cyanea.*

Stranding. Forbes, 1848, *Tima bairdi*; Gosse, 1853, *Cosmetira pilosella*; Browne, 1895, *Leuckartiara octona, Mitrocomella polydiademata*; Evans & Ashworth, 1909, *Tima bairdi*; Evans, 1916, *T. bairdi*; Storrow, 1922, *T. bairdi*; Bigelow, 1926, *Staurophora*; this monograph, p. 271, *Cosmetera pilosella*, p. 320, *Phialella quadrata* in boat.

Parasites and Commensals

Hincks, 1868, *Phoxichilidium* larvae in *Coryne eximia* hydroid; Haddon, 1888, larval anemones; M'Intosh, 1887, *Peachia* larvae; Vallentin, 1897, larval trematodes in *Tiaropsis*; Hallez, 1905*b*, *Phoxichilidium* in *Bougainvillia* hydroid; Delap, M. & C., 1905, *Halcampa* on *Phialella quadrata*; Evans & Ashworth, 1909, *Hyperia galba* and *Metopa alderi* on *Tima bairdi*; Neppi, 1910, *Halcampa* on *Helgicirrha* and *Eirene*; Mayer, 1910, larval *Cunina* on *Rhopalonema*; Tesch, 1911, *Hyperia galba* on *Melicertum* and *Leuckartiara*; Robson, 1914*a*, *Phoxichilidium* in *Coryne eximia* hydroid; Lebour, 1916*a*, larval *Anaphia petiolata* on *Leuckartiara octona, Cosmetira pilosella*, and *Phialidium hemisphaericum*; Lebour, 1916*b*, metacercaria of *Pharyngora* in *Leuckartiara octona*; Kramp, 1919, nematode in abnormal *Phialidium islandicum*; Hovasse, 1935, peridinian *Protoodinium chattoni* in *Podocoryne carnea* and *P. minima*; Künne, 1948, *Peachia* larvae on *Eutonina indicans*; actinian larvae and *Halcampa* (Nyholm, 1949); this monograph, larval trematodes (Hemiurids) in *Eirene* (p. 327), *Helgicirrha* (p. 333), *Tima bairdi* (p. 384), *Proboscidactyla stellata* (p. 392).

Rearing and Culture

Hartlaub, 1897, *Bougainvillia superciliaris*; Browne, 1898*a*, 1907*a*; Drzewina & Bohn, 1911, 1912*a*, *b*, 1913, *Eleutheria*; Russell, 1936*a*, *Laodicea*; Rees & Russell, 1937; this monograph, p. 246, *Melicertum* and p. 402, *Gonionemus.*

Experimental Observations

Embryology. Zoia, 1895*a*, *b*; Hargitt, C. W., 1904*b*; Maas, 1905*b*, 1908.

Regeneration. Morgan, 1899; Hargitt, G. T., 1902; Müller, H. C., 1913, 1914.

Reactions. Romanes, 1876*b*, *c*, 1877*b*, *c*, 1885; Nagel, 1893, 1894; Yerkes, 1902*a*, *b*, 1904; Yerkes & Ayer, 1903; Herbst, 1904; Murbach, 1903, 1907; Drzewina & Bohn, 1911, 1912*b*, 1913; Wolf, 1928; Rugh, 1929; Henschel, 1935.

Economics

As current indicators. Kramp, 1927, 1930; Wulff, Bückmann & Künne, 1934; Künne, 1937; Russell, 1938*a*, 1939*c*.

In fishing industry. Delap, M. & C., 1905, *Steenstrupia nutans* on fishing nets; Swithinbank & Bullen, 1913, *Obelia* and catches of pilchard; Lucas & Henderson, 1936, association with herring catches.

Preservation and Histological Methods

Hyde, 1902, nervous tissue; Bigelow, 1907, nuclear cycle; Bigelow, 1909*a*, p. 10; Müller, 1908, egg formation; Boulenger, 1910, *Moerisia*; Boulenger, 1911*a*, *Limnocnida*; Douglas, 1912, *Craspedacusta*; Apstein, I., 1913; Krasińska, 1914; Hargitt, G. T., 1917, p. 612; Kramp, 1919, p. 2; Dejdar, 1934, nematocysts of *Craspedacusta*; Weill, 1934*a*, nematocysts.

HISTORY AND CLASSIFICATION

General. L. Agassiz, 1862; Bigelow, 1909*a*; Forbes, 1848; Haeckel, 1879*a*; Hincks, 1862; Mayer, 1910; Ranson, 1936; Stechow, 1923.

Anthomedusae. Allman, 1871–2; Hartlaub, 1907, 1911, 1914; Kramp, 1926*a*; Lengerich, 1923 (Eleutheriidae); Rees, 1938 (Bougainvilliidae and Pandeidae); Kramp, 1949 (Corymorphidae).

Leptomedusae. Kramp, 1919, 1933*b*; Vanhöffen, 1902, 1911; Browne, 1907*b* (Laodiceidae); Kramp, 1932 (Mitrocomidae); Kramp, 1936 (Eirenidae); Rees, 1939*b* (*Campanulina*); Skogsberg, 1948 (Polyorchidae).

Limnomedusae. Kramp, 1939*a*; Hartlaub, 1917; Browne, 1904 (Williadae & Petasidae); Kramp, 1938*a* (Olindiidae); Uchida, 1929 (Olindiidae).

Trachymedusae. Broch, 1929; Kramp, 1947; Thiel, 1936; Uchida, 1928; Bigelow, 1915*b* (*Eperetmus*).

Narcomedusae. Broch, 1929; Kramp, 1947; Maas, 1904*c*; Uchida, 1928; Vanhöffen, 1907, 1908.

ON THE IDENTIFICATION OF MEDUSAE

It is not possible to produce any simple key for the identification of all species of British medusae on account of the different growth stages they pass through during their lives. In some species, especially among the Anthomedusae, there is no great change in general appearance during the growth of the medusa except for increase in size and the development of the gonads. But in the majority of species the changes are rather great, chiefly due to increase in the numbers of marginal tentacles. Thus the identification of the young stages will, as a rule, follow after the identification of the adult medusae has been learnt.

The main divisions of the group are based on the position of the gonads, and on the presence or absence of statocysts and on their structure when present. But the fact that there are a few species about whose systematic position there has been considerable divergence of opinion shows that sometimes in order to decide to which Order a species belongs attention must also be paid even to certain minor characters.

Briefly, the characters by which the Orders may be distinguished are as follows:

Gonads only on stomach, or occasionally both on stomach and extending for a short distance along radial canals; no statocysts . . . . . **Anthomedusae**

Gonads only on radial canals, but occasionally contiguous with base of stomach; with or without statocysts; statocysts velar ectodermal when present . . . . . **Leptomedusae**

Gonads either only on stomach, or both on stomach and extending for short distance along radial canals, or only on radials canals; with or without statocysts; statocysts in form of enclosed sensory clubs with endodermal axes when present. . . . . **Limnomedusae**

Gonads only on radial canals; with statocysts in form of free or enclosed sensory clubs with endodermal axes. . . . . **Trachymedusae**

Gonads only on stomach, without true radial canal system; with statocysts in form of free sensory clubs with endodermal axes . . . . . **Narcomedusae**

It will be seen that the characters of the Limnomedusae may overlap those of another Order. If they have gonads on the stomach only, or extending along the radial canals as well, and they have no statocysts, they might be placed in the Anthomedusae. If they have gonads on the radial canals only and have statocysts, they might be placed in the Trachymedusae. It is necessary then to examine other characters, namely the structure of the marginal tentacles and the histological structure of the hydroid. In Anthomedusae the marginal tentacles are either hollow, or solid when they have a central axis consisting of a single row of columnar endodermal cells; in the hydroids the endoderm of the tentacles is separated from the endoderm of the gastric cavity by a mesogloeal diaphragm. In Limnomedusae the marginal tentacles are hollow in that their axes are composed of a number of peripheral layers of endoderm cells whose inner walls may not always be quite contiguous; in the hydroids the endoderm of the tentacles is continuous with that of the gastric cavity. In Trachymedusae the marginal tentacles are solid (except in the Geryonidae in which there are also hollow tentacles), and there is no hydroid stage. This example at once shows the difficulties of constructing a key unless phylogeny is to be ignored, and all the genera of the five Orders are lumped together and treated as an artificial whole.

Fortunately, however, among the British medusae there are only five species of Limnomedusae and only four of these are marine. For general purposes they may therefore be disregarded, and the remaining medusae can be placed in their respective Orders with little difficulty.

But before attempting identification it should be realized that the state of preservation of the specimens must be taken into account. Preserved medusae rarely appear in their natural form unless carefully fixed when in a healthy free-swimming state (see p. 36). If, for any reason, a catch of plankton has been allowed to stand for some hours before preservation, many, if not most, of the medusae will be in an unhealthy or moribund condition. To show the change in appearance that may result I placed a specimen of *Phialidium hemisphaericum* in sea-water in a small glass vessel and drew it immediately with the aid of a camera lucida (Text-fig. 175 A); this drawing was made at 12 noon on 30 April 1940. The medusa was left in the dish on the stage of the microscope overnight, and drawn again at 9.15 a.m. on 1 May (Text-fig. 175 B). The medusa was still alive; its marginal tentacles were twitching, and it made feeble attempts at contraction of the umbrella. But a comparison of the two drawings shows that during the process of dying the bulk of the jelly of the umbrella had enormously decreased. As a result the relative proportions of the marginal tentacle bulbs and of the stomach and the gonads to the diameter of the umbrella became entirely altered. An inexperienced observer might well have hesitated to regard the two drawings as being of the same species, let alone the same specimen.

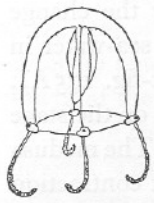
It is possible that dying medusae may be caught in the plankton, and these when preserved would thus look quite different from other healthy specimens caught at the same time (see Text-fig. 176). Many Anthomedusae also have a habit of turning inside out when dying owing to the shrinkage of the umbrella and consequent protrusion of the stomach (see Text-fig. 90). One can easily recognize such specimens among illustrations given in the past by earlier authors of medusae then supposed to be new species.

The possibility must, therefore, always be borne in mind that a specimen may have been moribund and that it may appear very different from descriptions which have been based on well-preserved or healthy living specimens. For this reason I have frequently given illustrations in the text showing the appearance of badly preserved specimens.

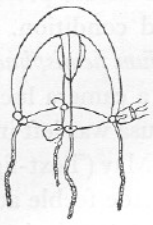
After the reader has placed a species in its Order he should turn the pages to that Order where detailed aids to the identification of the Families and their Genera will be found. Keys for the further identification into species are given under the genera.

As a general aid I have, however, given in Text-figs. 12–15 a pictorial key which includes diagrammatic drawings of all British species from which, by a process of elimination, the identification can be quickly narrowed down to a few remaining possible species.

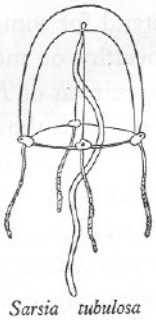
PICTORIAL KEY TO SPECIES OF BRITISH MEDUSAE



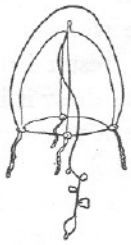
Sarsia eximia and *Stauridiosarsia producta*



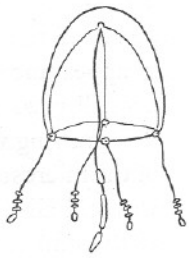
Sarsia prolifera



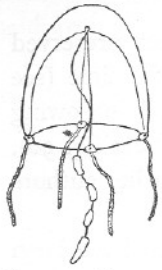
Sarsia tubulosa



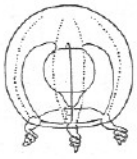
Sarsia gemmifera



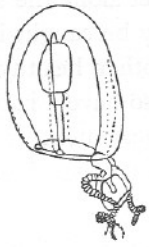
Dipurena halterata



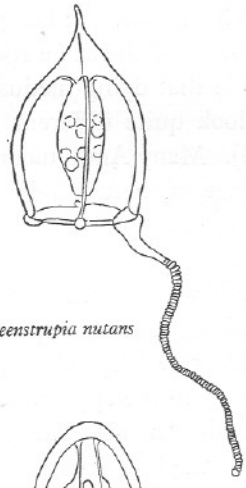
Dipurena ophiogaster



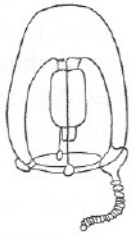
Ectopleura dumortieri



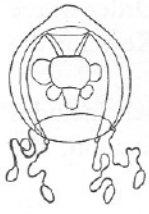
Hybocodon prolifer



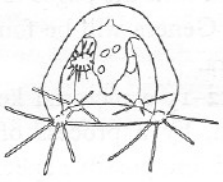
Steenstrupia nutans



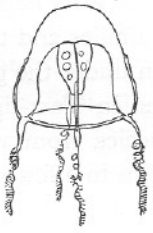
Euphysa aurata



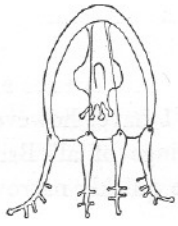
Eucodonium brownei



Margelopsis haeckeli



Zanclea costata



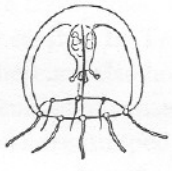
Cladonema radiatum



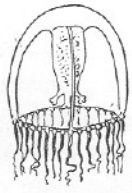
Eleutheria dichotoma



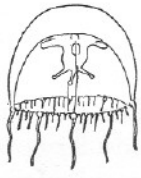
Turritopsis nutricula



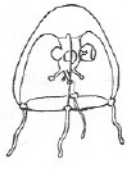
Podocoryne carnea



Podocoryne borealis



Podocoryne hartlaubi

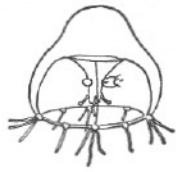


Podocoryne minima

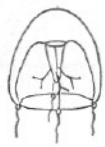
Text-fig. 12.



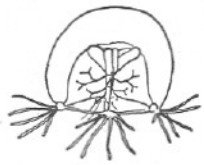
Rathkea octopunctata



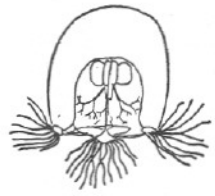
Lizzia blondina



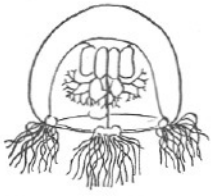
Thamnostoma sp.



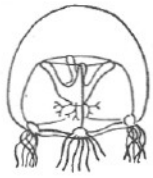
Bougainvillia ramosa



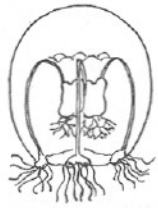
Bougainvillia britannica



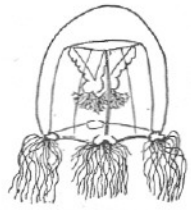
Bougainvillia principis



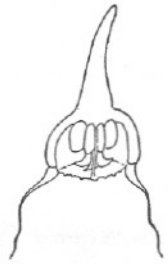
Bougainvillia pyramidata



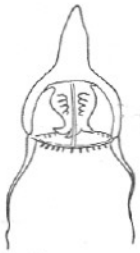
Bougainvillia superciliaris



Bougainvillia macloviana



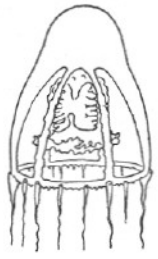
Amphinema dinema



Amphinema rugosum



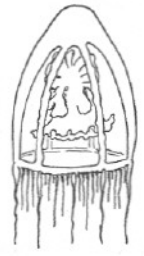
Annatiara affinis



Leuckartiara octona



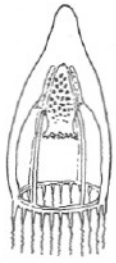
Leuckartiara nobilis



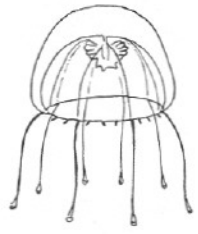
Leuckartiara breviconis



Neoturris pileata



Pandea conica
(and *P. rubra*)



Bythotiara murrayi

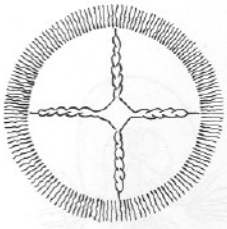


Tiaranna rotunda

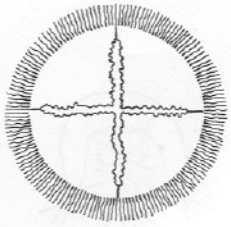


Chromatonema rubrum

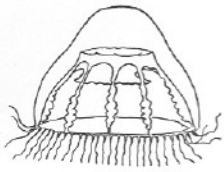
Text-fig. 13.



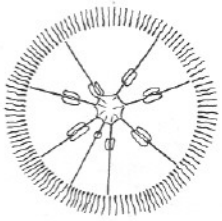
Laodicea undulata



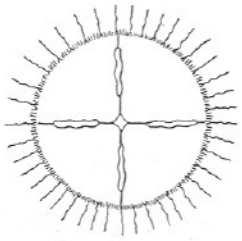
Staurophora mertensi



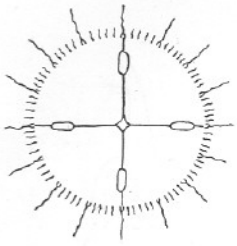
Melicertum octocostatum



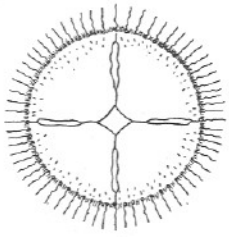
Dipleurosoma typicum



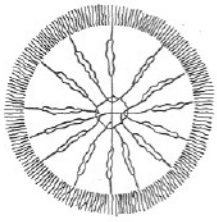
Mitrocomella polydiademata



Mitrocomella brownei



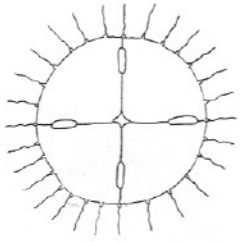
Cosmetira pilosella



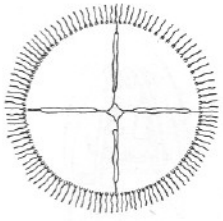
Halopsis ocellata



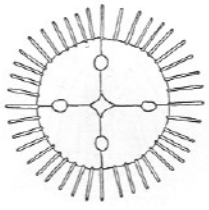
Tiaropsis multicirrata



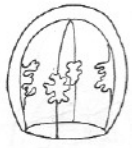
Phialidium hemisphericum and *Phialella quadrata*



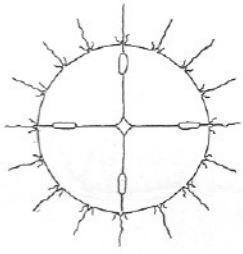
Phialidium islandicum



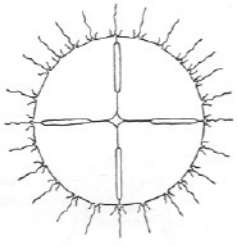
Obelia sp.



Agastra mira



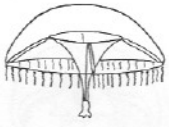
Lovenella clausa



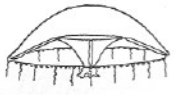
Eucheilota maculata



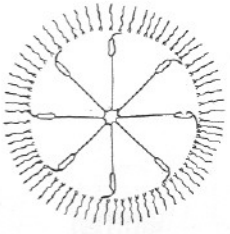
Eirene viridula



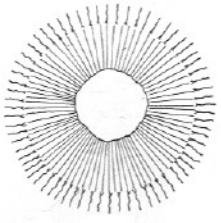
Helgicirrha schulzei



Phialopsis diegensis

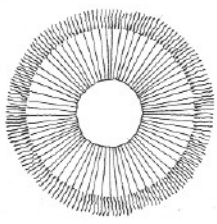


Octocanna funeraria

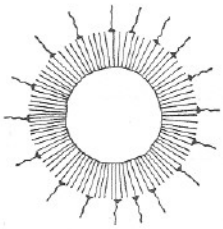


Aequorea forskalea

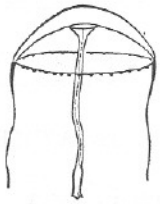
Text-fig. 14.



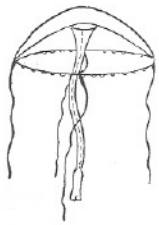
Aequorea vitrina



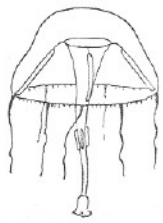
Aequorea pensilis



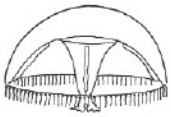
Eutima gracilis



Eutima gracilis var. *insignis*



Octorchis gegenbauri



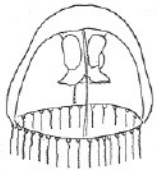
Eutonina indicans



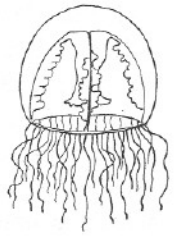
Tima bairdi



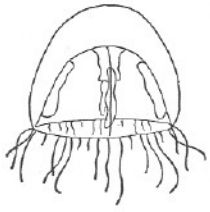
Proboscidactyla stellata



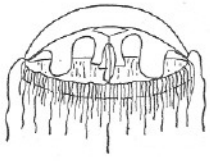
Pochella polynema



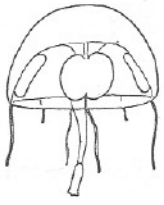
Gonionemus vertens



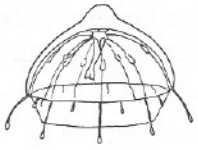
Gossea corynetes



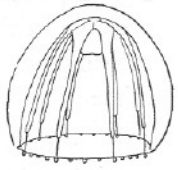
Craspedacusta sowerbii



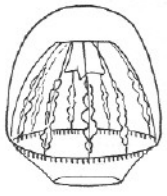
Liriope tetraphylla



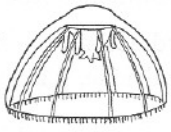
Rhopalonema velatum
(and *R. funerarium*)



Colobonema sericeum



Pantachogon haeckeli



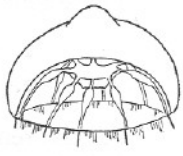
Crossota rufobrunnea



Aglantha digitalis



Haliscera bigelowi
(for *Halicreas minimum* see p. 453)



Botrynema brucei

Text-fig. 15.

ORDER

ANTHOMEDUSAE

(HYDROIDA ATHECATA)

Hydromedusae with considerable variation in form, with umbrella usually deep bell-shaped; with gonads almost invariably situated on stomach, very rarely extending perradially on subumbrella; with or without ocelli; without statocysts. Hydroids, as far as yet known, invariably athecate.

No single character can be used to define the Anthomedusae so as to separate them from the other Orders of the Hydromedusae. The characteristic bell-shape of the umbrella is found also in some Trachymedusae and Limnomedusae. Gonads may occur on the stomach in some Limnomedusae. There are also many Leptomedusae and Limnomedusae which have no marginal sense organs. Athecate hydroids are to be found among Leptomedusae and Limnomedusae. In a few Anthomedusae the gonads occur perradially, along the radial canals, on the subumbrella, which is one of the chief distinguishing characters of the Leptomedusae. Yet, when all the characters are taken together, the Anthomedusae can with very few exceptions be readily separated from medusae in the other Orders.

More diversity of form is shown in the Anthomedusae than within any of the other Orders. For this reason it is possible to split the Anthomedusae into more distinct groupings than is possible in the other Orders. This grouping can be made almost entirely on the form of the mouth, and a consideration of other characters shows that on the whole the grouping is that of related forms. There are four types of mouth:

1. Simple and tubular.
2. Simple and tubular, with oral tentacles inserted on the side of the mouth tube above its opening.
3. Divided into lips which are themselves armed with nematocyst clusters, so that they act virtually as tentacles.
4. Divided into lips with simple or folded margins.

These four types are divided among eight families of the Anthomedusae as follows:

1. Corynidae, Tubulariidae.
2. Bougainvilliidae, Eudendriidae.
3. Hydractiniidae, Rathkeidae.
4. Pandeidae, Tiarannidae.

For the remaining families other characters must be resorted to, but all the large families are included among these four categories based on the shape of the mouth.

The following twelve families of Anthomedusae are represented in British waters:

Corynidae, Tubulariidae, Margelopsidae, Eleutheriidae, Cladonemidae, Zancleidae, Clavidae, Hydractiniidae, Rathkeidae, Bougainvilliidae, Pandeidae, and Tiarannidae.

Among these there are twenty-six genera with forty-one species occurring or likely to occur in British waters.

It is possible to construct a simple key to family identification of these Anthomedusae on the following lines:

Mouth simple and tubular:
- Marginal tentacles solitary:
  - With ocelli . . . . . **Corynidae**
  - Without ocelli . . . . . **Tubulariidae**
- Marginal tentacles in four groups . . . . . **Margelopsidae**
- Marginal tentacles bifurcating . . . . . **Eleutheriidae**
- Marginal tentacles with several branches . . . . . **Cladonemidae**
- Marginal tentacles with stalked capsules containing nematocysts . . . . **Zancleidae**

Mouth with four lips with continuous row of nematocyst clusters along margin . . **Clavidae**

Mouth with four lips elongated to form tentacles each with one or a few nematocyst clusters:
- Marginal tentacles solitary . . . . . **Hydractiniidae**
- Marginal tentacles in eight groups . . . . . **Rathkeidae**

Mouth simple and tubular with oral tentacles inserted above mouth opening . **Bougainvilliidae**

Mouth with simple or folded lips:
- No marginal cordylus-like structures . . . . . **Pandeidae**
- With marginal cordylus-like structures . . . . . **Tiarannidae**

Family CORYNIDAE

Anthomedusae with simple circular mouths; with four radial canals; with gonads completely surrounding stomach; with four equally developed hollow marginal tentacles; with ocelli on marginal tentacle bulbs.

Hydroids *Coryne*-like, with tentacles irregularly distributed or in several whorls of few tentacles only; distal tentacles all capitate; single proximal whorl of four or five reduced filiform tentacles may be present.

The free-swimming medusae of the Corynidae are all characterized by having simple circular mouths and gonads which completely surround the stomach. These characters are common also to the Tubulariid medusae, but the Corynidae differ from the Tubulariidae in having conspicuous *ocelli* on the bases of the marginal tentacles. The ocellus is situated on a small area left clear by the large nematocyst pad which clasps the tentacle base.

The Corynid medusae are of the simplest type, having always only four marginal tentacles; these marginal tentacles are, however, well armed with nematocyst clusters or rings.

The medusae of the Corynidae are represented in British waters by three genera, *Sarsia* Lesson, *Stauridiosarsia* Mayer, and *Dipurena* McCrady.

Their chief distinguishing characteristics are as follows (see Text-fig. 16):

Gonads undivided:
- Hydroid without filiform tentacles . . . . . **Sarsia**
- Hydroid with filiform tentacles . . . . . **Stauridiosarsia**

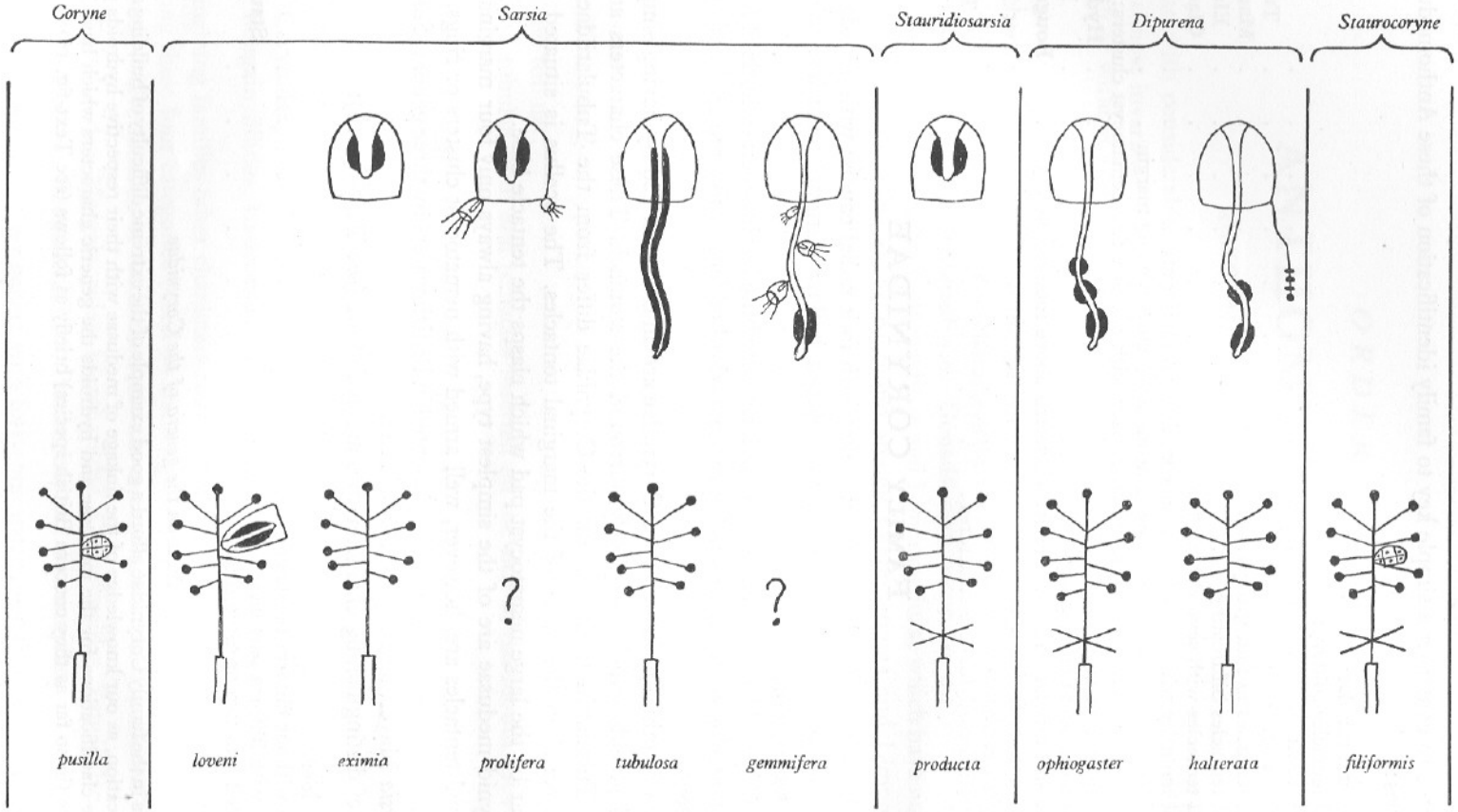
Gonads divided into two or more rings . . . . . **Dipurena**

Note on the genera of the Corynidae

The species in the family Corynidae afford a good example of the extreme difficulty of building a satisfactory single classification, as our knowledge of the linkage of medusae with their respective hydroids progresses.

In separate classifications for the medusae and hydroids the generic characters which have been chosen in the past are (in so far as they concern British species) briefly as follows (see Text-fig. 16):

MEDUSAE:
- With a single continuous gonad . . . . . **Sarsia**
- With more than one gonad . . . . . **Dipurena**



Text-fig. 16. Pictorial key to classification of Corynidae.

HYDROIDS:

With sporosacs and no reduced filiform tentacles	**Coryne**
With fixed or free-swimming medusae and no reduced filiform tentacles	**Syncoryne**
With free-swimming medusae and reduced filiform tentacles	**Stauridiosarsia**
With sporosacs and reduced filiform tentacles	**Staurocoryne**

It is necessary now to reduce this to a convenient single classification, in which the older generic names, whether that of medusa or hydroid, have priority.

On first approximation this means the retention of the following genera; *Coryne*, *Syncoryne*, *Dipurena*, *Stauridiosarsia*, and *Staurocoryne*. But it is agreed that the production of sporosacs or of medusoid gonophores should not constitute a generic difference (see, e.g., Kramp, 1935). On this basis, therefore, we must merge *Syncoryne* into *Coryne*. This in itself is satisfactory, but a difficulty arises when we have to decide into which genus *Staurocoryne* should be placed. It may as well be put either into *Stauridiosarsia* or *Dipurena*, for in both of these genera there are hydroids with reduced filiform tentacles. If *Staurocoryne* is kept separate, we have the inconsistency that the presence of sporosacs, which is regarded as a specific character in *Coryne*, is here used as a generic character. On first thoughts the easiest way out is to merge all genera into the one genus *Coryne*. This means that *Coryne* will become a very large and cumbersome genus, and it must be conceded that any system of classification should aim at a subdivision into convenient groups to aid in identification. On these grounds, therefore, it would seem better to retain the genus *Staurocoryne* even though it be inconsistent with the general scheme adopted for generic characters. The difficulty could be overcome by the use of subgenera in the place of genera, but in practice we should receive no help from this in identification since the name of the subgenus is rarely used.

It should, however, be pointed out that the hydroids of a number of Corynid medusae, including *Sarsia prolifera* and *S. gemmifera*, are not yet known for certain. Should it be found that one of these hydroids has reduced filiform tentacles it would strengthen the argument for the use of a single genus *Coryne*. But even in this instance the present generic classification could be retained by placing the species in the genus *Stauridiosarsia*, although perhaps the presence of reduced filiform tentacles in the hydroid is not strictly a good generic character, since it seems that in some polyps they apparently disappear with age.

Genus **Sarsia** Lesson, 1843

MEDUSAE. Corynidae with gonads forming a single continuous ring or cylinder surrounding stomach.

HYDROID. *Coryne*, with all tentacles capitate.

While the hydroid genus *Coryne* contains several British species which do not liberate medusae, it also contains several with free-swimming medusae. These medusae will be familiar to many as *Sarsia* and their hydroids as *Syncoryne*.

There are four species of *Sarsia* known for certain among British medusae.

They are *S. eximia* (Allman), *S. prolifera* Forbes, *S. tubulosa* (M. Sars) and *S. gemmifera* Forbes. There is also one species, *S. lovéni* (M. Sars) which has fully formed medusae, but these are not liberated (Pl. II, fig. 5; Text-fig. 23 B).

The distinguishing characters of the free-swimming medusae are as follows:

Stomach short, not extending beyond umbrella margin:	
No asexual budding	**S. eximia**
Asexual budding from bases of marginal tentacles	**S. prolifera**
Stomach long, extending far beyond umbrella margin:	
No asexual budding	**S. tubulosa**
Asexual budding from stomach	**S. gemmifera**

The identification of some *Sarsia* medusae may present considerable difficulties at first. While they are budding asexually, *S. prolifera* and *S. gemmifera* can be identified at once. In their sexual stages they can be distinguished from *S. eximia* and *S. tubulosa* respectively by their smaller size.

S. gemmifera is also readily distinguishable from *S. tubulosa* by the distal swelling on its stomach and by its short marginal tentacles.

It should also be mentioned that while length of stomach is given as a distinguishing character, in preserved specimens of *S. tubulosa* the stomach is often contracted within the subumbrellar cavity. On examination, however, it should be quite obvious that this shortening is due to contraction.

It is likely at present that, unless the medusae are seen liberated from their hydroids, *S. eximia* cannot be distinguished for certain from the medusa *Stauridiosarsia producta*, except possibly by size when mature.

The hydroids of *S. prolifera* and *S. gemmifera* have not yet been found.

Sarsia eximia (Allman)

Plate II, fig. 3; Text-figs. 17A, 18A, B

Coryne eximia Allman, 1859*b*, *Ann. Mag. Nat. Hist.* (August), ser. 3, vol. IV, p. 141.
Syncoryne eximia, Allman, 1864*a*, ibid., May, ser. 3, vol. XIII, p. 357.
Allman, 1872, *Monogr. Gymnobl. Hydroids*, p. 282, pl. v.
Sarsia eximia, Haeckel, 1879, *System der Medusen*, p. 17.
Browne, 1905*a*, *Proc. Roy. Soc. Edinb*, vol. XXV, pt. IX, p. 756.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 8, figs. 1, 2.
Mayer, 1910, *Medusae of the World*, vol. I, p. 57, fig. 21.

Specific Characters

Stomach short, not extending beyond umbrella margin. No asexual reproduction by budding.

Description of Adult

Umbrella bell-shaped, a little higher than broad; jelly moderately thick. Velum broad. Stomach cylindrical, in full extension about as long as subumbrellar cavity, but not extending beyond margin. Mouth simple, tube-like. Four simple radial canals and ring canal narrow. Radial canals enter marginal tentacle bulbs on adaxial side. Gonads completely surrounding stomach, extending from its base nearly to mouth. Eggs few and large. Four perradial marginal tentacles with many clusters of nematocysts and large terminal cluster. Marginal tentacle bulbs large and oval, each with large circular ocellus. Height about 4 mm. when fully grown (in British waters). Colour of marginal tentacle bulbs red to reddish brown; stomach may be reddish or greenish; ocelli black or dark chocolate in early stages, but crimson in adult.

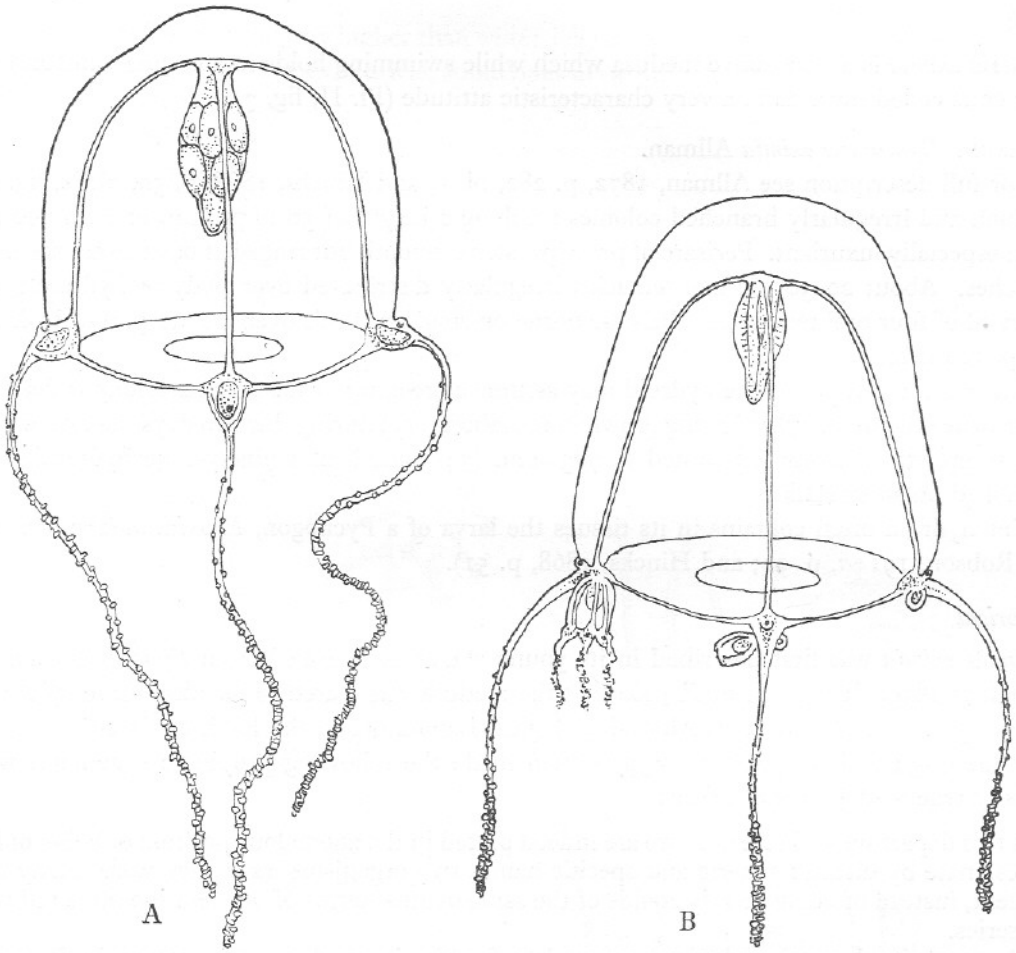
Distribution

Sarsia eximia is probably to be found in all coastal waters of the British Isles; coastal waters of North Sea, English Channel, Norway, N.W. Pacific (Bigelow, 1913, p. 4), Valparaiso (Vanhöffen, 1912*a*), and New Zealand(?) (Bale, 1924, p. 229). The medusa has rarely been recorded in the plankton and this may be because the hydroid is mainly coastal in its habitat, being common in harbours and estuaries and on floating objects.

Developmental Stages and Structural Details

Sarsia eximia shows little change in general structure during development. When first liberated from the hydroid, *Coryne eximia*, the medusae are comparatively large, being about 1·3 mm. or more in height. There are a few scattered nematocysts on the exumbrella, especially in the apical region. There are no interradial furrows on the umbrella as in the newly liberated *Sarsia tubulosa*. An apical chamber may sometimes be present. As development proceeds there is a general

increase in the size of the medusa and a slight lengthening of the stomach. Medusae reared by Browne (1905*a*, p. 756) in the Firth of Clyde reached an adult stage in about seven to ten days. The marginal tentacles are very extensile and have a large number of nematocyst clusters. These clusters vary somewhat in form, some being spherical cushions and others almost completely encircling the tentacle.



Text-fig. 17. A, *Sarsia eximia*, *c.* 2·4 mm. high (after Mayer, 1910, text-fig. 21, who drew it from life at Mousehole, Cornwall, on 14. xi. 07); B, *Sarsia prolifera*, *c.* 2·4 mm. high (after Mayer, 1910, text-fig. 23, who drew it from life at Mousehole, Cornwall, on 8. xi. 07).

In certain localities *S. eximia* grows to a greater size than has been recorded for British waters. Hartlaub (1894, p. 187) records specimens of over 10 mm. in height from Helgoland and specimens up to 10 mm. have been described by Bigelow (1913, p. 4) from the north-west Pacific coast of America. Hartlaub (loc. cit.) mentions that he has seen the tentacles of adult medusae stretch out to a length of 15–18 cm.

An unusual abnormality was found in a specimen of *S. eximia* reared in the laboratory at Plymouth. The mouth became fused with the umbrella margin, and two additional mouths developed.

NEMATOCYSTS. Stenoteles and desmonemes (Russell, 1938*b*).

Seasonal occurrence

Owing to the scarcity of this medusa in plankton collections its seasonal occurrence cannot be said to be fully known. Hydroids with medusa buds have, however, been recorded from different localities in most of the months from April to September.

Habits

Sarsia eximia is a very active medusa which while swimming holds its marginal tentacles with their ends coiled inwards in a very characteristic attitude (Pl. II, fig. 3).

HYDROID. *Syncoryne eximia* Allman.

(For full description see Allman, 1872, p. 282, pl. v, and Hincks, 1868, p. 50, pl. ix, fig. 2.)

Much and irregularly branched colonies reaching a height of 50 to 75 mm. or even 100 mm. when especially luxuriant. Perisarc of principal stems smooth but ringed at base, as are the lateral branches. About 20–30 capitate tentacles irregularly distributed over body of hydranth, with a verticil of four oral tentacles. Medusae borne on single pedicels over greater part of hydranth. Polyps reddish.

Under some conditions the hydroid may assume a creeping form. Such a colony is described by Browne (1907*a*, p. 37) as having grown in the laboratory; during thirteen days the total amount of new growth of stolon amounted to 773 mm. (34 inches), and ninety-nine hydranths were developed on short stalks.

This hydroid often contains in its tissues the larva of a Pycnogon, *Phoxichilidium femoratum* (see Robson, 1914*a*, p. 92; and Hincks, 1868, p. 51).

Historical

Sarsia eximia was first described in its young stages as liberated from *Syncoryne eximia* by Allman in 1859. It was not until 1902 that the medusa was reared to its adult stage by Browne (1905*a*, p. 756) at the Millport Marine Biological Laboratory in the Firth of Clyde.

In his original description in 1859 Allman made the following prophetic statement, which holds as true to-day as it did then:

> In this department of research, we are indeed placed in the anomalous position of being obliged to designate by distinct generic and specific names two organisms, as if they were totally independent, instead of being merely zooids of the same ovum—terms of one and the same unbroken life-series.
>
> The necessity, however, which we are under of subjecting to distinct treatment, in descriptive zoology, the polypal and the medusal terms of this series, renders it impossible to abandon the practice, even though it be to a certain extent modified when continued observation shall enable us to refer every polype-sprung Medusa to its proper zoophyte.

Sarsia prolifera Forbes

Plate II, fig. 1; Text-figs. 17B, 19, 20, 25D

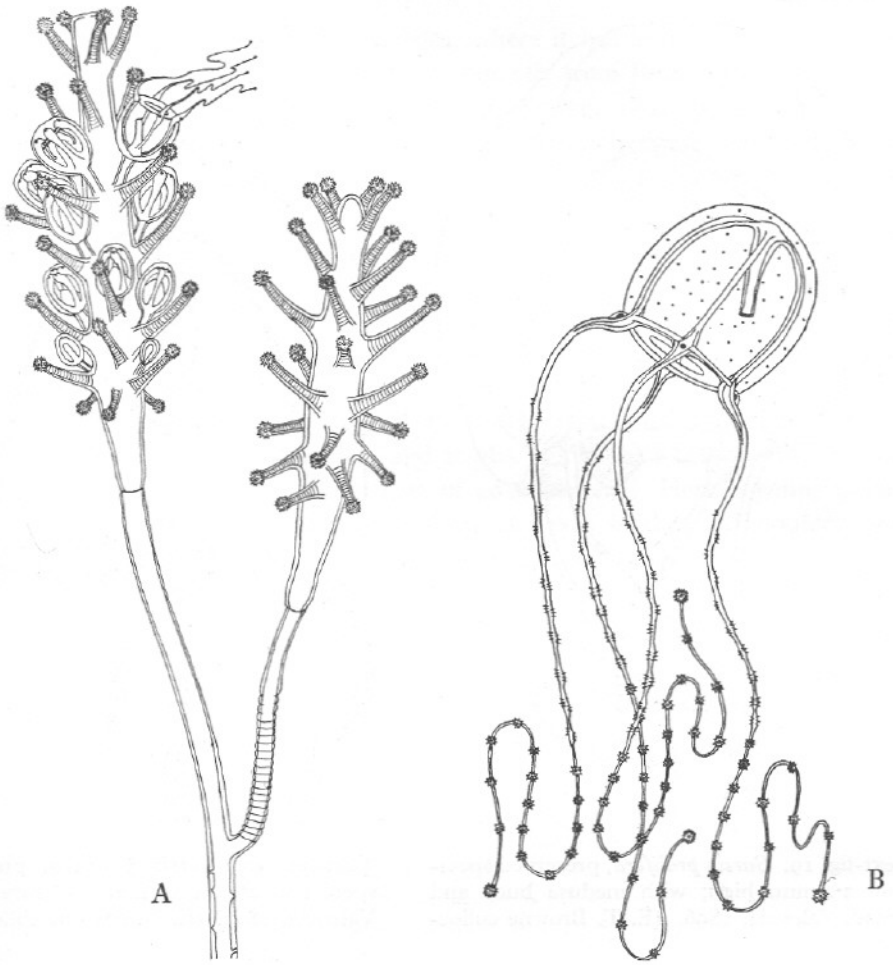
Sarsia prolifera Forbes, 1848, *Monogr. Brit. Medusae*, p. 59, pl. vii, fig. 3.
Busch, 1851, *Beobacht. wirbellos. Seeth.* p. 1, pl. i, figs. 1–6.
Haeckel, 1879, *System der Medusen*, p. 18.
Browne, 1900, *Proc. R. Irish Acad.*, ser. 3, vol. v, p. 711.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 15, figs. 7, 8.
Mayer, 1910, *Medusae of the World*, vol. I, p. 61, fig. 23.
Syncoryne sp., Allman, 1871, *Monogr. Gymnobl. Hydroids*, p. 83, fig. 38.

Specific Characters

Stomach not extending beyond margin. Asexual reproduction by budding from marginal tentacle bulbs.

Description of Adult

Umbrella bell-shaped, slightly higher than wide; jelly moderately thick. Margin quadrangular. Velum broad. Stomach small, cylindrical, about one- to two-thirds the length of the subumbrellar



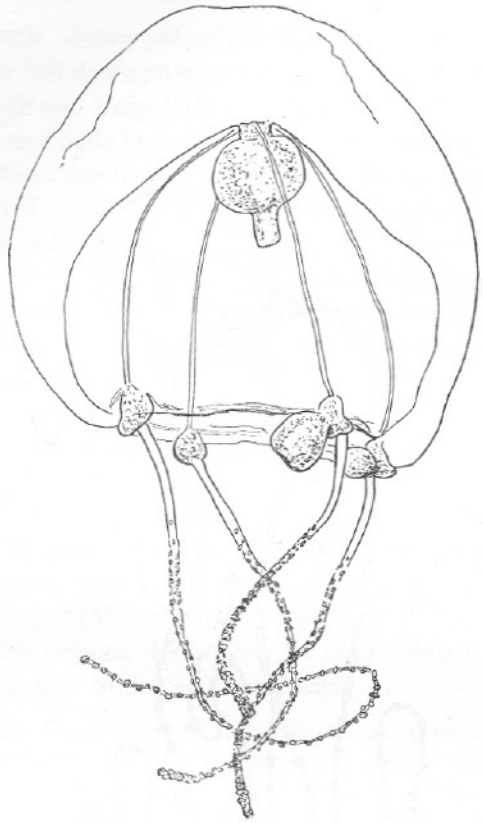
Text-fig. 18. *Syncoryne eximia* (A) with newly liberated medusa *Sarsia eximia* (B). (After Allman, 1871, pl. v, figs. 1, 3.)

cavity, never reaching beyond margin in full extension. Mouth simple, tube-like. Four radial canals and ring canal narrow. Apical knob may be present. Gonads completely surrounding stomach, leaving upper end and mouth free. Asexual reproduction by budding from the marginal tentacle bulbs. Four perradial marginal tentacles, very extensile, with irregularly scattered clusters of nematocysts. Marginal tentacle bulbs large and tapering, each with one ocellus. Colour of marginal tentacle bulbs and stomach sage green, yellowish brown or reddish brown; marginal tentacle tips may be light reddish brown; ocelli black or brownish. Height 2–3 mm. when fully grown, usually less than 2 mm.

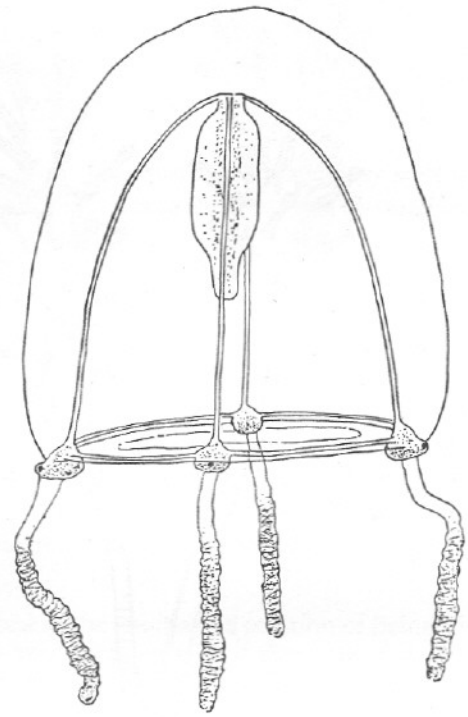
Distribution

Common off Devon, Cornwall and south Ireland coasts; recorded from Northumberland coast (Sanderson, 1930), St Andrews (M'Intosh, 1874), Orkney Islands (Busch, 1851), Atlantic coast of France (Ranson, 1925), Black Sea (Thiel, 1935).

Sarsia prolifera has a somewhat unusually restricted area of distribution having never been recorded from plankton catches other than round the British and French coasts, except for the Black Sea record.



Text-fig. 19. *Sarsia prolifera*, preserved specimen 2·2 mm. high, with medusa buds and gonad, Valencia, 1896. (E. T. Browne collection.)



Text-fig. 20. *Sarsia prolifera*, preserved specimen 2·3 mm. high, mature male, Valencia, 1896. (E. T. Browne collection.)

Developmental Stages and Structural Details

Sarsia prolifera shows hardly any change in general structure during its development. At the smallest stage, about 1 mm. in height, the first signs of the medusa buds are already apparent on the marginal tentacle bulbs. The development of these buds appears to be somewhat irregular and there may be as many as three buds on each bulb in progressive stages of development (see Ranson, 1925, p. 326, fig.; Forbes, 1848, pl. vii, figs. 3*e–i*). These medusa buds even before liberation may show the first rudiments of buds on their own marginal tentacle bulbs. In this way large numbers of medusae can be produced in a short time, accounting for their rapid increase in numbers in the plankton after their first appearance. At liberation the medusae are about 1 mm. in height and resemble their parents in every detail.

The generative cells appear on the stomach of the medusa while still carrying medusa buds, and they finally form a large oval swelling which completely surrounds the stomach (Text-figs. 19, 20). It is probable that at sexual maturity the production of medusa buds ceases and sexually ripe individuals occur towards the end of the season with no buds. It is not usual to find medusae much over 2 mm. in height though Ranson (1925, p. 325) mentions a size of 8 mm.

NEMATOCYSTS. Stenoteles and desmonemes (Weill, 1934*b*).

Seasonal occurrence

On the south-western coasts of the British Isles, where it has been most usually recorded, *Sarsia prolifera* becomes abundant in the plankton generally from June to October. Specimens have been recorded as early as March (Plymouth: Garstang, 1894, p. 232) and they may occasionally be found as late as November. Off the Northumberland coast they have been recorded in April, August and September, and as common in October (Sanderson, 1930, p. 222).

HYDROID. Not known.

Historical

Sarsia prolifera was first described by Forbes (1848, p. 59) from specimens of a large shoal in Penzance Bay, Cornwall, on 21 August 1846. It was the first example he had seen of a medusa which budded asexually from the marginal tentacle bulbs and he allowed his vivid imagination full play. 'What strange and wondrous changes!' he wrote, 'Fancy an elephant with a number of little elephants sprouting from his shoulders and thighs, bunches of tusked monsters hanging epaulette fashion from his flanks in every stage of advancement! Here a young pachyderm almost amorphous, there one more advanced, but all ears and eyes; on the right shoulder a youthful Chuny, with head, trunk, toes, no legs and a shapeless body; on the left an infant, better grown, and struggling to get away, but his tail not sufficiently organized as yet to permit of liberty and free action!' The budding was also studied by Busch (1851).

Sarsia tubulosa (M. Sars)

Plate I, fig. 2; Pl. II, fig. 6; Text-figs. 21, 22A, B, 23A

Oceania? *tubulosa* M. Sars, 1835, *Beskriv. og Jaggt.* p. 25, pl. v, figs. 11*a*, *b*.
Syncoryna sarsii Lovén, 1836, *K. svenska VetenskAkad. Handl.* 1835, pl. viii, figs. 7–10.
M. Sars, 1846, *Fauna Litt. Norveg.* pt. I, p. 2, pl. i, figs. 1–6 (hydroid and medusa).
Sarsia tubulosa, Lesson, 1843, *Hist. Nat. Acalèphes*, p. 333.
Forbes, 1848, *Monogr. British Medusae*, p. 55, pl. vi, fig. 2.
F. E. Schulze, 1873, *Über den Bau von* . . . Sarsia tubulosa, p. 14, pls. i–iii (hydroid and medusa).
Haeckel, 1879, *System der Medusen*, p. 16.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 19, figs. 10–15.
Mayer, 1910, *Medusae of the World*, vol. I, p. 52.
Kramp, 1926, *Danish Ingolf-Expedit.* vol. V, pt. X, p. 8, pl. i, figs. 5–7; text-figs. 6–16; chart VI.
Sverdrup, 1921, *Skrift. Vidensk. Christiania*, Mat.-Nat. Kl., Bd. I (1922), p. 14, pl. i, fig. 1.
Syncoryna decipiens, Dujardin, 1845, *Ann. Sci. nat. Paris* (3), Zool., tome IV, p. 275, pl. 14, figs. B1–B6; pl. 15, fig. B7 (hydroid and medusa = *Sthenyo*).
Sarsia pulchella Forbes, 1848, *Monogr. Brit. Medusae*, p. 57, pl. vi, fig. 3.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 34.
Medusa proboscidea Dalyell, 1848, *Rare and Remarkable Animals of Scotland*, vol. II, pp. 248–9, pl. lii, fig. 3; pl. liii, figs. 1–3.
Sarsia mirabilis L. Agassiz, 1849, *Contr. Nat. Hist. Acalephae*, p. 224, pl. iv, v.
Haeckel, 1879, *System der Medusen*, p. 17.
Fewkes, 1881, *Bull. Mus. Comp. Zoöl. Harvard*, vol. VIII, no. 8, p. 141, pl. iii, figs. 11, 12.

CORYNIDAE

Sarsia macrorhynchos Busch, 1851, *Beobacht. Wirbellos. Seeth.* p. 10, pl. iii, figs. 7–10; pl. iv, figs. 1, 2.
Coryne mirabilis, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 204, pls. xvii–xix, and pl. xx, figs. 1–9 (hydroid, in part, and medusa).
A. Agassiz, 1865, *N. Amer. Acalephae*, p. 175, figs. 283–8.
Coryne macrorhyncha, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 340.
Syncoryne pulchella, Allman, 1865, *Ann. Mag. Nat. Hist.*, Ser. 3, vol. XV, p. 465 (hydroid and medusa).
Hincks, 1868, *Brit. Hydroid. Zooph.* p. 57, pl. xv, fig. 3 (hydroid).
Allman, 1872, *Monogr. Gymnobl. Hydroids*, p. 279, pl. vi, figs. 1–3 (hydroid and medusa).
Syncoryne sarsii, Hincks, 1868, *Brit. Hydroid Zooph.* p. 52, pl. vii, fig. 3 (hydroid).
Allman, 1872, *Monogr. Gymnobl. Hydroids*, p. 275.
Jäderholm, 1909, *K. svenska VetenskAkad Handl.* Bd. XLV, p. 40, pl. i, figs. 5, 6 (hydroid and medusa).
?*Sarsia erythrops* Romanes, 1876*a*, *Journ. Linn. Soc. London, Zool.* vol. XII, p. 526.
Codonium pulchellum, Haeckel, 1879, *System der Medusen*, p. 15.
Browne, 1895, *Trans. Liverpool Biol. Soc.* vol. IX, p. 246.
Sarsia macrorhyncha, Haeckel, 1879, *System der Medusen*, p. 19.
?*Sarsia pattersoni* Haddon, 1886, *Proc. R. Irish Acad.*, vol. XIV (ser. 2, vol. IV), pt. 5, p. 525.
?*Sarsia densa* Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 26, figs. 17–19.
Sarsia decipiens, Hartlaub, 1907, ibid. p. 30, fig. 20.
Sarsia litorea Hartlaub, 1907, ibid. p. 32, figs. 23, 24.
Sarsia tubulosa var. *mirabilis*, Mayer, 1910, *Medusae of the World*, vol. I, p. 53, pl. iii, figs. 2, 4; pl. iv, figs. 1, 2.

Specific Characters

Stomach very extensile, extending far beyond umbrella margin in full extension. Radial canals smooth. Without asexual reproduction by budding. Gonad surrounding stomach continuous.

Description of Adult

Umbrella bell-shaped, slightly higher than broad; jelly moderately thick. Velum broad. Stomach cylindrical, slightly more than half the height of the subumbrellar cavity when completely contracted, in full extension reaching three or more times the length of umbrella. Mouth simple, tube-like. Four simple radial canals and ring canal narrow. Radial canals enter marginal tentacle bulbs on abaxial side. Apical knob or chamber usually present. Gonads completely surrounding stomach leaving short proximal region and mouth free. Four perradial marginal tentacles with many clusters of nematocysts. Marginal tentacle bulbs large and oval, each with large circular ocellus. Height up to 18 mm. Colour of stomach, apical knob and marginal tentacle bulbs yellow, orange, yellowish-brown, brown, green, scarlet, or blue; ocelli black or crimson.

Distribution

Sarsia tubulosa is to be found on all coasts of the British Isles. It is a circumpolar boreal neritic species and has been recorded from the English Channel, North Sea, Baltic, Danish waters, Norway, Murman Coast, White Sea, Iceland, Greenland; Black Sea; American coasts of North Atlantic as far south as Newport; Pacific coast of North America from San Francisco to Puget Sound; Japan.

Around the British Isles the species may be found in estuaries and most coastal waters; although it is probably scarcer in the eastern end of the English Channel and the southern North Sea (Kramp, 1930, p. 8). Kramp (1913*a*, p. 526) also says that in Danish waters this species appears to prefer a low salinity. Similarly it is characteristic of the low salinity waters of the German Bight (Künne, 1937*a*).

Developmental Stages and Structural Details

When first liberated from its hydroid the medusa *Sarsia tubulosa* is about 1·3 mm. in height. The umbrella is slightly higher than wide and there are a few scattered exumbrellar nematocysts.

An apical knob is usually present. The presence of an interradial furrow running down the centre of each interradius on the exumbrella is a characteristic feature, which distinguishes the medusa at once from *S. eximia*. The stomach is cylindrical and short and only slightly exceeds half the height of the subumbrellar cavity. The colour of the marginal tentacle bulbs is yellow (at Plymouth), and easily distinguishable from the more reddish tint of *S. eximia*.

As it grows the medusa alters little in appearance except for the greatly increased length of the stomach. As I have mentioned above, the stomach is very extensile and can contract well up into the subumbrellar cavity, or it may extend for three or more times the length of the umbrella. In full extension, especially when food is contained in the lower end, the stomach appears almost thread-like in its empty portion. Owing to the great contractility of the stomach the appearance of preserved medusae may vary greatly (Text-fig. 21).

The radial canals enter the marginal tentacle bulbs on the abaxial side (i.e. on the side nearer the exumbrella), a character which distinguishes this species from the arctic *S. princeps* (Haeckel), in which the entrance is on the adaxial side nearer the subumbrella (Kramp, 1926*a*) (Text-fig. 22).

A detailed histological study of the medusa has been made by Kramp (1926*a*). The endoderm of the stomach is cross-shaped in section, being divided by four major longitudinal furrows.

The ocellus has been described by Linko (1900*b*, as *Sarsia mirabilis*). It consists of a swelling with a central pit lined with pigmented ectoderm cells, amongst which are nerve cells—the retina; the cavity of the pit is filled with a transparent lens.

Sarsia tubulosa is somewhat variable in form and especially in colour. This, combined with the different shapes assumed by preserved specimens, has led to the description of a great many 'species'. Kramp (1926*a*, 1927) made an exhaustive study of the different colour varieties and has concluded that they probably form one variable species.

The three chief colour varieties are:

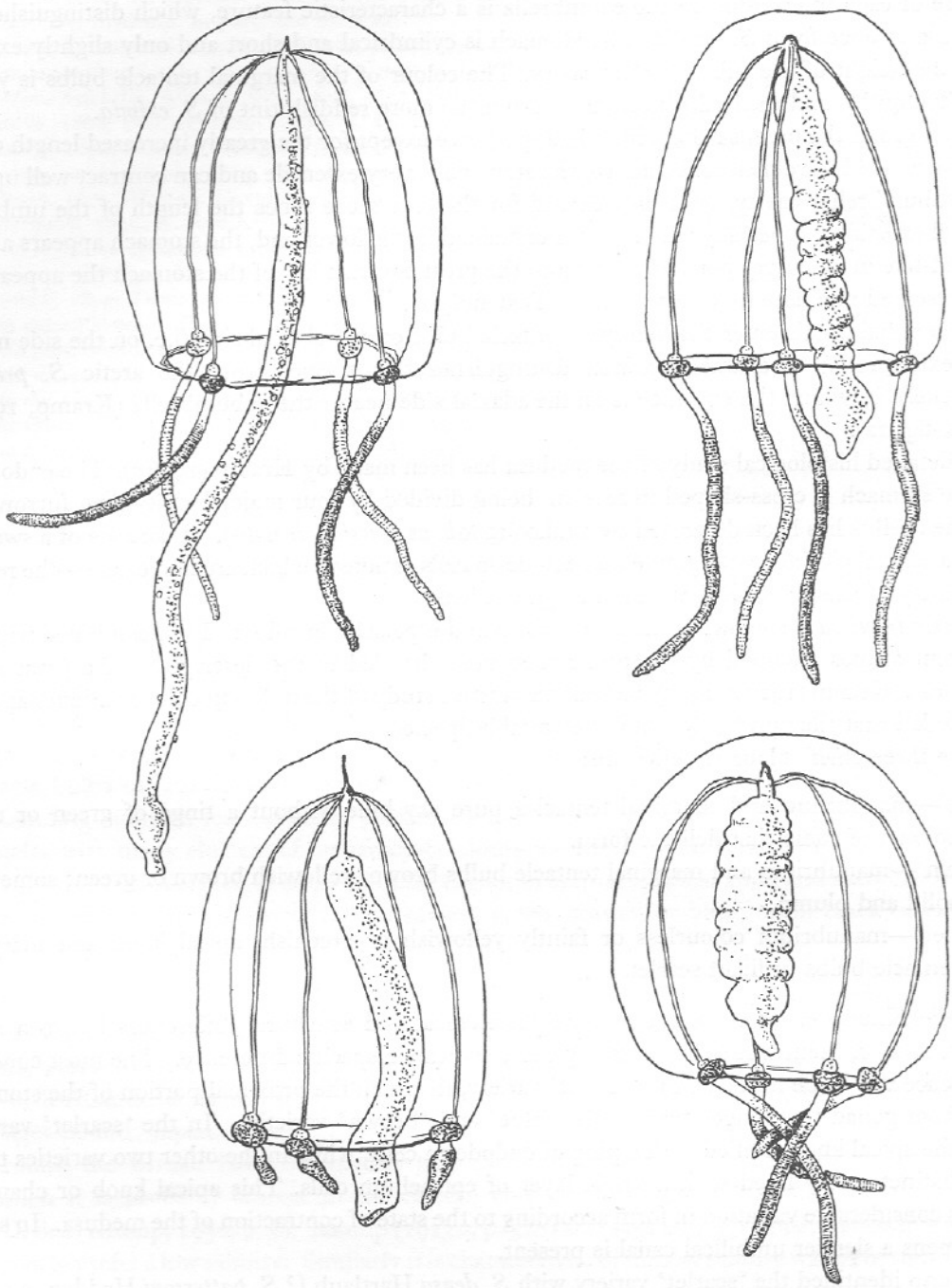
'Blue'—manubrium and marginal tentacles pure sky blue without a tinge of green or other colour; of somewhat delicate form.

'Brown'—manubrium and marginal tentacle bulbs brown, yellowish brown or green; somewhat solid and plump.

'Scarlet'—manubrium colourless or faintly yellowish or greenish, apical knob and marginal tentacle bulbs brilliant scarlet.

While Kramp could see certain minor histological and structural differences between these forms, none of them was constant enough to constitute a specific difference. The most constant difference was to be found in the 'scarlet' variety, in which the proximal portion of the stomach free from gonad was longer than in the 'blue' and 'brown' varieties. In the 'scarlet' variety, also, the apical knob is filled with a plug of endoderm cells, while in the other two varieties there is a distinct cavity lined with a single layer of epithelium cells. This apical knob or chamber shows considerable variation in form according to the state of contraction of the medusa. In some specimens a slender umbilical canal is present.

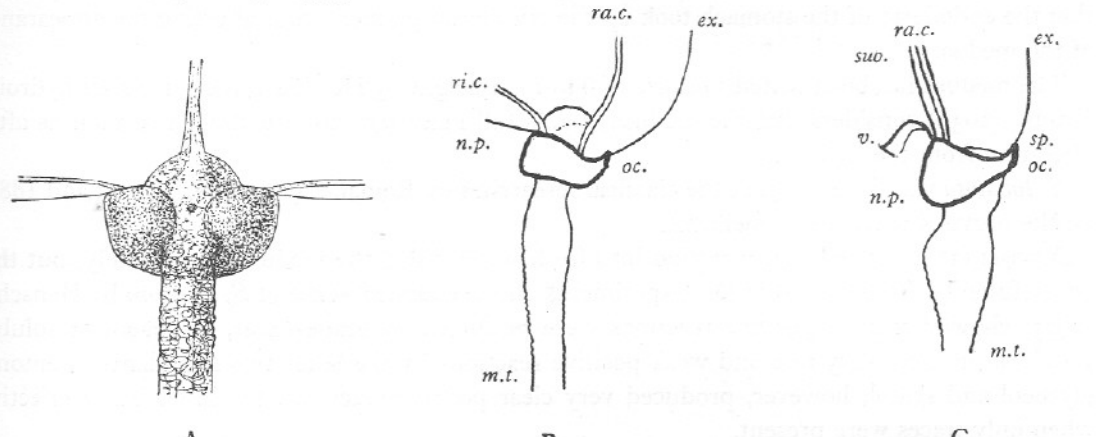
Kramp identified the 'scarlet' variety with *S. densa* Hartlaub [? *S. pattersoni* Haddon, a name given by Haddon to a medusa described by Forbes (1848) from Larne, Co. Antrim. It is worthy of note that this medusa had red ocelli, as had *S. erythrops* of Romanes (1876*a*)]. Kramp's final decision was that *S. densa* might be regarded as a distinct species, but that it was so closely related to *S. tubulosa* that it might possibly be regarded merely as a local variety.



Text-fig. 21. *Sarsia tubulosa*, preserved specimens 8–9 mm. high, from Isle of Muck, west Scotland, 9. vi. 37. (Collected by Mrs E. A. T. McEwen.)

Of these colour varieties it is probable that the 'brown' *Sarsia*, which may even appear with yellow marginal tentacle bulbs, is most typical of British waters. The 'blue' variety is, however, to be found in the north. It has been recorded from the Shetlands (Forbes, 1848). Nicol (1936) recorded the 'blue' variety in Loch Strumore, North Uist, at a salinity of 20–24‰, while at the same time, July 1935, the 'brown' variety was present at Oban a' Chlachain in a salinity of 28–32‰.

S. tubulosa probably does not grow to much more than 10 mm. in height in British waters, but specimens of as much as 18 mm. have been recorded from Arctic waters, and even of 21 mm. off West Greenland (Kramp, 1942).



Text-fig. 22. Base of marginal tentacle of: A, *Sarsia tubulosa*; with lateral views of those of B, *Sarsia tubulosa* and C, *Sarsia princeps* (after Kramp, 1926*a*, pl. i, figs. 1, 6). *ex.* exumbrella; *m.t.* marginal tentacle; *n.p.* nematocyst pad; *oc.* ocellus; *ra.c.* radial canal; *ri.c.* ring canal; *sp.* spur; *sub.* subumbrella; and *v.* velum.

Goette (1907) states that, while the sperm cells are ectodermal in origin, the ova originate in the endoderm and migrate later into the ectoderm.

Schulze (1873) reared the hydroid from the egg of the mature medusa.

Various abnormalities have been seen. Allman (1872, p. 202, fig. 76) recorded one in the form of a Siamese twin; and Hartlaub (1907) figures varying degrees of twinning (Text-fig. 9A, B). Kramp (1939*a*) described a specimen in which three marginal tentacles became fused to the stomach, and Mayer (1910) also recorded a tentacle growing from a stomach, which may have been produced as in Kramp's specimen. Kramp (1942) recorded a specimen with five radial canals, two of which united half-way down the subumbrella.

Seasonal occurrence

In British waters *S. tubulosa* generally appears in the plankton at the beginning of April. In the south it usually disappears by the end of June, although occasional specimens may be recorded in July, or even September and October. In the north it may continue in the plankton until August, but April, May and June are probably the months in which it is most abundant.

Habits

The habits of *S. tubulosa* have been studied by Agassiz (1862) who gives full descriptions of the graceful motions of this medusa with long marginal tentacles and stomach streaming in sinuous curves as the animal changes its direction of swimming.

Kramp & Damas (1925) state that off the Norwegian coast *S. tubulosa* comes to the surface on fine calm days in May, but that it usually keeps to the intermediate layers of 20–100 m.

Hansen (1951) gives *c.* 15° C. as the maximum temperature it will tolerate in the Oslo Fjord in summer.

Like most medusae, *S. tubulosa* is very voracious and this habit has been described by Forbes (1848) in characteristic vein: 'Being kept in a jar of salt water with small crustacea, they devoured these animals, so much more highly organized than themselves, voraciously; apparently enjoying the destruction of the unfortunate members of the upper classes with a truly democratic relish.'

Linko (1900*a*) records this species feeding on the crustacean amphipods *Hyperia*; he states that the endoderm of the stomach took up the crustacean pigment, thus affecting the appearance of the medusa.

The medusa has been reared to a size of 6 mm. in height by Hartlaub (1907) from its hydroid. Kramp (1930) considers that the medusa attains full maturity and size about two months after liberation from the hydroid.

S. tubulosa was the subject of the classical researches by Romanes (1876*a*, *b*; 1877*b*; and 1885) on the nervous reactions of medusae.

Agassiz (1862) stated that insertion into fresh water killed the medusa immediately, but this was refuted by Romanes (1877*b*). Experiments on the chemical sense of *S. tubulosa* by Henschel (1935) showed that no positive reactions were produced by grape-sugar, glycogen, or soluble starch, or at most very rare and weak positive reactions by the latter two stimulants. Peptone, glycocol and skatol, however, produced very clear positive reactions, the latter being effective when only traces were present.

HYDROID (Text-fig. 23A). (For a detailed discussion of this species, under the name of *Syncoryne decipiens* Dujardin, see Hartlaub, 1916.)

Delicate, simple or slightly branched colonies reaching a height of about 20 mm. Perisarc smooth, or slightly wrinkled, especially towards the base. Ten to twenty-five capitate tentacles irregularly distributed over body of hydranth. Medusae borne on short peduncles chiefly, but not exclusively, at the base of the lowest tentacles.

Historical

Sarsia tubulosa was first described by M. Sars (1835) under the name of *Oceania tubulosa*; the species was given the generic name of *Sarsia* by Lesson in 1843. L. Agassiz (1849) described in great detail the medusa of a *Syncoryne* which he called *Sarsia mirabilis*. Later (1862), he re-described the medusa together with its hydroid as *Coryne mirabilis*. Kramp (1928) examined specimens of this medusa from the Pacific and the coast of Greenland and was fully convinced that it is identical with *Sarsia tubulosa*.

As has already been pointed out, there have been many species described and the confusion cannot be said to have been fully cleared up. Observations on the colour varieties and forms of this medusa round the British coasts are badly needed.

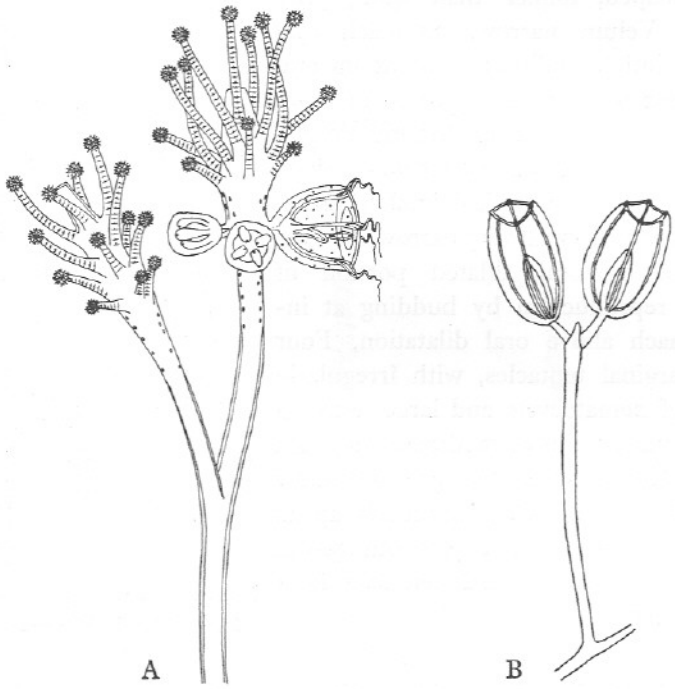
Much confusion has also been caused by the inclusion of two species of hydroids in the synonymy of the species. Some authors (including Agassiz in his 1862 description) included the hydroid *Coryne lovéni* (Sars), which does not produce free medusae.

This confusion was cleared up in a careful work by Hartlaub (1916). Briefly, Hartlaub combines *Syncoryne decipiens* Dujardin (1845) in part with Agassiz's *Coryne mirabilis*. This is the species which produces free medusae, and Dujardin remarks that interradial furrows are present in the

medusa, as seen in *Sarsia tubulosa*. Hartlaub also combines *Coryne gravata* Wright (1858*a*), in which the medusae mature on the hydroid, in part with Agassiz's *Coryne mirabilis*.

Coryne decipiens (Dujardin) can now be linked with the original *Coryne sarsii* (Lovén), from which Sars (1846) gives a description of the newly liberated medusa; *Coryne gravata* Wright is synonymous with *Coryne lovéni* (Sars) (of S. L. Lovén, 1836).

Coryne lovéni, in which the medusa matures on the hydroid has been figured by Robson (1914*a*, p. 92, pl. iii) under the name of *Syncoryne sarsii* Lovén. It had been suggested by Agassiz that this was a stage assumed towards the end of the breeding season when the polyps became degenerate and did not liberate their medusae. (Agassiz's figure is reproduced in Hincks, 1868, pl. x, figs. 1*e* and 1*f*, and fig. 1*d* is after Hodge). It is, however, now almost certain that *Coryne lovéni* is a distinct species, and figures of the species are given in Plate II, fig. 5 and Text-fig. 23 B.



Text-fig. 23. A, hydroid of *Sarsia tubulosa* (after Allman, 1871, pl. vi, fig. 4); B, *Syncoryne lovéni* (after Hincks, 1862, pl. x, fig. 1*d*, as *Syncoryne gravata*).

Sarsia gemmifera Forbes

Plate I, figs. 1, 4; Plate XXXIV, fig. 1; Text-figs. 24, 25 A–C

Sarsia gemmifera Forbes, 1848, *Monogr. Brit. Medusae*, p. 57, pl. vii, fig. 2.
Chun, 1895, *Bibliotheca Zoologica*, Heft 19, p. 4, text-fig. 1, pl. i, figs. 5, 6.
Browne, 1905, *Proc. Roy. Soc. Edinb.* vol. xxv, pt. ix, p. 757.
Mayer, 1910, *Medusae of the World*, vol. i, p. 62, fig. 25.
Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien*, Tom. xx, p. 31, pl. i, figs. 2, 3.
Sverdrup, 1921, *Skrift. Vidensk. Christiania*, Bd. i (1922), Mat.-Nat. Kl., p. 14, pl. i, fig. 3.
Sarsia clavata Keferstein, 1862, *Z. wiss. Zool. Leipzig*, Bd. xii, p. 27, pl. ii, figs. 1, 2.
*Dipurena fertilis** Metschnikoff, 1871, *Bull. Soc. Imp. des amis des Sci. Nat.* tome viii.
Sarsia sp., Allman, 1871, *Monogr. Gymnobl. Hydroids*, p. 83, fig. 37.

* Cited from Hartlaub, 1907, 1917.

CORYNIDAE

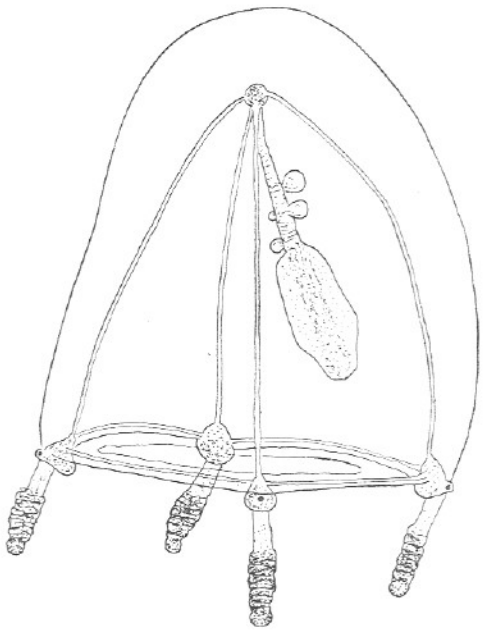
Codonium gemmiferum, Haeckel, 1879, *System der Medusen*, p. 15.
Dipurena dolichogaster (*non* Haeckel), Chun, 1895, *Bibliotheca Zoologica*, Heft 19, p. 4, pl. i, figs. 1–4.
?*Slabberia catenata*, Monticelli, 1897, *Atti Acc. Torino*, vol. xxxii, p. 888, 1 text-fig.
Dipurena ophiogaster, Johansen & Levinsen, 1903, *K. danske vidensk. Selsk. Skr.*, natur. og math. Afd., 6. Raekke, xii, 3, p. 276.
Purena gemmifera, Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, xii, p. 58, figs. 54–8.
Kramp, 1927, *K. danske vidensk. Selsk. Skr.* natur. og math. Afd., 6. Raekke, xii, p. 35.

Specific Characters

Stomach in full extension reaching far beyond umbrella margin, with dilatation at oral extremity. Asexual reproduction by budding from stomach.

Description of Adult

Umbrella bell-shaped, higher than wide; jelly moderately thick. Velum narrow. Stomach cylindrical, enlarging into a bulbous mass at its oral extremity, in full extension reaching three or more times the length of the umbrella. Mouth simple, tube-like, beset with nematocysts. Sometimes a short umbilical canal and always an apical knob present. Four radial canals and ring canal very narrow. Gonad completely surrounding oral, dilated portion of stomach. Asexual reproduction by budding at intervals along stomach above oral dilatation. Four short perradial marginal tentacles, with irregularly scattered clusters of nematocysts and large terminal knob. Marginal tentacle bulbs of moderate size, each with one ocellus. Height when full grown usually 2–3 mm., may reach 5 mm. Colour of mouth, apical knob and marginal tentacle bulbs pale orange-red or straw; terminal knob of marginal tentacles faint orange-red. Ocelli black.



Text-fig. 24. *Sarsia gemmifera*, preserved specimen 2·4 mm. high, Plymouth, 4. x. 39.

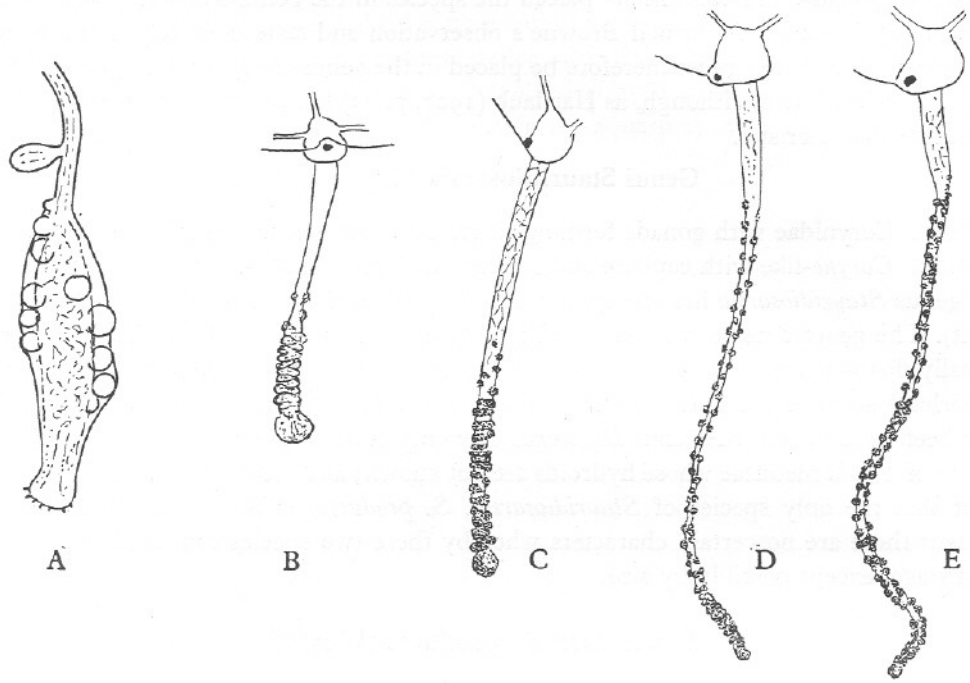
Distribution

All coasts of British Isles; Mediterranean; west European coasts as far north as Bergen, Norway; Faeroe-Shetland Channel; Danish Belt Sea.

Developmental Stages and Structural Details

Sarsia gemmifera shows hardly any change in general structure during growth. The hydroid is not known, so that the earliest stage has not been seen for certain, but at a size of 1 mm. in height the medusa buds are already present on the stomach. The sac-like dilatation of the stomach at its oral extremity is a characteristic feature of this medusa, and the gonads are developed on it. The medusa buds are attached by short pedicels at intervals along the stomach, above the oral dilatation, and are arranged in a spiral series. A primary medusa bud is first developed on each pedicel, and secondary and tertiary buds may develop on the sides of the pedicel. There are usually about five or six groups of medusa buds, though Hartlaub (1907, p. 62) records up to ten and M. & C. Delap (1905) one with thirteen. The disposition of these groups causes the stomach to have a distinct zigzag or kinked appearance, and even the free portion, which is extremely

tenuous, contracts in a sinuous manner. The oldest primary bud is borne at the proximal end of the stomach, and the youngest at the distal end. The young medusae thus produced already have buds just beginning to develop at the time of their liberation (Browne, 1905*a*). Chun (1896) after a study of the development of the medusa buds propounded a 'law of succession'. Sanderson (1930, p. 223), however, doubted the truth of this law on the grounds that the size distribution of the buds was irregular in very small specimens in which apparently only primary buds were present.



Text-fig. 25. *Sarsia gemmifera*, A, stomach of female; B and C, marginal tentacles; D, marginal tentacle of *Sarsia prolifera*; E, marginal tentacle of *Dipurena ophiogaster*.

The marginal tentacles of *Sarsia gemmifera* are rather short compared with those of other species in the genus (Text-fig. 25), when contracted having the upper half free of nematocysts. There is a well-developed terminal nematocyst knob which may be spherical or slightly elongated. There are also about thirty nematocyst clusters on each marginal tentacle but no nematocyst rings. The radial canals are extremely narrow. When expanded the marginal tentacles show a characteristic vibrational movement. This movement is produced by cilia which cover the tentacle: the cilia can already be seen on the tentacles while the young medusae are still attached to the stomach of the parent. The cilia appear to be confined to the nematocyst clusters and terminal knob.

NEMATOCYSTS. Stenoteles and desmonemes (Russell, 1938*b*).

Seasonal occurrence

In British waters *Sarsia gemmifera* has not been abundantly recorded, but it has been found in all months from May to September at Valencia, south-west Ireland. It is usually most plentiful in August and September. I have seen one specimen in October at Plymouth.

HYDROID. Not known.

CORYNIDAE

Historical

Sarsia gemmifera was first found in Shetland waters by Forbes and M'Andrew in 1845 (Forbes, 1848). The systematic position of the species depends upon the disposition of the gonads. Hartlaub (1907, p. 61), although he had not seen mature specimens himself, considered that the gonads observed by Browne (1905*a*) might only have been the beginning of the development of segmented gonads. He accordingly placed the species in the genus *Purena*. Neppi & Stiasny (1913*a*, p. 32), however, confirmed Browne's observation and state definitely that the gonad is continuous.* The species must therefore be placed in the genus *Sarsia* and is apparently closely related to *Sarsia tubulosa*, although, as Hartlaub (1907, p. 62) has pointed out, the short marginal tentacles are characteristic.

Genus **Stauridiosarsia** Mayer, 1910

MEDUSAE. Corynidae with gonads forming single continuous ring surrounding stomach.

HYDROID. *Coryne*-like with capitate and reduced filiform tentacles.

The genus *Stauridiosarsia* has one species occurring in British waters, *Stauridiosarsia producta* (Wright). The generic name was first used by Mayer as a subgenus of *Sarsia*. It is here kept generically distinct from *Sarsia* on account of the presence of filiform tentacles in the hydroid. This perhaps seems somewhat illogical in view of the fact that this character of the hydroid has not been used to split the genus *Dipurena*. My only grounds are, first, that there still remain a number of *Sarsia* medusae whose hydroids are not known; and secondly, the need to emphasize the fact that the only species of *Stauridiosarsia*, *S. producta*, is distinct from *Sarsia eximia*. At present there are no certain characters whereby these two species can be separated in their medusa stage, except possibly by size.

Stauridiosarsia producta (Wright)

Text-figs. 26A–C, 27A, B

Stauridia producta Wright, 1858, *Edinb. New Philos. Journ.* (April), vol. VII, p. 285, pl. vii, figs. 6, 8 (hydroid).
Stauridium productum, Hincks, 1862, *Ann. Mag. Nat. Hist.*, ser. 3, vol. X, p. 459, pl. ix.
Hincks, 1868, *Brit. Hydroid Zooph.* p. 68, pl. xii, fig. 1.
Hartlaub, 1895, *Z. wiss. Zool. Leipzig*, Bd. LXI, Heft 1, p. 142, pl. vii–ix (hydroid and medusa).
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 53, figs. 47–50.
Sarsia (*Stauridiosarsia*) *producta*, Mayer, 1910, *Medusae of the World*, vol. I, p. 65, figs. 28–30.

Specific Characters

Stomach short, extending at most for about one-third its length beyond umbrella margin in full extension.

Description of Adult

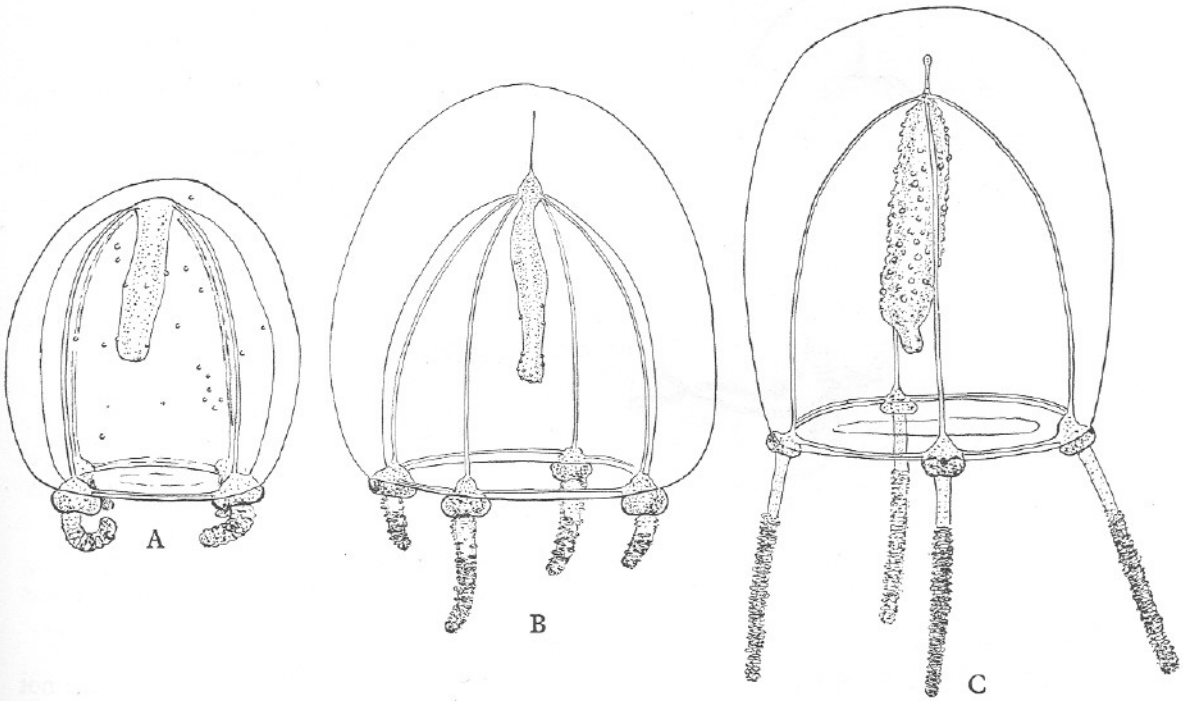
Umbrella bell-shaped, higher than wide; jelly thick. Velum moderately broad. Stomach short, cylindrical, extending at most for about one-third of its length beyond umbrella margin in full extension. Mouth simple, tube-like. Four radial canals and ring canal narrow. Apical knob present, with vestiges of umbilical canal. Gonad completely surrounding stomach from

* In all northern specimens more than one gonad has never been seen; Hartlaub (1907), however, says that in the Mediterranean they may probably be numerous, but he quotes no author. This contention appears to me to be doubtful, especially since Neppi & Stiasny (1913*a*) say that they have never seen specimens in the Mediterranean with more than one gonad.

its base to mouth. Four perradial marginal tentacles with irregularly scattered nematocyst clusters and a terminal nematocyst cluster. Marginal tentacle bulbs well developed, each with one ocellus. Height when full grown 10 mm. Colour of apical knob and marginal tentacle bulbs reddish; ocelli black or deep brown.

Distribution

This medusa has never been recorded for certain from British waters. The hydroid, *Stauridiosarsia producta*, liberating medusae has been recorded from Ilfracombe (Hincks, 1862). Adult medusae have been reared in an aquarium at Helgoland (Hartlaub, 1895), and at Valencia by Miss Delap. Robson (1914*a*) recorded the hydroid in the aquarium tanks at Cullercoats.



Text-fig. 26. *Stauridiosarsia producta*, preserved specimens of medusae reared from the hydroid by Miss Delap at Valencia, June 1903 (E. T. Browne collection). A, 0·95 mm. high; B, 2·5 mm. high; C, 6 mm. high.

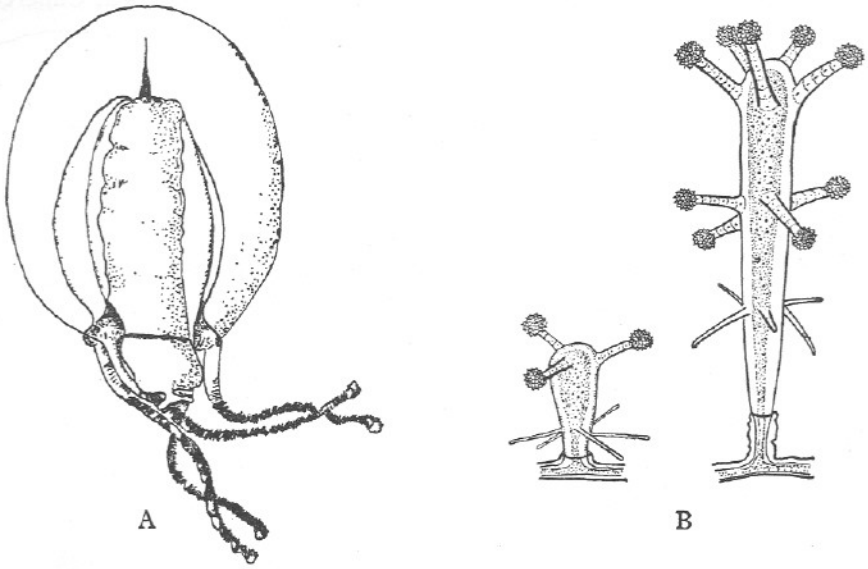
Developmental Stages and Structural Details

The growth and development of the medusa *Stauridiosarsia producta* have been fully described by Hartlaub from material reared in the laboratory. Little change in structure was shown during the course of development. The newly liberated medusae were about 1 mm. in height and had an umbilical canal. The stomach was about two-thirds the length of the subumbrellar cavity; there were scattered nematocysts on the exumbrella, which soon disappeared as the medusa increased in size. After eleven days the medusae reached a size of 5 mm. in height, and the gonads began to develop. The gonad which surrounded the stomach from its base to the mouth appeared as a whitish yellow mass in contrast to the brown of the stomach endoderm. At sixteen days the medusae were 6 mm. in height and the stomach reached the margin of the umbrella. The coloured parts had become more intense and the apical knob was crimson red

and the marginal tentacle bulbs a bright red yellow. Four weeks after liberation the medusae were 10 mm. in height. The stomach had increased in length until one-third of it extended beyond the margin of the umbrella. The marginal tentacles could stretch to a length of 14 or 15 cm.

The medusae have also been reared from the hydroid to a height of 8 mm. by Miss Delap at Valencia. Text-fig. 26 A–C are of drawings I have made from her preserved specimens which were in Mr E. T. Browne's collections.

In all respects this medusa seems to be identical with *Sarsia eximia*, though it appears to have fewer nematocysts round the mouth and grows to a larger size.



Text-fig. 27. *Stauridiosarsia producta*. A, medusa (after Hartlaub, 1907, fig. 49); B, young and fully developed hydranths, Herdla, Norway, 20. viii. 37 (after Rees, 1938, fig. 11).

Seasonal occurrence

The seasonal occurrence of *Stauridiosarsia producta* medusae is not known as they have not been recorded from the plankton in British waters. Hartlaub's specimens were reared in May and he records one young specimen taken in the plankton at Helgoland in the same month. Miss Delap's specimens were reared at Valencia in June 1903.

HYDROID. *Stauridiosarsia producta* (Wright) (Text-fig. 27 B).

(For full description see Hartlaub, 1895, p. 142, pls. vii–ix, and Hincks, 1868, p. 68, pl. xii, fig. 1.)

Hydrocaulus simple or slightly and irregularly branched. Perisarc pale yellowish brown, smooth. Hydranths elongate, reddish, with oral extremity opaque white. Medusae borne at the base of the lower capitate tentacles. Three or four whorls of capitate tentacles with four to six tentacles in a whorl; one proximal whorl of four to six reduced filiform tentacles.

Habits

There have been no observations on the habits of this medusa, except for our knowledge of its rate of growth in aquaria. Hartlaub's medusae reached a height of 6 mm. in sixteen days and 10 mm. in a month.

Historical

The hydroid was first described by Wright (1858) as *Stauridia producta*, but no medusae were observed from his specimens. Hincks (1862) was the first to obtain medusae liberated from the hydroid and he pointed out that it appeared identical with the newly liberated *Sarsia eximia* medusae.

Hartlaub (1895) reared medusae to the adult stage from hydroids growing in an aquarium at Helgoland. He indicated certain differences between his hydroid and that described by Hincks. The rearing of an *eximia*-like medusa from the hydroid *Stauridiosarsia producta* has been confirmed by Miss M. Delap at Valencia (unpublished and recorded here for the first time).

The name *Stauridie* (French) was first used by Dujardin (1843) for *Cladonema* and Strethill Wright used it imagining that his hydroid would produce a *Cladonema*-like medusa. Actually he failed to get medusae. Mayer (1910) on these grounds suggested a new subgeneric name *Stauridiosarsia*. Stechow (1919) pointed out that in any case the name *Stauridium* was invalid as it was already preoccupied for a Protozoan; he also noted that Kölliker first used it in 1853 for *Cladonema*.

Genus **Dipurena** McCrady, 1858

MEDUSAE. Corynidae with gonad divided into two or more distinct rings surrounding stomach.

HYDROID. *Dipurena*, *Coryne*-like with all tentacles capitate, or with capitate and reduced filiform tentacles.

The genus *Dipurena* has two British representatives, *D. halterata* (Forbes) and *D. ophiogaster* Haeckel. The genus was erected by McCrady (1858) for *D. strangulata* from the American coast, which is the genotype. Forbes (1846) had already erected the genus *Slabberia* for *Dipurena halterata* but the name was preoccupied by Oken (1815) (see Mayer, 1910, *Medusae of the World*, Vol. III, p. 719).

The two species of medusae can be distinguished by the structure of their marginal tentacles.

Marginal tentacles with three to six large nematocyst rings and a terminal cluster . . **D. halterata**
Marginal tentacles with irregularly distributed nematocyst clusters and no distinct rings **D. ophiogaster**

While the early stages of *D. halterata* are quite distinctive owing to the structure of the marginal tentacles, care must be taken in separating *D. ophiogaster* from some species of *Sarsia*, such as *S. tubulosa*; the youngest stages are, however, remarkable for the distribution of their exumbrellar nematocysts in adradial zones.

The hydroids of both species are now known. That of *Dipurena halterata* was found at Plymouth by Rees (1939*a*); it is a *Coryne*-like hydroid with no reduced filiform tentacles. The hydroid of *Dipurena ophiogaster* was found at Valencia by Miss M. J. Delap (unpublished) and was described by Rees (1941*c*). It resembles *Stauridiosarsia* in having reduced filiform tentacles, which constitutes a further specific difference from *Dipurena halterata*.

Dipurena halterata (Forbes)

Plate I, fig. 3; Plate II, fig. 2; Text-figs. 28, 29A–C

Slabberia halterata Forbes, 1846, *Ann. Mag. Nat. Hist.*, ser. 1, vol. v, p. 286.
Forbes, 1848, *Monogr. Brit. Medusae*, p. 53, pl. vi, fig. 1.
Allman, 1867, *Brit. Assoc. Report*, p. 77.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 64, figs. 60–2.
Mayer, 1910, *Medusae of the World*, vol. I, p. 75.

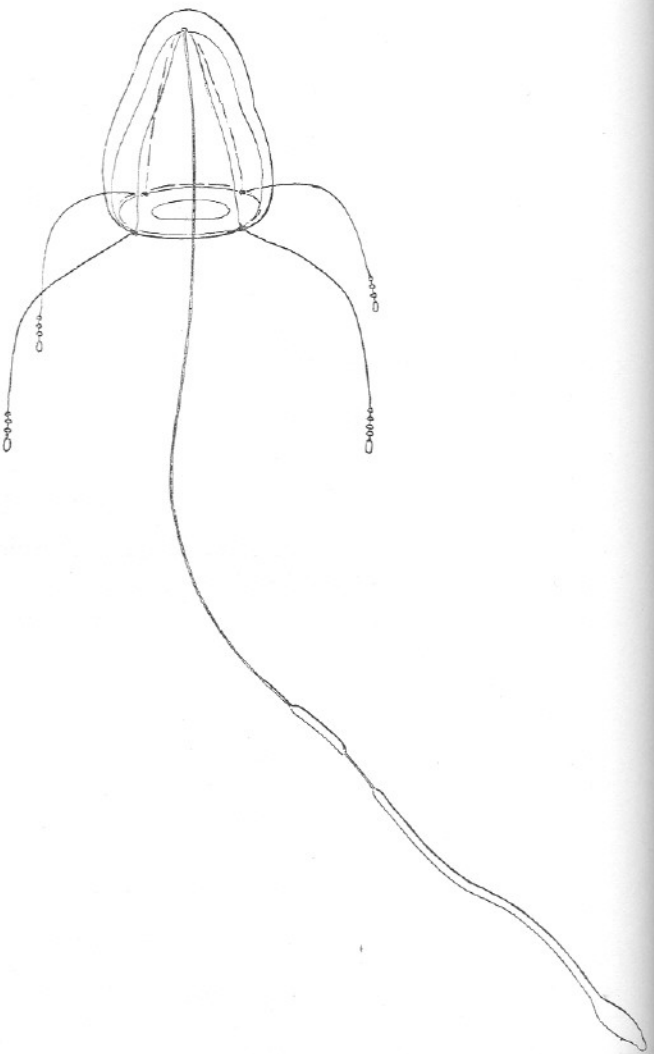
Dipurena halterata, Haeckel, 1879, *System der Medusen*, p. 24.
Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 473.
Browne, 1897*a*, ibid. p. 816, pl. xlix, fig. 2.
Browne, 1900, *Proc. R. Irish Acad.*, ser. 3, vol. v, p. 704.
Rees, 1939*a*, *Journ. Mar. Biol. Assoc.* vol. xxiii, p. 343, figs. 1–3 (hydroid and young medusa).
Slabberia catenata Forbes & Goodsir, 1851, *Trans. Roy. Soc. Edinb.* vol. xx, p. 311, pl. x, fig. 3.
Haeckel, 1879, *System der Medusen*, p. 655.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, xii, p. 63, fig. 59.
Mayer, 1910, *Medusae of the World*, vol. i, p. 77 (? in part), pl. viii, figs. 8, 9.

Specific Characters

Gonad with two to three segments. Linear swellings on radial canals. Marginal tentacles each with one large terminal cluster of nematocysts, and three to six nematocyst rings.

Description of Adult

Umbrella bell-shaped, higher than wide; jelly thick. Velum moderately broad. Stomach cylindrical, enlarging into bulbous mass at its oral extremity, in full extension reaching two to three times the length of the umbrella. Mouth simple, tube-like. Four radial canals and ring canal narrow; linear swellings on radial canals. Apical knob present. Gonad with two or more segments surrounding stomach, leaving upper half free. Four per-radial marginal tentacles, each with large terminal knob of nematocysts, with three to six nematocyst rings immediately above. Marginal tentacle bulbs moderately large, each with large ocellus. Height about 8 mm. when fully grown. Colour of marginal tentacle bulbs, orange, red, reddish brown or brown below, with bright green tinge above; terminal knobs of marginal tentacles red or brownish; ocelli black or deep crimson; apical knob reddish or green.



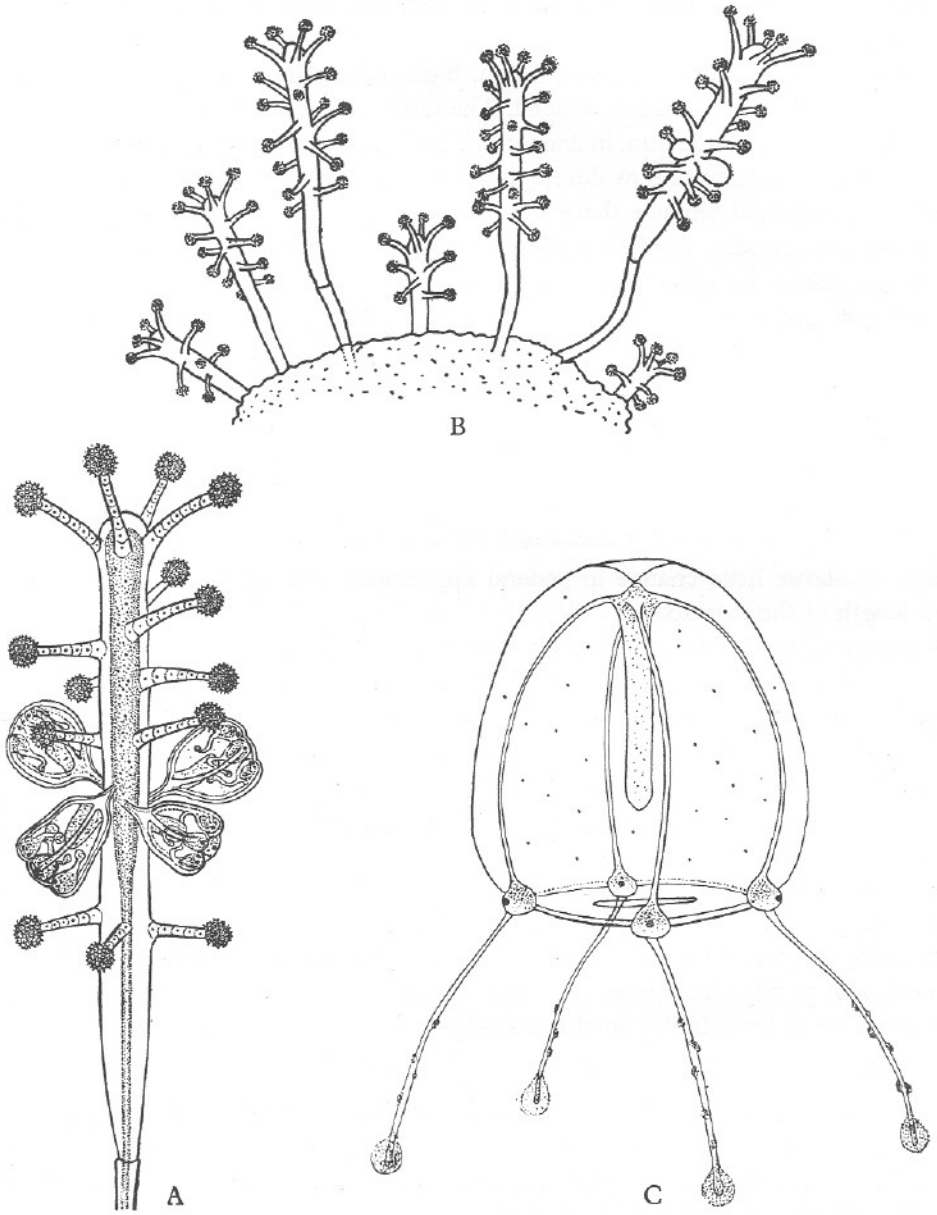
Text-fig. 28. *Dipurena halterata*, sketch of living medusa made on S.S. *Salpa* off Plymouth, 25. v. 34.

Distribution

There are many records of this species from the English Channel and at Valencia, south-west Ireland. In the north it has been recorded from Port Erin (Browne, 1895); Northumberland Coast (Sanderson, 1930); Tobermory, Mull, and west coast of Scotland (as *Slabberia catenata*, Forbes & Goodsir, 1851, and Haeckel, 1879, p. 655); and Dover Straits (Kramp, 1930).

Developmental Stages and Structural Details

The medusa *Dipurena halterata*, when newly liberated from its hydroid has been described by Rees (1939*a*). The umbrella is bell-shaped, a little higher than wide, being 1·5–1·6 mm. high



Text-fig. 29. *Dipurena halterata*, Plymouth, May 1938. A, hydranth with four medusa buds; B, portion of hydroid colony; C, medusa liberated from hydroid. (After Rees, 1939*a*, figs. 1, 2*b*, 3.)

and 1·3–1·4 mm. wide (Text-fig. 29C). The jelly is fairly thin and there are a few scattered nematocysts on the exumbrella. The velum is broad. The stomach is cylindrical and its length is about two-thirds the height of the subumbrellar cavity. There is a slight apical knob. The four radial canals and ring canal are narrow, and there are no signs of the linear swellings on the

radial canals. The four marginal tentacles each have a large terminal cluster of nematocysts, and on the distal halves of each tentacle there are a few irregularly scattered small batteries of nematocysts. The colour of the stomach is pale green; the basal bulbs of the marginal tentacles and their terminal endoderm are brick red. The ocelli are black. Later the green colour appears in the marginal tentacle bulbs.

Rees reared a specimen until it was 2·8 mm. high and 2·5 mm. wide. At this size the linear swellings on the radial canals had developed. The terminal knobs on the marginal tentacles were now larger and were 0·16–0·22 mm. in diameter. The irregularly scattered batteries of nematocysts on the marginal tentacles were now developing into complete rings of nematocysts. In the most fully developed marginal tentacle there were three complete rings and one incomplete ring as well as the terminal cluster. In older individuals these rings may vary from one to six in number, the uppermost one of the series being the youngest.

Browne (1900, p. 704) gives the following counts for a number of specimens:

Umbrella length (mm.)	No. of rings on each of the four marginal tentacles*
5	1, 2, 2, 3
5	2, 2, 2, 2
5	4, 4, 4, 4
6	3, 3, 3, 3
7	3, 4, 3, 5
8	1, 3, 3, 4

* Excluding large terminal cluster.

The species shows little change in general appearance with growth, except for the greatly increased length of the stomach.

The linear swellings on the radial canals were originally thought by Forbes to be gonads, but Browne (1897*a*) has examined sections which show that each is formed by 'a considerable enlargement of the endoderm cells, which are crowded with small nuclei'. 'In general appearance the swelling resembles an immature gonad, as usually seen upon the radial canal of a Leptomedusa, but more specimens must be examined to settle the question whether there are generative cells among endoderm cells of the swelling, or not' (Browne, 1897*a*, p. 813). Similar swellings are to be seen on the radial canals of *Zanclea*.

The gonads which are situated on the lower half of the stomach completely surround it. There is usually one long gonad extending from the mouth upwards about a third the length of the stomach, and there may be one or two shorter gonads situated at short intervals above it.

Browne (1900, p. 705) records an abnormal specimen in which there was an extra marginal tentacle with a small basal bulb joined to its neighbour.

Seasonal occurrence

Dipurena halterata has never been recorded in very large numbers. In south-western waters of the British Isles occasional specimens have been caught in the months April to November, and 'a good many in July' (M. & C. Delap, 1905). It has been recorded from the Northumberland coast in September, and Port Erin in August.

Habits

In life the stomach can be extended to a great length, and the marginal tentacles may be held directed outwards gradually curving downwards to their ends (Text-fig. 28).

HYDROID (Text-fig. 29A, B).

(For full description see Rees, 1939*a*, *Journ. Mar. Biol. Assoc.* vol. XXIII, p. 343, figs. 1, 2.)

Simple unbranched colonies reaching a height of 2·5 mm. Perisarc smooth. Seventeen to twenty-four irregularly distributed capitate tentacles. Hydranth reddish. Medusa buds borne on lower half of hydranth or on blastostyles.

This hydroid was found at Plymouth with its stolon embedded in a sponge.

Historical

Dipurena halterata was first found by Forbes (1848) in Mount's Bay, Cornwall, in 1836. He named it *Slabberia halterata* (Forbes, 1846). He described the species from a young specimen as having one terminal cluster of nematocysts on each marginal tentacle. Later Forbes & Goodsir (1851) found a specimen off Mull having five to six rings of nematocysts in addition to the terminal cluster; this was described as a new species, *Slabberia catenata*. Haeckel (1879) also took similar medusae off the west coast of Scotland and was convinced that they were the same as *Dipurena dolichogaster* Haeckel (1879, p. 25). Browne (1900, p. 705), however, considered *Slabberia catenata* to be the fully developed adult stage of *Dipurena halterata*. The medusa *Slabberia catenata* of Forbes & Goodsir differs from Haeckel's description of *Dipurena dolichogaster* in having far fewer nematocyst rings and in the presence of linear swellings on the radial canals. Hartlaub (1907, p. 63) kept *Slabberia catenata* as a distinct species. Mayer (1910, p. 77) followed Haeckel in regarding *S. catenata* and *Dipurena dolichogaster* as synonymous. Chun (1896) described and figured a medusa which he regarded as Haeckel's *D. dolichogaster* in which medusa buds were developed on the stomach much as in *Sarsia gemmifera*. No Corynid medusa has ever been recorded in British waters with medusa buds arranged in this manner except *S. gemmifera*. In view of the number of specimens of *Dipurena halterata* which have been seen from the British coasts, including all stages from the very young to the adult, it seems unlikely that such a medusa-producing species exists here. This fact, coupled with the small number of nematocyst rings on the marginal tentacles and the presence of linear swellings on the radial canals, seems sufficient evidence that *D. halterata* and *Slabberia catenata* may for the time be regarded as the same species. It should, however, be remarked that in the *S. catenata* described by Forbes & Goodsir the terminal nematocyst cluster on the marginal tentacles was not larger than the accessory rings.

The hydroid of this medusa was discovered at Plymouth in 1938 by Rees (1939*a*).

Dipurena ophiogaster Haeckel

Plate I, fig. 5; Plate II, fig. 4; Text-figs. 25E, 30A, B, 31

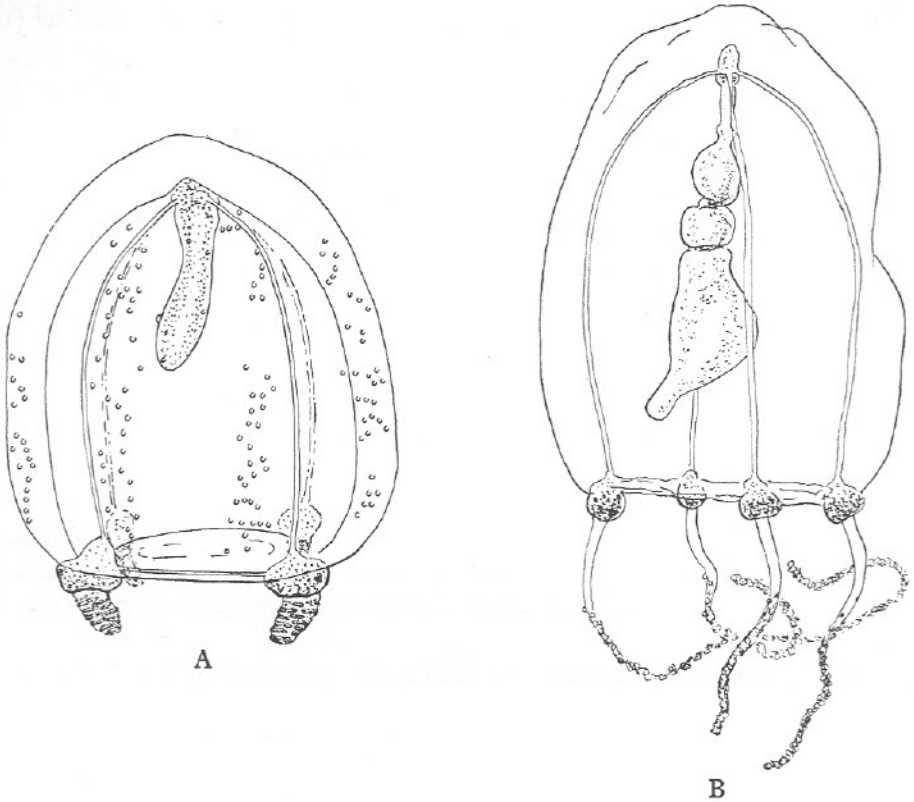
Sarsia strangulata Allman, 1871, *Monogr. Gymnobl. Hydroids*, p. 46, fig. 17.
Sarsia dolichogaster Spagnolini, 1876, *Atti Soc. Ital. Milano*, vol. XIX, fasc. 2, p. 18, pl. ii, fig. 3
Tetrapurena ophiogaster Haeckel, 1877, *Prodrom. Syst. Medusen*, no. 19.
Dipurena ophiogaster, Haeckel, 1879, *System der Medusen*, p. 25.
Browne, 1900, *Proc. R. Irish Acad.*, ser. 3, vol. v, p. 703.
Uchida, 1927, *J. Fac. Sci. Univ. Tokyo, Zool.* vol. I, pt. 3, p. 187, fig. 27.
Rees, 1941*c*, *Journ. Mar. Biol. Assoc.* vol. XXV, p. 131, fig. 2 (hydroid and medusa bud).
?*Dipurena* sp., Browne, 1905*b*, Ceylon Pearl Oyster Fisheries, *Roy. Soc. London, Suppl. Rep.* no. XXVII, p. 133, pl. ii, figs. 1, 2.
?*Purena brownei* Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 183, pl. vii, fig. 7; pl. xliv, figs. 8–10.
Mayer, 1910, *Medusae of the World*, vol. II, p. 489.
Purena strangulata, Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 55, figs. 51–3.
Slabberia ophiogaster, Mayer, 1910, *Medusae of the World*, vol. I, p. 79, figs. 36, 37.

Specific Characters

Gonad with two to six segments. Marginal tentacles with many irregularly distributed clusters of nematocysts, and without distinct nematocyst rings.

Description of Adult

Umbrella bell-shaped, higher than wide; jelly thick. Velum moderately broad. Stomach cylindrical, enlarging into bulbous mass at its oral extremity, in full extension reaching up to several times the length of umbrella. Mouth simple, tube-like. Four radial canals and ring canal narrow. Apical knob present. Gonad with two to six segments surrounding stomach, leaving upper part free. Four perradial marginal tentacles beset with irregularly distributed nematocyst



Text-fig. 30. *Dipurena ophiogaster*, preserved specimens. A, 1·3 mm. high, reared from hydroid by Miss Delap, Valencia, 2. v. 04 (nematocysts shown only on near side); B, 3·5 mm. high, Valencia, 6. vii. 97. (Both from E. T. Browne collection.)

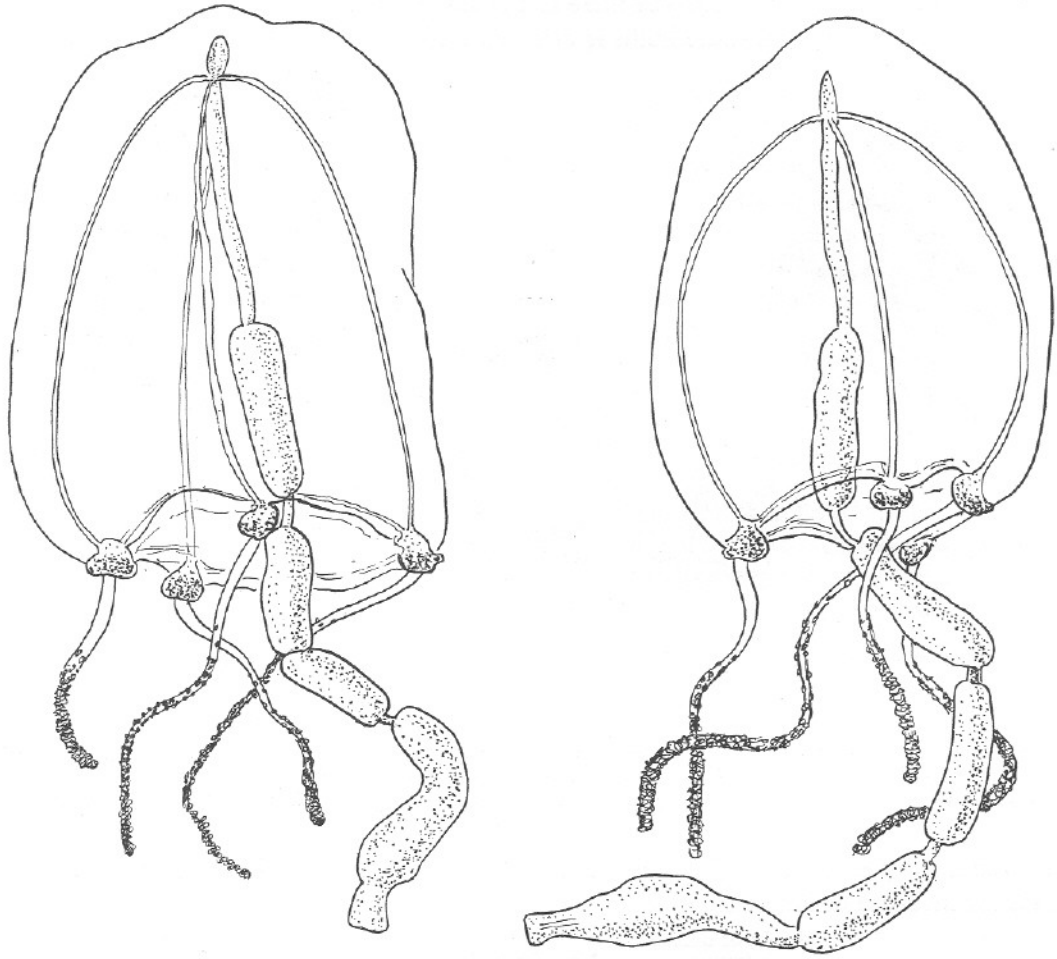
clusters and small terminal cluster. Marginal tentacle bulbs moderately large, each with one ocellus. Height when full grown about 5 mm. Colour of marginal tentacle bulbs and apical knob yellowish brown or reddish yellow; stomach and gonads sometimes rose-coloured; marginal tentacles when contracted pale brownish. Ocelli black.

Distribution

Dipurena ophiogaster has been recorded from Valencia, south-west Ireland; Plymouth; Jersey; and Normandy; the Mediterranean (Naples, Mayer, 1910); Ceylon (Browne, 1905*b*); Pacific and Indian Oceans (Bigelow, 1909*a*; Uchida, 1947) and Japan (Uchida, 1927*a*).

Developmental Stages and Structural Details

The medusa *Dipurena ophiogaster* has been reared by Miss Delap (unpublished) from the hydroid, and I have seen her specimens in Mr Browne's collection (Text-fig. 30A). The most striking feature of the earliest stages of the medusa is the abundance of exumbrellar nematocysts. These appear to be concentrated in eight perradial zones. These nematocysts probably disappear

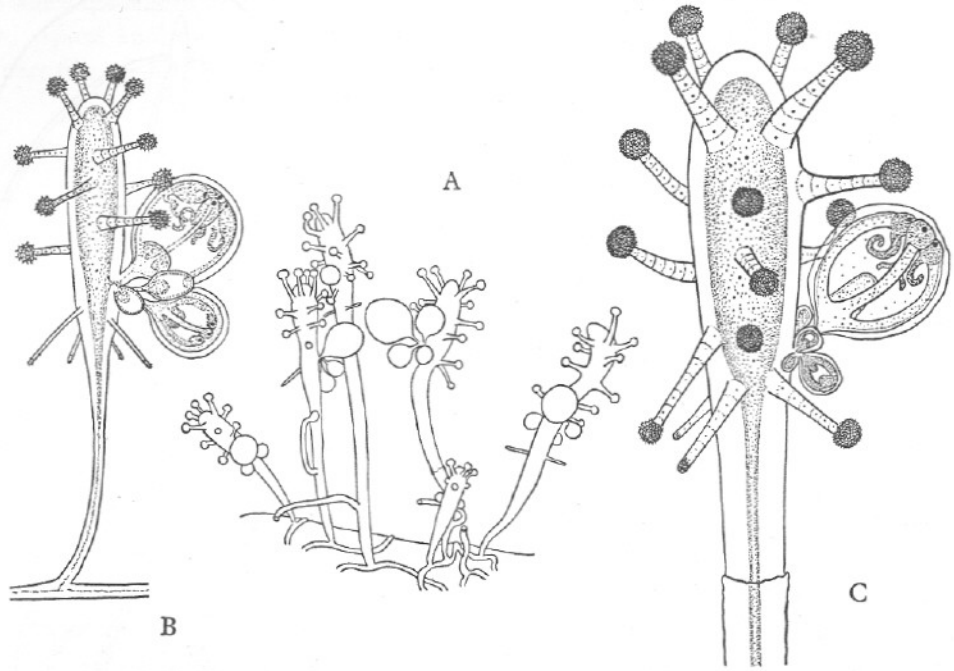


Text-fig. 31. *Dipurena ophiogaster*, preserved specimen 4·5 mm. high, Valencia, 6. vii. 97. (E. T. Browne collection.)

very soon, since in quite a small specimen I caught at Plymouth (Pl. II, fig. 4) they were already much less numerous though still sufficiently so to form a noticeable feature. Hartlaub (1907, p. 57 and fig. 52) records and figures these nematocysts on a specimen he observed at Concarneau; he thought that these had been missed by earlier observers, but while present in the earliest stages they evidently disappear in most adults.

In the young medusa about 1 mm. in height the stomach is only about half the height of the subumbrellar cavity. It increases very quickly in length however. In a specimen I found at Plymouth which was 1·2 mm. high the stomach was slightly less than half the height of the subumbrellar cavity, although when feeding it could be extended nearly to the margin of the

umbrella. Two days later the medusa was 2·2 mm. high and the stomach already extended beyond the umbrella margin. On the next day the medusa was 2·5 mm. high, and the stomach was two or three times the height of the umbrella and had one short and one long gonad. The stomach is very extensile and Browne (1900) records a specimen 5 mm. in height in which the stomach measured 40 mm. in length. In a medusa of similar size the marginal tentacles may extend to 20 mm. in length. In young medusae there is a slight apical knob, and the colour of this, the stomach and the marginal tentacle bulbs is brick red. The ocelli are deep brown.



Text-fig. 32. *Dipurena ophiogaster*. A, general appearance of a portion of the hydroid 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. (After Rees, 1941, fig. 2.)

Examination of a number of specimens caught at Valencia gives the following numbers of gonads for medusae of different sizes:

Height of umbrella (mm.)	No. of gonads	Sex
5	4	—
*3·5	4	—
5	4	♂
4	3	♂
3	2	♂
4·5	2	♂
5	4	♀ ripe
4	4	♀ ripe
4	2	—

* Plymouth.

Uchida (1927*a*; see below) records a specimen 6 mm. in height with nine gonads.

Seasonal occurrence

The records for Valencia give *Dipurena ophiogaster* as occurring fairly commonly at times between the months of May and September, with 'many' in July (M. & C. Delap, 1905).

HYDROID (Text-figs. 32A–C).

The hydroid of *D. ophiogaster* was found by Miss M. J. Delap (unpublished) in 1899 and 1904, and she reared the medusa. A description of the colony found by her at Valencia in May 1904 is given by Rees (1941*c*, *Journ. Mar. Biol. Assoc.* vol. XXV, p. 131, fig. 2).

Simple unbranched colonies reaching a height of 4 mm. Perisarc smooth. Ten to eighteen irregularly distributed capitate tentacles; one proximal whorl of four or fewer reduced filiform tentacles. Medusa buds borne on hydranth anterior to filiform tentacles, singly or in clusters of two to four.

Historical

Dipurena ophiogaster was first briefly described and figured by Allman (1871), from a specimen he caught off the south-west coast of Ireland, under the name of *Sarsia strangulata*. The specific name *strangulata* cannot, however, be retained because it is preoccupied by the genotype of *Dipurena* described by McCrady (1858), which resembles *D. halterata* but has only a single terminal cluster on each marginal tentacle and no accessory nematocyst rings (see Mayer, 1910). The specific name *ophiogaster* was given to Allman's medusa by Haeckel (1879).

Browne (1905*b*) described a medusa from Ceylon, which was apparently identical with *D. ophiogaster*, under the name *Dipurena* sp.(?). Bigelow (1909*a*) renamed this species *Purena brownei*, and recorded it as having 'a very wide range over the Pacific and Indian oceans'. Bigelow's figure depicts this medusa with very short cylindrical gonads. Uchida (1927*a*) described and figured *Dipurena ophiogaster* from Japan. He recorded a fully developed specimen with nine gonads which in his figure have the same shape as those in Bigelow's. Uchida, however, says: 'So far as I have observed, the gonads are ovate and the manubrium longer in living specimens, but the former become short cylindrical and the latter shorter by preservation.' There are therefore good grounds for identifying *Purena brownei* Bigelow as *Dipurena ophiogaster*. This identity, however, cannot yet be certain. Bigelow (1909*a*), in remarking on the oceanic distribution of *Purena brownei*, says that it suggests reproduction by budding. Chun (1896) describes and figures budding in *Dipurena dolichogaster*; in Haeckel's figure of the sexual stage of *D. dolichogaster* the tentacles are shown with nematocyst rings, but in other respects it resembles *D. ophiogaster*. Since Haeckel uses also the word 'Nesselringen' for the tentacles of *D. ophiogaster* it is impossible to say whether his figure is correct.

FAMILY TUBULARIIDAE

Anthomedusae with umbrella with or without apical projections; with or without exumbrellar nematocyst tracks; with stomachs not extending beyond umbrella margin; with simple circular mouths; with four radial canals; with gonads completely surrounding stomach; with four or fewer hollow marginal tentacles; without ocelli on marginal tentacle bulbs.

Hydroids *Tubularia*-like, with two whorls of many tentacles of which one whorl at least is filiform or moniliform.

The family may be divided into two subfamilies,* the Tubularinae and the Corymorphinae, based on differences in the structure of the hydroid.

Tentacles all filiform; perisarc well developed; without rooting filaments . . . . **Tubularinae**
Tentacles either all filiform, or with capitate oral tentacles; aboral tentacles may be moniliform; perisarc weakly developed; rooting filaments present . . . . . **Corymorphinae**

* Kramp (1949) has concluded that these should be distinct families, Tubulariidae and Corymorphidae.

TUBULARIIDAE

The free-swimming medusae of the Tubulariidae are all characterized by having simple, circular mouths and gonads which completely surround the stomach. These characters are common also to the Corynid medusae, but the Tubulariidae differ from the Corynidae in having *no ocelli* on the bases of the marginal tentacles.

The Tubulariid medusae are all of simple type, never having more than four marginal tentacles. These tentacles are, however, usually conspicuous for their heavy nematocyst armature.

Subfamily TUBULARINAE

The medusae of the Tubularinae are represented in British waters by two genera, *Ectopleura* L. Agassiz and *Hybocodon* L. Agassiz, each with a single species.

They are easily distinguishable by the number of their marginal tentacles.

With four marginal tentacles . . . . . **Ectopleura**
With one marginal tentacle, or a cluster of two or three arising from a common bulb . . **Hybocodon**

Genus **Ectopleura** L. Agassiz, 1862

MEDUSAE. Tubularinae without pointed apical process to umbrella; with eight meridional exumbrellar nematocyst tracks; without asexual budding; with two opposite, or four perradial, equally developed marginal tentacles.

HYDROID. *Tubularia*-like.

There is only one species of *Ectopleura* in British waters, *E. dumortieri* (Van Beneden). This medusa cannot be confused with any other British species.

Ectopleura dumortieri (Van Beneden)

Plate III, figs. 5, 6; Text-figs. 33 A–C

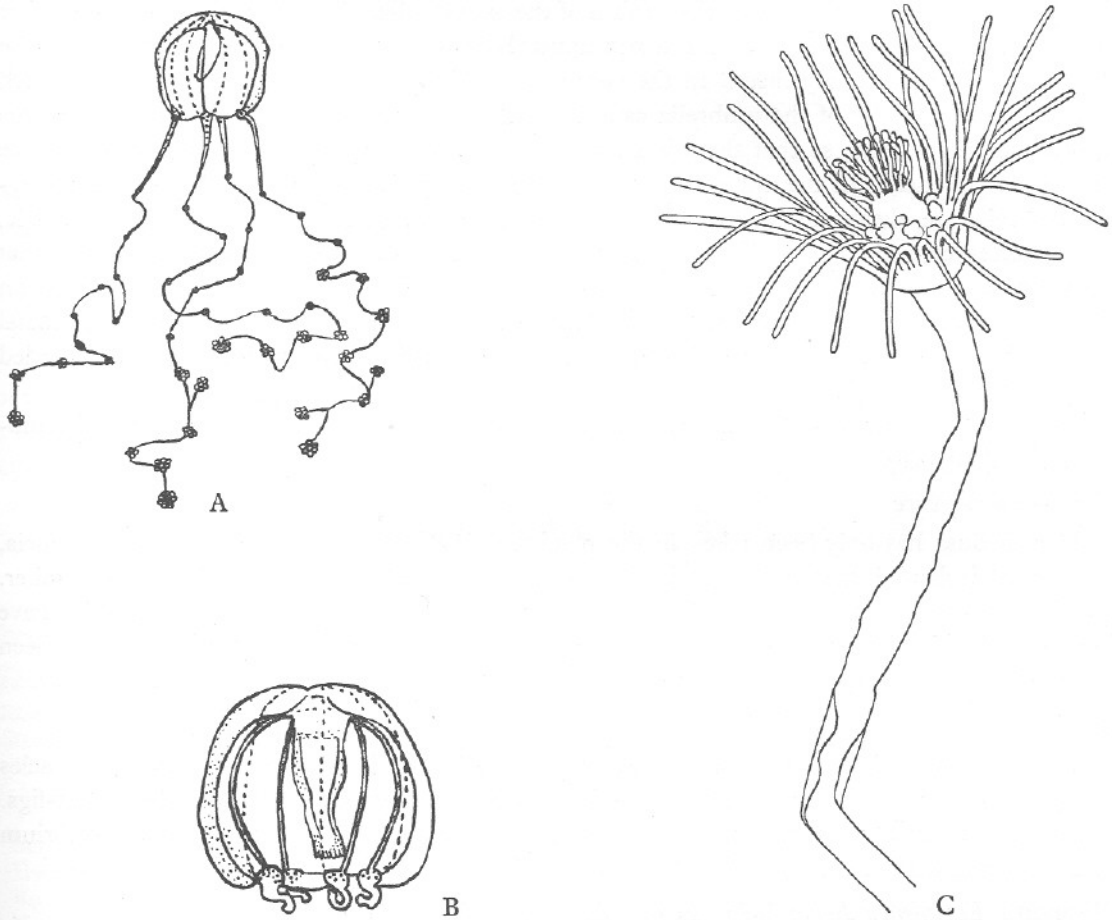
Tubularia dumortierii Van Beneden, 1844*a*, *Mém. Acad. R. Belg.* tome XVII, p. 50, pl. ii (hydroid and medusa).
Van Beneden, 1866, ibid. vol. XXXVI, p. 111.
L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 242.
Ectopleura dumortieri, L. Agassiz, 1862, ibid. vol. IV, p. 342.
Hincks, 1868, *Brit. Hydroid Zooph.* p. 124, pl. xxi, fig. 4*a*.
Böhm, 1878, *Jena Z. Naturw.* vol. XII, p. 198, pl. vii, figs. 10–13.
Haeckel, 1879, *System der Medusen*, p. 22.
Hartlaub, 1894, *Wiss. Meeresuntersuch.* N.F., Bd. I, Abt. Helgoland, Heft 1, IV, p. 188.
Browne, 1905*a*, *Proc. Roy. Soc. Edinb.* vol. XXV, pt. IX, p. 748.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 94, figs. 90, 91.
Mayer, 1910, *Medusae of the World*, p. 69, pl. v, figs. 4, 5; pl. vi, figs. 1, 1′, 2.
?*Ectopleura ochracea* L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 343.
A. Agassiz, 1865, *North American Acalephae*, p. 191, figs. 320–3.
Haeckel, 1879, *System der Medusen*, p. 22.
Fewkes, 1882*b*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. IX, no. 8, p. 295, pl. i, figs. 15, 16, 35, 36.
A. Agassiz & Woodworth, 1896, *Bull. Mus. Comp. Zoöl. Harvard*, vol. XXX, no. 2, pl. vi, fig. 6.
Nutting, 1901*a*, *Bull. U.S. Fish. Commission*, vol. XIX (1899), p. 373, fig. 82.
Hargitt, 1905, *Bull. U.S. Bur. Fish. Washington*, vol. XXIV (1904), p. 32, pl. ii, fig. 1.
Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 184, pl. vi, fig. 5, pl. xxxviii, figs. 12, 13.
?*Ectopleura prolifica* Hargitt, 1908, *Biol. Bull. Woods Hole*, vol. XIV, no. 2, p. 106, figs. 8–11.

Specific Characters

Umbrella nearly spherical. Exumbrella with four pairs of nematocyst tracks. Four perradial marginal tentacles with abaxial clusters of nematocysts.

Description of Adult

Umbrella nearly spherical; jelly thick, especially in apical region. Subumbrellar cavity about two-thirds the length of medusa. Velum fairly broad. Exumbrella with four pairs of nematocyst tracks. Stomach very large, spherical at base, tapering towards mouth; extensile, stretching beyond umbrella margin in full extension. Mouth simple and tube-like, armed with nematocysts.



Text-fig. 33. *Ectopleura dumortieri*. A, expanded (after Hartlaub, 1907, fig. 91); B, contracted (after Hartlaub, 1907, fig. 90); C, hydroid, drawn from preserved specimen, off Plymouth, 27. iii. 33.

Four radial canals and ring canal narrow. Gonads completely surrounding stomach, leaving mouth free. Four perradial marginal tentacles with round nematocyst clusters on abaxial surface. Height usually about 1·75 mm. Colour of marginal tentacle bulbs brownish or yellow flecked with red; mouth orange or crimson; with band of fine red spots round centre of stomach, and brownish or yellow circle of pigment round base of stomach near junctions of radial canals.

Distribution

Probably all British coasts. Recorded from west Ireland, Valencia, Firth of Clyde, Isle of Man (hydroid, Thornely, 1894), St Andrews, English Channel, North Sea, and in Danish waters outside the Skaw (Kramp, 1933*a*, p. 241). Never abundant. Atlantic coasts of North America from Cape Cod to South Carolina. ? Mediterranean. ? Philippine Islands.

TUBULARIIDAE

Developmental Stages and Structural Details

Ectopleura dumortieri changes little in general form during the course of its development. When first liberated the medusa is nearly 1 mm. in height. It grows generally to about 2 mm. in diameter, though a specimen has been recorded by Browne (1900, p. 705) 4 mm. in length and 2·5 mm. wide. A very fine umbilical canal is sometimes present. A characteristic feature is the presence of four pairs of nematocyst tracks on the surface of the exumbrella. These tracks spring from either side of the marginal tentacle bulbs and run upwards over the exumbrella to the summit of the crown, but do not actually meet. In the very young individuals the upper end of the stomach stretches into the jelly of the umbrella as a dome-shaped summit, but in older specimens this appearance is reversed, so that there is a funnel-shaped concavity giving rise to the semblance of a slight peduncle. In the upper half of the stomach large globules and vacuolated parenchymatous cells are always to be seen. The four perradial marginal tentacles are very extensile, but are often carried rolled up into a thick short spiral. When fully extended it can be seen that there are a large number of spherical clusters of nematocyst cells situated at intervals on the exterior or abaxial surface only of the tentacle. An abnormal specimen with eight radial canals, eight marginal tentacles and sixteen exumbrellar nematocyst tracks has been recorded (M. & C. Delap, 1905).

NEMATOCYSTS. Desmonemes; anisorhize haplonemes; micro-basic mastigophores; and stenoteles (Weill, 1934*b*).

Seasonal occurrence

This medusa has only been taken in the plankton singly or in small numbers. At Valencia, south-west Ireland, it has been found in all months from March to December, except November. At Plymouth it has been taken in May, September, October and November, and hydroids have been found which liberated medusae in the laboratory in April and in September. It has been recorded at St Andrews in Scotland in June.

Habits

Ectopleura dumortieri is an active medusa, at times swimming jerkily with its marginal tentacles rolled up and then resting motionless in the water with tentacles fully expanded (Text-figs. 33A, B). Hartlaub (1894, p. 188) has remarked upon the great extensibility of the manubrium and suggested that the medusa may cling to algae to get its food.

HYDROID. *Ectopleura dumortieri* (Van Beneden) (Text-fig. 33C).

(For full description see Van Beneden, 1844, *Mém. Acad. R. Belg.* tome XVII, p. 50, pl. ii; and Hincks, 1868, *Brit. Hydroid Zooph.* p. 124, pl. xxi, fig. 4.)

Hydrocaulus 25 mm. or more in height, slender, simple or slightly branched, solitary. Perisarc horn-coloured, sometimes with a few annular constrictions. About twenty-four short oral tentacles; twenty to thirty longer aboral tentacles. Medusae borne on short, slightly branched peduncles just above aboral tentacles.

Historical

This medusa with its hydroid was first described by Van Beneden (1844*a*, p. 50, pl. ii) under the name *Tubularia dumortieri*, being named after M. Dumortier. L. Agassiz (1862, p. 342) erected a new genus *Ectopleura*. *Ectopleura dumortieri* medusae from the North American coasts of the Atlantic differ slightly in that they are larger and have thicker apical jelly than those from the European side. Mayer (1910, p. 69) has shown, however, that the American and European

hydroids are apparently identical, and the American medusa which had been called *E. ochracea* L. Agassiz is now united with *E. dumortieri* (Van Beneden). This opinion was, however, not upheld by C. W. Hargitt (1924).

Neppi & Stiasny (1913*a*, p. 15, pl. i, fig. 7) record *E. dumortieri* from the Adriatic; their specimens had, however, only two marginal tentacles as has *E. minerva* Mayer, which Mayer (1910, p. 70) regards as a separate species. The hydroid is recorded from the Mediterranean at Naples by Stechow (1921, p. 249 and 1923, p. 50).

Genus **Hybocodon** L. Agassiz, 1862

MEDUSAE. Tubularinae without pointed apical process to umbrella; with five meridional exumbrellar nematocyst tracks; with umbrella margin at oblique angle; with asexual budding from marginal tentacle base; with one simple or compound marginal tentacular bulb with one to three tentacles; remaining three non-tentacular marginal bulbs greatly reduced to mere endodermal swellings.

HYDROID. *Hybocodon*, indistinguishable from *Tubularia* on hydroid characters alone.

The genus *Hybocodon* contains only one British species, *Hybocodon prolifer* L. Agassiz. This medusa is liable to be confused with *Euphysa aurata* if specimens are found without medusa buds. It can, however, be distinguished by the greatly reduced nature of the non-tentacular marginal bulbs, by the oblique angle of the umbrella margin, and by the exumbrellar nematocyst tracks.

Hybocodon prolifer L. Agassiz

Plate III, figs. 3, 4; Text-fig. 34

Coryne fritillaria Steenstrup, 1845, *Alternation of Generations*, Ray Soc. Publ. p. 27, pl. i, figs. 43–7 (medusa *non* hydroid).
?*Diplonema islandica* Green, 1857, *Nat. Hist. Rev.* vol. iv, p. 27, pl. v, fig. 7.
?*Steenstrupia owenii* Green, 1857, ibid. p. 28, pl. v, fig. 8.
?*Steenstrupia globosa* Sars, 1860, *Forhandl. Vidensk. Selsk. Christiania* (1859), p. 101.
M. Sars, 1877, *Fauna litt. Norveg.* pt. 3, p. 20, pl. i, figs. 1–6.
Hybocodon prolifer L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. iv, p. 243, pl. xxiii*a*, figs. 10, 11, pl. xxv (hydroid and medusa).
Böhm, 1878, *Jena Z. Naturw.* Bd. xii, p. 195, pl. vii, figs. 7–9.
Haeckel, 1879, *System der Medusen*, p. 33.
Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 466.
Nutting, 1901*a*, *Bull. U.S. Fish. Comm. Washington*, vol. xix (1899), p. 370, fig. 76.
Hargitt, 1901, *Biol. Bull. Woods Hole*, vol. ii, p. 222.
Hargitt, 1904, *Bull. U.S. Bur. Fish. Washington*, vol. xxiv, p. 33, pl. ii, fig. 2.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, xii, p. 98, figs. 94–7.
Mayer, 1910, *Medusae of the World*, vol. i, p. 38, pl. ii, fig. 1, pl. iii, fig. 3.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. v, pt. 10, p. 33, text-figs. 29–32, pl. i, fig. 9.
Steenstrupia fritillaria, L. Agassiz, 1862, *Contrib. Nat. Hist. U.S.* vol. iv, p. 343.
Amphicodon fritillaria, Haeckel, 1879, *System der Medusen*, p. 36.
Browne, 1895, *Trans. Liverpool Biol. Soc.* vol. ix, p. 253.
Amphicodon amphipleurus Haeckel, 1879, *System der Medusen*, p. 37, pl. i, figs. 7–9.
Auliscus pulcher Saemundsson, 1899, *Vidensk. Medd. naturh. Foren. Kbh.* p. 425, pl. iv (hydroid with medusa buds).
Tubularia prolifer, Bonnevie, 1899, *Norweg. North Atlantic Expedit.* 1876–8, p. 28, pl. i, fig. 6.
Hybocodon pulcher, Hartlaub, 1907, *Nordisches Plankton*, p. 96, figs. 92, 93.
?*Hybocodon islandicus*, Hartlaub, 1907, ibid. p. 104, fig. 99.
?*Steenstrupia occidentalis* Fewkes, 1889, *Zoölogical Excursions*, p. 11, pl. iii, fig. 1; *Bull. Essex Inst.* vol. xxi, p. 110.

TUBULARIIDAE

Specific Characters

Umbrella asymmetrical, with margin oblique to vertical axis, without apical process. Exumbrella with five nematocyst tracks. Asexual reproduction by budding from one fully developed, simple or compound, marginal bulb having one to four tentacles.

Description of Adult

Umbrella bell-shaped, higher than wide with rounded summit; without apical process; jelly thick, especially on tentacular side. Exumbrella with five meridional nematocyst tracks; umbrella margin oblique to vertical axis sloping upwards from tentacular side. Velum moderately broad. Stomach large, cylindrical, about half to two-thirds the length of umbrella cavity, never reaching beyond margin in full extension. Mouth simple and tube-like, surrounded by narrow ring of nematocyst batteries. Four radial canals and ring canal fairly broad; radial canal on tentacular side longer than that opposite it. Gonads completely surrounding stomach, leaving peduncle and mouth free. Eggs amoeboid, developing into actinulae in umbrella cavity. Asexual reproduction by budding from marginal tentacle bulb. One fully developed simple or compound perradial marginal bulb with one, two, or three tentacles or even four. Marginal tentacles heavy and ringed with nematocyst batteries. Three perradial non-tentacular marginal bulbs, small compared with marginal tentacular bulb. Height 2–4 mm. when fully grown. Colour: bulbs, mouth and upper end of stomach bright red or reddish brown; stomach pale yellow; marginal tentacle endoderm and subumbrella surface pink; exumbrellar nematocyst tracks pink.

Distribution

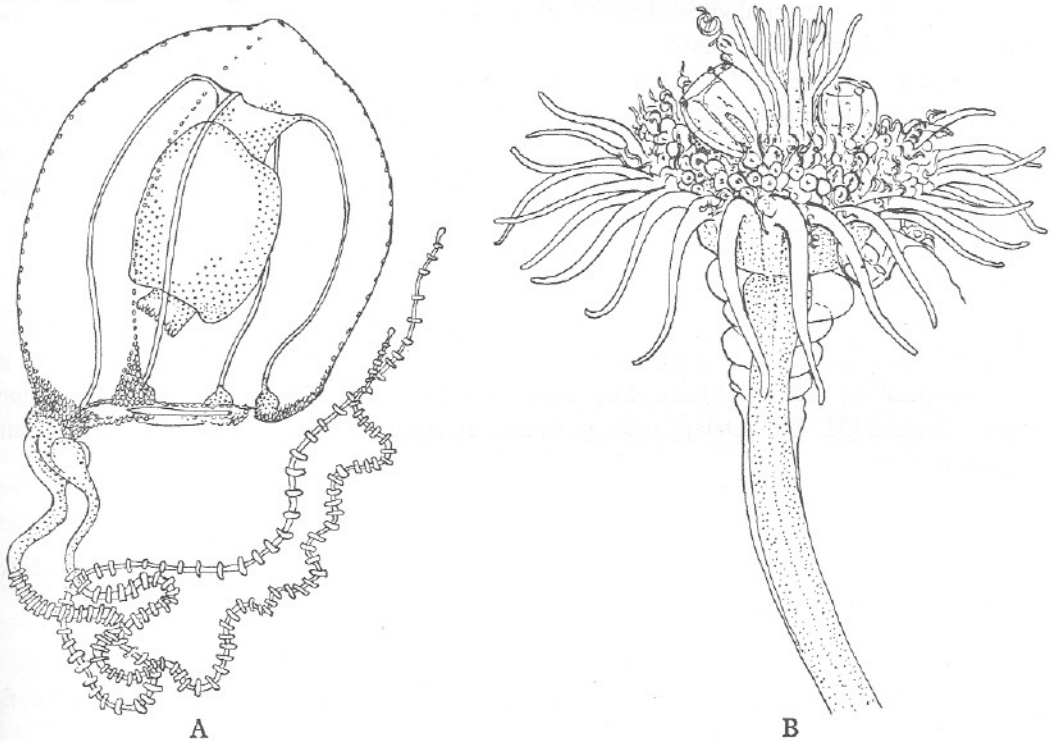
All coasts of British Isles, north European coasts to northern Norway, Iceland, west Greenland, Hudson Strait, Atlantic coast of North America; Pacific coast of North America, Japan. Probably world-wide; northern boreal circumpolar. On the coasts of the British Isles this species becomes more abundant towards the north.

Developmental Stages and Structural Details

Hybocodon prolifer shows little change in general structure during the course of its development. When first liberated from the hydroid, *H. prolifer*, the medusae are about 1 mm. high. An umbilical canal is probably present in the earliest stages but soon disappears. It may occasionally persist in the adult (Browne, 1895, p. 258; Hartlaub, 1907, p. 102). A conspicuous feature of this medusa is the asymmetry of the umbrella by which even the young single tentacle stage can be distinguished from *Euphysa aurata*. There is unequal development of the radial canals during growth (while still on the hydroid) so that the canal on the tentacular side becomes the longest and that opposite it the shortest. The remaining two radial canals are of equal length, but intermediate between the longest and the shortest. The umbrella margin thus slopes upwards from the marginal tentacle side. The marginal bulb on the tentacular side may be simple or compound with one to three, or even four tentacles. In compound bulbs the component basal bulbs may be unequal in size, the smaller bulbs appearing to develop from the sides of the larger. The largest marginal tentacles have about fifty closely set nematocyst rings (Sanderson, 1930, p. 224). The remaining three perradial non-tentacular marginal bulbs are small and poorly developed, being actually mere internal dilatations of the gastro-vascular system (Kramp, 1926*a*, p. 38). Three perradial nematocyst tracks arise in the vicinity of the three non-tentacular bulbs and extend upwards over the exumbrellar surface; two similar nematocyst tracks also arise one on either side

of the tentacular bulb so as to become adradial in position. These two tracks may be joined at their base. The histological detail of these tracks has been examined by Kramp (1926*a*, p. 38). The nematocysts are most numerous in the neighbourhood of the bulbs. It has been stated by C. W. Hargitt (1902*a*, p. 20, and 1904, p. 34) that the tracks appear in diminishing strength on medusae from the Woods Hole, U.S.A., region as the season advances, and that they are entirely absent in August.

The vesicular endoderm of the upper part of the stomach has been shown by Kramp (1926*a*, p. 36, fig. 29) to be separated from the ectodermal layer of epithelium by a thick mass of jelly



Text-fig. 34. *Hybocodon prolifer*. A, medusa. (After Hartlaub, 1907, fig. 94.) B, hydroid. (After L. Agassiz, 1862, vol. IV, pl. XXV, fig. 2.)

which surrounds the stomach base in a gelatinous ring. The lower end of the mouth tube is surrounded by several prominent knobs to form a ring-shaped mound of nematocyst-bearing ectoderm (Kramp, 1926*a*, p. 36). The ectodermal muscle layer surrounds the stomach, but is more strongly developed perradially (Kramp, 1932).

Hybocodon prolifer is remarkable for its methods of reproduction. This may be sexual or asexual. Medusa buds may be produced on the marginal tentacle bulb and these develop into miniatures of the parent, and may themselves produce buds before liberation. Thus three generations may be attached at one moment, resulting, when the tentacular bulb is compound, in a considerable number of medusae.

In sexual female medusae the ripe eggs are few in number and amoeboid, having developed at the expense of other cells (see H. Müller, 1908; G. T. Hargitt, 1917, p. 624; Kramp, 1926*a*). Development of the fertilized egg takes place *in situ*, and the new hydroid generation reaches the actinula stage while still in the umbrella cavity.

Sexual development and asexual budding can proceed at the same time, actinulae having been observed in medusae carrying medusa buds (Browne, 1895, p. 254; C. W. Hargitt, 1904, p. 33, pl. ii, fig. 2). It is, however, not known whether the first medusae which are liberated from the hydroid eventually become sexual.

A detailed study of the germ cells was made by G. T. Hargitt (1917). The development of the young actinula is described below under the description of the hydroid.

C. W. Hargitt (1901, p. 222) examined about 200 specimens of *Hybocodon* in a study of variation in medusae. He found that apart from the variability in tentacular budding the medusae showed marked constancy in morphological detail. Uchida (1927*a*, p. 193, fig. 29) records two specimens from Japan with eight radial canals.

The marginal tentacle bulbs show considerable variation in colour, those of the younger specimens being yellowish or yellowish brown and of the adults brilliant crimson to reddish brown. In many specimens the crimson pigment extends into the radial and ring canals, and this is not in circulation but occurs as small particles in the endoderm cells (Pl. III, figs. 3, 4) (Browne, 1895, p. 254).

Seasonal occurrence

Hybocodon prolifer occurs in the plankton in British waters in spring and early summer. It usually first makes its appearance about March, and becomes most abundant during April and May; it disappears by the end of June. The latest records for British waters are 5 July off Valencia, south-west Ireland (M. & C. Delap, 1906, p. 6) and 29 August in the Straits of Dover (Kramp, 1930, p. 11).

Habits

This medusa has been shown by Lebour (1922, p. 661) to feed on copepods, and by M'Intosh (1926) on 'young cuttlefish'.

HYDROID. *Hybocodon prolifer*, L. Agassiz, 1862.

(For full description see L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 243, pl. xxiii*a*, figs. 10, 11; pl. xxv; and Allman, 1872, *Monogr. Gymnobl. Hydroids*, p. 422.)

Hydrocaulus solitary or sparingly aggregated, reaching height of about 50 mm., gradually enlarging to just below hydranth. Perisarc covering whole hydrocaulus; wide and annulated at summit. About thirty-two oral tentacles in two verticils each of sixteen, the more distal being the shorter; about twenty-five to thirty aboral tentacles.

The medusae are produced just above the aboral tentacles, the older medusae themselves carrying buds while still on the hydranth.

The early development of the hydroid, which takes place inside the umbrella cavity of the medusa has been described by Browne (1895, p. 254). The aboral tentacles are the first to appear, being eleven to seventeen in number. When these are about 2 mm. long eight oral tentacles appear. 'The body of the young hydra behind the aboral tentacles becomes covered with a thin perisarc. Sometimes the young hydra breaks away from the manubrium before the appearance of the second row of tentacles and remains free in the umbrella cavity. The young hydra with the two verticils of tentacles is about 2 mm. long, and the tentacles of the posterior verticil are a little longer than the body.' Browne watched the further growth of these hydroids after leaving the medusae. They fixed themselves to the bottom of the glass aquarium and grew to about 10 mm.

in length. The body became long and stem-like, and the coenosarc showed longitudinal striae of an orange-red colour. As in the young *Corymorpha* the oral tentacles are capitate. Free-floating actinulae are sometimes common in the plankton.

On the British coasts the adult hydroid has only been recorded from Plymouth where it is found growing in the sponge *Desmacidon fruticosum* (*Mar. Biol. Assoc.* 1931, p. 70). The stems of the hydroid penetrate deep down into the sponge.

Historical

Hybocodon prolifer (hydroid and medusa) was first fully described by L. Agassiz in 1862 from specimens taken off the east coast of North America. The hydroid was described in great detail and the description was accompanied by a very beautiful plate. Agassiz gave the name *Hybocodon* on account of the asymmetrical form of the medusa.

In his original description Agassiz stated that the medusae 'have no common peduncular axis of attachment', but 'arise directly from the actinal area of the disk'. It appears that this statement was incorrect. C. W. Hargitt (1927, p. 498) says: 'I am able to correct some incidental errors of the original description of Agassiz, such as, for example, that young medusae "arise singly on very short peduncles direct from the body of the parent hydranth". On the contrary the medusae arise on peduncles which branch, producing numerous medusae, as in *Tubularia* and *Ectopleura*, but never in dense and pendulous racemes characteristic of the Tubulariidae.' Hargitt made these observations on specimens from Woods Hole, U.S.A.

Kramp (1926*a*, pp. 34–5) and Broch (1916, p. 22) had pointed out this discrepancy between Agassiz's description of the hydroid and that described by Saemundsson (1899, p. 425) from Reykjavík, Iceland, under the name of *Auliscus pulcher*.

Hargitt's observation, however, appears to settle the question that the European and American *Hybocodon* are one and the same species.

The medusa, *Hybocodon prolifer*, can also be identified with that figured and described by Steenstrup (1845, pp. 27–8, pl. i, figs. 43–7) which he caught in the plankton and associated with his hydroid *Coryne fritillaria*. This latter name, however, refers to the hydroid and *Hybocodon prolifer* therefore has priority since Steenstrup's *Coryne fritillaria* is definitely not a *Hybocodon*, but resembles rather *Coryne lovéni* Sars.

Subfamily CORYMORPHINAE

The medusae of the Corymorphinae are represented in British waters by two genera. These are *Steenstrupia* Forbes and *Euphysa* Forbes. They are easily distinguishable by the character of the apex of the umbrella.

With pointed apical process	**Steenstrupia**
Without pointed apical process	**Euphysa**

Genus **Steenstrupia** Forbes, 1846

MEDUSAE. Corymorphinae with pointed apical process to umbrella; without exumbrellar nematocyst tracks; without asexual budding; with one fully developed marginal tentacle, and the remaining three small and rudimentary, or completely reduced to rudimentary, spur-like marginal bulbs.

HYDROID. *Corymorpha*.

TUBULARIIDAE

There is one British species in the genus, namely *Steenstrupia nutans* (M. Sars), and it is unlikely to be confused with any other species.

NOTE. *Corymorpha nana* Alder 1857, from the Northumberland coast, remains a somewhat uncertain species. The newly liberated medusa had no pointed apical process, and its further development is unknown. The species was figured twice by Alder (1857, p. 108, pl. ix, figs. 7, 8; 1862, p. 233, pl. xi, figs. 1–5). The hydroid was also recorded at Plymouth and figured by Stechow (1912, p. 404, text-fig. 1, pl. vii).

Steenstrupia nutans (M. Sars)

Plate III, fig. 1; Plate XXXIV, fig. 2; Text-figs. 35A–D, 36, 37A–C

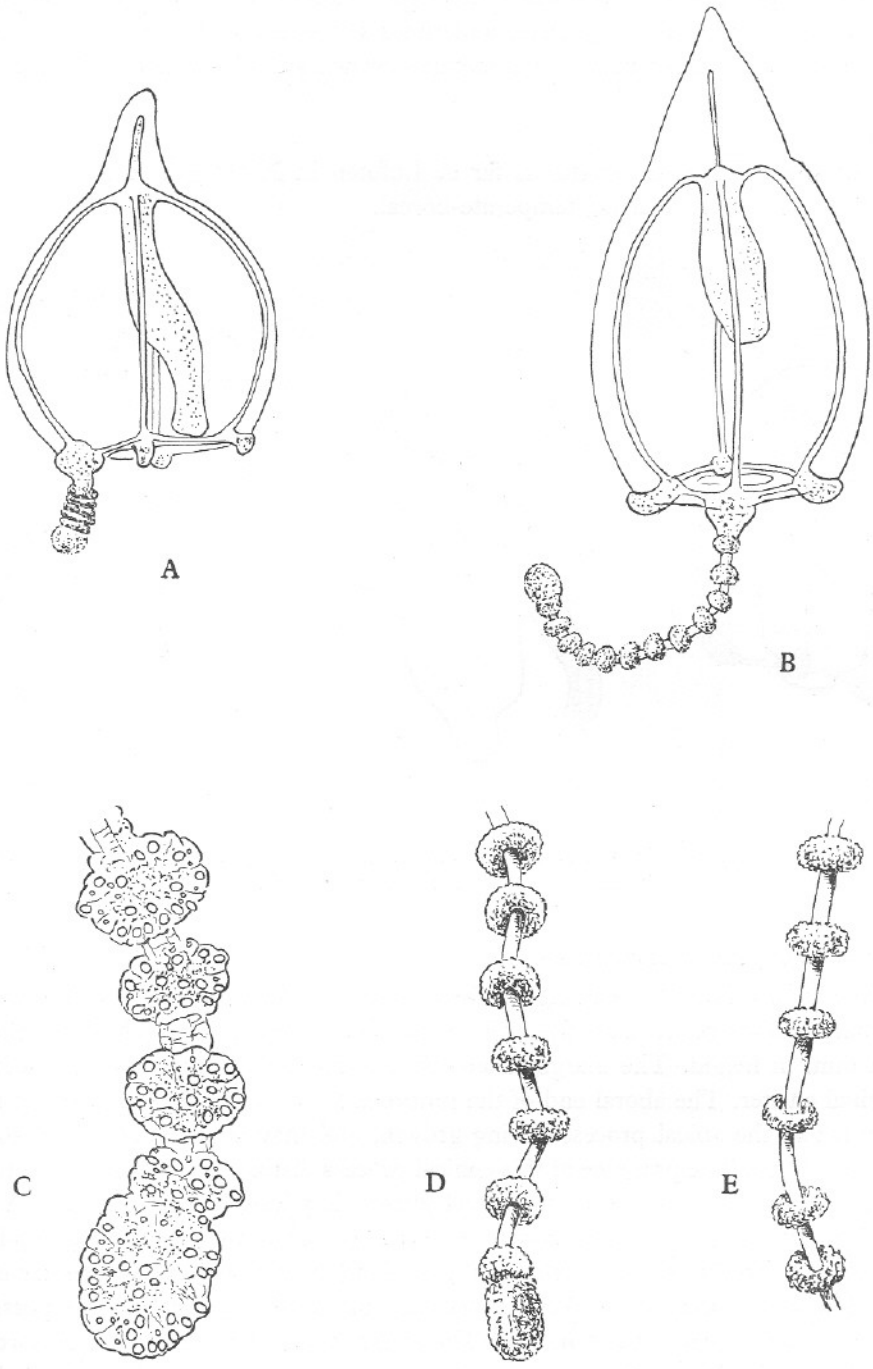
Corymorpha nutans M. Sars, 1835, *Beskrivelser og Iagttagelser*, p. 7, pl. i, fig. 3 (hydroid with medusa buds).
Hodge, 1861, *Trans. Tyneside Nat. Field Club*, vol. v, pt. II, p. 80, pl. ii, figs. 1–9 (hydroid and medusa).
Allman, 1863, *Ann. Mag. Nat. Hist.* (January, Ser. 3), vol. XI, p. 1 (hydroid and medusa).
Hincks, 1868, *Brit. Hydroid Zooph.* p. 127, pl. xxii, fig. 2.
Allman, 1871–2, *Monogr. Gymnobl. Hydroids*, pp. 77, 210, 338, text-fig. 34, pl. xix.
M. Sars, 1877, *Fauna litt. Norveg.* pt. 3, p. 1, pl. ii, figs. 25–8.
Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 463, pl. xvi, fig. 1.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 76, figs. 72–5.
Steenstrupia rubra Forbes, 1848, *Monogr. Brit. Medusae*, p. 73, pl. xiii, fig. 1.
Hartlaub, 1904, *Wiss. Meeresuntersuch.* N.F., Bd. v, Abt. Helgoland, Heft 2, p. 105, fig. 3.
Mayer, 1910, *Medusae of the World*, vol. I, p. 31, text-figs. 4–6.
Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien*, Tom. XX, p. 28.
Ranson, 1925, *Bull. Mus. Hist. nat. Paris*, vol. XXXI, p. 324, fig.
Steenstrupia flaveola Forbes, 1848, *Monogr. Brit. Medusae*, p. 74, pl. xiii, fig. 2.
Steenstrupia lineata Leuckart, 1856, *Arch. Gesch. Natw.* Jahrg. XXII, p. 29, pl. ii, fig. 6.
Spagnolini, 1876, *Atti Soc. Ital. Milano*, vol. XIX, fasc. II, p. 17, pl. i, figs. 1–4.
Haeckel, 1879, *System der Medusen*, p. 30.
Steenstrupia cranoides Haeckel, 1864, *Jena Z. Naturw.* Bd. I, p. 329.
Haeckel, 1879, *System der Medusen*, p. 30, pl. ii, figs. 10–14.
Steenstrupia galanthus Haeckel, 1879, *System der Medusen*, p. 31.
Hybocodon nutans, Haeckel, 1879, ibid. p. 34.
?*Steenstrupia gracilis* Brooks, 1882, *Johns Hopkins. Univ. Stud. Biol. Lab.* vol. II, p. 144.
Steenstrupia nutans, Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. v, pt. 10, p. 28, text-figs. 23–7.
Ranson, 1936, *Rés. Camp. Sci. Monaco*, fasc. XCII, p. 51.

Specific Characters

Umbrella with pointed conical apical process, and with umbilical canal. Margin at right angles to vertical axis. Exumbrella without nematocyst tracks. One simple perradial marginal tentacle with annular nematocyst rings.

Description of Adult

Umbrella bell-shaped, nearly twice as high as broad, with a pointed conical apical process and an umbilical canal; jelly thick. Umbrella margin at right-angles to vertical axis; no exumbrellar nematocyst tracks. Velum fairly wide. Stomach large, cylindrical, on short peduncle; about two-thirds the length of subumbrellar cavity, in full extension reaching slightly beyond margin. Mouth simple and tube-like, armed with nematocysts. Four radial canals and ring canal fairly broad. Gonads completely surrounding stomach and leaving peduncle and mouth free; eggs amoeboid. One single stout perradial marginal tentacle with many well-developed nematocyst rings and terminal cluster; three perradial non-tentacular marginal bulbs, smaller than the tentacular bulb. Height about 5–6 mm. Colour very variable; marginal tentacle, marginal bulbs

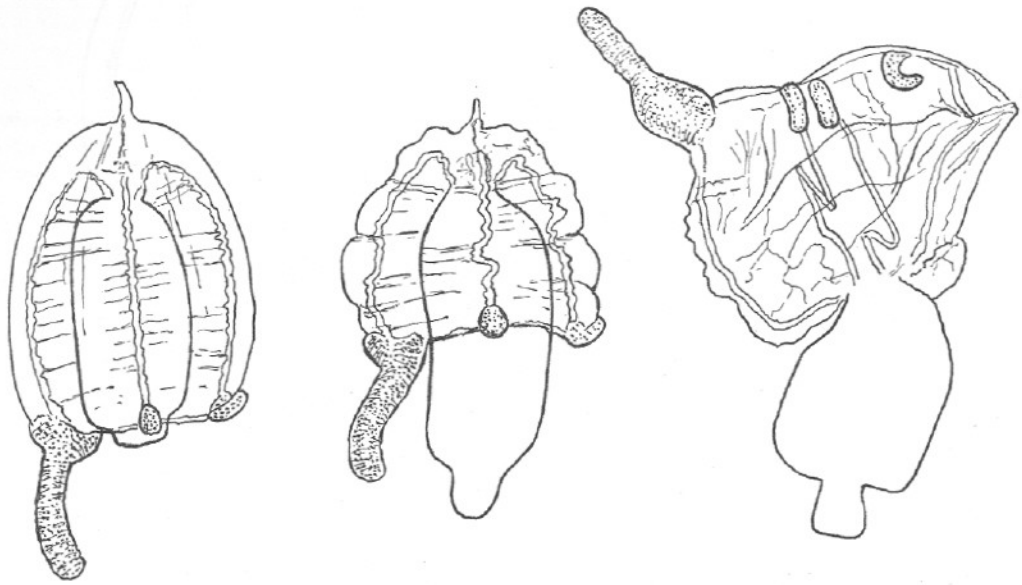


Text-fig. 35. *Steenstrupia nutans*: A, 1·4 mm. high, newly liberated from hydroid, Plymouth, 13. v. 35. B, 1·8 mm. high, Plymouth, 7. v. 34; C, enlarged portion of marginal tentacle of B; D, portion of marginal tentacle of preserved specimen, 5 mm. high, Plymouth, 28. iv. 37. *Euphysa aurata*: E, portion of marginal tentacle of preserved specimen 3·3 mm. high. (Collected in Norway by W. J. Rees.)

and stomach light pink, flecked with carmine, bright yellow, straw coloured or reddish brown; apical process often pinkish; subumbrella sometimes suffused with pink; radial canals and ring canal often with bright yellow pigment; sometimes brown granules at apex of stomach.

Distribution

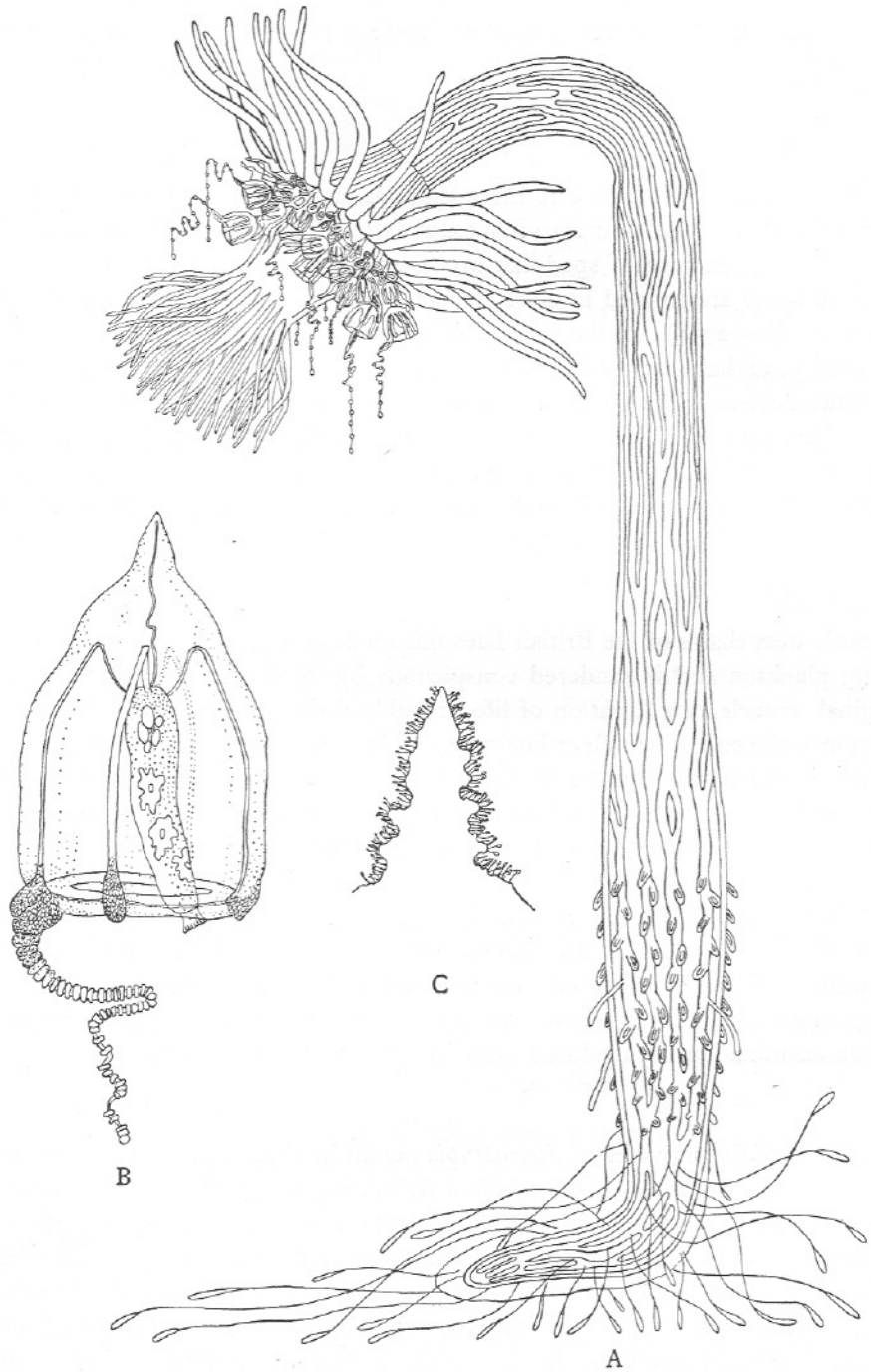
All British coasts, European coasts as far as Lofoten in Norway, Faeroe Islands, Iceland, Mediterranean, Black Sea. Neritic, temperate-boreal.



Text-fig. 36. *Steenstrupia nutans*, showing attitudes assumed by dying medusae and often found in preserved plankton collections.

Developmental Stages and Structural Details

Steenstrupia nutans shows little change in the course of its development, its form on liberation being a miniature of the adult (Text-fig. 35 A). When first set free from the hydroid, the medusae are 1·1–1·4 mm. in height. The marginal tentacle has about five nematocyst rings in addition to the terminal cluster. The aboral end of the umbrella shows variation according to the degree of development of the apical process during growth, and may at times assume a conspicuous spine-like appearance. The presence of this conical process distinguishes the species at once from *Euphysa aurata*. In many specimens the apical process is pilose, being covered with numerous small papillae varying in size from scarcely perceptible points to well-marked papillae (Text-fig. 37 C). Kramp (1926*a*, p. 29, text-fig. 23) has shown that these are unicellular ectodermal structures. The apical process is very contractile and sensitive, the papillae possibly being nervous structures (Hartlaub, 1904, p. 105). The stomach, which is attached to a short peduncle, is capable of considerable contraction and expansion; it has four broad ectodermal perradial longitudinal bands of muscle (Kramp, 1926*a*, p. 29). The single marginal tentacle when fully elongated is about four times the height of the umbrella, and carries a very large number of complete narrow rings of nematocyst batteries beginning a short distance below the marginal bulb (Text-fig. 35 D).



Text-fig. 37. *Steenstrupia nutans*. A, the hydroid, *Corymorpha nutans* (after Allman, 1872, pl. xix, fig. 1); B, medusa (after Hartlaub, 1907, fig. 74); C, apical process of medusa with papillae (after Hartlaub, 1907, fig. 74).

A few observations on Plymouth specimens gave the following results:

Umbrella height (mm.)	No. of rings on marginal tentacles	Umbrella height (mm.)	No. of rings on marginal tentacles
1·8	12	3·0 (contracted)	*c.* 60
1·9	11	4·0	61
2·0	15	4·25	*c.* 70
3·25	39	5·0	*c.* 120

The marginal tentacle bulb is two to three times as large as any of the remaining three non-tentacular marginal bulbs. All four marginal bulbs extend for a short distance up the exumbrellar surface giving the appearance of spur-like processes when slightly contracted or in preserved material. These spurs are formed both of ectoderm and of endoderm and are hollow (Kramp, 1926*a*, p. 30, text-figs. 27–8). In the female full-grown eggs are few in number and amoeboid. H. Müller (1908, p. 52) has described the development of the eggs which have been nourished at the expense of other degenerating egg-cells. The development of the hydroid from the egg has been described by Rees (1937*a*). The medusa often turns inside out when dying, and this and the shrinkage of the umbrella cause it to assume many unusual shapes on preservation (Text-fig. 36).

NEMATOCYSTS. Large and small stenoteles; ? anisorhize heterotrichous haplonemes; ? microbasic mastigophores or microbasic euryteles; and desmonemes (Russell, 1938*b*).

Seasonal occurrence

On the south-west coasts of the British Isles this medusa is in some years a common member of the spring plankton and is rendered conspicuous by its bright coloration and by the long heavy marginal tentacle. Its duration of life probably does not exceed two months, appearing in the plankton at the end of March or beginning of April and reaching maturity in May or June. Occasional specimens may be found as late as August or even September or October (M. & C. Delap, 1905), but these are likely to have been survivors of the last medusae liberated from the hydroid, the majority having died off in June. In the north the season is likely to be slightly later, and anywhere may vary slightly from year to year.

A remarkable instance of the abundance that some medusae may reach at times was recorded in May 1900, and in 1901. The mackerel fishermen off the coast of Valencia Island, south-west Ireland, had their nets so badly fouled by small jellyfish that they had to be cleaned no less than three times in one week. Scrapings from these nets were fortunately obtained by the Misses Delap (1905) and on examination the medusae were found to be *Steenstrupia nutans*.

Habits

A vivid account of the activities of *Steenstrupia nutans* has been given by Forbes (1848, p. 73). 'It is very active and tenacious of life; before dying, assuming all manner of strange shapes, doubling itself up, and turning inside out in a terrific manner, giving up the ghost with convulsions as fearful as those of a popular actor in the death scene of a tragedy.... But when well and uninjured, it is an extremely active and regularly formed creature, though, owing to the weighty and unbalanced tail which it is doomed perpetually to drag as its train, it cannot advance through the water with the easy grace and rapidity for which its allies are remarkable, but struggles forward with frantic energy, contracting and expanding rapidly, and without ceasing, reminding us of an escaped felon impeded in his course by the dragging of his heavy fetters.' The medusa has been shown by Lebour (1922, p. 661; 1923, p. 84) to feed on copepods, crustacean larvae, *Sagitta*, fish eggs and young fish.

In the day-time the medusae are usually caught below 20 m.; at night they sometimes migrate upwards as far as 12 m. and occasional specimens may even reach the surface (Russell, 1925, p. 781; 1927, p. 569; 1928, pp. 83, 85; and 1931).

HYDROID (Text-fig. 37 A). *Corymorpha nutans* M. Sars, 1835.

(For full description see Allman, 1872, pp. 210–11, 388–90, pl. xix; and Hincks, 1868, p. 127, pl. xxii, fig. 2.)

Hydrocaulus subcylindrical, 50–115 mm. in height. Solitary. Basal end with short papillary projections, with numerous fine long filaments below. Perisarc a transparent membranous tube. About eighty short oral tentacles arranged in several series; about thirty-two longer aboral tentacles. Medusae borne in clusters on fifteen to twenty branching peduncles above aboral tentacles without ectothecal covering.

This hydroid lives rooted in the bottom, and may be found in silty sand, clean sand, and clean shell gravel (Ford, 1923).

Allman (1872, p. 211) has recorded reproduction in the hydroid, *Corymorpha*, by asexual budding and it is possible that considerable fields of the hydroid may be developed in this way. The hydroid has been taken in various localities off Plymouth in the Petersen grab, the largest numbers being in the Eddystone shell gravel where as many as sixteen were found in one square metre (Ford, 1923, p. 204). Occasional specimens are also taken in plankton tow-nets after rough weather.

Historical

The hydroid was first described by Michael Sars in 1835 as producing medusae, and the first descriptions of the adult medusa were made by Forbes (1848). The generic name *Steenstrupia* was given by Forbes (1846) for the medusa to perpetuate the name of Japetus Steenstrup in honour of his classical memoir on Alternation of Generations, *Corymorpha* being one of the first hydroids in which the relationship of medusa to hydroid was demonstrated. A closely allied medusa, *Steenstrupia gracilis*, was described by Brooks (1882, p. 144) on the American side of the Atlantic. This species has been regarded by Mayer (1910) and apparently Bigelow (1915*a*, p. 318) as synonymous with *S. nutans*, but its identity is uncertain. The most important difference is the development of a short marginal tentacle opposite the main tentacular bulb. In this respect it resembles *S. lineata* Leuckart from the Mediterranean which Neppi & Stiasny (1913*a*, p. 28) have united, with *S. cranoides* Haeckel, to *Steenstrupia nutans*, as has also Mayer (1910).

Genus **Euphysa** Forbes, 1848

MEDUSAE. Corymorphinae without pointed apical process to umbrella; without exumbrellar nematocyst tracks; with umbrella margin horizontal; without asexual budding; with one to four marginal tentacles.

HYDROID. *Heteractis*.

The genus *Euphysa* was erected by Forbes (1848). The only known British species is *Euphysa aurata* Forbes.

The genus contains also two other North Atlantic species, *E. tentaculata* (Linko) and *E. flammea* (Linko). It is possible that they may one day be found in waters north of the British Isles.

Their distinguishing characters are:

E. aurata	One marginal tentacle.
E. tentaculata.	Three marginal tentacles.
E. flammea	Four marginal tentacles.

Both *E. tentaculata* and *E. flammea* have only one marginal tentacle in their youngest stages. For descriptions of these two species see Kramp (1926*a*).

The medusa *Euphysa aurata* is liable to be confused with *Hybocodon prolifer* if specimens of the latter species are found not bearing medusa buds. *Euphysa aurata* may, however, be distinguished by the fact that the non-tentacular marginal bulbs are in the form of exumbrellar spurs and by the horizontal umbrella margin (see p. 92).

Euphysa aurata Forbes

Plate III, fig. 2; Text-figs. 35E, 38, 39

Euphysa aurata Forbes, 1848, *Monogr. Brit. Medusae*, p. 71, pl. xiii, fig. 3.
Haeckel, 1879, *System der Medusen*, p. 32.
Browne, 1895, *Trans. Liverpool Biol. Soc.* vol. IX, p. 248.
Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 474.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. V, pt. X, p. 25, text-figs. 21, 22; pl. i, figs. 10, 11.
Rees, 1938, *Journ. Mar. Biol. Assoc.* vol. XXIII, p. 26 (hydroid and young medusa).
Corymorpha annulicornis M. Sars, 1860, *Christiania Vidensk. Selsk. Forhandl.* p. 96.
Euphysa mediterranea Haeckel, 1864, *Jena Z. Naturw.* Bd. I, p. 338.
Haeckel, 1879, *System der Medusen*, p. 32, pl. ii, figs. 8, 9.
Hybocodon annulicornis, Haeckel, 1879, ibid. p. 35.
?*Trichorhiza brunnea* E. S. Russell, 1906, *Proc. Zool. Soc. London*, p. 99, pl. v (hydroid and young medusa ?abnormal).
Corymorpha aurata, Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 81, figs. 77, 78.
Sverdrup, 1921, *Skrift. Vidensk. Christiania*, Bd. I (1922), mat.-nat. Kl., p. 15, pl. i, fig. 5, pl. ii, fig. 7.
Rees, 1938, *Journ. Mar. Biol. Assoc.* vol. XXIII, p. 32.
Steenstrupia aurata, Mayer, 1910, *Medusae of the World*, vol. I, p. 35.
Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien*, Tom. XX, p. 30.
Corymorpha (*Euphysa*) *annulicornis*, Broch, 1937, *Avh. norske Vid. Akad. Oslo*, I. mat.-nat. Kl., no. 8, p. 1, figs. 1–4 (hydroid and young medusa).
Corymorpha annulicornis, Rees, 1938, *Journ. Mar. Biol. Assoc.* vol. XXIII, p. 25, figs. 8, 9 (hydroid and young medusa).

Specific Characters

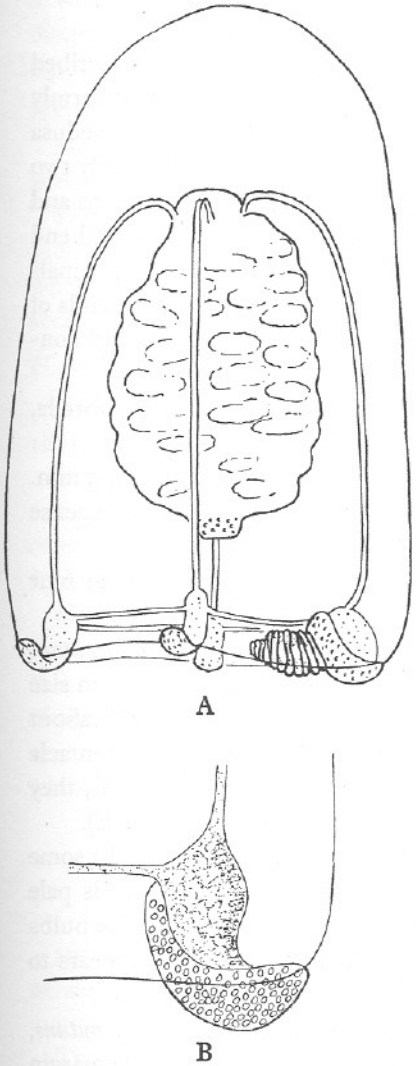
One short simple perradial marginal tentacle with nematocyst rings. Height up to 6 mm.

Description of Adult

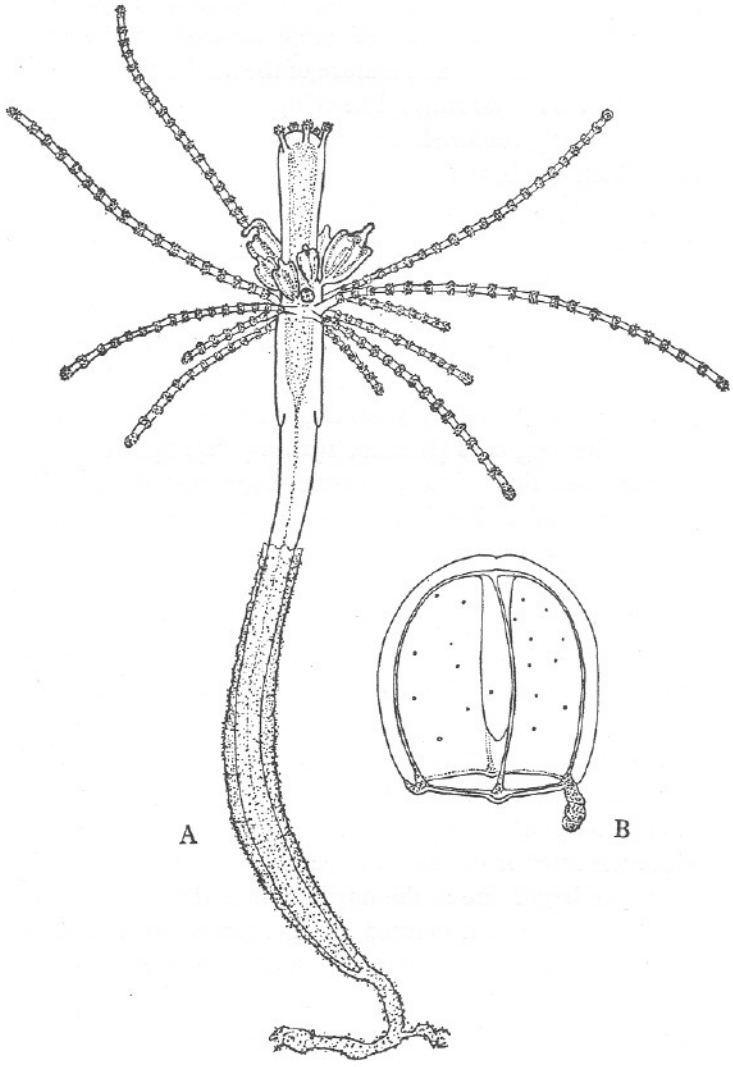
Umbrella bell-shaped, higher than broad; apex rounded, without pointed apical process; jelly thick, especially in apical region; umbrella margin at right angles to vertical axis; without exumbrellar nematocyst tracks. Velum fairly wide. Stomach large, cylindrical, about two-thirds the length of subumbrellar cavity; with rounded apex; in full extension never reaching beyond umbrella margin. Mouth simple and circular, surrounded by nematocysts. Four radial canals and ring canal narrow. Gonads completely surrounding stomach, leaving upper end of stomach and mouth free; eggs amoeboid. One single short perradial marginal tentacle with numerous nematocyst rings; three non-tentacular perradial marginal bulbs, smaller than tentacular bulb, extending as spurs slightly up exumbrellar surface. Height from 3·5 to 6 mm. Colour of stomach yellow, often splashed with crimson at oral end; ring canal occasionally with crimson pigment; tentacular and non-tentacular marginal bulbs yellowish to crimson, sometimes colourless; marginal tentacle yellow.

Distribution

The medusa *Euphysa aurata* occurs commonly in British waters along the western, northern and north-eastern coasts of the British Isles. Thus it has been recorded at various points from



Text-fig. 38. *Euphysa aurata*. A, preserved specimen 5 mm. high, showing marginal tentacle bent inwards, Isle of Muck, west Scotland, 9. vi. 37 (collected by Mrs E. A. T. McEwen); B, enlarged view of non-tentacular marginal bulb of same, slightly contracted inwards.



Text-fig. 39. *Euphysa aurata*. A, the hydroid, *Heteractis aurata*, Herdla, Norway, 12. viii. 37; B, newly liberated medusa, Herdla, Norway, 11. viii. 37. (After Rees, 1938, fig. 8.)

Plymouth to the Northumberland coast, including Valencia, Ireland. It does not appear to have been recorded from the south-eastern region of the British Isles either in the North Sea or English Channel. It is common off the mouth of the English Channel but is not common as far east as Plymouth.

Elsewhere it has been recorded along the north-east European coasts as far as the Murman coast, from west Greenland, and from the Mediterranean. Künne (1937*b*) states that it is a visitor in the western Baltic. Thiel (1938) records this species from the Patagonian Bank in the South Atlantic.

Developmental Stages and Structural Details

The living medusa, when newly liberated from its hydroid (Text-fig. 39B), has been described by Rees (1938). The umbrella is bell-shaped, *c.* 0·6–1·0 mm. in height; the jelly is uniformly thin and there are a few scattered nematocysts on the exumbrella. In other respects the medusa is at this stage merely a miniature of the adult. The solitary marginal tentacle has at first only two or three nematocyst rings. The coloration is variable, some medusae being almost colourless and others brightly coloured. In the latter the stomach is yellow with a crimson spot at its oral end and sometimes brownish pigment at its base; the ring canal and junctions of the radial canals with the ring canal are vivid scarlet or crimson, with a few black pigment granules at the ends of the radial canals; the marginal tentacle is golden yellow, and the marginal tentacle bulb and non-tentacular marginal bulbs are crimson above and yellow below.

The only change with the growth of the medusa is the thickening of the jelly of the umbrella, especially in the apical region, and the lengthening of the marginal tentacle.

The gonads develop rapidly and specimens may already be mature when the medusa is 2·5 mm. in height. The mature eggs are large, amoeboid, and few in number, having grown at the expense of the other egg cells (Kramp, 1926*a*, p. 25, fig. 21).

A cross-section of the stomach shows that the ectodermal musculature is confined to four narrow, perradial, longitudinal bands (Kramp, 1926*a*, p. 26).

In adult medusae the marginal tentacle is considerably shorter than that of *Steenstrupia nutans* and the nematocyst rings are consequently fewer. In preserved specimens up to 2·5 mm. in size Sanderson (1930, p. 223) counted six to twenty-six nematocyst rings, there being mostly about fifteen. According to Hartlaub (1907, p. 83, fig. 78) the nematocyst rings of the marginal tentacle of this species are wider than those of *S. nutans*. In specimens I have examined, however, they appear to be approximately the same size and shape in the two species (Text-fig. 35D, E).

The colour of the tentacular and non-tentacular marginal bulbs varies considerably. In some specimens the three non-tentacular bulbs may be colourless, while the tentacular bulb is pale yellow. Most specimens, however, have yellow or orange pigment in the lower part of the bulbs while the interior of the bulb may be crimson (Browne, 1895, p. 249). The medusa appears to grow to a larger size in the north than in the south.

The absence of a pointed apical process distinguishes this species at once from *S. nutans*, and the horizontal umbrella margin distinguishes it from *Hybocodon prolifer* in which the margin slopes at an angle to the horizontal axis. In preserved specimens of *Euphysa aurata*, however, the side opposite the tentacular bulb is sometimes more contracted giving the umbrella margin the sloping appearance characteristic of *Hybocodon prolifer*. The characters which then distinguish *Euphysa aurata* from sexual specimens of *Hybocodon* with a single marginal tentacle are to be found in the form and structure of the non-tentacular marginal bulbs. In *Euphysa aurata* these bulbs are continued up the exumbrellar surface as short clasping spurs (Text-fig. 38B), while in *Hybocodon prolifer* they are almost completely reduced, consisting merely of endodermal dilatations of the canal system. In many preserved specimens of *Euphysa aurata* the marginal tentacle will be found to be tucked inwards towards the subumbrellar cavity (Text-fig. 38A). The stomach also may be contracted up to half the subumbrellar height.

Seasonal occurrence

On the northern coasts of the British Isles *E. aurata* is common in the plankton during the summer months June to August; it first appears usually in March or April, and may continue in small numbers throughout the autumn and winter until January. In the south-west its seasonal distribution is somewhat similar, the medusa having been recorded at Valencia, for instance, from April to November.

HYDROID. *Heteractis aurata* (Forbes).

(For full description see Rees, 1938, *Journ. Mar. Biol. Assoc.* vol. XXIII, p. 25, figs. 8, 9; and Broch, 1937, *Avh. Norske Vid. Akad. Oslo*, I. Mat.-Nat. Kl., no. 8, p. 1.)

Polyp solitary, up to *c.* 4–8 mm. in height; perisarc of hydrocaulus a transparent membranous tube with adhering mud particles; basal end with anchoring filaments. Hydranth with one whorl of three to ten short capitate oral tentacles and one whorl of six to twenty long moniliform aboral tentacles. Medusa buds borne on hydranth just above aboral tentacles.

Historical

The medusa *Euphysa aurata* was first described by Forbes (1848) from a specimen taken in 1835 in Brassay Sound, Shetland Islands. He placed it in his new genus *Euphysa*.

It was not until quite recently that the identity of its hydroid was discovered by Broch (1937) and Rees (1938). This proved to be the species described by M. Sars (1860) as *Corymorpha annulicornis*. This is probably the same hydroid as that described by E. S. Russell (1906) as *Trichorhiza brunnea*.

Euphysa aurata has its counterpart on the American side of the North Atlantic in the medusa *E. virgulata* (A. Agassiz, 1865). It has been suggested by some authors (e.g. Bigelow, 1914*b*, p. 5) that the two species may be synonymous, the only difference being the considerably larger size of the American medusa. The hydroid of *E. virgulata* has not yet been identified, but it seems quite possible that it will prove to be that described by Miles (1937) as *Dahlgrenella farcta*, which closely resembles the European hydroid (see Kramp, 1949).

INCERTAE SEDIS

Genus **Eucodonium** Hartlaub, 1907

MEDUSAE. ? Tubulariidae with umbrella without pointed apical process; without exumbrellar nematocyst tracks; with stomach attached to peduncle; with asexual budding; with four perradial marginal tentacles each with terminal knob of nematocysts.

The genus *Eucodonium* was erected by Hartlaub (1907) for the rare species *E. brownei* (Hartlaub) first recorded by Browne as *Dipurena* sp. (?). Since so little is known of its life history its relationship is uncertain, but it is provisionally regarded as a tubulariid since it has a simple mouth and there are no ocelli on the marginal tentacle bulbs.

Eucodonium brownei Hartlaub

Text-fig. 40

Dipurena sp.? Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 473, pl. xvi, fig. 2.
Eucodonium brownei Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 71, fig. 67.
Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien*, Tom. XX, p. 36, pl. i, fig. 6.
Kramp, 1927, *K. danske vidensk. Selsk. Skr.* natur. og math. Afd., 8. Raekke, XII, p. 37.

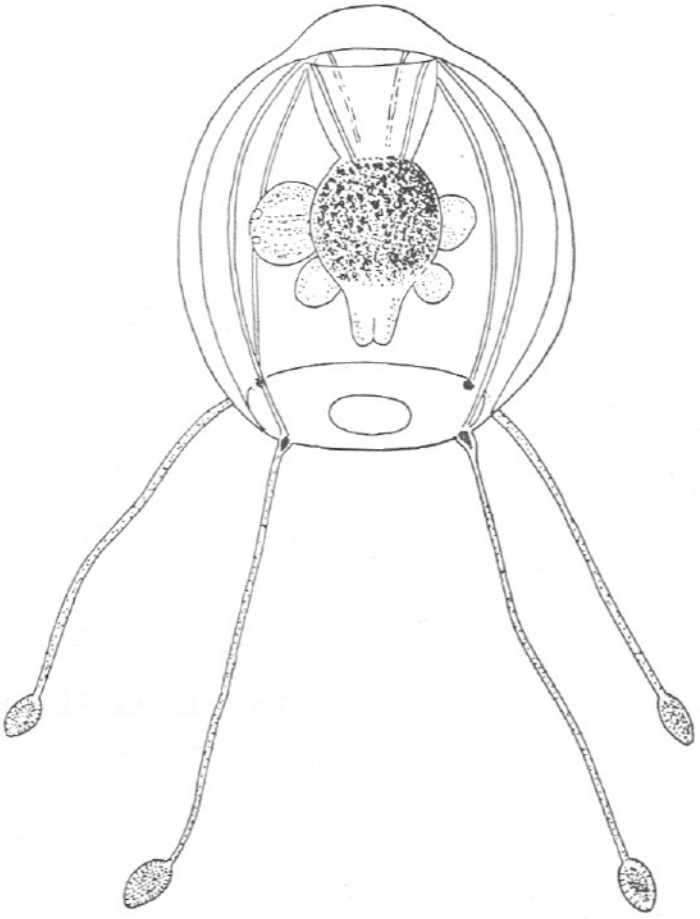
TUBULARIIDAE

Specific Characters

Stomach attached to peduncle; medusa buds borne on stomach; four perradial marginal tentacles each with terminal knob of nematocysts.

Description of Adult

Umbrella nearly hemispherical, with slight rounded apical projection; margin of umbrella somewhat four-cornered; jelly fairly thin. Velum broad. Stomach short, cylindrical, with conical peduncle; mouth simple, tube-like. Four narrow radial canals. Medusa buds carried on stomach. Four perradial marginal tentacles, thin, thread-like, extending to twice the height of umbrella, with irregularly distributed nematocysts and large terminal knob containing nematocysts. Marginal tentacle bulbs small, apparently without ocelli. Diameter about 1 mm. Colour of marginal tentacle bulbs blackish, stomach blackish brown, and terminal knobs of marginal tentacles brownish.



Text-fig. 40. *Eucodonium brownei*. Plymouth, 10. ix. 95. (After Browne, 1896, pl. xvi, fig. 2.)

Distribution. Plymouth, North Sea, Adriatic.

Historical

This species was first found by Browne (1896*a*, p. 473) at Plymouth on 10 September 1895. Browne found two medusae on which he based his description of the species as *Dipurena* sp. (?). It has not been again recorded in British waters. Hartlaub (1907, p. 71) raised for it a new genus, under the name *Eucodonium brownei*. Neppi (1912) and Neppi & Stiasny (1913*a*, p. 36, pl. i, fig. 6) found this species in the Adriatic and described and figured it, and it was later recorded again by Neppi (1922). Their description agrees in all essentials with that of Browne, except that the manubrium is shorter, and the marginal tentacles shorter and thicker. These differences may only be due to contraction. They record the species as rare and found in October. Kramp (1927, p. 38) records one specimen from Schultz's Ground in the Kattegat on 20 March 1901.

The sexual stage of this species of medusa has not yet been found, nor is its hydroid known.

FAMILY MARGELOPSIDAE

Anthomedusae with umbrella without apical projection; without exumbrellar nematocyst tracks; with stomach not extending beyond umbrella margin; with simple circular mouth; with gonads completely surrounding stomach; with solid marginal tentacles in perradial clusters on margin or at different levels on exumbrella; without ocelli on marginal tentacle bulbs.

Hydroids pelagic.

The family Margelopsidae is represented in British waters by a single genus *Margelopsis* Hartlaub.

Genus **Margelopsis** Hartlaub, 1897

Margelopsid medusae with marginal tentacles in perradial clusters on margin of umbrella.

HYDROID. *Margelopsis.*

The only species of this genus which might occur in British waters is *Margelopsis haeckeli* Hartlaub. It cannot be confused with any other British medusa.

Margelopsis haeckeli Hartlaub

Text-figs. 41 A–C, 42 A, B

Margelopsis haeckeli Hartlaub, 1897, *Wiss. Meeresuntersuch.* N.F., Bd. II, Abt. Helgoland, Heft 1, x, p. 482, pl. xvi*b*, figs. 12–18.
Hartlaub, 1899, *K. Gesellsch. Wiss. Göttingen*, math.-phys. Kl., Heft 2, p. 219, figs. 1–3 (hydroid).
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, pp. 89, 91, figs. 84–6 (hydroid and medusa).
Mayer, 1910, *Medusae of the World*, vol. I, p. 80, fig. 38.
Kramp, 1930, *Mém. Mus. Roy. Hist. Nat. Belgique*, Mém. no. 45, p. 12.
Leloup, 1929, *Ann. Soc. Zool. Belge*, tome LX, p. 97, 1 fig. (hydroid).

Specific Characters

Marginal bulbs each with three to five rather stiff, solid tentacles.

Description of Adult

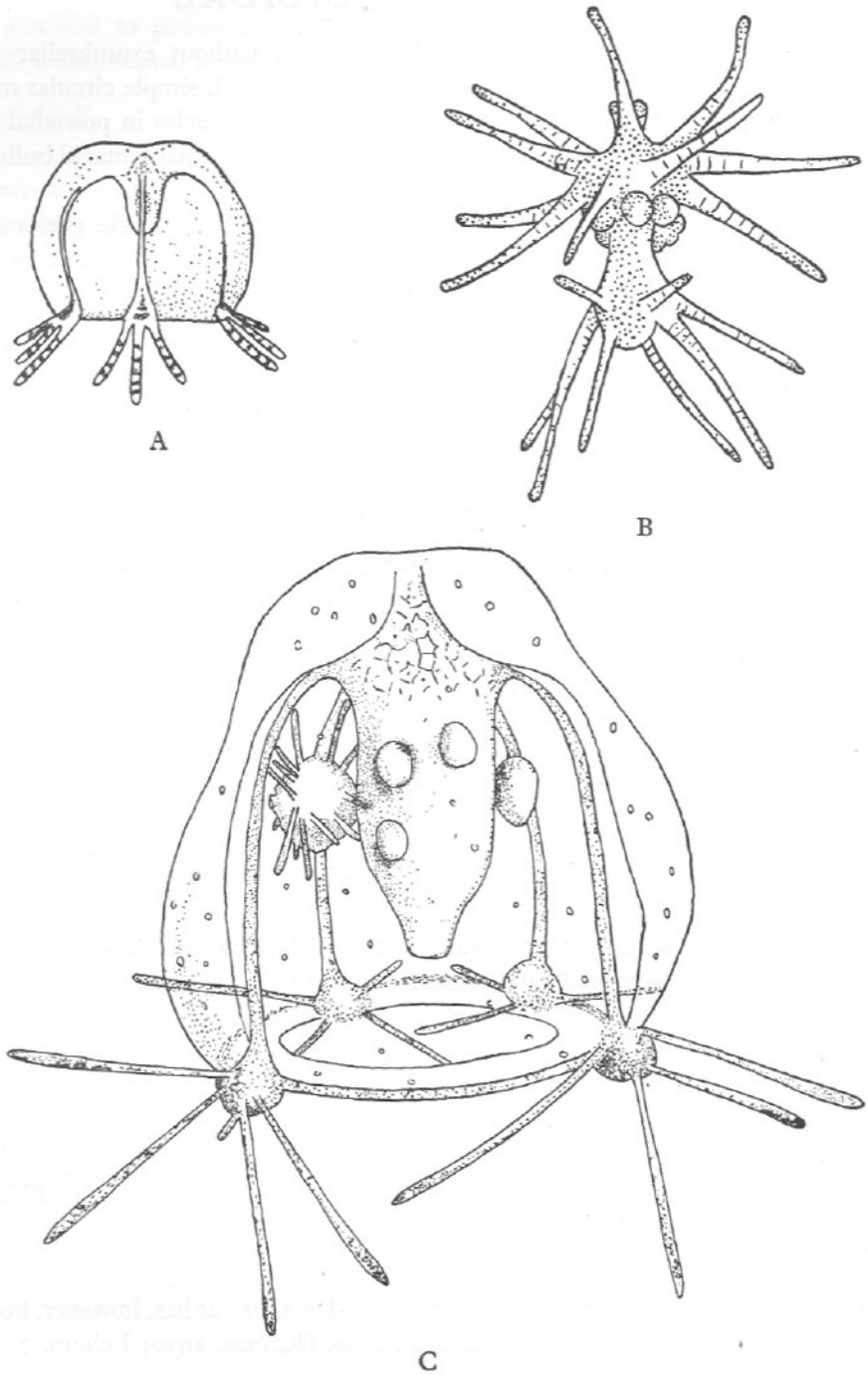
Umbrella bell-shaped, slightly higher than wide, without apical process; with scattered exumbrellar nematocysts; jelly moderately thick. Velum broad. Stomach short cylindrical, not extending beyond umbrella margin; basal portion with large transparent endoderm cells. Mouth simple, circular, armed with nematocysts round margin. Four radial canals and ring canal narrow. Gonad completely surrounding stomach, leaving basal third free. Amoeboid eggs developing into actinulae in subumbrellar cavity. Four perradial rounded marginal bulbs, each with three to five rather stiff, solid tentacles irregularly distributed, with scattered clusters of nematocysts. No ocelli. Height of umbrella 2 mm. Colour of stomach dark grey with dark brown pigment granules; marginal bulbs brown.

Distribution

Margelopsis haeckeli has not been recorded from British waters. It has, however, been recorded from Helgoland (Hartlaub, 1907) and the Belgian coast (Kramp, 1930; Leloup, 1929, hydroid only), and might be expected off our south-eastern coasts.

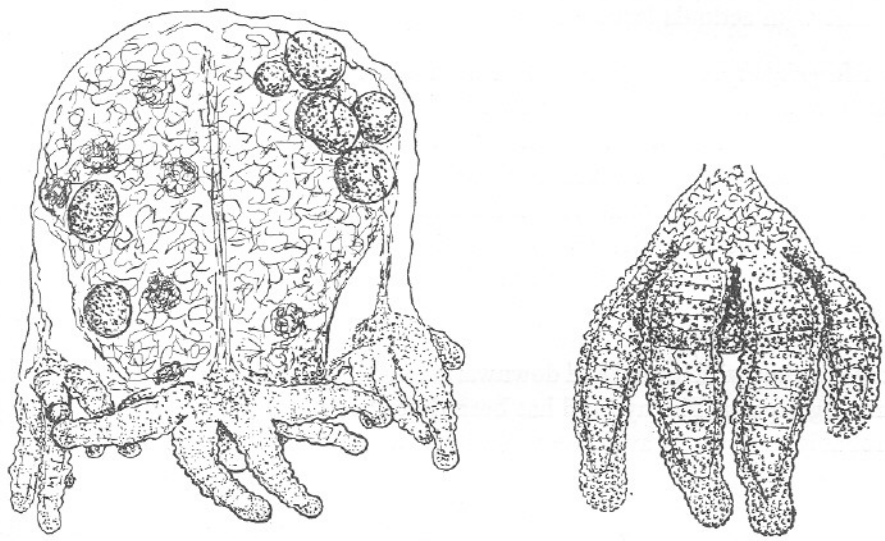
Developmental Stages and Structural Details

The medusa *Margelopsis haeckeli* is budded from a free-swimming hydroid. The early development of the medusa has been described by Hartlaub (1897).



Text-fig. 41. *Margelopsis haeckeli*. A, young medusa 0·5 mm. high; B, free-swimming hydroid with medusa buds; C, adult medusa with ripe gonad and actinula larva. (After Hartlaub, 1907, figs. 84–6.)

The umbrella of a very young specimen is 0·5 mm. in height (Text-fig. 41 A). It is relatively wider than in the adult. The apical jelly is thin. Nematocysts are evenly scattered over the exumbrella. There is a very broad umbilical canal. The stomach is half as long as in the adult and its length is less than half the height of the subumbrellar cavity. A circle of nematocysts surrounds the mouth-opening. The four radial canals and ring canal are narrow. There are no signs of gonads. The four perradial marginal bulbs each have three tentacles. The tentacles are covered with scattered clusters of nematocysts, but the base of the tentacle is free from nematocysts. The umbilical canal and marginal bulbs have black pigment.



Text-fig. 42. *Margelopsis haeckeli.* A, preserved specimen, much contracted, 51° 09′ N., 2° 43′ E., 10. vi. 14 (sent by P. L. Kramp); B, marginal tentacle cluster of above.

With further growth the umbrella becomes higher. In a specimen 1·5 mm. high the apical jelly is considerably thicker than that of the sides of the umbrella. There are many exumbrellar nematocysts. The umbilical canal has narrowed. The stomach is considerably longer. The upper third of the stomach is without gonads and has large transparent endoderm cells, covered with a thin layer of ectoderm. The gonad, which covers the lower two-thirds of the stomach, is still thin. The marginal bulbs each have three or four tentacles irregularly placed on the bulb. They have irregularly scattered nematocysts which appear as ring-like bands when the tentacle is contracted. The upper basal third of the stomach is clear and transparent in contrast to the opaque brownish grey appearance of the lower two-thirds.

Only a few of the amoeboid eggs ripen and these give rise to planulae attached to the stomach wall (Text-fig. 41 C). The structure and development of the eggs, the larger of which devour the smaller, have been described by H. Müller (1908).

Seasonal occurrence

Hartlaub recorded *Margelopsis haeckeli* in July and August from Helgoland. Kramp (1930) and Leloup (1929) recorded medusae and hydroids respectively from the Belgian coast in June.

According to Hartlaub the occurrence of the medusae is not constant from year to year. They may at times occur in great quantities, since Kramp (1930) records more than 2000 specimens in each sample taken in June 1910 off Ostende.

Habits

Hartlaub (1907) describes the medusa as swimming very energetically and jerkily. The short marginal tentacles are held out stiffly.

The planulae develop to the actinula stage in the subumbrellar cavity, and Kramp (1930) records that among thousands of specimens from the Belgain coast the vast majority were mature females with actinula larvae; there were very few males.

HYDROID. *Margelopsis haeckeli* Hartlaub (Text-fig. 41 B).

(For full description see Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 89, fig. 84; and Leloup, 1929, *Ann. Soc. Zool. Belge*, tome LX, p. 97, 1 fig., for histological details.)

Solitary free-swimming hydranth about 1 mm. in size. Hypostome conical; base handle-shaped. Two whorls of tentacles, twelve aboral, and six to seven oral. Aboral tentacles nearly as long as hydranth, oral tentacles somewhat shorter. Medusa buds borne on body of hydranth just above aboral tentacles and alternating with them. Older medusa buds have rudiments of tentacles on four marginal bulbs.

The hydroid swims with its oral end downwards, and the tentacles are spread out and apparently act as swimming organs. The hydroid has been described more fully in Hartlaub (1899) but this paper is probably less readily available to readers than Hartlaub (1907).

Historical

Margelopsis haeckeli was first described and figured, in considerable detail, by Hartlaub (1897) from Helgoland. The hydroid was described for the first time by Hartlaub (1899).

FAMILY ZANCLEIDAE

Anthomedusae with, or without, exumbrellar nematocysts confined to specialized tissue in form of oval or club-shaped patches or elongated tracks; with simple circular mouth; with four radial canals; with interradial gonads; with two or four hollow marginal tentacles, each with abaxial stalked capsules (or cnidophores) containing nematocysts, or without marginal tentacles; without ocelli.

Hydroids with irregularly distributed tentacles, either all capitate, or all filiform, or of both types.

The family Zancleidae is represented in British waters by one genus, *Zanclea* Gegenbaur.

Genus **Zanclea** Gegenbaur, 1856

MEDUSAE. Zancleidae with exumbrellar nematocyst armature; with two or four marginal tentacles.

HYDROID. *Zanclea*, with tentacles all capitate.

The only British species of the genus is *Z. costata* Gegenbaur. The structure of the marginal tentacles makes the medusa at once distinguishable from all other British species.

Zanclea costata Gegenbaur

Plate IV, figs. 1–3; Text-figs. 43–8

Zanclea costata Gegenbaur, 1856, *Z. wiss. Zool. Leipzig*, Bd. VIII, p. 229, pl. viii, figs. 4-7.
Haeckel, 1879, *System der Medusen*, p. 103.
Mayer, 1910, *Medusae of the World*, vol. I, p. 87, text-fig. 41; pl.viii, figs. 2, 3, 6, 7.
Vanhöffen, 1911, *Wiss. Ergebn. 'Valdivia'*, Bd. XIX (1925), Heft 5, p. 199, fig. 3.
Russell, 1938*c*, *Journ. Mar. Biol. Assoc.* vol. XXIII, p. 151, figs. 19-22.
Zanclea gemmosa McCrady, 1857, *Proc. Elliott Soc. Nat. Hist.* vol. I, p. 151, pl. viii, figs. 4, 5.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, figs. 115-18.
Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 188, pl. vii, fig. 3; pl. xliv, figs. 1, 2.
Mayer, 1910, *Medusae of the World*, vol. I, p. 88, pl. vi, fig. 7; pl. vii, fig. 5; pl. viii, figs. 4, 5.
Russell & Rees, 1936, *Journ. Mar. Biol. Assoc.* vol. XXI, p. 107, figs. 1-12 (hydroid and medusa).
Gemmaria gemmosa, McCrady, 1858, *Proc. Elliott Soc. Nat. Hist.* vol. I, p. 151.
A. Agassiz, 1865, *N. Amer. Acaleph.* p. 184, fig. 306.
Haeckel, 1879, *System der Medusen*, p. 104.
Fewkes, 1881*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. VIII, p. 150, pl. i, figs. 8-12.
Weill, 1934*b*, *Trav. Stat. Zool. Wimereux*, tome XI, p. 417, figs. 257–60.
Coryne implexa Alder, 1862, *Trans. Tyneside Nat. Field Club*, vol. V, pt. III, p. 227, pl. x, fig. 4.
Zanclea implexa, Allman, 1864*a*, *Ann. Mag. Nat. Hist.* (May), ser. 3, vol. XIII, p. 357.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 116, figs. 104, 106–11, 115.
Mayer, 1910, *Medusae of the World*, vol. I, p. 89, text-figs. 43, 44.
Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien*, Tom. XX, p. 38.
Gemmaria cladophora A. Agassiz, 1865, *N. Amer. Acaleph.* p. 184, figs. 307-10.
Haeckel, 1879, *System der Medusen*, p. 104.
Gemmaria implexa, Allman, 1871–2, *Monogr. Gymnobl. Hydroids*, pp. 224, 290, pl. vii (hydroid and medusa).
Hargitt, 1904, *Mitt. Zool. Stat. Neapel*, Bd. XVI, Heft 4, p. 574, pl. xxii, fig. 29.
Browne, 1905*a*, *Proc. Roy. Soc. Edinb.* vol. XXV, pt. ix, p. 750.
'Corynitis agassizii' Murbach, 1899, *Quart. Journ. Micr. Sci. Lond.* vol. XLII, pt. 3, p. 341, pl. xxxiv, figs. 11, 13.
Zanclea cladophora, Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 121, figs. 112-13.
Mayer, 1910, *Medusae of the World*, vol. I, p. 90.
Gemmaria implexa var. *neapolitana* Bruckner, 1914, *Z. wiss. Zool. Leipzig*, Bd. CXI, p. 460, text-figs. 7-24, pl. viii, figs. 3–14; pl. ix, figs. 16–25 (hydroid and medusa).
Güntherella implexa, Weill, 1934*b*, *Trav. Stat. Zool. Wimereux*, tome XI, p. 417.

Specific Characters

Two or four marginal tentacles each with stalked capsules or cnidophores on abaxial side which are oval, 0·02–0·03 mm. in length, and each containing two to five nematocysts.

Description of Adult

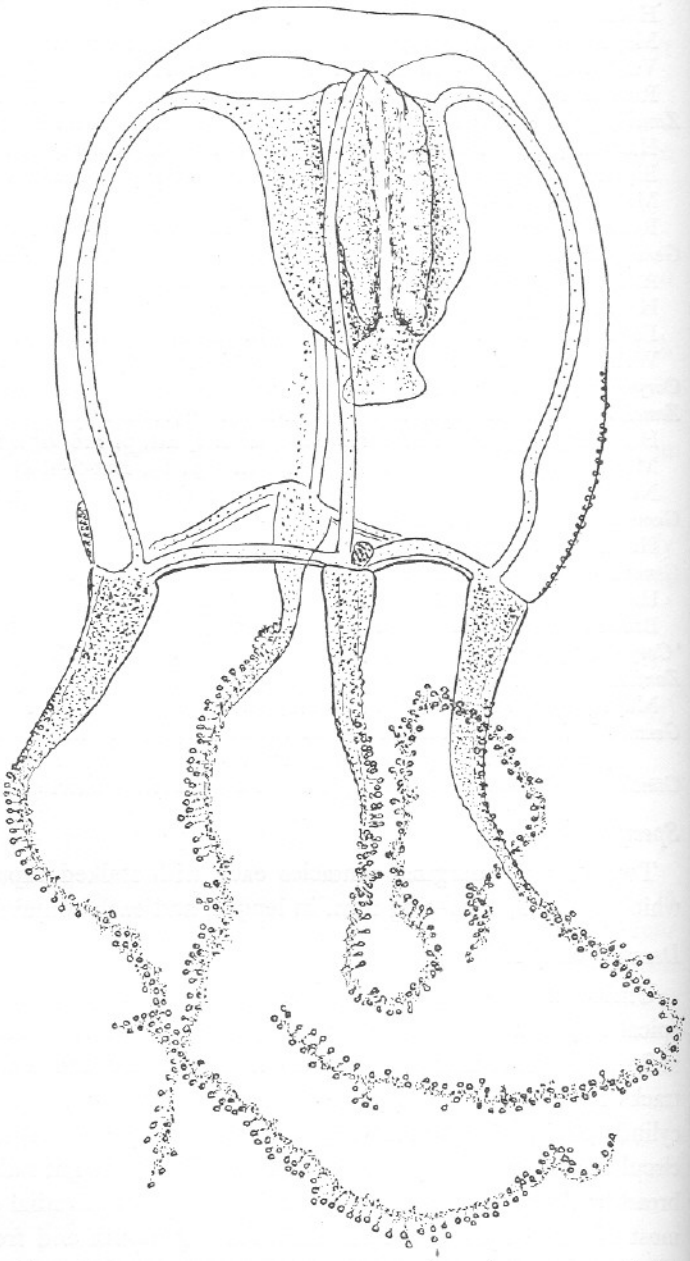
Umbrella bell-shaped, about as high as wide; jelly moderately thick, sometimes thicker in apical region and at sides near margin; exumbrellar nematocysts confined to specialized tissue in form of oval or club-shaped patches immediately above marginal bulbs or elongated meridional tracks running for varying lengths towards summit of umbrella. Velum fairly broad. Stomach cylindrical, in full extension reaching nearly to, but not beyond, umbrella margin. Mouth simple, circular, with nematocysts along margin. Four straight radial canals and ring canal of moderate breadth; linear thickenings along middle regions of radial canals. Gonads interradial, covering most of the length of the stomach, leaving mouth end free. Two opposite perradial marginal tentacles and two opposite perradial non-tentacular marginal bulbs, or four perradial marginal tentacles. Marginal tentacles with elongated conical bases and stalked capsules or cnidophores along their abaxial surfaces; each cnidophore oval in shape, 0·02–0·03 mm. in length, and containing two to five nematocysts. Height of umbrella usually 1·5–3·0 mm. Colour of stomach pale yellow, radial canals and ring canal pink; marginal tentacle bulbs reddish or orange.

ZANCLEIDAE

Distribution

The medusa *Zanclea costata* has been recorded in the plankton from British waters from the Firth of Clyde, Port Erin, Plymouth and Valencia. Its hydroid has also been recorded from the south-east of Scotland and off the Northumberland coast. From its known distribution it is likely to be found all round the British coasts but it is usually taken only in small numbers.

Elsewhere it has been recorded from Norway, the Belgian coast, the Mediterranean, the American coasts of the North Atlantic, the Tortugas, the Red Sea, and the Pacific. It is apparently a very widespread species.



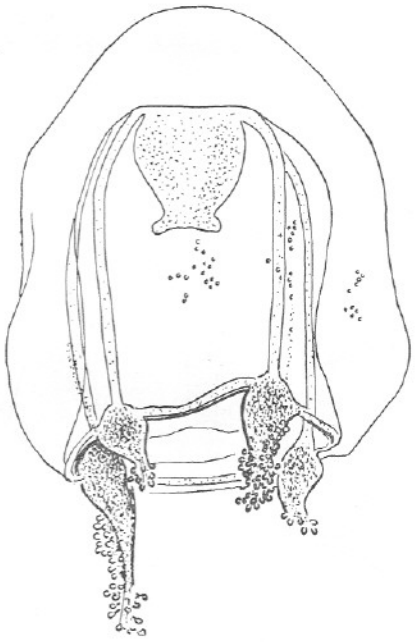
Text-fig. 43. *Zanclea costata*, preserved specimen 2 mm. high, male, off Plymouth, 30. viii. 37.

Developmental Stages and Structural Details

When newly liberated from the hydroid the medusa is about 0·6–0·7 mm. in height (but 1·8 mm. in American waters, Weill, 1934*b*). The umbrella is bell-shaped and its margin appears somewhat square. The jelly is uniformly thin. There are four perradial patches of exumbrellar nematocysts, each of which is narrow basally and enlarges distally into an oval; each aggregation is thus somewhat spoon-shaped. Each arises from the base of a tentacular or non-tentacular marginal bulb and extends upwards over the exumbrella for about one-third of its height. The oval portions contain four to seventeen large nematocysts, and there may be none to four in the narrow basal portions. When seen in side view the triggers of the cnidoblasts appear to be pushing up the thin covering membrane. There are usually fewer exumbrellar nematocysts on the non-tentacular radii than on the tentacular radii. The stomach is cylindrical and its length is about half the height of the subumbrellar cavity. The mouth is simple and

circular and its margin is armed with nematocysts. The four radial canals and ring canal are narrow. The gonads are not apparent. There are two opposite perradial marginal tentacles and two opposite perradial non-tentacular marginal bulbs. Each marginal tentacle has about fifty stalked capsules or cnidophores along its abaxial side, each containing two to five nematocysts. The capsules are about 0·018–0·02 mm. long and 0·013 mm. broad. Medusae are occasionally liberated in which the marginal tentacles are greatly reduced in size and have much fewer, or (rarely) no, capsules. The bases of the marginal tentacles are filled with nematocysts. The colour of the stomach and tentacular and non-tentacular marginal bulbs is salmon pink.

The development of the medusa has been described by Russell & Rees (1936). As the medusa grows the jelly of the umbrella may become thickened at the apex and in the regions of the lower perradii. A number of fine opaque dots appear on the umbrella arranged roughly in circles. At the same time the exumbrellar nematocyst patches change in shape and elongate to form continuous narrow lines extending upwards over half the height of the umbrella or more. The nematocysts are then arranged in a single row, with an occasional pair lying side by side. The stomach increases in length but does not extend beyond the umbrella margin. Each of the four radial canals increases in width and linear swellings are developed along the middle portion of each canal. The gonads develop interradially on the stomach wall. The two opposite perradial marginal tentacles increase greatly in length and when fully developed may have as many as 300 or more stalked capsules each about 0·022–0·03 mm. in length. At the same time the two opposite perradial marginal bulbs, which at the time of the liberation of the medusa have no tentacles, may or may not develop tentacles. Adults may thus be found with either two or four marginal tentacles. Although medusae with four marginal tentacles have not yet been reared from the hydroid, intermediate stages have been found in the plankton which show that adult medusae with four tentacles have only two when young. The colour of the tentacular or non-tentacular marginal bulbs becomes yellowish and a diffuse patch of red is developed on the abaxial side of the bulb.

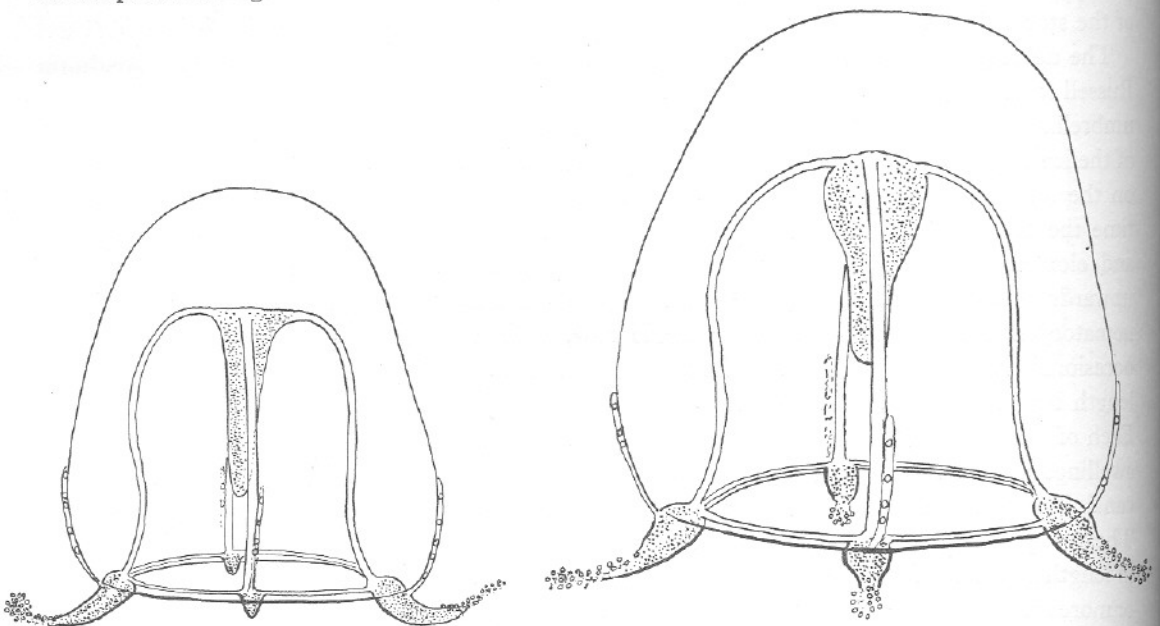


Text-fig. 44. *Zanclea costata*, preserved specimen 1·5 mm. high, Plymouth, 20. v. 37.

The formation of the patches of exumbrellar nematocysts has been a subject of discussion (see, e.g. Weill, 1936*a* and Ranson, 1937). The nematocysts appear at first glance to be in oval vesicles on the exumbrella connected with the marginal bulb by a hollow canal. Actually this structure is not hollow, but solid. The nematocysts probably migrate through this solid tissue from the marginal bulbs. It has been mentioned above that as the medusa grows these patches elongate to form narrow lines of nematocysts. It is probable that eventually their connexion with the marginal bulb may be broken, for I have seen a specimen (Text-fig. 43) in which, while two were normal and elongated, two consisted of large oval patches just above the bases of the marginal tentacles. It appears that these latter two may have been regenerating and we must be cautious against laying too much stress on the form of the nematocyst patch in the adult medusa as a possible specific character.

ZANCLEIDAE

The structure of the marginal tentacles in *Zanclea costata* is remarkable (Text-figs. 46, 47). They are extremely extensile and carry on their abaxial surfaces the numerous small capsules or cnidophores which are attached by contractile stalks. The capsules themselves consist of a single layer of cells completely enclosing the cavity in which the nematocysts lie. The capsules have long cirri which when in motion impart a curious vibrating movement, which is only occasionally seen. The nematocysts in the capsules have no cnidoblasts. The cnidophores are not developed on the proximal region of the basal bulb.



Text-fig. 45. *Zanclea costata*, Plymouth, 20. v. 37. A, 1·5 mm. high; B, 2 mm. high.

Both the stalks by which the capsules are attached and the marginal tentacles themselves are composed of a remarkably contractile tissue which is capable of putting out pseudopodia-like processes. The capsule stalks may contract spirally or in quite an irregular fashion.

Brückner (1914) made a careful histological examination of the medusa from the Mediterranean. He found that the stalks and marginal tentacles are composed of a number of nucleated ectoderm cells which are able to alter their shapes considerably, and that through the stalk there runs a fine thread, which he considered to be a muscle. Allman (1872) on the other hand thought that the stalks consisted of a simple granular protoplasm; and Weill (1934*b*, p. 421), working on American medusae, emphatically denied that the stalk is composed of cellular tissue. He could see no nuclei and considered that it was composed of a completely hyaline protoplasmic mass; he maintained that the structure of the marginal tentacle itself was similarly composed of hyaline protoplasm. Specimens from Plymouth stained and mounted by Dr W. J. Rees show nuclei exactly as Brückner has figured them. Zoia (1895*b*, pl. iv, figs. 121–3) gives figures of the blastula and primary polyps reared from medusae in the Mediterranean.

NEMATOCYSTS. Stenoteles; macrobasic telotrichous euryteles; and ? atrichous haplonemes (Russell, 1938*b*).

Seasonal occurrence

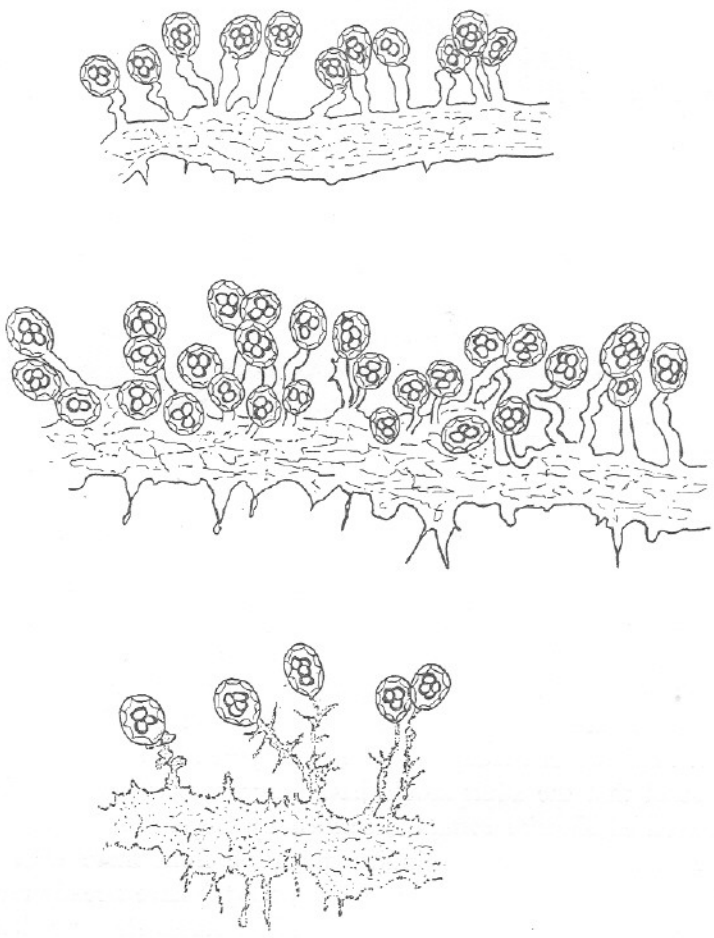
Zanclea costata has been recorded from the plankton off the south-west coasts of the British Isles in May, June, July, August and September; it has been recorded from the Firth of Clyde in May and Port Erin in September.

Habits

The curious structure of the marginal tentacles gives the living medusa a remarkable appearance that has always excited the attention of those who have seen it. The marginal tentacles and the stalks of the capsules are capable of very great extension. Allman (1872) says: 'The peduncles of these sacs are singularly extensile, and may sometimes be seen stretched out to a great length, carrying the sacs on their extremities, and giving to the tentacles the appearance under the naked eye of being covered with a dense growth of some parasitic mould. On being touched they immediately contract, and become closely aggregated along the tentacles.'

Medusae were reared from the hydroid by Russell & Rees (1936) but considerable difficulty was experienced in getting the medusae to grow. They were fed on copepod nauplii and other small plankton organisms but showed no desire to feed on their own, having usually to be forcibly fed by pushing the food through the velar aperture to the mouth.

The medusa swims quite normally and energetically like other medusae, with its marginal tentacles contracted.



Text-fig. 46. *Zanclea costata*, Plymouth. Portions of marginal tentacles of preserved specimen 2 mm. high.

HYDROID. *Zanclea costata* Gegenbaur (Text-fig. 48).

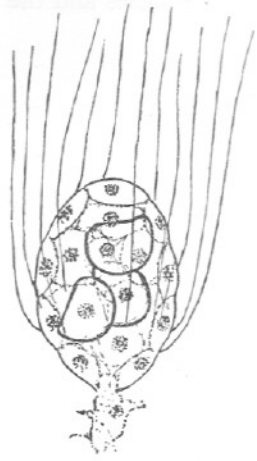
(For full description see Allman, 1872, *Monogr. Gymnobl. Hydroids*, pp. 223, 290, pl. vii, figs. 1–10; and Russell & Rees, 1936, *Journ. Mar. Biol. Assoc.* vol. XXI, p. 107, figs. 1–12. For synonymy see Russell & Rees, 1936, p. 124.)

Colonies of single hydranths from 2 to 10 mm. in height. Perisarc surrounding base of each hydranth irregularly corrugated, sometimes ringed at base. No visible perisarc in young colonies.

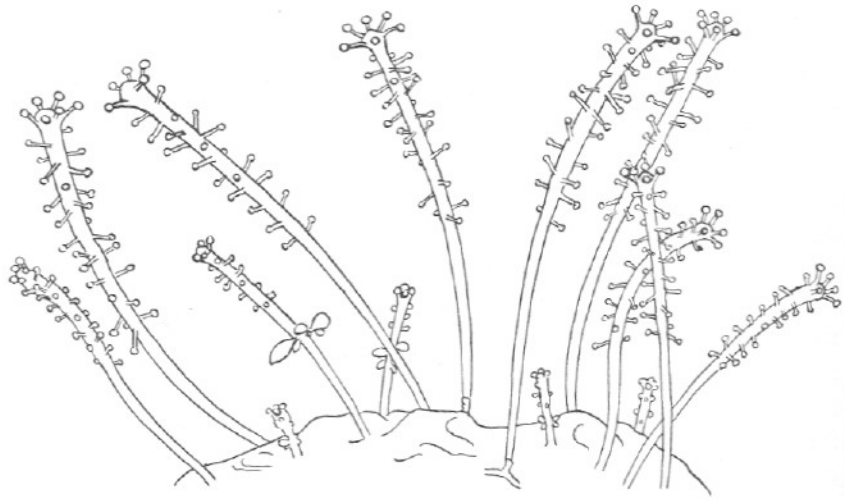
ZANCLEIDAE

About forty to fifty capitate tentacles irregularly distributed over body of hydranth, with a tendency sometimes towards verticillate arrangement, and always an apical whorl of four to six tentacles. Medusa buds borne usually at base of hydranth below tentacles, but may occur among tentacles; medusiferous hydranths often reduced to mere blastostyles. Hydranths reddish with opaque white probosces.

This hydroid is commonly found in association with the encrusting polyzoa, *Cellepora avicularis* Hincks, at Plymouth, and has also been recorded elsewhere associated with polyzoa.



Text-fig. 47. *Zanclea costata*. Cnidophore of marginal tentacle of newly liberated medusa.



Text-fig. 48. *Zanclea costata*. Hydroid. Plymouth, 28. iii. 36. Height of tallest polyp *c.* 10 mm. (After Russell & Rees, 1936, fig. 3.)

Historical

The medusa *Zanclea costata* was first described and figured by Gegenbaur (1856) from the Mediterranean. The young stages of the medusa were described by McCrady (1858) from Charleston Harbour on the American coast of the Atlantic as *Z. gemmosa*. The first description in British waters was given by Alder (1862) from medusae liberated by the hydroid, as *Z. implexa*. McCrady suggested the generic name *Gemmaria* for his medusa if it should be found that the adult should have only two marginal tentacles, to distinguish it from the four-tentacled *Zanclea costata* described by Gegenbaur (1856). The medusae with four marginal tentacles are otherwise indistinguishable from those with two marginal tentacles and some authors (e.g. Mayer, 1910; Browne, 1905*a*) have already regarded them as probably the same species. The occurrence of intermediate stages showing that the medusae with four marginal tentacles have at first only two strengthens this view and they are here regarded as one species.

There has also been considerable discussion on the identity of the European and American species of *Zanclea* based chiefly on the fact that the American hydroid had apparently no visible perisarc on the hydrocaulus while the European species had a hydrocaulus. On these grounds the two hydroids were placed by some workers in different genera, the American hydroid being regarded as *Gemmaria* McCrady or *Halocharis* Agassiz, and the European species as *Zanclea* Gegenbaur. Russell & Rees (1936) have, however, shown that the development of the perisarc in the British hydroid is dependent on the age of the colony, the young colonies having none visible. A specimen had also been recorded from America by Murbach (1899) with well developed

perisarc. On these grounds the European and American species were united. A full bibliography of the genus *Zanclea* is given by Russell & Rees.

It appears that attention must be paid by future workers to the size and shape of the stalked capsules on the marginal tentacles. Vanhöffen (1911, p. 200, fig. 4) records specimens in which these capsules are three times as large as in *Z. gemmosa*, reaching a length of 0·06 mm. Vanhöffen (1911) and Mayer (1910) also refer to *spherical* capsules in species with two marginal tentacles which they regarded as *Z. costata*. It is, however, to be noted that on preservation the oval capsules of *Z. gemmosa* often contract slightly so as to assume a spherical form.

Workers in the past have also based specific or generic distinction on the form of the exumbrellar nematocyst canals, regarding specimens with long narrow canals as distinct from those in which the canal dilated into an apical sac. This also is only a matter of the extent of development of the medusa. In this connexion it seems possible that *Zanclea orientalis* Browne (1916), from the Indian Ocean, may prove to be the same species.

Family CLADONEMIDAE

Creeping and swimming Anthomedusae; with mouth with short lips armed with nematocyst clusters; with stomach with perradial pouches; with variable number of radial canals, some branched, some simple, final number of canals entering ring canal usually of same number as marginal tentacles; with gonads completely surrounding stomach; with variable number of hollow branching marginal tentacles, each furnished with organs of adhesion; with ocelli.

Hydroid with single oral whorl of capitate tentacles, and aboral whorl of reduced filiform tentacles.

The family Cladonemidae is represented in British waters by one genus, *Cladonema* Dujardin, 1843.

Genus **Cladonema** Dujardin, 1843

Characters as family.

The only British species of the genus is *Cladonema radiatum* Dujardin. Its characters are so distinctive that it cannot be confused with any other British species.

Cladonema radiatum Dujardin

Text-figs. 49–51

Cladonema radiatum Dujardin, 1843*a*, *Ann. Sci. nat. Paris* (2), tome xx, p. 271, pl. xv; 1843*b*, *C.R. Acad. Sci. Paris*, tome xvi, p. 1132.
Dujardin, 1845, *Ann. Sci. nat. Paris* (3), tome iv, p. 271, pl. xiv, figs. C1–C7; pl. xv, figs. C8–C19.
Krohn, 1853, *Müller's Arch. Anat. Physiol.* p. 420, pl. xiii.
Keferstein & Ehlers, 1861, *Zool. Beiträge . . . Neapel und Messina*, p. 85, pl. xiii, fig. 5.
Van Beneden, 1866, *Mém. Acad. R. Belg.* vol. xxxvi, p. 139, pl. xii.
Hincks, 1868, *Brit. Hydroid Zooph.* p. 62, pl. 11.
Allman, 1871–2, *Monogr. Gymnobl. Hydroids*, pp. 96, 216, 217, 257, pl. xvii.
Hincks, 1872*b*, *Ann. Mag. Nat. Hist.* ser. 4, vol. x, p. 391, pl. xxi, fig. 6.
Haeckel, 1879, *System der Medusen*, p. 109.
Hartlaub, 1887, *Zool. Anz. Leipzig*, x. Jahrg., no. 266, p. 651.
Billard, 1905, *Bull. Mus. Hist. Nat. Paris*, tome xi, p. 500.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, xii, p. 132, figs. 123–5.
Coryne stauridia Gosse, 1853, *Naturalist's Rambles on Devonshire Coast*, p. 257, pl. xvi, figs. 1–5 (hydroid only).
Eleutheria radiata, Lengerich, 1922*a*, *Zool. Anz. Leipzig*, Bd. liv, p. 210, fig. 1.
Lengerich, 1923, *Zool. Jahrb. Jena* (Anat.), Bd. xliv, p. 313, figs. G–S.

CLADONEMIDAE

Specific Characters

One to four, usually three, adhesive organs on base of each marginal tentacle.

Description of Adult

Umbrella bell-shaped, slightly higher than broad; jelly moderately thin, sometimes with a slight apical projection. Velum very broad. Stomach spindle-shaped, with usually five, sometimes four, perradial pouch-like outgrowths in its middle region. Mouth with usually five, sometimes four, short protuberances or lobes, each armed with nematocyst clusters. Stomach not extending beyond umbrella margin. Usually five, sometimes four, thin primary radial canals some of which bifurcate to form usually eight, sometimes ten, radial canals in all; ring canal narrow. Gonads completely surrounding stomach on its upper two-thirds. Usually eight, sometimes ten, marginal tentacles, corresponding to the number of radial canals. Marginal tentacles branched, with elongated thickened bases from the under side of which grow one to four, usually three, adhesive organs. The branched portions of the marginal tentacles are beset with numerous nematocyst clusters. There is an ocellus on the abaxial side of the base of each marginal tentacle bulb. Height when full grown about 4 mm. Colour of stomach and marginal tentacles red, bright-red or brown; ocelli black or deep crimson.

Distribution

Round the British Isles *Cladonema radiatum* has been recorded from Falmouth, Ilfracombe, Bournemouth, Kent, and Valencia in south-west Ireland.* The hydroid and medusa turn up at times in aquaria, having been found at the Zoological Gardens and University College in London, and at Plymouth from material sent from Falmouth. It has been recorded elsewhere from the coasts of France, Belgium, Denmark (Limfjord), and Sweden and from the Mediterranean and Black Sea.

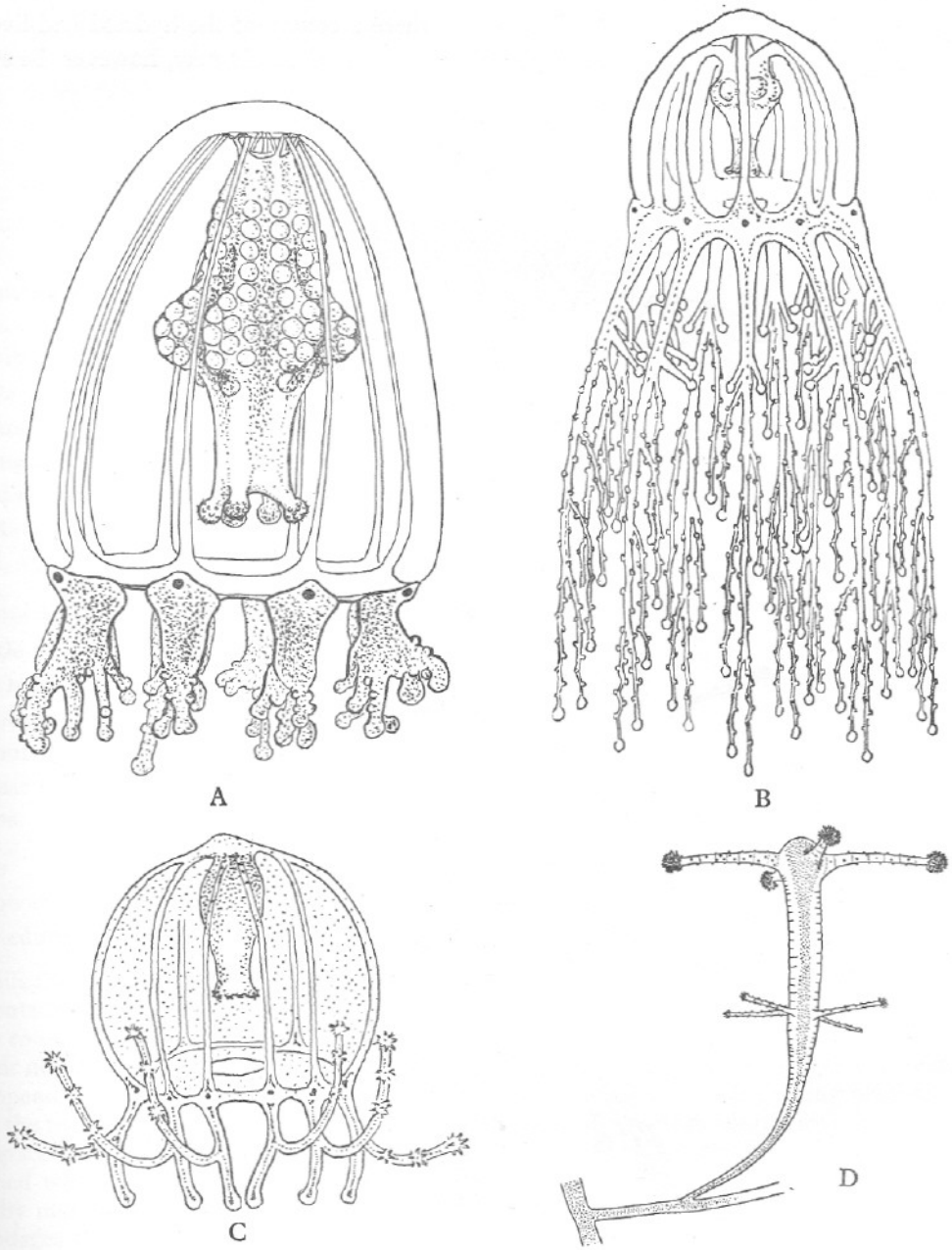
Developmental Stages and Structural Details

On liberation from the hydroid the medusae are about 1 mm. in height (Text-fig. 49C). The marginal tentacles are unbranched and there is only one adhesive organ. There are about five clusters of nematocysts on each marginal tentacle. At this stage it bears a close resemblance to young medusae of the genus *Eleutheria*.

As development proceeds the marginal tentacles increase in length and branch two or three times; additional adhesive organs are also developed until there are usually three. The stomach develops usually five pouch-like outgrowths in its middle region and is somewhat five-sided in cross-section. There are usually five primary radial canals, some of which bifurcate to form secondary canals, the others remaining unbranched throughout their courses. The final number of radial canals thus formed is usually eight. Billard (1905) examined fifty specimens of the same size from Saint Vaast-la-Hougue, France, with the following results:

No. of specimens	No. of radial canals
4	7
39	8
1	9
5	10
1	11

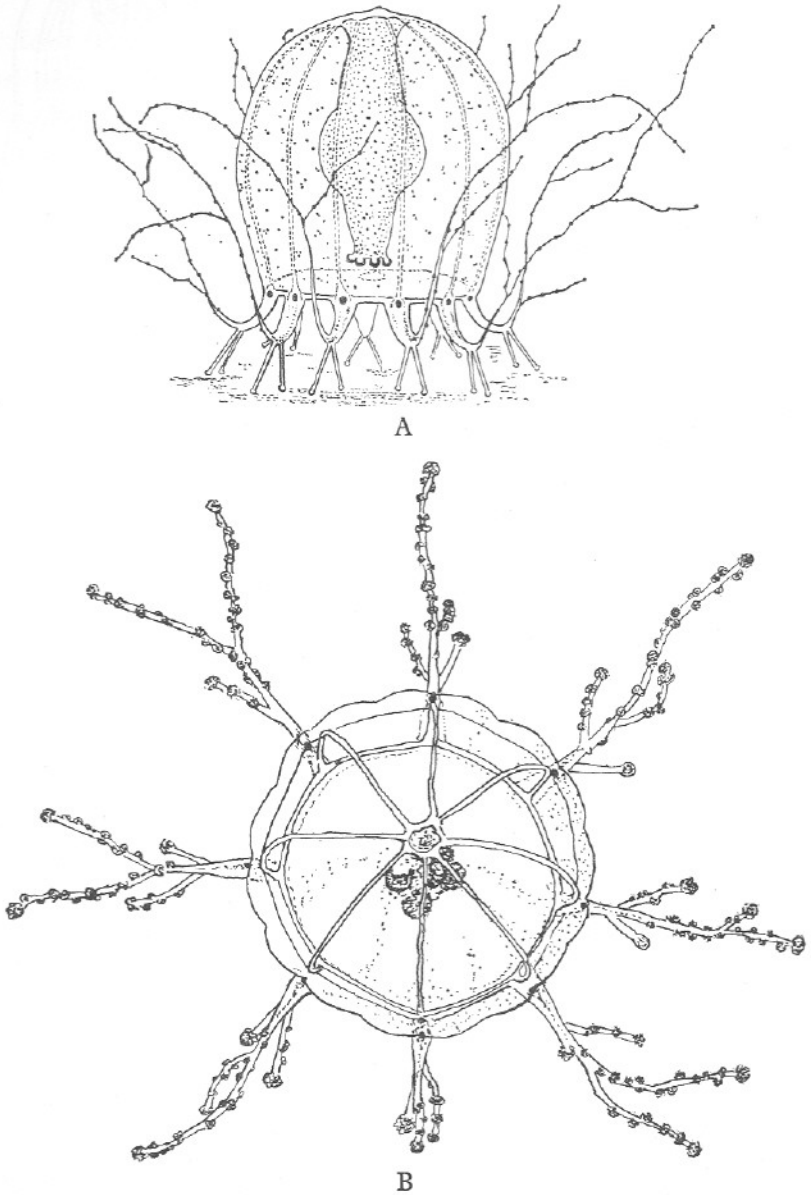
* Dr W. J. Rees tells me that he has seen specimens in the British Museum collected by Mr F. J. Lambert at Leigh-on-Sea, Essex.



Text-fig. 49. *Cladonema radiatum*. A, preserved specimen 2·25 mm. high from West Cove, Kenmare Bay, County Kerry, Ireland, August 1939 (collected by S. W. Kemp); B, adult medusa floating in water (after Allman, 1872, pl. xvii, fig. 3); C, newly liberated medusa (after Hincks, 1872*b*, pl. xxi, fig. 6); D, hydroid (ibid. pl. xi, fig. *b*).

In those with eight canals thirty-six out of the thirty-nine had three branched and two unbranched canals, so arranged that each unbranched canal had two branched canals on one side and one on the other. Hartlaub (1887) found a similar disposition to be usual in medusae from Naples; and Lengerich (1923) found the same in twenty-eight out of thirty-five specimens from

the aquarium at the Zoological Institute in Berlin where a colony of the hydroid had lived for about thirty years. The branching and disposition of the radial canals may, however, be subject



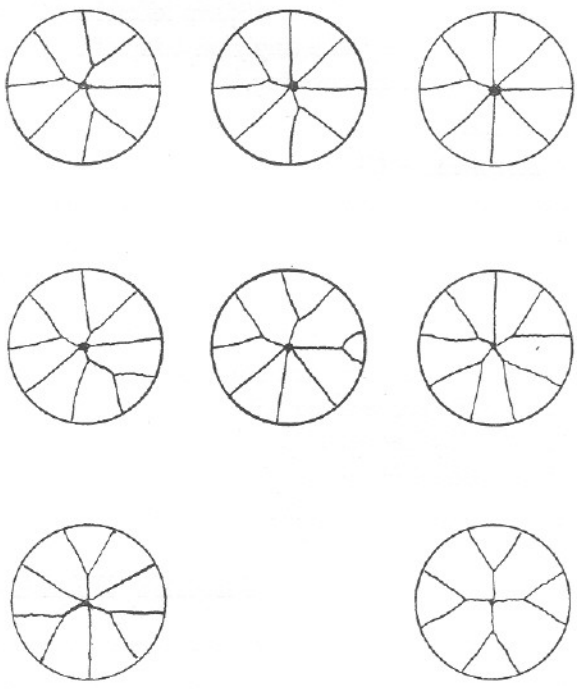
Text-fig. 50. *Cladonema radiatum*. A, adult medusa creeping on bottom (after Hincks, 1868, pl. xi, fig. *c*'); B, young medusa from subumbrellar side (after Lengerich, 1923, fig. H).

to considerable variation (Text-fig. 51). The primary trunk of the branched canals is usually rather short.

The eggs are small and not amoeboid (H. Müller, 1908). Hartlaub (1887) observed successive hermaphroditism in the medusae, which could begin either as males or females. This, however, was never observed by Müller in the specimens he examined.

The abaxial ocelli have ectodermal cuticular lenses and according to unpublished observations by Heider (Lengerich, 1923) the ectoderm cells surrounding the ocelli have long stiff hairs. Joseph (1920) records the occurrence of crystalloid concretions in the endoderm of the marginal tentacle bases. These concretions appeared to be fewer in number than in the closely related species *Cladonema mayeri* Perkins (1908).

The histology of this species is dealt with in detail by Lengerich (1923). Brien (1942) found that the sexual cells were formed by dedifferentiation from ectoderm cells. Pasteels (1939) records a number of very interesting abnormalities in a culture of *Cladonema* in a marine aquarium at the Institute of Anatomy in Brussels. Among a large number of individuals about 1% showed varying stages of twinning. A complete series was obtained showing apparent binary fission of the medusa starting at the mouth.



Text-fig. 51. *Cladonema radiatum*. Variations in arrangements of the radial canals (after Lengerich, 1923, fig. L).

NEMATOCYSTS. Desmonemes and stenoteles (Weill, 1937).

Seasonal occurrence

Little is known of the seasonal occurrence of the medusa *Cladonema radiatum*. Medusae have been caught in the autumn in Falmouth Harbour (Browne, 1900). In aquaria the medusae may be liberated during the summer months.

Habits

A good description of the movements of this medusa has been given by Allman (1872):

While the medusa is in the act of swimming the tentacles are contracted and curved upwards round the margin of the umbrella. The cirri, or nodulated appendages of the tentacles, are at the same time more strongly contracted, but the appendages destined for attachment always remain extended. While floating passively in the water the tentacles with their appendages are extended to their entire length, and then hang down in a graceful tassel-like cluster from the margin. The most remarkable attitude, however, is assumed when the medusa has fixed itself to the side of the aquarium. It then adheres to the glass by means of the sucker-like capitula, which terminate the organs of attachment. On these appendages the medusa is elevated as on so many feet, while all the rest of tentacle is extended to the utmost, and thrown back over the umbrella.

Lengerich (1923) calls this latter the 'defence attitude' (Schutzstellung); and Kramp (1927) remarks that when at rest and undisturbed the tentacles extend horizontally with only their extreme ends lifted free of the substratum.

Browne (1900) records that 'they remain at rest for long periods, with their tentacles expanded on the wait for prey, generally a copepod. Directly a copepod is caught by a tentacle the Medusa starts swimming, and with great skill conveys the unfortunate Copepod into its mouth. In the sea the Medusa probably lives amongst seaweed.'

Browne and Lengerich both remark that the adhesive organs are only used for attachment and not for crawling as in *Eleutheria*. The medusae are very sensitive to light.

Graeffe (1884) records that in aquaria the medusae attain maturity in about four weeks.

HYDROID. *Cladonema radiatum* Dujardin. (Text-fig. 49D.)

(For full description see Hincks, 1868, p. 62, pl. xi; and Allman, 1872, pp. 216, 357, pl. xvii.)

Slender, simple or slightly branched, colonies reaching a height of 12–25 mm. Perisarc smooth, light yellowish brown in colour. Hydranth with an oral whorl of four capitate tentacles, and a basal whorl of four filiform tentacles. Colour of hydranth pale reddish.

Medusa buds borne singly on body of hydranth immediately above basal whorl of tentacles, without ectothecal covering.

Historical

The medusa *Cladonema radiatum* was first described by Dujardin in 1843 from its hydroid, which he called 'Stauridie'. Subsequently he (1845) and Krohn (1853) observed the development of the hydroid from eggs of medusae which they had previously liberated from the parent hydroid. They were thus the first observers to see the complete cycle of alternation of generations from a hydroid to the medusa and back.

Two* other, non-British, species of *Cladonema* are known, *C. perkinsi* Mayer and *C. mayeri* Perkins. On account of the variability of the species Mayer (1910) was inclined to believe that both might prove to be only varieties of *C. radiatum*. This view has at any rate been held for *C. mayeri* by Lengerich (1922*a*; 1923) and Uchida (1927*a*). More recently Weill (1937) has found at Bermuda *Cladonema* of the three varieties, indicating that there may be one cosmopolitan species, *C. radiatum*, with three geographical races. (See also *C. myersi*, Rees, 1949.)

FAMILY ELEUTHERIIDAE

Creeping Anthomedusae with thickened ring of nematocysts round umbrella margin; with simple circular mouth; with variable number of radial canals (corresponding with, or more usually fewer than, number of marginal tentacles) which may or may not branch; with gonads on subumbrellar surface or in special dorsal brood pouch; with variable number of hollow bifurcating marginal tentacles, each furnished with an organ of adhesion; with ocelli.

Hydroid with single oral whorl of capitate tentacles, with or without aboral whorl of reduced filiform tentacles.

The family Eleutheriidae is represented in British waters by one genus, *Eleutheria* Quatrefages.

Genus **Eleutheria** Quatrefages, 1842

Characters as family.

The only British species of the genus is *Eleutheria dichotoma* Quatrefages. Its characters are so distinctive that it cannot be confused with any other British species.

Eleutheria dichotoma Quatrefages

Plate IV, figs. 4–6; Text-figs. 52, 53

Eleutheria dichotoma Quatrefages, 1842, *Ann. Sci. nat. Paris*, sér. 2, tome XVIII, p. 270, pl. viii (medusa).
Krohn, 1861, *Arch. Naturgesch. Berlin*, 27. Jahrg. Bd. I, p. 157.

* There is now a third species, *C. californica* Hyman (1947).

de Filippi, 1865, *Mem. R. Accad. Torino*, ser. II, vol. XXIII, p. 375, pl. i.
Haeckel, 1879, *System der Medusen*, p. 106.
Hartlaub, 1886, *Zool. Anz. Leipzig*, 9. Jahrg. no. 239, p. 706, 1 text-fig.
Hartlaub, 1907, *Nordisches Plankton*, Lief. 6, XII, p. 127, figs. 119–20.
Mayer, 1910, *Medusae of the World*, p. 94, figs. 46–8.
Lengerich, 1923, *Zool. Jahrb. Jena* (Anat.), Bd. XLIV, p. 359, figs. R′–Z′, D^2.

Clavatella prolifera Hincks, 1861, *Ann. Mag. Nat. Hist.* ser. 3, vol. VII, p. 73, pl. vii–viii (hydroid and medusa).
Hincks, 1868, *Brit. Hydroid Zooph.* pp. 73, 320, pl. xii, fig. 2.
Allman, 1871–2, *Monogr. Gymnobl. Hydroids*, p. 30, fig. 5, pp. 212, 384, pl. xviii.

Eleutheria krohni Krumbach, 1907*a*, *Beiträge zur Kenntnis der Medusa Eleutheria* . . . Inaugural Dissertation, Breslau.

Herpusa ulvae O. Schmidt, 1869, in Brehm, *Illustriertes Thierleben*, Bd. VI, p. 993.

Non *Eleutheria dichotoma*, Claparède, 1863, *Beob. wirbellos. Thiere*, p. 4, pl. i, figs. 4–10.

Specific Characters

Usually six radial canals; usually six, deeply bifurcated marginal tentacles each with single terminal nematocyst cluster on one branch. Gonads developed entirely in dorsal brood-pouch. Medusa-buds borne on exumbrella.

Description of Adult

Umbrella somewhat flattened-hemispherical, with its ventral surface more or less six-sided: with well-developed thickened marginal ring of nematocysts. Velum broad. Stomach cylindrical, extending slightly beyond umbrella margin; mouth simple and tubular. Radial canals short, usually six in number. Ring canal narrow, widening at junctions with radial canals. Gonads in specialized umbrella cavity or brood pouch situated above the stomach, in which the embryos develop to planula stage. Asexual reproduction by medusa-bud formation from ring canal on exumbrellar side. Marginal tentacles solid, four to fourteen in number, usually six or five, perradial, twice the diameter of umbrella in length, bifurcating into an upper branch with single terminal nematocyst cluster and a lower unarmed branch terminating in adhesive disk. One abaxial ocellus on base of each marginal tentacle. Diameter of umbrella about 0·4–0·5 mm. Colour of terminal suckers, stomach and radial canals yellowish, reddish or brilliant orange; ocelli deep chocolate red; adhesive disk pink; core of fine straw pigment down marginal tentacles to adhesive disk.

Distribution

Eleutheria dichotoma has been recorded from the British Isles from the coasts of Cornwall, Dorset, Devon, Yorkshire, west Scotland and south Ireland. It has also been found on the coasts of the Skagerak, Sweden, France, the Mediterranean, and the Black Sea (Thiel, 1935). It frequents small rock pools in the tidal regions, on weeds such as *Ulva* and *Gigartina*.

Developmental Stages and Structural Details

On liberation from its hydroid the young medusa closely resembles the adult in general appearance. The subumbrellar cavity is very restricted and limited to a ring-shaped space between the marginal nematocyst pad, the broad velum, and the stomach. The radial canals are very short and appear almost as mere outgrowths from the stomach; they generally correspond in number with the usual six marginal tentacles. Canal-shaped cavities are formed above the stomach from the ectoderm of the umbrella which eventually communicate distally with the subumbrellar cavity and join above the stomach itself to form an enlarged cavity or brood-pouch. The connexions from this brood-pouch with the subumbrellar cavity are situated interradially

between the radial canals. The endoderm of the stomach becomes completely separated from the umbrella ectoderm dorsally by the development of the brood-pouch, which thus has no connexion with the alimentary cavities. The pouch was shown by Hartlaub to have no homology with an umbilical canal as was suggested by Haeckel. The sexual cells develop in the upper and lower walls of this pouch, the eggs apparently predominating ventrally and the sperm dorsally. The eggs are fertilized *in situ* and develop to the planula stage before liberation. The planulae, which have many nematocysts, are liberated by the bursting of the upper wall of the umbrella. Hermaphroditism is frequent, Hartlaub (1886) recording 12% hermaphrodites in the material he examined and H. Müller (1908) 25%. The eggs are small and not amoeboid. Histological studies of the developing germ cells have been made by H. Müller (1908) and Nekrassoff (1911).

In the asexual reproduction the medusa-buds begin as ectodermal swellings on the exumbrellar surface into which endodermal outgrowths from the ring canal develop. Sexual and asexual reproduction can proceed simultaneously, and the medusa-buds may themselves develop buds before liberation so that there are three generations united.

The number of marginal tentacles is variable. Most authors have given six as the usual number. Krumbach (1907*a*) found the following results in an examination of 155 specimens from the Gulf of Trieste:

No. of specimens	No. of marginal tentacles in each
14	4
58	6
71	5
9	7
2	10
1	11

In this instance five was the most prevalent number. Drzewina & Bohn (1913) record that out of thirty-eight specimens examined from Saint Vaast-la-Hougue, seven had five marginal tentacles each, thirty had six, and one had seven. H. Müller (1908) observed one specimen with fourteen marginal tentacles, and also recorded an abnormal specimen with a marginal tentacle with three branches, two of which had adhesive disks. He also noted that occasionally specimens had two ocelli in the place of one, and that sometimes the back was covered with a number of dark pigment granules, both of which facts I have observed myself. The rarity of specimens with eight marginal tentacles is remarkable (see Drzewina & Bohn, 1913) and it is perhaps significant that eight is the characteristic number of marginal tentacles in another species *Eleutheria claparedi* Hartlaub.

Seasonal occurrence. The production of medusae occurs in the summer months.

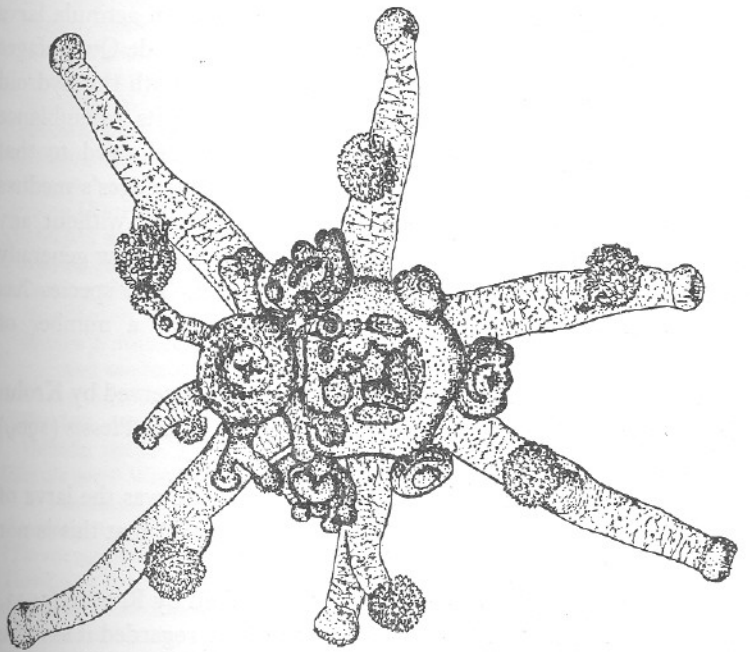
Habits

The medusae are adapted for creeping about among the weeds at the bottoms of the small intertidal rock pools in which the hydroid lives. When moving, the adhesive disk of one marginal tentacle is lifted from the ground and the whole marginal tentacle thrown out in the direction of motion so that the adhesive disk becomes once more attached to the substratum a little farther on. The other marginal tentacles are held out rather sideways, in contradistinction to *E. claparedi* in which species they are held more aloft (H. Müller, 1911).

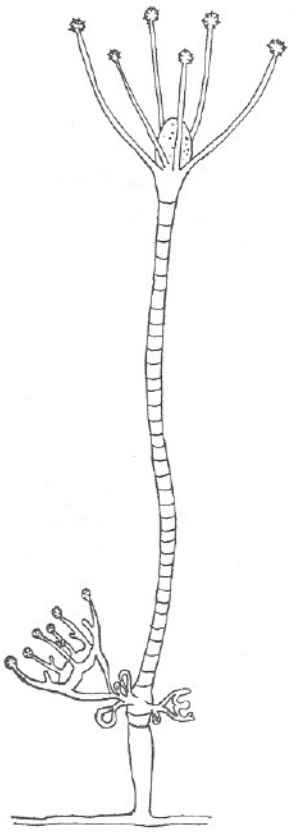
E. dichotoma medusae are apparently very hardy and able to withstand high temperatures and deficiency of oxygen. Drzewina & Bohn (1913) found that they lived quite well in the laboratory at Concarneau in the hot summer of 1911 when the temperature rose to 29° and 30° C. They are thus evidently well adapted for conditions in the small rock pools in which they live. It has also

been suggested by Krumbach (1907*a*) that the closure of the subumbrellar cavity by the manubrium and velum may allow the retention of water in case of desiccation.

Drzewina & Bohn (1911, 1912*a*, 1913) studied the effects of oxygen decrease and of potassium cyanide and the resulting increase in the number of marginal tentacles. They also made observations on its powers of regeneration, and the decrease in size due to starvation.



Text-fig. 52. *Eleutheria dichotoma*. From subumbrellar side showing six different stages of medusa buds (after Lengerich, 1923, fig. 8′).



Text-fig. 53. *Clavatella prolifera*, the hydroid of *Eleutheria dichotoma* (after Hincks, 1868, pl. xii, fig. 2).

These authors kept cultures of *E. dichotoma* in Petri dishes and fed them on the littoral Harpacticid copepod *Harpacticus fulvus* (= *Tigriopus*). The medusae thus fed soon took on the intense red-orange colour of the copepod. The nematocyst armature was very efficient for the capture of prey and evidently contained a potent paralysing poison. As soon as the copepod touched one of the nematocyst batteries it was caught and the marginal tentacle slowly transferred it to the mouth. Copepods which were liberated immediately after capture died, and the authors record having seen a copepod rendered immediately motionless when only the point of a furca had touched the stinging battery. The medusae would not feed on oyster larvae. On contact with a larva the nematocysts were discharged, and the oyster larva quickly shut its valves and remained shut, although the cilia continued to beat. The larvae did not adhere to the nematocyst battery as did the copepods, and the medusa did not move its marginal tentacle towards its mouth.

HYDROID. *Clavatella prolifera* Hincks. (Text-fig. 53.)

(For full description see Hincks, 1868, *Brit. Hydroid Zooph.* p. 73, pl. xii, fig. 2; Allman, 1871–2, *Monogr. Gymnobl. Hydroids*, pp. 212, 384, pl xviii.)

Simple unbranched colonies reaching a height of about 9 mm. Perisarc smooth and delicate. Hydrocaulus short. Hydranth elongated cylindrical, very extensile. A single oral whorl of capitate tentacles up to eight or ten in number. Oral extremity and centre of body of hydranth opaque white. Medusa buds borne in clusters on short branched peduncles at base of unprotected part of hydranth body; without ectothecal covering.

Historical

The medusa was found and described for the first time by A. de Quatrefages (1842) in 1841 at the Isles of Chansey. He thought that it was a free-living hydroid and named it *Eleutheria dichotoma*. It was suggested by Van Beneden (1844*b*, 1845) that it resembled an actinula larva and that its hydroid would be found to be a tubularian. This was refuted by M. de Quatrefages (1845). In 1861 Hincks found the hydroid stage at Torquay and described both the hydroid and the medusa under the name *Clavatella prolifera*. He drew attention to its resemblance to de Quatrefages's *Eleutheria* and remarked that the medusa no doubt belonged to that genus. But he regarded it as a distinct species on the grounds that de Quatrefages's medusa had terminal nematocyst clusters on both branches of each marginal tentacle, without any adhesive disk, and that it walked with its manubrium upwards. It is, however, now generally agreed that de Quatrefages's medusa was probably an abnormal specimen. The species has been shown to be very variable and Haeckel described these variations as a number of subspecies.

The early stages of development of the hydroid from the planula were first observed by Krohn (1861*b*), and subsequently by de Filippi (1865) and Drzewina & Bohn (1913). Du Plessis (1909) obtained the medusa liberated from a hydroid previously reared from the egg.

Krumbach (1907*b*) thought that the mesozoan *Trichoplax adhaerens* Schulze was the larva of *Eleutheria*; it has, however, been shown by Schubotz (1912) and Schulze (1914) that this is not very probable.

A species of medusa found in a laboratory tank at Cullercoats was described by Robson (1913, 1914*b*). She at first thought that this might be a*Cladonema* species, but later regarded it as more likely to be a Leptomedusan. Lengerich (1922*b*) considered that it was an *Eleutheria* and named it *E. robsoni*. It has, however, been shown by Joseph (1924, 1925) that it was a young *Gonionemus* and it is referred to later (p. 402) under the Limnomedusae.

FAMILY CLAVIDAE

Anthomedusae with umbrella without apical process; without exumbrellar nematocyst tracks; with stomach not extending beyond umbrella margin; with or without peduncle; with mouth with four simple lips with numerous sessile clusters of nematocysts along whole margin; with numerous solid marginal tentacles; with ocelli.

HYDROID. Where known, *Clava*-like, with irregularly distributed filiform tentacles.

The Clavidae are represented in British waters by one genus in which free-swimming medusae are produced, *Turritopsis* McCrady.

Genus **Turritopsis** McCrady, 1856

MEDUSAE. Clavidae with stomach having apical mass of vacuolated endoderm cells; without peduncle.

HYDROID. *Corydendrium.*

There is one British species, *Turritopsis nutricula* McCrady. This medusa is not likely to be confused with any other species in British waters; it is made conspicuous by its brilliant red stomach.

Turritopsis nutricula McCrady

Plate V, figs. 1–5; Plate XXIX, figs. 1–3; Text-figs. 54A–C, 55, 56

?*Cyanaea coccinea* Davis, 1841, *Ann. Mag. Nat. Hist.* vol. VII, p. 235, pl. ii, figs. 1–3.
?*Turris neglecta* Lesson, 1843, *Acalèphes*, p. 284.
Forbes, 1848, *Monogr. Brit. Medusae*, p. 23, pl. iii, fig. 2.
Busk, 1848, *Trans. Micr. Soc. London*, vol. III (1852), p. 14, pl. v, figs. 1–12.
Gosse, 1853, *Devonshire Coast*, pp. 348, 410, pl. xiii, figs. 6–10 (medusa and young hydroid).
Allman, 1864, *Ann. Mag. Nat. Hist.*, ser. 3, vol. XIII, p. 352.
Hincks, 1868, *Brit. Hydroid Zooph.* p. 13, pl. iii, fig. 1 (medusa and young hydroid).
Allman, 1871–2, *Monogr. Gymnobl. Hydroids*, pp. 97, 259.
Mayer, 1910, *Medusae of the World*, p. 122, fig. 65.
Oceania (*Turritopsis*) *nutricula* McCrady, 1856, *Proc. Elliott Soc.* vol. I, p. 55, pl. iv, figs. 1–10.
Turritopsis nutricula, McCrady, 1858, ibid. vol. I (1859), p. 127, pl. viii, fig. 1.
Non A. Agassiz, 1865, *N. Amer. Acaleph.* p. 167, figs. 269–70.
Brooks, 1886*a*, *Mem. Boston Soc. Nat. Hist.* vol. III, no. 12, p. 388, pl. xxxvii (hydroid and medusa).
Non Hargitt, 1905, *Bull. U.S. Bur. Fish. Washington*, vol. XXIV (1904), fig. on p. 37.
Brooks & Rittenhouse, 1907, *Proc. Boston Soc. Nat. Hist.* vol. XXXIII, no. 8, p. 429, pls. xxx–xxxv (hydroid and medusa).
Mayer, 1910, *Medusae of the World*, vol. I, p. 143, text-figs. 75–7; pl. xiv, figs. 10–13; pl. xv, figs. 10–13.
Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, p. 8.
Uchida, 1927*a*, *J. Fac. Sci. Univ. Tokyo, Zool.* vol. I, pt. 3, p. 217 (in part, see Kramp, 1928, p. 53).
Clavula gossii Wright, 1859*a*, *Edinb. New Philos. Journ.*, vol. X, p. 106, pl. viii, fig. 1 (hydroid reared from medusa).
Oceania polycirrha Keferstein, 1862, *Z. Wiss. Zool. Leipzig*, Bd. XII, p. 26, pl. ii, figs. 11–13.
?*Turritopsis nutricola*, Haeckel, 1879, *System der Medusen*, p. 66 (in part).
Turritopsis polynema Haeckel, 1879, ibid. p. 66.
Modeeria multitentaculata, Fewkes, 1881*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. VIII, p. 149, pl. iii, figs. 7–9.
Modeeria nutricula, Fewkes, 1882, ibid. vol. IX, p. 294.
Dendroclava dohrnii Weismann, 1883, *Sexualzellen bei Hydromedusen*, p. 26, pl. xii, figs. 6–9 (hydroid and medusa bud).
Zoia, 1892, *Ann. Mag. Nat. Hist.* ser. 6, vol. IX, p. 409 (hydroid and medusa).
Turritopsis polycirrha, Hartlaub, 1897, *Wiss. Meeresuntersuch.* N.F., Bd. II, Abt. Helgoland, Heft 1, p. 480, pl. xvi*c*, fig. 2.
Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 202, figs. 179–84.
Corydendrium nutricula, Kramp, 1935, *Göteborgs VidenskSamh. Handl.* ser. B, Bd. IV, no. 11, p. 11.

Specific Characters

Marginal tentacles in a single row.

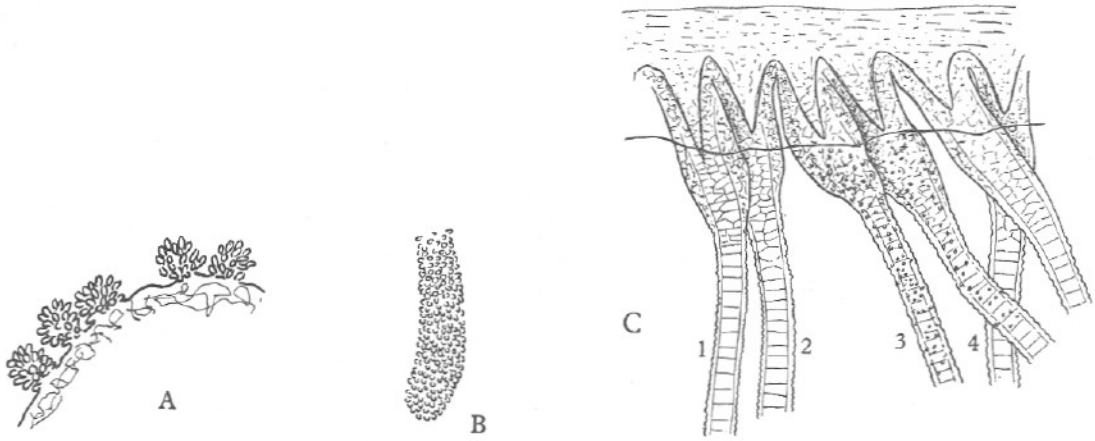
Description of Adult

Umbrella bell-shaped, slightly higher than wide; jelly uniformly thin. Velum broad. Stomach cross-shaped in section, not extending beyond umbrella margin. Four radial masses of large vacuolated endoderm cells coalescing to form compact mass above stomach. Mouth four-lipped with numerous spherical clusters of nematocysts along its margin. Four radial canals and ring

canal fairly broad; radial canals continued through endodermal masses to stomach. Gonads in four pairs on interradial walls of stomach; eggs developing to planulae in subumbrellar cavity and on stomach wall (in European form). Eighty to ninety marginal tentacles closely spaced round umbrella margin in a single row; marginal tentacles solid, with core of single cylindrical endodermal cells. Small adaxial ocelli on marginal tentacle bulbs. Height when full grown 4–5 mm. Colour of interradial regions of stomach, gonads and ocelli brilliant red; pale red pigment on marginal tentacle bulbs; sometimes faint reddish tinge in radial canals.

Distribution

Turritopsis nutricula is found commonly in the plankton in the English Channel and southern North Sea. Elsewhere round the British coasts it has only been recorded from Queensferry (Firth of Forth), the Mersey, Tenby, and Ilfracombe.



Text-fig. 54. *Turritopsis nutricula.* A, margin of mouth lip; B, tip of marginal tentacle; C, bases of marginal tentacles, ocelli omitted (1 and 2 in optical section; 3 and 4 including surface nematocysts). Preserved specimens, Plymouth, 16. ix. 35.

The species has been shown to be useful as an indicator of the drift of Channel water into the southern North Sea (Kramp, 1930; Wulff, Bückmann & Künne, 1934; Russell, 1938*a*).

T. nutricula is also found in the Adriatic; Mediterranean; the American coast of the Atlantic from Cuba to New England, but not north of Cape Cod; Bahamas; Tortugas; St Thomas, West Indies; ? Amboina; Pacific from Hokkaido, Japan, to Tsingtao, China; Chagos Archipelago, Indian Ocean.

Developmental Stages and Structural Details

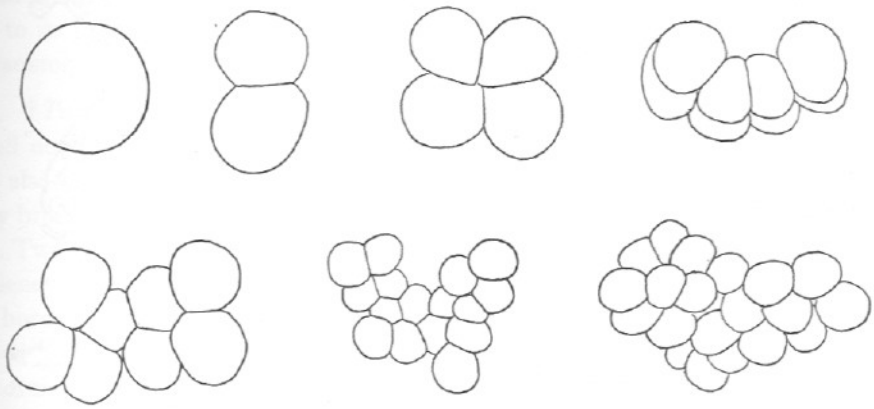
Turritopsis nutricula has not been observed at the moment of liberation from its hydroid in European waters for certain as the identity of its hydroid has not been proved. On the American coast, however, this stage has been described by Brooks (1883, 1886*a*) (see also Brooks & Rittenhouse, 1907). The young medusa (Text-fig. 56) has eight marginal tentacles, four radial and four interradial. The stomach is cone-shaped and there is a large peduncle formed of the vacuolated endoderm cells. The mouth is at first simple (?), but the nematocyst clusters soon develop on the margin of the lips. McCrady (1858) recorded a specimen 0·8 mm. high by 0·6 mm. wide and he and Mayer (1910) both figured this eight-tentacle stage from the plankton. Although many medusae have been seen by different workers there appear to be hardly any records showing

the increase in the numbers of marginal tentacles with growth; Brooks (1886*a*) gave drawings of various stages. Mayer (1910) figures a medusa *c.* 2 mm. in height with twenty marginal tentacles and one slightly smaller with twelve.

A few specimens examined at Plymouth gave the following results:

Height (preserved) (mm.)	Marginal tentacles
1·8	48
2·2	56
2·5	56
2·9	*c.* 70
3·3	88
3·5	80
3·6	87
3·6	*c.* 90
4·2	86

The increase in the number of marginal tentacles is evidently rapid.



Text-fig. 55. *Turritopsis nutricula*. Segmentation of the egg (after Brooks & Rittenhouse, 1907, pl. xxxii, figs. 19, 20, 21; pl. xxxiii, figs. 24, 27).

The vacuolated endoderm cells grow outwards from the radial canals until the four sections meet and form a compact mass occupying the upper third of the subumbrellar cavity. Through this mass the radial canals can be seen running to the stomach. In preserved specimens it is sometimes not possible to see these continuations of the radial canals owing to the opacity of the endodermal mass and because the walls of the radial canals are not so clearly defined as they are outside the mass; they can, however, be shown by sections. These endoderm cells also often appear to form one compact mass, but with suitable lighting under the microscope it is possible to see four interradial lines of more transparent cells showing where the four masses meet one another.

Cavities are commonly seen in the endodermal mass (Pl. XXIX, fig. 3), and occasionally there may be four of these interradially disposed.

Viewed from the aboral surface the radial canals can be seen to run up a short distance over the endodermal mass before diving downwards to the stomach. The stomach appears as a large radial cross.

The gonads develop as paired cushions on the interradial walls of the stomach and in this region the developing eggs and planulae can be seen. Apparently this development to the planula stage *in situ* only occurs in the European medusa. In medusae from other regions the eggs are

cast loose into the water. Keferstein (1862) stated that he had observed male and female medusae, but Hartlaub (1911) after examining sections said that they were hermaphrodite.

The marginal tentacles (Text-figs. 54B, C) are smooth and beset with numerous irregularly but closely spaced nematocysts. There is a core of single cylindrical endoderm cells, which becomes multicellular in the marginal tentacle bulb. In preserved specimens many of the marginal tentacles are often missing, being represented only by fusiform bulbs. In fully developed specimens the marginal tentacles are crowded very closely round the umbrella margin. The marginal tentacle bulbs also tend to be directed alternately outwards and downwards; this gives the appearance of a double row of marginal tentacles, whereas there is in reality only a single row. The marginal tentacles are slightly swollen and club-shaped at their extremities.

The adaxial ocelli disappear in preserved specimens. Gosse (1853, p. 411) observed a globular, highly refractile, crystalline lens in the ocellus.

The planulae were reared to young hydroids by Gosse (1853) and Strethill Wright (1859*a*); the latter developed a polyp with twelve tentacles which he named *Clavula gossii*. Young polyps have also been reared in the Plymouth laboratory (Pl. V, figs. 2, 5). The planulae are crimson lake or reddish in colour and 0·47 mm. long and 0·09 mm. wide; the anterior end is blunt and pale, and the posterior end pointed. The development of the eggs and planulae of American medusae was studied by Brooks & Rittenhouse (1907). Segmentation is very irregular (Text-fig. 55). The planula becomes attached to the substratum by its side to form a root from the middle of which the first hydranth develops. Rittenhouse developed normal small planulae from divided developing eggs.



Text-fig. 56. *Turritopsis nutricula*. Hydroid. (After Brooks, from Mayer, 1910, fig. 76.)

NEMATOCYSTS. Microbasic euryteles and desmonemes (Russell, 1940*a*).

Seasonal occurrence

Turritopsis nutricula occurs in the plankton in autumn and winter months, from August to February. It is most abundant in September and October. The latest record is April from the southern North Sea (Kramp, 1930).

Habits

In life the marginal tentacles can be extended to two to three times the length of the umbrella. When fully extended they are held at first straight outwards or upwards from the umbrella margin and then hanging downwards in a graceful curve (Pl. V, fig. 1). When partially contracted the

ends may be coiled, and when swimming they are tightly coiled except for a short straight basal portion.

Gosse (1853 as *Turris neglecta*) recorded this species, which he called the 'Ruby medusa', as so frequent at Ilfracombe in the autumn that it was even to be found in rock pools. He states: 'when resting in a phial of water, the tentacles are elongated, like white threads of an equal thickness throughout, and are extended in every direction, some perpendicularly upwards, some downwards, and some arching outwards. Thus it lies quite motionless, but on the slightest jar being given to the vessel, or to the table on which it stands, all the tentacles at the same instant are contracted into minute contorted balls, so suddenly that it seems the work of magic.' In captivity the medusae tend to float near the surface of the water.

Gosse observed that it was the custom for the medusa to turn inside out before death, when the red interradial portions of the stomach show clearly as red crosses; and I have noticed the same.

A good drawing showing various positions of living medusae was made by Brooks (1886*a*, reproduced in Mayer, 1910, p. 145, fig. 76).

Owing to its brilliant red colour *T. nutricula* is one of the most conspicuous medusae in the British plankton.

Hydroid. ? *Turritopsis dohrnii* (Weismann) (=*Dendroclava*). (Text-fig. 56.)

(For full description see Weismann, 1883; Brooks, 1886; Zoia, 1892; Mayer, 1910; Fraser, 1912; see also Stechow, 1923 and Kramp, 1935.)

Slightly branched colonies up to 20 mm. in height; perisarc smooth, ending abruptly below hydranth. Twelve to twenty thick filiform tentacles irregularly distributed over body of hydranth with tendency to form indefinite whorls or rows. Body of hydranth elongated and fusiform. Medusae borne on short pedicels, invested with perisarc, at base of hydranth. Colour of hydranth pale yellowish red.

The hydroid *Turritopsis dohrnii* has not yet been found in British waters. On European coasts it has only been recorded from the Mediterranean. Many authors have pointed to the similarity between the hydroid of *T. nutricula* originally described by Brooks (1886*a*) from the American coast and *Dendroclava dohrnii* described by Weismann (1883). Stechow (1923) regards them as identical, the only difference being that in the European hydroid the perisarc is smooth while in the American it is encrusted with foreign matter. If the European and American medusae are to be regarded as synonymous, then it seems most probable that the hydroid described by Brooks and *Turritopsis dohrnii* of Weismann (1883) are identical; albeit the European medusa has not yet been connected with certainty to *T. dohrnii*.

The occurrence of the hydroid in harbours on the American coast and the presence of *T. nutricula* commonly in the English Channel suggests that its hydroid should be found in such localities as Southampton.

Mention might be made of the resemblance between *T. dohrnii* and *Tubiclava fruticosa* described by Allman (1872) from Tenby but whose method of reproduction is not known.

Historical

It is probable that the first description of *Turritopsis nutricula* was that of Davis (1841) who described a medusa from Tenby under the name *Cyanaea coccinea*. His description, however, was inadequate for certain identification. A medusa was inadequately described by Lesson (1843) as *Turris neglecta*; under this name Forbes (1848) described and figured a medusa which is almost certainly *Turritopsis nutricula*. Unless Forbes has confused two species it seems that he was

mistaken as to the structure of the endodermal mass, for he describes and figures this rather as convoluted pandeid ovaries. His figures of the marginal tentacles and mouth certainly refer to *T. nutricula*. The first satisfactory description was given by McCrady (1856, 1858) under the name now adopted, from the American coast.

In 1862 Keferstein described the European medusa as a separate species, *Oceania polycirrha*, from St Vaast on the Normandy coast.

Although Mayer (1910) could detect no specific differences between *nutricula* and *polycirrha*, Hartlaub (1911) and Browne (1916) kept them distinct. Hartlaub maintained that in *polycirrha* the endodermal mass was not in four sections, and that the radial canals did not penetrate the endodermal mass nor widen into chambers as figured by Brooks. Later (1917) he recorded a specimen from Helgoland that agreed with Brooks's figure as regards the widening of the radial canal, though he maintained that the identity of the two species still remained unproved. Their identity has, however, been accepted by Mayer (1910), Bigelow (1913) and Kramp (1930); it is accepted here on the grounds that all specimens seen at Plymouth showed the endodermal mass divided into four sections which were traversed by the radial canals. Cavities were also frequently seen in the endodermal mass which might give rise to the appearance figured by Brooks.

There remains, however, one difference between the European and American forms. While in the latter the eggs are shed loose in the water, in the former development to the planula takes place in the subumbrellar cavity. As this, however, seems to be a matter of difference in rate of development it should be regarded as having varietal rather than specific value.

Family HYDRACTINIIDAE

Anthomedusae with umbrella with or without slight apical process; without exumbrellar nematocyst tracks; with stomach not extending beyond umbrella margin; with or without peduncle; with mouth with four simple or branching lips armed with terminal nematocyst clusters; with four radial canals; with gonads either only on interradial walls of stomach, or on proximal portions of radial canals as well; with four, eight, or more, solid marginal tentacles; with or without ocelli.

HYDROID. *Hydractinia*-like, with single whorl of filiform tentacles.

The family Hydractiniidae is represented in British waters by one genus in which free-swimming medusae are produced, *Podocoryne* M. Sars.

The Hydractiniid medusae are chiefly characterized by the structure of the mouth. If the lips are unbranched each has a single terminal cluster of nematocysts; otherwise the lips themselves branch, and each branch has a terminal cluster of nematocysts. They thus differ from the Bougainvilliid medusae in which the oral tentacles are inserted above the opening of the tubular mouth, but are very similar to the Rathkeid medusae in which the mouth-lips themselves have a number of nematocyst clusters distributed on a definite pattern.

Genus **Podocoryne** M. Sars, 1846

MEDUSAE. Hydractiniidae with stomach without peduncle; without ocelli.

HYDROID. *Podocoryne*.

There are probably four species of the genus in British waters which produce free-swimming medusae, *Podocoryne carnea* M. Sars, *P. borealis* (Mayer), *P. minima* Trinci and *P. hartlaubi*

Neppi & Stiasny. They can be distinguished by the form of the mouth-lips, the position of the gonads, and by whether they reproduce asexually.

Lips unbranched, each with terminal nematocyst cluster:
  Gonads on stomach only:
    Without asexual budding from stomach . . . . . **P. carnea**
    With asexual budding from stomach . . . . . **P. minima**
  Gonads on stomach and proximal portions of radial canals . . . . . **P. hartlaubi**
Lips branched, each branch with terminal nematocyst cluster; gonads on stomach; without asexual budding from stomach . . . . . **P. borealis**

It is possible that *P. carnea* may be confused with *Lizzia blondina* when it is in the stage with eight marginal tentacles. It can, however, be distinguished at this stage by the absence of a peduncle and by the form of the mouth-lips.

Some difficulty may also be encountered in distinguishing small *Podocoryne carnea* from *P. minima* when it has become sexually mature and has ceased budding asexually. *P. carnea* has usually, however, signs of more than four marginal tentacles.

The identification of *Podocoryne* spp. requires further research. The hydroid of *P. carnea* is well known; that of *P. borealis* has only been recorded once for certain; while those of *P. minima* and *P. hartlaubi* have not yet been found. There remain the hydroids *P. areolata* Hincks (Text-fig. 62) and *P. proboscidea* Hincks (1868, p. 317), but it is possible that in the latter the medusa is never liberated.

Podocoryne carnea M. Sars

Plate VI, figs. 2, 3; Text-figs. 57A, 58A, B, 59B

Podocoryna carnea M. Sars, 1846, *Fauna Littoralis*, vol. I, p. 4, pl. i, figs. 7–18 (hydroid in part and medusa).
Sarsia nodosa Busch, 1851, *Beobacht. wirbellos. Seeth.* p. 17, pl. ii, figs. 6–8.
Podocoryne carnea, Krohn, 1851, *Wiegmann's Arch. Naturgesch.* Jahrg. XVII, p. 263 (hydroid and medusa).
Allman, 1859*a*, *Ann. Mag. Nat. Hist.* ser. 3, vol. IV, p. 50 (hydroid and medusa).
Hincks, 1868, *Brit. Hydroid Zooph.* p. 29, pl. v, fig. *c* (hydroid and medusa).
Allman, 1872, *Monogr. Gymnobl. Hydroids*, p. 349, pl. xvi, figs. 1–9 (hydroid and medusa).
Grobben, 1875, *Sitzb. Akad. Wiss. Wien.* math.-nat. Kl. Bd. LXXII, p. 455, pls. i, ii (hydroid and medusa).
Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 463.
Mayer, 1910, *Medusae of the World*, p. 136, pl. xiv, figs. 3, 6, text-fig. 74 (? not pl. xiv, figs. 2, 5; nor pl. xv, fig. 14).
Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 213, figs. 187–90, and end piece on p. 235.
Kramp, 1927, *D. Kgl. Danske Vidensk. Selsk. Skrift.* natur. og math. Afd., 8. Raekke, XII, p. 72, fig.1, chart 8.
Ectopleura nodosa, L. Agassiz, 1862, *Contrib. Nat. Hist. U.S.* vol. IV, p. 343.
Turritopsis nutricola, A. Agassiz, 1862, *Proc. Boston Soc. Nat. Hist.* vol. IX, p. 97, figs. 22, 23.
A. Agassiz, 1865, *N. Amer. Acalephae*, p. 167, figs. 269, 270.
Fewkes, 1881*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. VIII, p. 153, pl. iv, figs. 4, 7–10.
Hargitt, 1905, *Bull. U.S. Bur. Fish. Washington*, vol. XXIV (1904), p. 37, text-fig.; pl. iv, fig. 5.
Syndictyon nodosum, Haeckel, 1879, *System der Medusen*, p. 21.
Dysmorphosa carnea, Haeckel, 1879, ibid. p. 77.
Cytaeis exigua Haeckel, 1879, ibid. p. 634.
Calycidion formosum Fewkes, 1882*b*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. IX, p. 294.
Podocoryne conchicola Hargitt, 1904*a*, *Mitt. Zool. Stat. Neapel*, Bd. XVI, p. 581, pl. xxii, fig. 26.
Hydractinia carnea, non Sverdrup, 1921, *Skrift. vidensk. Christiania*, Bd. I (1922), p. 18, pl. ii, fig. 9.

Specific Characters

Four perradial mouth-lips each with single cluster of nematocysts. No asexual reproduction by medusa buds. Never more than eight marginal tentacles (in British waters).

Description of Adult

Umbrella bell-shaped, a little higher than wide; no apical process; jelly thin; scattered nematocysts on exumbrella. Velum broad. Stomach cylindrical, not more than half the length of subumbrellar cavity; no peduncle. Mouth with four single round perradial clusters of long-stalked nematocysts on its margin. Four radial canals and ring canal narrow. Gonads interradial. Four perradial marginal tentacles, and one to four interradial marginal tentacles, making five to eight in all (in British waters). No ocelli. Height when full grown *c.* 1 mm. (in British waters). Colour of stomach and marginal tentacle bulbs yellow, reddish or reddish brown.

Distribution

Probably owing to its short life the medusa *Podocoryne carnea* has not often been recorded from the plankton in British waters. It has been found at St Andrews, Firth of Clyde, Port Erin, Thames Estuary, Plymouth, off coast of Cornwall, and Valencia, south-west Ireland. The distribution of its hydroid is, however, such that the medusa is likely to occur on all British coasts, though possibly rarer in the eastern end of the English Channel and in the southern North Sea. Elsewhere the medusa or its hydroid has been recorded from Oslofjord, Norway, to North Cape; Iceland; Spitsbergen; Atlantic and Channel coasts of France; Mediterranean; Saldanha Bay, South Africa; West Greenland; and Atlantic coasts of North America at Newport, Narragansett and Buzzard Bays, but not at Beaufort, North Carolina or farther south.

Developmental Stages and Structural Details

The medusa *Podocoryne carnea* is about 0·8–1·0 mm. in height when first liberated from its hydroid; an umbilical canal may at first be present. It shows no structural difference from the fully developed medusa. The four perradial marginal tentacles are always developed, but the interradial marginal tentacles may vary in number from one to four. When the medusa is newly liberated the gonads are already partially developed and some specimens may be almost sexually mature so that there is little time for further development of the interradial tentacles. Thus mature specimens may be found with anything from five to eight marginal tentacles. Kramp (1927) figures a mature medusa from Middlefart Sound with eight marginal tentacles and an umbilical canal still in evidence. Hartlaub (1911) figures a specimen from Roscoff with ripe ovaries and only four marginal tentacles (see also C. W. Hargitt, 1904*a*, from Naples as *Podocoryne conchicola*).

On the American coast of the North Atlantic it has been stated that this species grows considerably larger, to as much as 3·5 mm. in height, and develops as many as thirty-two marginal tentacles (see Mayer,* 1910). Graeffe (1884) recorded what was presumably this species in the Mediterranean with sixteen marginal tentacles.

The nematocyst clusters on the mouth margin are a characteristic feature of this species (Text-fig. 57 A). These are situated on the margin of the mouth itself at the four perradial corners. Each cluster is spherical and consists of thirty to forty elongated nematocysts each with a filamentous stalk. These nematocysts are *c.* 0·01 mm. in length and 0·003 mm. in width (Grobben, 1875).

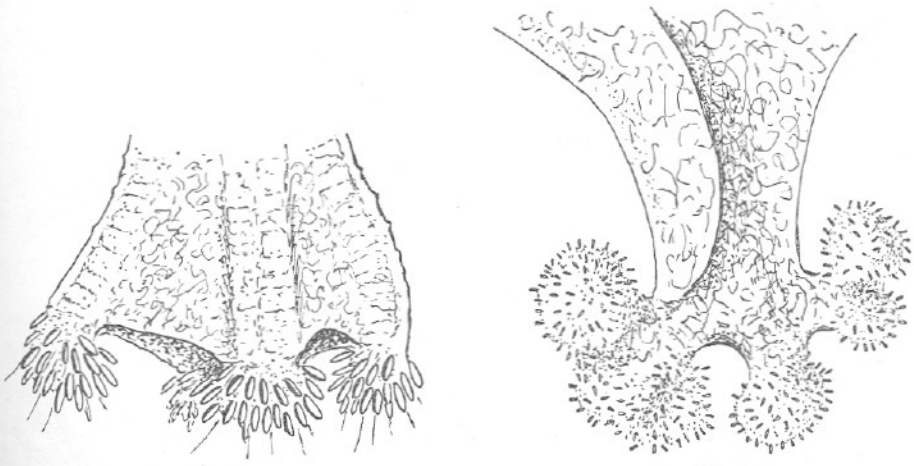
The marginal tentacles are solid, with a core of large cylindrical endoderm cells. The whole surface of the marginal tentacle is covered with irregularly but closely packed nematocysts.

* But Rees (1941*a*) showed that it is possible that *P. borealis* is also included in Mayer's description.

The gonads develop on the interradial surfaces of the stomach; when fully mature the few large eggs appear to surround the stomach, occupying its whole length and being divided by four longitudinal ridges.

The origin and movements of the sexual cells have been studied by de Varenne (1882), Weismann (1883), Ishikawa (1888), Bunting (1894), and Goette (1907). While there was some divergence of opinion amongst the earlier workers, Goette has summed up as follows. The primitive female germ cells originate in the ectoderm of the hydroid blastostyle mostly in the region of bud proliferation. They pass into the endoderm of the developing bud where differentiation takes place; and then by various routes they come to lie in the ectoderm of the stomach where they form four interradial ovaries. The male cells originate in the interradii of the ectoderm of the stomach.

Goette (1907) described the formation of the medusa buds in great detail.



Text-fig. 57. A, *Podocoryne carnea*, mouth of newly liberated medusa with eight tentacles and developing gonads, *c.* 1 mm. diameter, Plymouth, 9. iii. 37; B, *Podocoryne borealis*, one mouth lip of preserved specimen, off Plymouth, 1. vi. 32.

Grobben (1875) described two abnormal specimens: one had only three marginal tentacles from one of which arose a bifurcated radial canal; the other was a twin (figure reproduced by Hartlaub, 1911, p. 235).

C. W. Hargitt (1901), in an examination of over 100 specimens from America, found that the characters of the medusae showed a fair degree of constancy; he recorded three trimerous specimens.

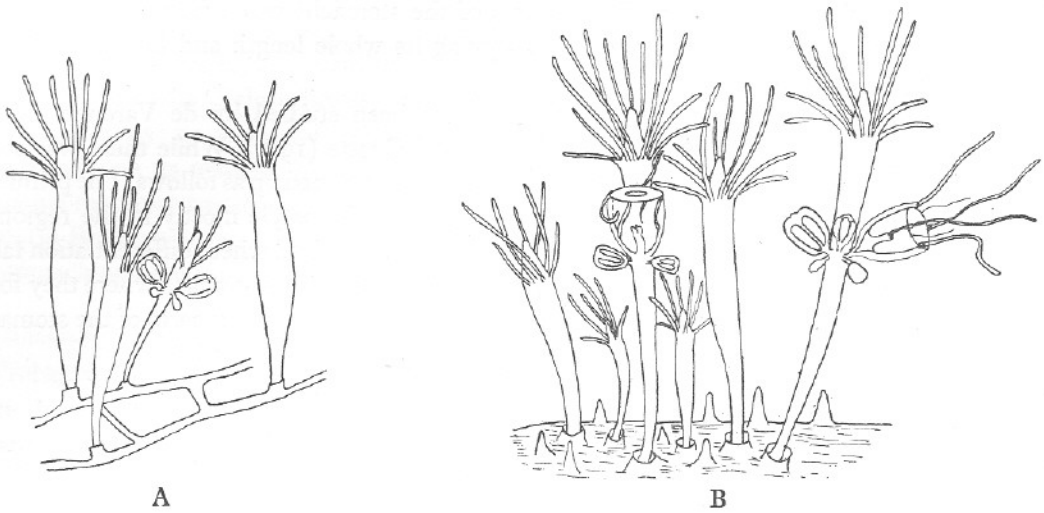
Young hydroids have been reared from the egg by de Varenne (1882).

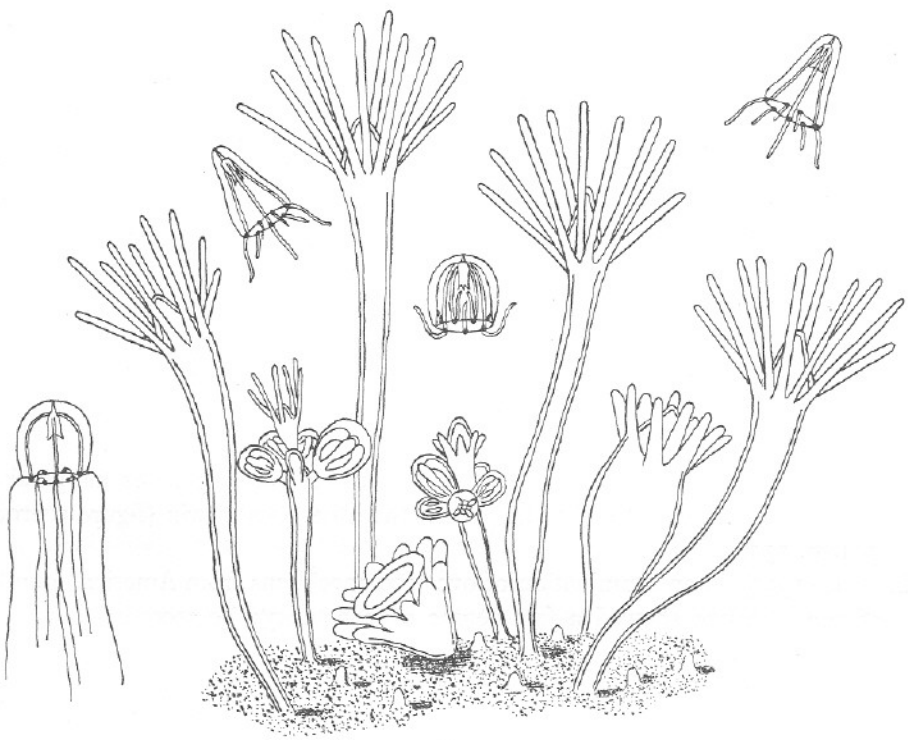
H. C. Müller (1913) studied regeneration and degeneration in the developing medusa.

Podocoryne carnea might at first glance be confused with the eight-tentacled stage of *Lizzia blondina*. It can, however, be distinguished by the absence of a peduncle, by the nematocyst knobs on the mouth margin, which are not stalked and originate above the mouth margin as in *Lizzia*, and by the fact that it does not produce medusa buds.

Seasonal occurrence

While the medusae are not commonly taken in the plankton they may be obtained in almost any month of the year by bringing the hydroid into the laboratory. The main season of medusa production is probably spring and summer.





Text-fig. 58. *Podocoryne carnea*. A and B, portions of hydroid colonies (after Hincks, 1868, pl. v, figs. *b*, *c*); C, hydroid (after Allman, 1871–2, pl. xvi, fig. 1).

Habits

In life the marginal tentacles, which can extend to two or three times the length of the umbrella, are carried somewhat stiffly, curling at first upwards for a short distance round the exumbrella margin. They are never spirally coiled. A very lifelike drawing of the newly liberated medusae was made by Brooks (reproduced in Mayer, 1910, p. 138, fig. 74).

Allman (1859*a*) and de Varenne (1882) have recorded constant movement of the nematocysts in the clusters on the mouth margin. Allman suggested that this was due to currents set up in the water by cilia in the mouth.

Hovasse (1935) records the peridinian *Protoodinium chattoni* as parasitizing a medusa of this species.

Hydroid. *Hydractinia carnea* (M. Sars). (Text-figs. 58A–C.)

(For full description see Hincks, 1868, *Brit. Hydroid Zooph.* p. 29, pl. v; and Allman, 1872, *Monogr. Gymnobl. Hydroids*, p. 349, pl. xvi, figs. 1, 2.)

Colonies of single naked hydranths 5–15 mm. in height springing from creeping stolon which at first forms a network and later spreads to form a thin layer with short blunt spines. Hydranth with a single whorl of twelve filiform tentacles. Specialized spiral appendages are sometimes present arising from the stolon.

Medusa buds borne singly in a collar round hydranth stem a short distance below tentacles. These hydranths are often reduced to form blastostyles of small size and with reduced number of tentacles.

Colour of hydranths varying from white to flesh colour. Commonly found on shells of *Nassarius* and other gastropods.

Historical

The medusa *Podocoryne carnea*, together with its hydroid, was first described by Michael Sars in 1846 from Floröe and Manger in Norway. It was later placed by Haeckel in the genus *Dysmorphosa* in which he also placed the first stage of the medusa *Lizzia blondina*. The name *Dysmorphosa* was first used by Philippi (1842) for a hydroid from the Mediterranean which he named *D. conchicola*. The hydroid was not mature and it is impossible to say whether it was *Hydractinia carnea* or a non-medusa-bearing species of *Hydractinia*.

The first specimen to be recorded in British waters was found off the Cornish coast by Busch (1851) and named *Sarsia nodosa*. This was subsequently placed by L. Agassiz into the genus *Ectopleura* and by Haeckel into *Syndictyon*.

Podocoryne borealis (Mayer)

Plate VI, fig. 5; Text-figs. 57B, 59A, C–F

Cytaeandra areolata, Browne, 1895, *Trans. Liverpool Biol. Soc.* vol. ix, p. 262.
?Browne, 1897*a*, *Proc. Zool. Soc. London*, p. 817, pl. xlviii, figs. 1, 2.
Browne, 1903, *Bergens Mus. Aarb.* no. 4, p. 12.
Lymnorea borealis Mayer, 1900*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. xxxvii, p. 6, pl. 5, figs. 16–18.
Mayer, 1910, *Medusae of the World*, vol. i, p. 154, pl. xv, figs. 1–3; ?pl. xiv, figs. 2, 5 (?pl. xv, fig. 14).
Peacock, 1924, *Dove Marine Lab. Rep.* p. 58.
Limnorea norvegica Broch, 1905, *Bergens Mus. Aarb.* no. 11, p. 5.
Podocoryne areolata, Mayer, 1910, *Medusae of the World*, vol. i, p. 140.
Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, xii, p. 219, figs. 192–4.
Kramp & Damas, 1925, *Vidensk. Medd. Dansk. naturh. Foren*, Bd. lxxx, p. 268.
Podocoryne borealis, Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, xii, p. 225, fig. 195.
Rees, 1941*a*, *Journ. Mar. Biol. Assoc.* vol. xxv, p. 307, fig. 1.
Lymnorea norvegica, Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, xii, p. 227.

HYDRACTINIIDAE

Specific Characters

Four mouth-lips extending to form four tentacles branching dichotomously once or twice, each branch with terminal cluster of nematocysts. No asexual reproduction by medusa buds. More than eight marginal tentacles.

Description of Adult

Umbrella bell-shaped, nearly as high as wide; jelly thin, somewhat thicker in apical region with tendency towards apical projection; scattered nematocysts on exumbrella. Velum broad. Stomach four-sided, not extending beyond umbrella margin; with no, or very short, peduncle. Mouth with four lips extending to form four tentacles, each branching dichotomously once or twice, each branch with terminal cluster of nematocysts. Four radial canals and ring canal narrow. Gonads interradial, covering upper half of stomach and separated radially. Marginal tentacles usually sixteen to thirty-two in number, four of which are perradial and four interradial; closely spaced round umbrella margin. No ocelli. Height when full grown *c.* 5 mm. Colour of marginal bulbs dark red, reddish yellow, reddish brown, brown, or deep yellow brown. Stomach in region of gonad yellowish brown.

Distribution

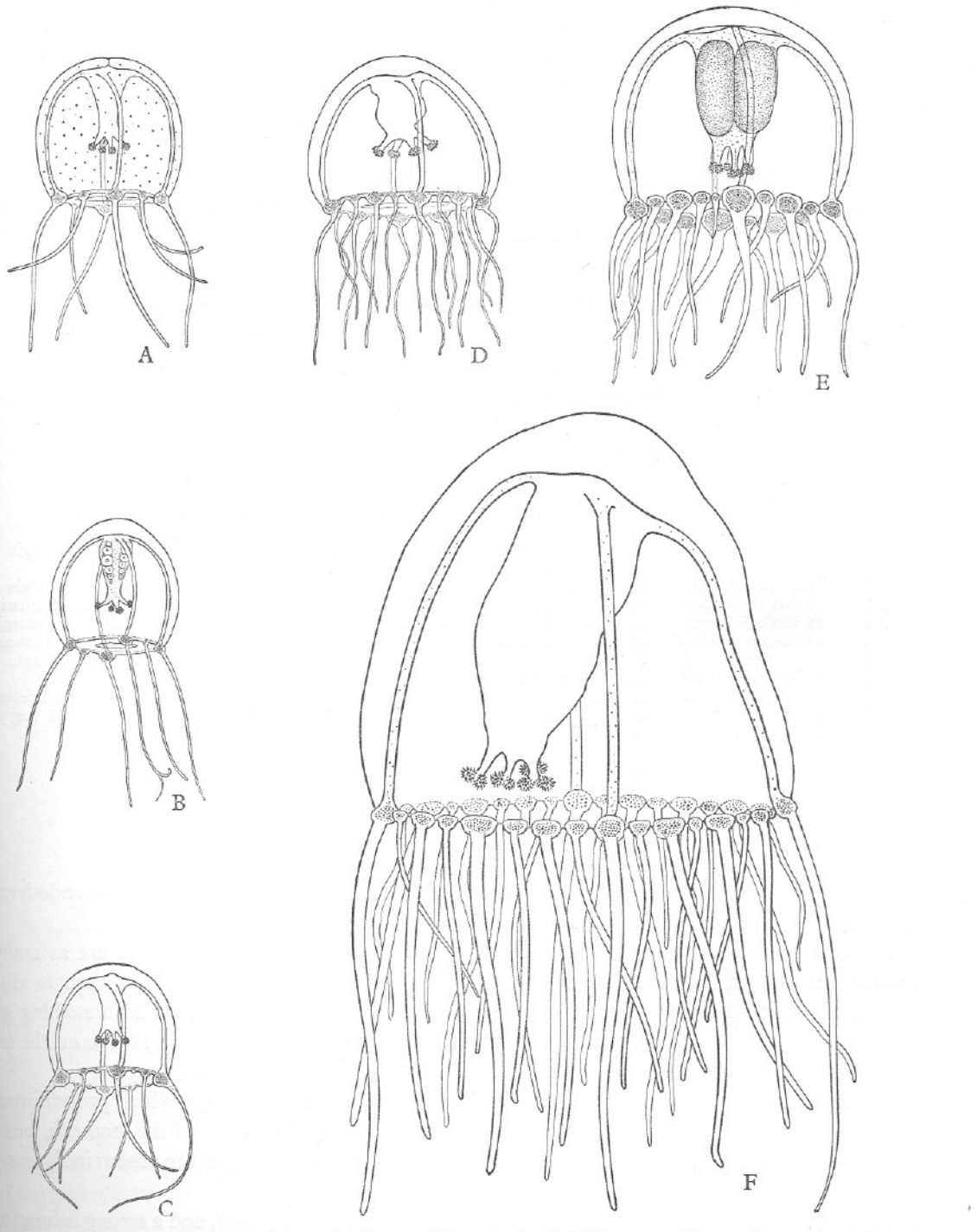
Podocoryne borealis has never been recorded as very numerous in the plankton. Round the British Isles it has been recorded from the Northumberland coast; Firth of Clyde; Port Erin; Plymouth; Valencia and Duvillaunmore, Ireland. Elsewhere it has been recorded from the coast of Norway; Iceland; the North Sea south of Jutland Bank; Helgoland, Zeebrugge, Ostende; Eastport Harbour, Maine, U.S.A.

Developmental Stages and Structural Details

The only certain description of the liberation of *Podocoryne borealis* from its hydroid is that given by Rees (1941*a*). The newly liberated medusae (Text-fig. 59A) were 0·8–1·0 mm. high and 0·9–1·2 mm. wide. There were scattered nematocysts on the exumbrella and the jelly was uniformly thin. The stomach was about half the length of the subumbrellar cavity. The mouth had four distinct lips, each terminating in a cluster of nematocysts. The four radial canals and ring canal were narrow. There were four large perradial marginal tentacles and four smaller interradial tentacles. The four perradial tentacular bulbs were the larger, each being 0·1 mm. in diameter. There was no trace of a gonad. The colour of the base of the stomach and of the marginal tentacle bulbs was brownish.

Rees obtained exactly similar medusae from the plankton, 0·65–1·0 mm. high and 0·65–1·1 mm. wide. In the next stage (Text-fig. 59C) the interradial marginal tentacles were further increased in size and there were now eight adradial developing tentacular bulbs, none of which as yet had signs of tentacles. The medusa was 1·1 mm. high and 1·2 mm. wide. There were scattered nematocysts on the exumbrella. The stomach was 0·8 mm. long. The mouth had four lips each terminating in a nematocyst cluster. There was no trace of developing gonads. The colour of the marginal bulbs was brownish.

As the medusa grew, marginal tentacles developed on the eight adradial bulbs so that a stage with sixteen tentacles was produced (Text-fig. 59D). At this stage the umbrella was 1·7 mm. high and 1·8 mm. wide. The stomach had a slight peduncle and the mouth still had four lips. The first signs of the gonads were now appearing.



Text-fig. 59. *Podocoryne borealis*. A, newly liberated from hydroid, Millport, 7. iii. 40; C and D, eight and sixteen tentacle stages, Millport, 6. v. 40; E, mature male with seventeen tentacles, Millport, 6. v. 40; F, mature female with thirty-one tentacles, Millport, 2. v. 40; B, *Podocoryne carnea*, mature female reared from the hydroid, Plymouth, 2. x. 36. (After Rees, 1941*a*, fig. 1.)

The medusa continues to grow and develop new marginal tentacles. The largest number of marginal tentacles yet recorded for any specimen is that described by Rees (1941*a*) which had thirty-one (Text-fig. 59F). It was a mature female 3·55 mm. high and 4·0 mm. wide. The umbrella was thickened at its apex, thinning towards the margin. The stomach reached nearly to the umbrella margin. The four mouth-lips were completely divided so that there were eight nematocyst clusters. As well as the thirty-one marginal tentacles there was one developing tentacular bulb. The four gonads were interradial in position and occupied the greater part of the length of the stomach. The mature eggs on the interradii were dark and granular in appearance, while the more immature eggs at the edges of the gonads were transparent. This gave the surface of the gonad a reticulate appearance.

TABLE IV. *Podocoryne borealis* (Mayer). Series of Medusae caught at Keppel Pier, Millport, 2 May 1940

Diameter (mm.)	Marginal tentacles	Total	Sex	No. of nematocyst clusters on oral lips	Remarks
0·85	4 large+4 small	8	—	4, round	Newly liberated
1·2	8 large+8 small	16	—	4, round	Young specimen
1·7	8 large+8 small	16	—	4, round	Fairly young specimen
1·1	8 large+8 small	16	—	4, round	Stomach full
1·7	12 large+4 small	16	Imm. male	4, oval	Stomach reaching bell margin
1·9	8 large+8 small	16	?Imm. female	4, oval dividing	Gonads just appearing
2·0	8 large+8 small	16	Imm. male	4, oval	Stomach reaching bell margin
2·2	8 large+8 small	16	Imm. male	—	Mouth and part stomach missing
2·1	12 large+4 small	16	Imm. male	4, oval	Stomach nearly reaching margin
2·1	16 large+3 small	19	Imm. female	4, all dividing	Stomach reaching half-way to margin
2·1	—	16	Male	4, 2 oval, 2 dividing	Stomach reaching bell margin
2·15	16 large+3 small	19	Imm. female	4, 2 oval, 2 dividing	Gonads just appearing
2·6	17 large+4 small	21	Male	—	Mouth and part stomach missing
2·8	16 large+4 small	20	Imm. female	4, all dividing	The 4 small tentacles are very small
2·65	16 large+4 small	20	Male	4, all dividing	Gonads mature
2·4	16 large+4 small	20	Male	8 distinct clusters	Gonads mature
3·0	22 large+3 small	25	Male	8 distinct clusters	Gonads mature
3·0	19 large+5 small	24	Male	8 distinct clusters	Gonads mature
3·4	22 large+4 small	26	Male	8 distinct clusters	Gonads mature
4·0	30 large+1 small	31	Female	8 distinct clusters	Gonads mature

The stomach, radial canals and ring canal were a delicate pinkish red and the endoderm of the marginal tentacle bulbs deep reddish brown.

In some specimens the mouth-lips may be further subdivided so that there are as many as sixteen nematocyst clusters. The nematocysts are on fine stalks and have been seen to vibrate and quiver. The dividing of the nematocyst clusters and somewhat irregular branching gives these oral tentacles a foliaceous appearance (Text-fig. 57B). There is a deep groove on the inner face of each oral tentacle, running along the branches (Kramp & Damas, 1925).

In cross-section the stomach shows four longitudinal endodermal ridges which project inwards into the alimentary cavity; they extend over the upper gonadial region of the stomach, but not throughout its whole length to the mouth (Hartlaub, 1911). These ridges are absent in *Podocoryne carnea*.

In preserved specimens the marginal tentacles may be spirally coiled, and a strong coloration is retained in the tentacular bulbs.

Rees obtained a good series of this medusa at Millport in the Firth of Clyde and details of specimens of different sizes are given in Table IV. Some details of other specimens which have been recorded in the literature or seen at Plymouth are given in Tables V and VI.

P. areolata can be distinguished from *P. carnea* in British waters by the presence of more than eight marginal tentacles and the branching of the oral tentacles.

Seasonal occurrence

As already stated *Podocoryne borealis* has never been recorded in large numbers from the plankton. It has, however, been recorded in British waters in one locality or another in every month of the year, except February, October and November. In the Firth of Clyde Browne (1905 *a*) records that while generally very scarce it was more plentiful in May than in the other months; Rees (1941 *a*) obtained the majority of his specimens at Millport also in May, while medusae were liberated from the hydroid in March.

TABLE V. *Podocoryne borealis* (Mayer)

Diameter (mm.)	Marginal tentacles	Total	Locality
1·0	16 large+4 small	20	Plymouth
1·0	16 large+10 small	26	Plymouth
1·0	8 large+8 small	16	Plymouth
1·0	16 large+4 buds	20	Plymouth
1·5	8 large+15 very small (in pairs)	23	Plymouth
1·5	8 large+8 small+7 bulbs	23	Plymouth
1·5	8 large+8 small	16	Plymouth
1·5	8 large+5 small+3 bulbs	16	Port Erin
1·5	4 large+4 smaller+8 small+1 bulb	17	Port Erin
1·5	19 tentacles	19	Valencia
1·75	28 (some not fully grown)	28	Northumberland coast
1·75	18 (some not fully grown)	18	Northumberland coast
2·0	16 large+10 small	26	Port Erin
2·0	18 tentacles	18	Valencia
2·0	22 large+2 small	24	Valencia
2·0	29 (some not fully grown)	29	Northumberland coast
2·0	28 (some not fully grown)	28	Northumberland coast
3·0	16 large+6 small	22	Port Erin
4·0	25 large (uniform size)	25	Port Erin
4·0	28 large (uniform size)	28	Port Erin
4·0	30 large (uniform size)	30	Port Erin
5·0	22 large+2 small	24	Valencia
5·0	24 tentacles	24	Valencia

TABLE VI. *Podocoryne borealis* (Mayer)

Size (height in mm.)	Marginal tentacles	Total	Locality
1·25	4 large, 4 smaller, 8 developing	16	Norway
1·25	5 large	5	Norway
3·0	26 all different sizes	26	Norway
2·0	8 large+4 small	12	Herløfjord
2·0	24 tentacles	24	Hjeltefjord
3·0	22 large+3 small	25	Herløfjord
3·0	23 tentacles	23	Herløfjord
3·0	16 large+6 very small	22	Osterfjord

Habits

Rees (1941 *a*) states that when swimming the medusae frequently had their marginal tentacles coiled in tight spirals.

HYDROID.

The only certain description of the hydroid of this species is that given by Rees (1941 *a*); they were in colonies of single naked hydranths, springing from a creeping stolon; there was no encrusting base or spines, though Rees suggests that their absence might depend on the age

of the colony. The hydranths had a single whorl of nine to fourteen filiform tentacles. Medusa develop on the hydranth; a hydranth may have three to eight medusa buds.

Rees found this hydroid on a dead *Buccinum* shell dredged off the north end of Cumbrae on 6 March 1940.

Historical

The medusa *Podocoryne borealis* was for some time wrongly identified with a newly liberated medusa described by Alder (1862) in his account of the hydroid *Hydractinia areolata*. Haecke (1879) placed this medusa in his genus *Cytaeandra*. Browne (1895, 1897*a*) described a number of stages of the medusa under the provisional name of *Cytaeandra areolata*. Later Mayer (1900) described a medusa from Eastport, Maine, under the name *Lymnorea borealis*, and Broch (1905) described one from Norway as *Limnorea norvegica*. The similarity between *L. borealis* and *L. norvegica* was commented on by Bigelow (1909*a*), and Mayer (1910) was inclined to believe that these two species and *Podocoryne areolata* were one and the same. Hartlaub, (1911) while keeping all three provisionally separate, was evidently inclined to believe that they were the same.

Kramp & Damas (1925) accepted the synonymy of the three species, and by examination of one of Broch's original specimens removed all doubt as regards *L. norvegica* and *P. areolata*.

It was not until 1940 that Rees (1941*a*) showed that the medusa came from a hydroid differing from *Hydractinia areolata* in that the medusa buds were borne on the hydranths and not on the stolon. On these grounds Rees points out that the specific name *borealis* has priority for the medusa.

A re-examination of Norwegian and Danish specimens by Kramp (1947) has shown that all recorded as *Podocoryne areolata* are *P. borealis*.

Podocoryne hartlaubi Neppi & Stiasny

Plate VI, figs. 1, 4; Text-figs. 60A–D, 61A, B

Podocoryne hartlaubi Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. xx, p. 47, pl. ii, fig. 14.
Russell, 1940*b*, *Journ. Mar. Biol. Assoc.* vol. xxiv, p. 525, fig. 1.

Specific Characters

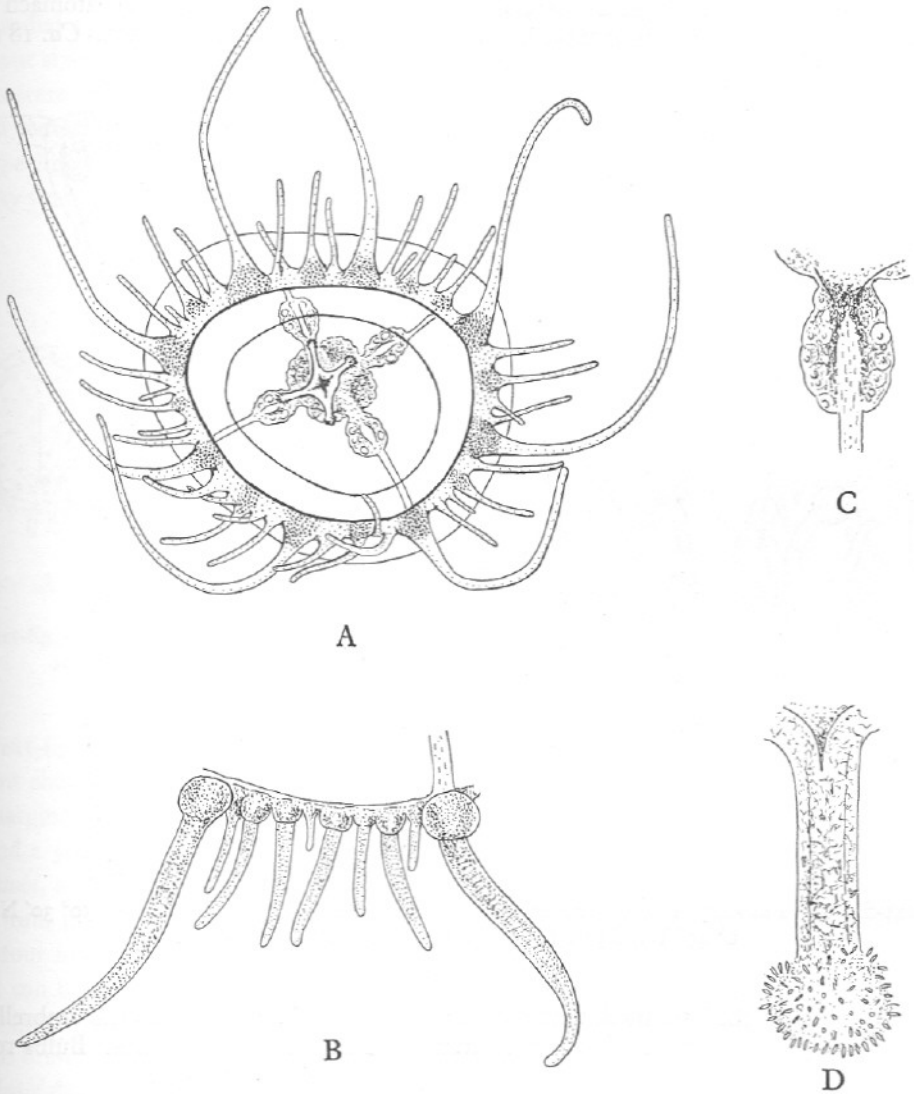
Mouth-lips each with single terminal cluster of nematocysts; gonads on proximal portions of radial canals as well as on stomach; up to forty-four marginal tentacles of which four perradial and four interradial are large.

Description of Adult

Umbrella bell-shaped, about as high as wide; no apical process; jelly thin, thicker in apical region. Velum broad. Stomach cylindrical, about half the height of subumbrellar cavity in length; very slight peduncle. Four radial canals and ring canal narrow. Mouth with four elongated perradial lips each with single terminal nematocyst cluster. Gonads interradial on stomach wall and perradial for short distance along proximal portions of each radial canal. Up to fifty-seven solid marginal tentacles with swollen basal bulbs; four perradial and four interradial marginal tentacles large and approximately of same size, remaining marginal tentacles small and of different sizes. No ocelli. Diameter of umbrella 2·0–3·8 mm. Colour of stomach, gonads, and basal bulbs of larger marginal tentacles yellow or brownish.

Distribution

Podocoryne hartlaubi was recorded for the first time from British waters in 1938 when I caught one specimen while on a cruise on S.S. *George Bligh* in the mouth of the English Channel (50° 30′ N.; 6° 49′ W.) and what is probably a young stage at Plymouth. Subsequently I found



Text-fig. 60. *Podocoryne hartlaubi*, preserved specimens. A, 2 mm. diameter, Valencia, 11. viii. 99; B, octant of umbrella margin of specimen 3·8 mm. diameter; C, gonads on proximal portion of radial canal; D, mouth lip. (After Russell, 1940*b*, fig. 1.)

one specimen in Mr Browne's collection from Valencia, and two more in collections made by Mr P. G. Corbin in the mouth of the English Channel (Russell, 1940*b*).

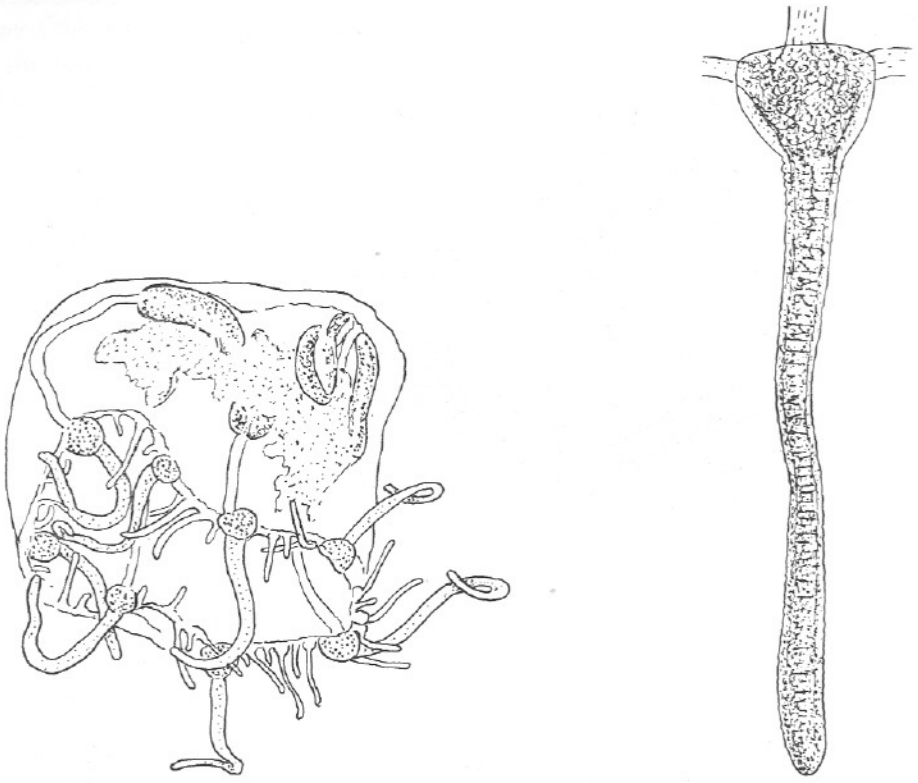
The only other locality from which the species has been recorded is the Gulf of Trieste (Neppi & Stiasny, 1913*a*).

HYDRACTINIIDAE

Developmental Stages and Structural Details

The early stages of *Podocoryne hartlaubi* have not been described, nor is its hydroid known. The species was described by Neppi & Stiasny (1913*a*) from the Gulf of Trieste and it has apparently not been recorded since. The species-diagnosis given by these authors was as follows:

Umbrella bell-shaped, as high as broad. Peduncle short, broad conical, stomach cubical, filling half the umbrella cavity; four mouth tentacles half as long as the stomach. *Ca.* 18 tentacles



Text-fig. 61. *Podocoryne hartlaubi.* A, preserved specimen 3·0 mm. diameter, 50° 30′ N.; 6° 49′ W., April 1938; B, marginal tentacle of above.

of different lengths: eight long thick tentacles, approximately half as long as the umbrella height and between every two long tentacles one to three much shorter thin tentacles. Bulbs roundish, small. Gonads only on the stomach or both on it and on the manubrium.

Umbrella height and breadth *ca.* 2 mm.

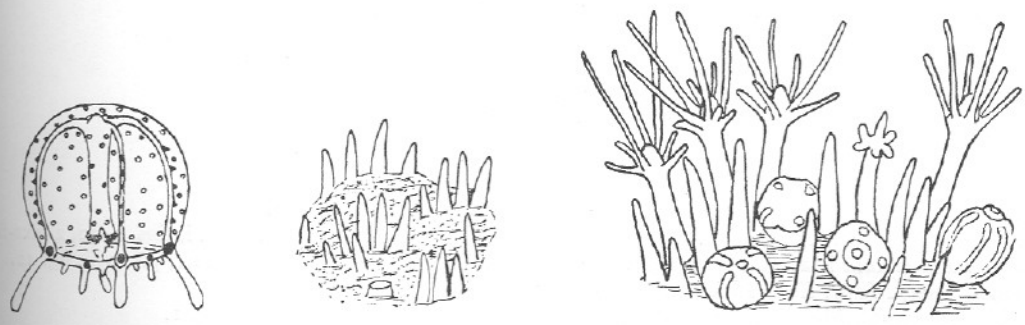
Colour: The eight larger bulbs strong dark brown, stomach flecked with dark brown, gonads yellowish brown.

They add that the species comes nearest to *Podocoryne borealis* but differs from it in the unequal lengths of the marginal tentacles in adult specimens and in the unbranched mouth tentacles. Their expression as regards the disposition of the gonads is not quite clear, but their figure (pl. ii, fig. 14) shows them quite clearly both on the stomach and on the proximal portions of the radial canals.

The specimens I have seen differ only in having a greater number of marginal tentacles. I do not regard this difference as specific since it is such as might be expected from the geographical localities if the Mediterranean medusae mature earlier.

The specimens from the mouth of the English Channel were 3·0, 3·5 and 3·8 mm. in diameter. They had forty-eight, thirty-four and fifty-seven marginal tentacles respectively, of which the four perradial and four interradial were large and of the same size, the remainder being small and of different sizes (Pl. VI, fig. 4). In a living specimen the basal bulbs of the eight large marginal tentacles were yellow and this colour was also shown in the larger bulbs of the series of small marginal tentacles; the stomach and gonads were flecked with yellow.

The specimen from Valencia (labelled by Mr Browne '*Cytaeandra* n.sp.') was 2 mm. in diameter after forty years' preservation. It had forty-four marginal tentacles of which again only eight were



Text-fig. 62. *Podocoryne areolata* Alder. A, newly liberated medusa; B, spines on encrusting stolon of hydroid; C, hydroid colony. (After Hincks, 1868, pl. vi, fig. 1*a–c*.)

large (Text-fig. 60A). The fact that only eight of the marginal tentacles are large appears to be a constant character and constitutes a specific difference from *Podocoryne borealis* in which most of the marginal tentacles grow to a large and uniform size.

I found a young medusa at Plymouth whose identity puzzled me until I had seen the adult *P. hartlaubi*, and I think now that there can be little doubt that it is this species. The medusa was 1·4 mm. in diameter and had twenty-three marginal tentacles, of which the four perradial and the four interradial were large (Pl. VI, fig. 1).

There can be no difficulty in distinguishing adult *P. hartlaubi* from adult *P. borealis*, but it is possible that confusion may have arisen over the young stages, before the mouth-lips have started to branch in *P. borealis*. I think it should probably be possible to distinguish them in the future if the degree of development of the marginal tentacles is watched. The colour of the basal bulbs in *P. borealis* is also much redder than in *P. hartlaubi* and becomes conspicuous on all the basal bulbs.

In *P. hartlaubi* each mouth-lip is continued outwards to form a solid tentacle with several rows of endodermal cells and a single large terminal nematocyst cluster (Text-fig. 60D).

The gonads on the proximal portions of the radial canals are situated on the sides of the canals and are not continuous over the lower surfaces of the canals. Each of these gonads appears to be continuous with its neighbouring portion on the interradial wall of the stomach (Text-fig. 60C).

Seasonal occurrence

The five specimens recorded here from British waters were taken on the following dates 14 January 1936 (Plymouth), 4 April 1938 (mouth of Channel), and 11 August 1899 (Valencia)

Neppi & Stiasny give for the Gulf of Trieste 'December and January, rare'.

Habits. Nothing known.

HYDROID. Not known.

It must not be overlooked that there is a possibility that the hydroid *P. areolata* of Alder may belong to this species (Text-fig. 62A–C).

Historical

Podocoryne hartlaubi was first described and figured by Neppi & Stiasny (1913*a*) from the Gulf of Trieste. It was not recorded again until 1938 (Russell, 1940*b*).

Podocoryne minima (Trinci)

Text-figs. 63A–C, 64

Cytaeis sp. (?) Browne, 1898*b*, *Journ. Mar. Biol. Assoc.* vol. v, pp. 189, 190.
Cytaeis minima Trinci, 1903, *Mitt. Zool. Stat. Neapel*, Bd. XVI, Heft 1, 2, p. 1, pl. i, figs. 1–30, 2 text-figs.
?*Dysmorphosa minuta* Mayer, 1900*b*, *Bull. Mus. Comp. Zoöl. Harv.* vol. XXXVII, p. 41, pl. xviii, fig. 42.
Trinci, 1904, *Monit. Zool. Ital.* vol. XV, p. 304.
?*Podocoryne minuta*, Mayer, 1910, *Medusae of the World*, vol. I, p. 140, pl. xiv, fig. 1.
Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. XX, p. 46 (in part), pl. i, fig. 12.
?*Podocoryne simplex* Kramp, 1928, *Vidensk. Medd. Naturh. Foren. Kbh.* Bd. LXXXV, p. 46, fig. 20.
Podocoryne minima, Russell, 1940*b*, *Journ. Mar. Biol. Assoc.* vol. XXIV, p. 528.

Specific Characters

Four perradial marginal tentacles; asexual budding from stomach.

Description of Adult

Umbrella bell-shaped, slightly higher than wide; jelly moderately thick with slight apical thickening. Velum well developed. Stomach short cylindrical, on short peduncle. Four perradial mouth-lips elongated to form four simple tentacles each terminating in single cluster of nematocysts. Four radial canals and ring canal narrow. Four interradial gonads. Asexual reproduction by budding from stomach wall. Four solid perradial marginal tentacles, each with large rounded basal bulb. No ocelli. Height of umbrella up to about 1 mm. Colour of marginal tentacle bulbs and stomach yellowish brown or brown.

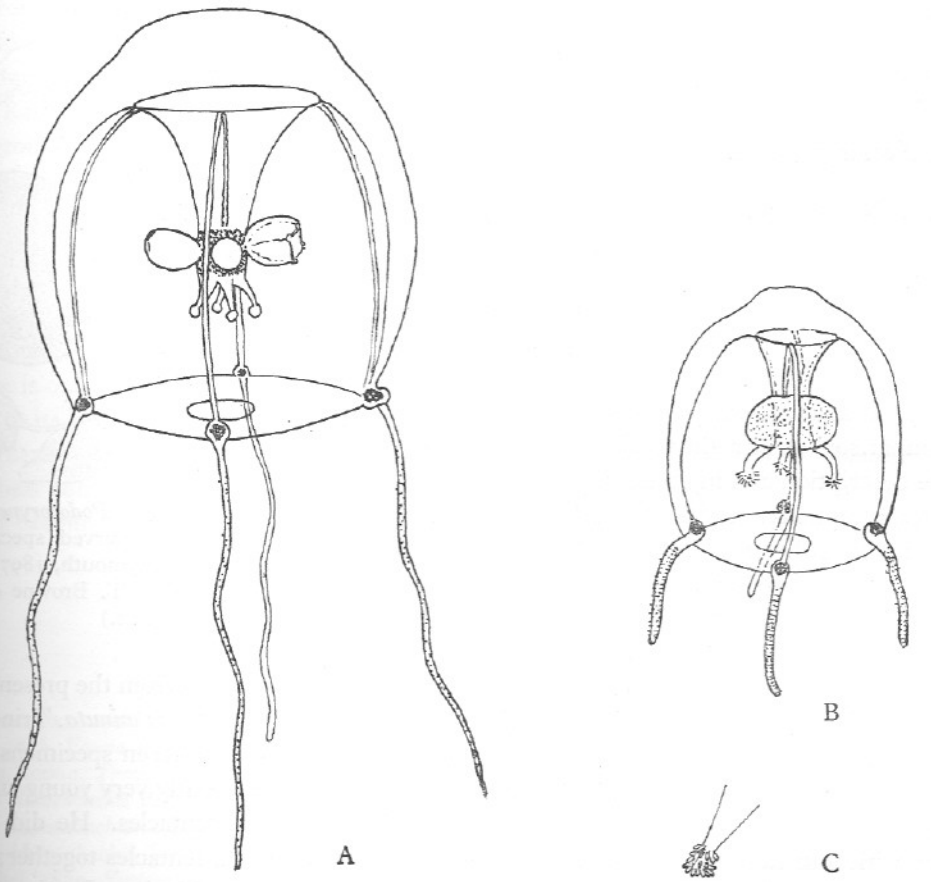
Distribution

Podocoryne minima has not previously been recorded as such from British waters. Specimens of this medusa were collected by Mr Browne from the Sound and Cawsand Bay, Plymouth, and recorded by him (1898*b*) as *Cytaeis* sp.(?). He stated that a description of the medusae was in preparation. I have seen these specimens in Mr Browne's collection (Russell, 1940*b*) and I have no doubt that they are the same species as that later described by Trinci (1903).

Elsewhere the species has been recorded from the Mediterranean and (?) Japan as *Podocoryne simplex* (Kramp, 1928).

Developmental Stages and Structural Details

The earliest stage of *Podocoryne minima* is not known for certain since its hydroid has not been found. It is, however, quite possible that when newly liberated from its hydroid the medusa differs little in general appearance from the adult. Mr Browne mentions in his notes having seen 'a very early stage, about 1 mm. long, with two medusa buds. Stomach not on a peduncle. There is a trace of an apical canal. Exumbrella covered with scattered nematocysts.'



Text-fig. 63. *Podocoryne minima*. A, medusa budding, Plymouth, September 1897; B, sexually mature medusa, Plymouth, 4. x. 93; C, mouth lip of A. (Tracings of drawings by E. T. Browne.)

There is thus little to add to the general description given above. I have examined Mr Browne's specimens and the mouth-lips (Text-fig. 63 C) are quite definitely of the *Podocoryne* type and there are no oral tentacles such as in *Lizzia*.

The medusa buds are borne on the stomach walls in the interradii and develop successively in the manner typical of such species as *Rathkea* and *Lizzia*, that is according to the formula $4\frac{1}{2}3$.

The early development of the medusa buds has been studied in detail by Trinci (1903) who states that they are entirely ectodermal in origin.

Medusa buds and gonads may occur simultaneously. The gonads are interradial, but it appears from a drawing made by Mr Browne (Text-fig. 63 B) that when fully developed they may completely surround the stomach as in *Rathkea* and *Lizzia*.

In his notes Mr Browne also says: 'The tentacles are usually contracted and then look somewhat rudimentary, but when expanded are slightly longer than the length of the umbrella.' The marginal tentacle bulbs are very conspicuous on account of their dark colour.

Hovasse (1935) records the peridinian parasite *Protoodinium chattoni* from a medusa taken at Séte which he identified as *Lizzia blondina*, although in a footnote (p. 60) he raised a doubt as to the correct identification. His drawing (pl. ii, fig. 1) agrees with *Podocoryne minima*.

Seasonal occurrence

The Plymouth specimens were found in September and October.

Habits. Nothing known.

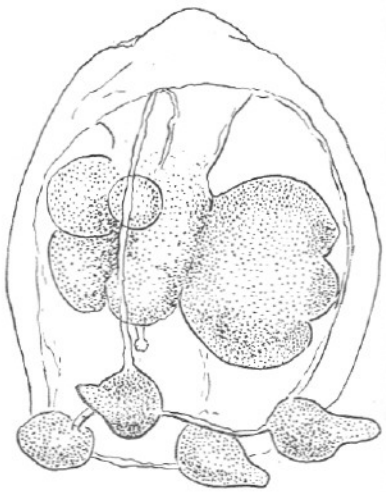
HYDROID. Not known.

Historical

Podocoryne minima was first described by Trinci (1903) from the Gulf of Naples as *Cytaeis minima*, Browne (1898*b*) having previously recorded the occurrence of the species at Plymouth without a description as *Cytaeis* sp.(?).

A comparison of Mr Browne's specimens and drawings with the description and figures given by Trinci shows no real difference except that of size. Trinci's specimens were only 0·27–0·33 mm. in height; this is hardly a specific difference.

I think it most probable that the medusa described by Kramp (1928) from Japan as *Podocoryne simplex*, which was 0·75 mm. in height, is the same species.



Text-fig. 64. *Podocoryne minima*. Shrunken preserved specimen 0·6 mm. high, Plymouth, 1897. (Specimen from E. T. Browne collection drawn 16. v. 40.)

Mayer (1900*b*) described a species from Tortugas which only differed from the present species in having eight marginal tentacles instead of four. He called it *Dysmorphosa minuta*. Trinci (1904) found similar specimens from the Mediterranean. He found about a dozen specimens all with eight marginal tentacles; they were 0·28 mm. high. Some were apparently very young and newly liberated from the hydroid, but they already had eight marginal tentacles. He did not find medusae with four marginal tentacles and those with eight marginal tentacles together; nor did he see any intermediate stages between four and eight marginal tentacles. In view of these observations he hesitated to regard his *Podocoryne minima* as the same species as that described by Mayer.

It is, however, known that *P. carnea* shows variation in the number of marginal tentacles at liberation from the hydroid, and it may be proved eventually that Trinci's and Mayer's medusae are the same species. Should this be so the name must become *P. minuta* (Mayer).

P. minima was recorded by Neppi & Stiasny (1913*a*) from the Gulf of Trieste, as *P. minuta*. But it seems that they may have included *P. minima* and *P. carnea* in their account; for they state that the medusae with four marginal tentacles had medusa buds, while those with eight marginal tentacles had only gonads. Although *P. carnea* may sometimes be liberated from its hydroid with four marginal tentacles there are no records of these medusae ever having been found with medusa buds. They mature very quickly after liberation, and there can, I think, be little doubt that *P. minima* is a distinct species.

Family RATHKEIDAE

Anthomedusae with umbrella with slight apical process; without exumbrellar nematocyst tracks; with stomach not extending beyond umbrella margin; with peduncle; with mouth with four lips armed with terminal and lateral nematocyst clusters; with four (or eight?) radial canals; with gonads completely surrounding stomach; with asexual budding from stomach wall; with eight groups of solid marginal tentacles; without ocelli.

HYDROID. *Rathkea*, with single whorl of very extensile threadlike filiform tentacles.

The family Rathkeidae is represented in British waters by one genus, *Rathkea* Brandt.

The Rathkeid medusae are characterized by the structure of the mouth and the presence of eight groups of marginal tentacles. In the former character they somewhat resemble the Hydractiniidae and in the latter the Bougainvilliidae.

Genus **Rathkea** Brandt, 1837

MEDUSAE. Rathkeidae with four radial canals.

HYDROID. *Rathkea*.

There is one species of the genus occurring in British waters, *Rathkea octopunctata* (M. Sars). Owing to its power of increasing its numbers by asexual budding it is at times very abundant in the plankton. The only medusa it is likely to be confused with is *Lizzia blondina*, adults of which bear some resemblance to very young *Rathkea*. The two species can be distinguished at once by examination of the mouth; in *Lizzia* oral tentacles grow out above the mouth opening.

Rathkea octopunctata (M. Sars)

Plate VII, figs. 3, 4; Text-figs. 65A–E, 66, 67A, B

Cytaeis octopunctata M. Sars, 1835, *Beskriv. og Jagttag.* p. 28, pl. vi, fig. 14*a–g*.
Sars, 1846, *Fauna Littor. Norveg.* Heft I, p. 10, pl. iv, figs. 7–13.
Linko, 1900*a*, *Trav. Soc. Imp. Nat. St.-Pétersbourg*, tome XXIX, livr. 4, p. 152, fig. 2.
Oceania blumenbachii Rathke, 1835, *Mém. Acad. Imp. Sci. St.-Pétersbourg*, tome II, p. 321.
Rathkia blumenbachiana Brandt, 1837, *Bull. Sci. Acad. Imp. St.-Pétersbourg*, tome I, no. 24, p. 187.
Rathkea blumenbachii, Brandt, 1838, *Mém. Acad. Imp. Sci. St.-Pétersbourg*, tome IV, p. 353.
Haeckel, 1879, *System der Medusen*, p. 96.
Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 229, figs. 196–9.
Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest.* Tom. XX, p. 56, pl. ii, fig. 23.
Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, p. 11.
Hartlaub, 1917, *Nordisches Plankton*, Lief. 19, XII, p. 408.
Hippocrene octopunctata, Forbes, 1841, *Ann. Mag. Nat. Hist.* vol. VII, p. 84.
Bougainvillea octopunctata, Lesson, 1843, *Acalèphes*, p. 292.
Lizzia octopunctata, Forbes, 1848, *Monogr. Brit. Medusae*, p. 64, pl. xii, fig. 6.
L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 345.
Van Beneden, 1866, *Mém. Acad. R. Belg.* vol. XXXVI, p. 94, pl. iii, figs. 7–13.
Böhm, 1878, *Jena Zeitschr. Nat.* Bd. XII, p. 186, pl. iv–vi.
Fewkes, 1883, *Bull. Mus. Comp. Zoöl. Harvard*, vol. XI, p. 79.
Bigelow, 1909, *Proc. U.S. Nat. Mus.* vol. XXXVII, p. 306, pl. xxxi, figs. 3–5.
Rathkia blumenbachii, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.*, vol. IV, p. 345.
Lizzia grata A. Agassiz, 1862, *Proc. Boston Soc. Nat. Hist.* p. 100, figs. 28, 29.
A. Agassiz, 1865, *North Amer. Acaleph.* p. 161, figs. 251–8.
Fewkes, 1881*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. VIII, p. 142, pl. i, figs. 1–7.

RATHKEIDAE

Margellium octopunctatum, Haeckel, 1879, *System der Medusen*, p. 95.
Browne, 1895, *Trans. Liverpool Biol. Soc.* vol. IX, p. 270.
Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 477.
Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. V, p. 710 and tables.
Margellium gratum, Haeckel, 1879, *System der Medusen*, p. 95.
Rathkea octopunctata, Haeckel, 1879, *System der Medusen*, p. 97.
Giard, 1888, *Bull. Sci. France Belg.* ser. 3, tome XIX, p. 317, pl. XXI.
Garstang, 1894, *Journ. Mar. Biol. Assoc.* (N.S.), vol. III, p. 213.
Chun, 1895, *Bibliotheca Zoologica*, Bd. VII, Heft 19, p. 15, pl. ii.
Mayer, 1910, *Medusae of the World*, vol. I, p. 177, pl. XX, fig. 11.
Kramp, 1913*b*, *Vidensk. Medd. Danske naturh. Foren., Kbh.*, Bd. LXV, pp. 266, 284.
Kramp, 1914, *Medd. om Grønland*, vol. XXIII, p. 408.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. V, pt. 10, p. 58, chart X.
Kramp, 1927, *K. danske vidensk. Selsk.* natur. og math. Afd., 8. Raekke, XII, p. 76, chart 10.
Uchida, 1927*a*, *Journ. Fac. Sci. Imp. Univ., Tokyo*, Sect. IV, Zool. vol. I, p. 225.
Lizzia blondina, Wagner, 1885, *Wirbellosen des Weissen Meeres*, Bd. I, p. 73, pl. ii, figs. 2–5 (and pl. ii, figs. 5–7 as *Bougainvillea*).
Rathkea octopunctata var. *grata*, Mayer, 1910, *Medusae of the World*, p. 179, pl. XVIII, fig. 5.
Lizzia shimiko Kishinouye, 1910, *Journ. Coll. Sci. Imp. Univ. Tokyo*, vol. XXVII, Art. 9, p. 25, pl. V, fig. 24.

Specific Characters

Four radial canals. Eight marginal tentacular bulbs, four perradial each with five tentacles, four interradial each with three tentacles.

Description of Adult

Umbrella somewhat globular, with rounded apical process, slightly higher than wide; jelly moderately thick, especially in the apical region. Velum broad. Stomach short, cylindrical, with conical peduncle, not reaching beyond umbrella margin in full extension. Mouth with four lips, each divided at its extremity into two short stalked nematocyst knobbed arms and having one or two pairs of lateral stalked nematocyst clusters and one central cluster between the two terminal arms, when fully developed. Four radial canals and ring canal narrow. Gonads completely surrounding stomach; asexual reproduction by budding from stomach wall. Eight marginal tentacular bulbs, four perradial each with five tentacles, four interradial each with three tentacles, at full development. No ocelli. Height when full grown 3–4 mm. Colour of marginal tentacular bulbs pale yellowish, dark yellowish brown, or deep vandyke brown appearing black by transmitted light. Colour of stomach brownish yellow.

Distribution

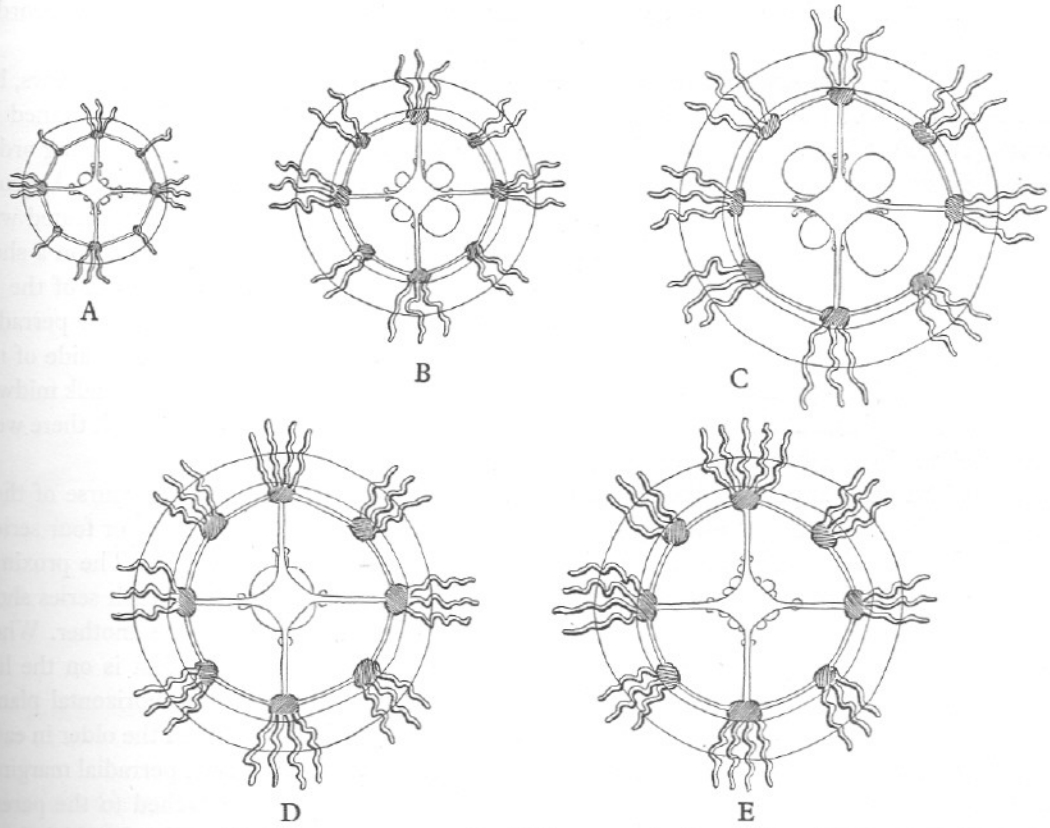
Rathkea octopunctata occurs all round the coasts of the British Isles. It is a widely distributed circumpolar arctic boreal species. North European coasts from France to Novaya Zemlya; Iceland; Mediterranean; Black Sea; western Atlantic from Chesapeake Bay to Greenland; ? Bermuda; Pacific coasts of Japan; Bering Sea; Alaska.

Developmental Stages and Structural Details

The earliest stage of the medusa at liberation from its hydroid has not been described. The smallest specimens found in the plankton (whether first liberated from the hydroid or budded from another medusae, it is not certain) are about 1 mm. in height. At this stage there are usually three tentacles on each perradial marginal bulb and four single interradial marginal tentacles. Occasionally there are only two tentacles on the perradial bulbs. As the medusa grows the number of tentacles increases to five on each perradial marginal bulb and to three on each interradial bulb

(Text-fig. 65). Thus many intermediate stages may be met with. This led to the erection of distinct genera and species by the earlier workers.

Increase in the number of tentacles appears to alternate between the perradial and interradial groups. After the stage in which there are three tentacles on each perradial bulb, the interradial bulbs develop a further pair of tentacles one on either side of the original tentacles; a stage is thus reached with three tentacles on each of the eight marginal bulbs. A further pair of tentacles is now developed on each perradial bulb, one on either side of the original three. The fully



Text-fig. 65. *Rathkea octopunctata*. Semi-diagrammatic illustration of five stages of development, seen from above.

developed stage is thus reached with five tentacles in each perradial group and three in each interradial group (Text-fig. 66B). The typical growth is thus somewhat as follows, as illustrated by the examination of a number of specimens from the plankton (Browne, 1896*a*):

P.	3333	3333	5344	5454
I.	1112	3333	3333	3333
P.	3333	3334	5433	5553
I.	2222	3333	3333	3333
P.	3333	4343	5444	5554
I.	3231	3333	3333	3333
P.	3333	5334	4454	5555
I.	2333	3333	3333	3333

P. = perradial. I. = interradial.

Similar observations have been given by Linko (1900*a*).

These examples show that the increase in the numbers of tentacles does not follow a strictly co-ordinated plan either on the perradial or the interradial marginal bulbs, the growth of one being apparently independent of that of another. It appears, however, to be a general rule that once all four perradial marginal bulbs have developed three tentacles further increase does not take place until each interradial marginal bulb has developed three tentacles.

Bigelow (1913) records that in the Bering Sea specimens are found in which five tentacles are developed on each interradial marginal bulb as well as on the perradial marginal bulbs. This is possibly the extreme development of the species, but such specimens have so far not been recorded from the Atlantic.

Not only do the numbers of tentacles on the marginal bulbs increase as the medusa grows, but also the numbers of nematocyst clusters on the lips of the mouth. Specimens examined by Browne (1896*a*) at Valencia showed that these nematocyst clusters develop in the following order. The earliest stage has each of the four lips terminating in a single cluster of nematocysts. A second cluster appears on a short stalk near the first cluster; each lip thus appears to be bifurcated with a round cluster of nematocysts at the end of each branch. Two lateral clusters, each on a short stalk, now develop on each lip, one on either side at about the middle of the length of the lip (Text-figs. 66A, C). In the largest specimens with four or five tentacles on each perradial marginal bulb a second pair of lateral clusters is developed on each lip on the basal side of the first lateral pair. Finally, there is a single central cluster on each lip borne on a short stalk midway between the two terminal clusters on each lip. Browne described a variation in which there were three terminal clusters but only one lateral pair.

The medusa buds appear on the stomach wall at a very early stage, and the course of their development has been fully studied by Chun (1896). The buds are borne in three or four series, and in each series there are four interradial buds approximately at right-angles. The proximal series, nearest the base of the stomach, is the first to develop and the buds in each series show a graded order of development, in that the two older buds stand opposite one another. When viewed from the aboral pole with the oldest bud lying dorsally the third oldest is on the left side. While the four buds in the oldest series are approximately in the same horizontal plane, the younger buds in the later series tend to be slightly more distally placed than the older in each series. The budded medusae are liberated usually with three tentacles on each perradial marginal bulb and single tentacles on the interradial marginal bulbs. While still attached to the parent medusa the buds themselves are already developing buds on their stomach walls, the oldest have already two series of four buds forming at liberation.

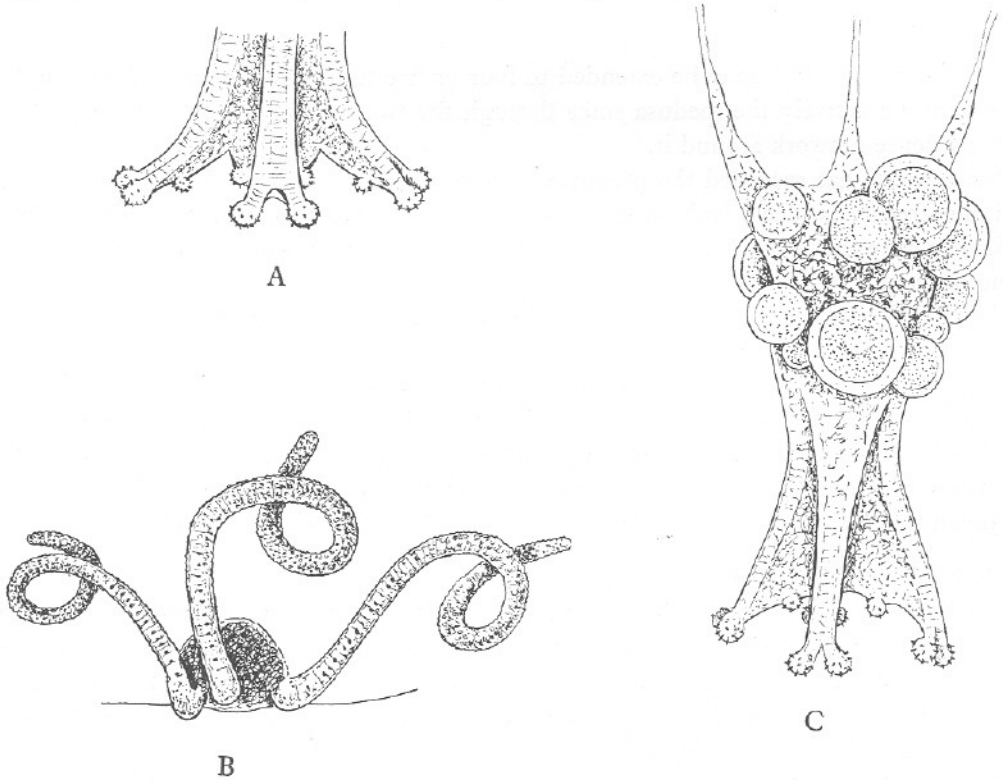
Bigelow (1913) states that among the Bering Sea specimens mentioned above he found a specimen with a medusa bud almost ready for liberation which had five tentacles on each perradial marginal bulb and three on each interradial marginal bulb. As with the number of marginal tentacles in fully grown specimens this implies extreme development compared with medusae in the Atlantic.

Böhm (1878) and Chun (1895) have studied the histology of the process of bud formation. The former showed that both endoderm and ectoderm took part in the first formation of the bud; but Chun maintained that they were purely ectodermal in origin and that the endoderm cells were later differentiated from the ectoderm (see also Braem, 1908). This, however, is rightly doubted by Kramp (1926*a*).

The gonads start to ripen at the termination of the period of asexual reproduction and may be present when the last buds are still unliberated. The gonads first appear upon the perradial ridges

of the stomach and as they increase in size they form a mass completely surrounding the stomach (Pl. VII, fig. 4). Kramp (1942) considers that in Danish and Greenland waters sexual reproduction is not preceded by asexual reproduction in the same individual.

The four perradial ridges of the stomach are formed of supporting endodermal cells stretching from the radial canals to the lips of the mouth (Text-fig. 66C).



Text-fig. 66. *Rathkea octopunctata*. Specimen 2·5 mm. high, Plymouth, 20. iv. 39. A, mouth; B, interradial marginal tentacle group; C, stomach and gonads.

Littleford (1939) records that the colour of medusae from Chesapeke Bay was brilliant orange to bright red.

Browne (1895) described an abnormal specimen from Port Erin. This had six radial canals. The two additional canals ran down to two adjacent interradial marginal bulbs each of which had four tentacles. There were also five mouth-lips, four of which had two terminal and two lateral clusters of nematocysts while the fifth had a single terminal and two lateral clusters.

Mereschkowsky (1879) described and figured an abnormal specimen, from the White Sea, devoid of a stomach (as a species of *Bougainvillia*).

The hydroid has been reared from the egg by Rees & Russell (1937). The eggs are opaque white, and 0·14 mm. in diameter. The planulae are 0·20–0·24 mm. in length and 0·08–0·09 mm. wide.

NEMATOCYSTS. Microbasic euryteles and desmonemes (Russell, 1938*b*).

Seasonal occurrence

Rathkea octopunctata occurs in the plankton typically as a winter and spring species. The medusae first appear in January or February, becoming abundant by April. Up to this month

they mostly carry medusa buds, but in April and May asexual bud formation gives rise to sexual maturity, although sexually mature specimens have been found in March on the west coast of Ireland. The medusae mostly disappear from the plankton by June and July. Occasional specimens have however been recorded in all remaining months of the year except December. Specimens taken at Valencia in October and November had medusa buds.

Habits

The marginal tentacles may be extended to four or five times the height of the umbrella and after swimming actively the medusa sinks through the water in any position with its tentacles forming a dense network around it.

Lebour (1923) has recorded the presence of many different organisms in their stomachs, on examining freshly landed plankton catches. Fish were frequently taken, although Crustacea and *Sagitta* were the commonest food. Specimens were seen in which unliberated medusae were feeding on young sprat.

Hollowday (1947) records specimens in the Marine Lake, Southport, as feeding on the rotifer, *Synchaeta*, in November 1946.

Littleford (1939) observed that these medusae were eaten by *Cyanea*.

Kramp (1927) found in Danish waters that reproduction by gemmation appeared to be controlled by temperature, the percentage of gemmiferous individuals being much reduced above 5° C. The temperature would thus limit their period of occurrence in the plankton.

In Japan this medusa is popularly known as 'Shimiko' (Kishinouye, 1910).

Hydroid (Text-figs. 67A, B).

(For full description see Rees & Russell, 1937, *Journ. Mar. Biol. Assoc.* vol. XXII, p. 71, figs. 7, 8.)

Colonies of small single hydranths rising from a creeping stolon. Base of hydranth surrounded by very thin gelatinous perisarc. Hydranths *c.* 0·15–0·20 mm. in height, with single whorl of four to six delicate threadlike filiform tentacles. Position of medusa buds not known. Hypostome opaque white, remainder of polyp colourless.

This hydroid has not yet been recorded for certain from the wild, and the description is from specimens reared in the laboratory from the medusae. If these were normal specimens, it seems likely that the hydroid will be very difficult to find in the sea on account of its minute size.

Historical

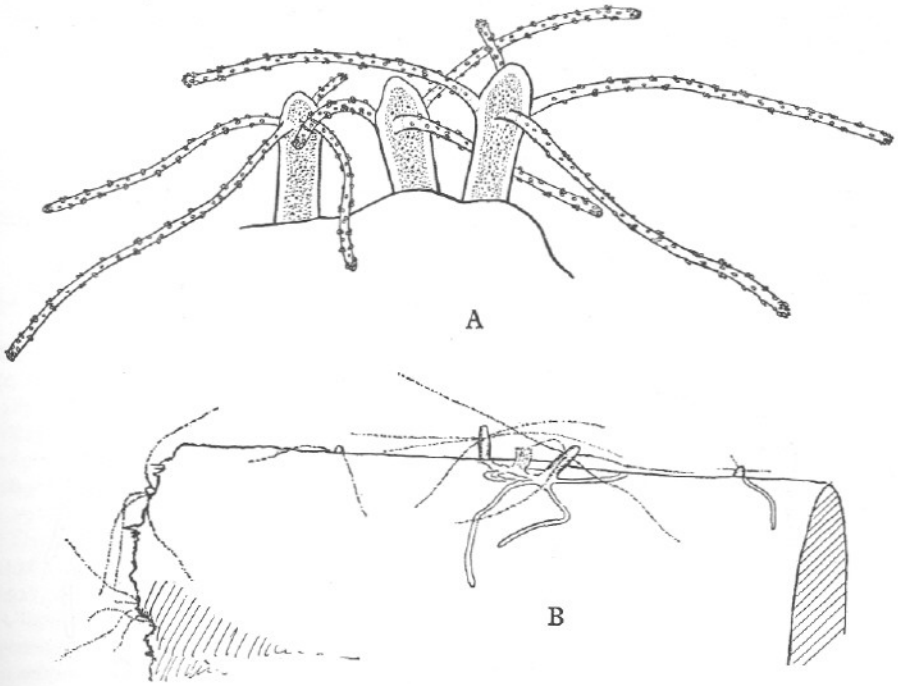
Rathkea octopunctata was first described by Sars (1835) as *Cytaeis octopunctata*. In the same year a medusa was described by Rathke from the Black Sea as *Oceania blumenbachei*. This according to Rathke had eight radial canals. Haeckel (1879) presumed that Rathke had been mistaken in the number of radial canals, and the two species have generally been regarded as being identical, especially as typical *Rathkea octopunctata* have since been recorded from the Black Sea (e.g. Markow, 1908).

Hartlaub (1911) used Rathke's specific name *blumenbachei*, but Kramp (1926*a*) having gone carefully into the question of the actual dates of publication of the two descriptions by Sars and by Rathke in 1835 has shown that the more usually accepted name *octopunctata* probably actually has priority.

The generic name *Rathkia* was erected by Brandt in 1837; the spelling has since been altered to *Rathkea*. Haeckel (1879), on the grounds of the difference in the number of tentacles, which are now known to be due to development, split the species into two genera *Margellium* and *Rathkea*.

The characteristic of *Margellium* was inequality between the number of tentacles on the perradial and interradial marginal bulbs, and that of *Rathkea* their equality. Garstang (1894) and Browne (1895, 1896*a*) showed that these generic distinctions arose from an insufficient knowledge of the development of the medusa.

In this species medusa production by gemmation was recorded for the first time in medusae by Sars (1835, 1846).



Text-fig. 67. *Rathkea octopunctata.* A, hydroid reared from medusa, attached to piece of *Eunicella*, with tentacles partially contracted; B, colony of same showing creeping stolon and typical attitude of tentacles; Plymouth, May 1937. (After Rees and Russell, 1937, figs. 7 and 8*b*.)

Van Beneden (1866, p. 95) described a medusa with eight radial canals under the name *Circe hyalina*.* It seems very possible that this may have been an abnormal *Rathkea octopunctata*, and supports the view that Rathke's original specimen was also abnormal. Uchida (1927) has described a somewhat similar medusa for which he has erected a new genus *Octorathkea*.

The hydroid was first described by Rees & Russell (1937).

Family BOUGAINVILLIIDAE

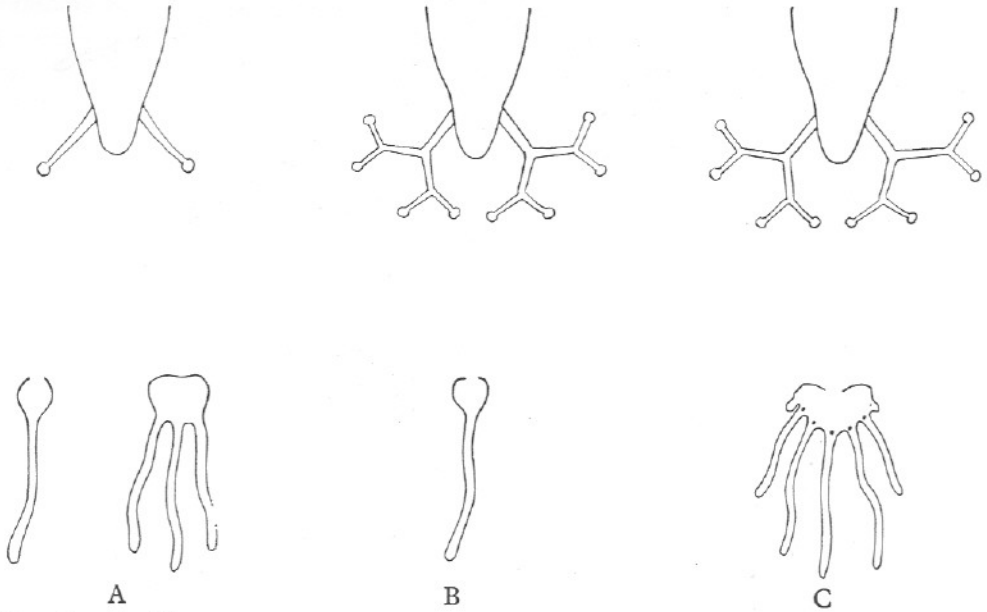
Anthomedusae with umbrella without exumbrellar nematocyst tracks; with short stomach not extending beyond umbrella margin; with or without peduncle; with simple tubular mouth with four or eight unbranched or four dichotomously branching oral tentacles inserted above mouth opening; with four radial canals; with gonads situated adradially or interradially on or completely surrounding stomach; with or without asexual budding; with two, four, or more solitary solid

* Placed by Haeckel (1879) in the genus *Lizzella* (see also Hartlaub, 1911).

marginal tentacles, or with four, eight or sixteen large marginal bulbs each with a group of solid marginal tentacles; with or without ocelli.

Hydroids with a single whorl of filiform tentacles.

The Bougainvilliidae are above all characterized by the four unbranched or dichotomously branching oral tentacles. These are inserted on the mouth tube some way above its opening and are distinctly different from the mouth tentacles of the Hydractiniidae and Rathkeidae. Another frequent character is the occurrence of the marginal tentacles in groups, each group arising from a single large marginal bulb.



Text-fig. 68. Diagram showing sub-family characters of the Bougainvilliidae. A, Lizziinae; B, Thamnostominae; C, Bougainvilliinae.

The Bougainvilliidae may be conveniently divided into three subfamilies according to whether the oral tentacles are branched or unbranched, and to whether the marginal tentacles are solitary or in groups (Text-fig. 68). These subfamilies are the Lizziinae, Thamnostominae and Bougainvilliinae and they may be distinguished as follows:

Oral tentacles unbranched:
  Marginal tentacles solitary or in groups . . . . . **Lizziinae**
Oral tentacles branched:
  Marginal tentacles solitary . . . . . **Thamnostominae**
  Marginal tentacles in groups . . . . . **Bougainvilliinae**

All three families are represented in the British fauna, the Lizziinae and Thamnostominae each with one genus with a single species, and the Bougainvilliinae with one genus with five (or six) species.

Subfamily LIZZIINAE

Bougainvilliid medusae with four or eight unbranched oral tentacles; with gonads completely surrounding stomach; with asexual budding from stomach; with four, eight or more solitary marginal tentacles or with marginal tentacles in eight groups; without ocelli.

The Lizziinae are represented in British waters by one genus, *Lizzia* Forbes, and a single species.

Genus **Lizzia** Forbes, 1849

MEDUSAE. Lizziinae with stomach with short peduncle; with marginal tentacles, when grouped, more numerous on perradial bulbs than on interradial bulbs.

HYDROIDS. Not known.

There is only one British species of the genus, *Lizzia blondina* Forbes. It is a small species which, on account of its power of increasing its numbers by asexual budding from the stomach, may at times be exceedingly abundant. It can, however, be rather easily confused at first with *Podocoryne* or *Rathkea* in some of its stages of development. On this account great care should be taken to note whether the oral tentacles are inserted above the opening of the mouth.

The hydroid of *Lizzia blondina* is not known, but there is a suggestion that it might be *Trichydra pudica* Wright (Rees, 1941*c*); should this be so, *Lizzia* might have to be removed from the Bougainvilliidae.

Lizzia blondina Forbes

Plate VII, figs. 1, 2; Plate XXXIV, figs. 5, 6; Text-figs. 69, 70A–C, 71, 72A, B

Lizzia blondina Forbes, 1848, *Monogr. Brit. Medusae*, p. 67, pl. xii, fig. 4.
L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 345.
Haeckel, 1879, *System der Medusen*, p. 82.
Browne, 1895, *Trans. Liverpool Biol. Soc.* vol. IX, p. 265.
Browne, 1896*a*, *Proc. Zool. Soc. Lond.* p. 475.
Browne, 1898*b*, *Journ. Mar. Biol. Assoc.* (N.S.), vol. V, p. 188.
Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 145, figs. 131–5.
Kramp & Damas, 1925, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. LXXX, p. 266.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. V, pt. X, p. 52, chart IX.
Kramp, 1927, *K. danske vidensk. Selsk.* natur. og math. Afd., 8. Raekke, XII, p. 65, chart 9.
Lizzia sp.? Claparède, 1860, *Z. wiss. Zool. Leipzig*, Bd. X, p. 401, pl. xxxii, figs. 1, 2.
Cubogaster gemmascens Haeckel, 1879, *System der Medusen*, p. 76, pl. vi, figs. 8–11.
Dysmorphosa minima Haeckel, 1879, ibid. p. 78, pl. vi, fig. 7.
Hartlaub, 1894, *Wiss. Meeresuntersuch.* N.F., Bd. I, Abt. Helgoland, p. 189.
Browne, 1895, *Trans. Liverpool Biol. Soc.* vol. IX, p. 260.
Lizzia claparedei Haeckel, 1879, *System der Medusen*, p. 82.
Chun, 1895, *Bibl. Zool.* Bd. VII, Heft 19, p. 36, text-figs. 2–4.
Hartlaub, 1897, *Wiss. Meeresuntersuch.*, N.F., Bd. II, Abt. Helgoland, p. 455.
?*Lizzia elizabethae* Haeckel, 1879, *System der Medusen*, p. 83, pl. vi, fig. 12.
?*Lizzia minuta* M'Intosh, 1893, *11th Rep. Fish. Bd. Scotland*, pt. iii, Sci. Invest. p. 344.
Rathkea blondina, Mayer, 1910, *Medusae of the World*, vol. I, p. 181.
Hydractinia carnea, Sverdrup, 1921, *Skrift. Vidensk. Kristiania*, Bd. I (1922), p. 18, pl. ii, fig. 9.

Specific Characters

Four unbranched oral tentacles. Eight marginal bulbs, four perradial each with one to three tentacles, four interradial each with a single tentacle.

Description of Adult

Umbrella semiglobular, sometimes a little higher than wide, usually with rounded apical process; jelly moderately thick, especially in apical region. Velum broad. Stomach short, cone-shaped, with broad quadrangular base attached to a broad-based conical peduncle; not reaching beyond umbrella margin in full extension. Four unbranched oral tentacles arising above mouth margin, each with one terminal nematocyst cluster. Four radial canals and ring canal narrow. Perradial columns of large endodermal cells stretching from stomach below medusa buds and along radial canals throughout length of peduncle. Gonads completely surrounding stomach;

asexual reproduction by budding from stomach wall. Eight marginal bulbs, four perradial each with one to three tentacles, four interradial each with a single tentacle, rarely two. No ocelli. Height up to 2·0 mm.* Colour of marginal tentacle bulbs and stomach pale straw, yellow, or yellowish brown.

Distribution

Lizzia blondina occurs all round the coasts of the British Isles, being scarcest in the eastern end of the English Channel and the southern North Sea. Elsewhere it has been recorded from Iceland; Iceland and Faeroe-Shetland Channels; south-west coast of Norway; Skagerak; Kattegat, North Sea and (?) Mediterranean.

Developmental Stages and Structural Details

The hydroid of *Lizzia blondina* is not known; it is not therefore certain whether the earliest stage found in the plankton has arisen direct from the hydroid or by budding from other medusae. The smallest stages seen are less than 0·75 mm. in height. They have eight marginal bulbs on some or all of which there may be a single tentacle. There are scattered nematocysts on the exumbrella. In other respects they differ little in general appearance from the older stages.

During the course of development additional tentacles grow on each of the perradial marginal bulbs until in fully developed specimens there are three on each (Text-figs. 69, 70C). Occasional specimens are found in which some of the interradial bulbs have two tentacles, but none has yet been seen with a complete series of two tentacles on each interradial bulb.

Examination of samples of twenty-two specimens from Plymouth in the month of August and fifteen from Mounts Bay in June gave the following tentacle arrangement for individuals which had passed the first single tentacle stage.

		No. of individuals			No. of individuals
P.	2111	2	P.	3222	4
I.	1111		I.	1111	
P.	2211	1	P.	3322	1
I.	1111		I.	1111	
P.	2121	2	P.	3322	1
I.	1111		I.	1112	
P.	2221	10	P.	3332	2
I.	1111		I.	1111	
P.	2222	13	P.	3332	1
I.	1111		I.	1121	

P. = perradial. I. = interradial.

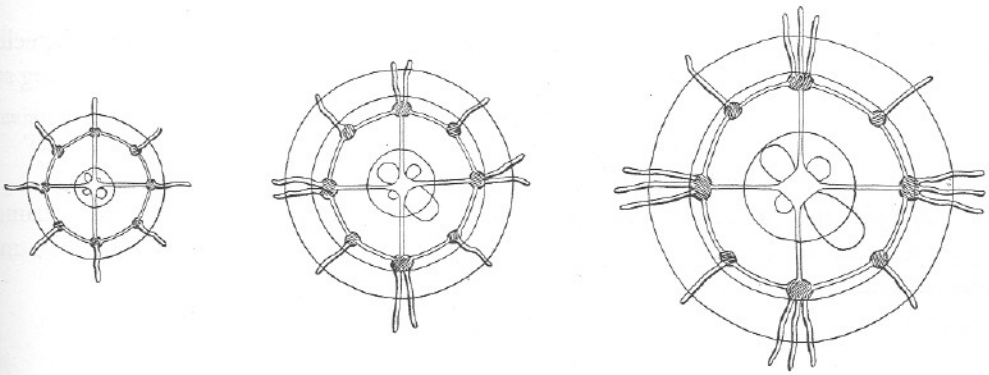
Development of tentacles on any perradial marginal bulb thus appears to proceed independently of that of the others, although it would seem that the third tentacles do not grow fully on a bulb until all four have developed their two tentacles. The fully developed stage with three tentacles on each of the perradial marginal bulbs is not as commonly seen as the earlier stages. Many individuals are to be found in intermediate stages with their second or third tentacles not fully grown. The marginal bulbs have small nematocyst cushions on their adaxial sides.

The stomach is variable in length and has somewhat concave sides.

The medusa buds appear on the stomach wall at a very early stage. The course of their development was studied in detail by Chun (1895). The buds are borne in two, or rarely three, series,

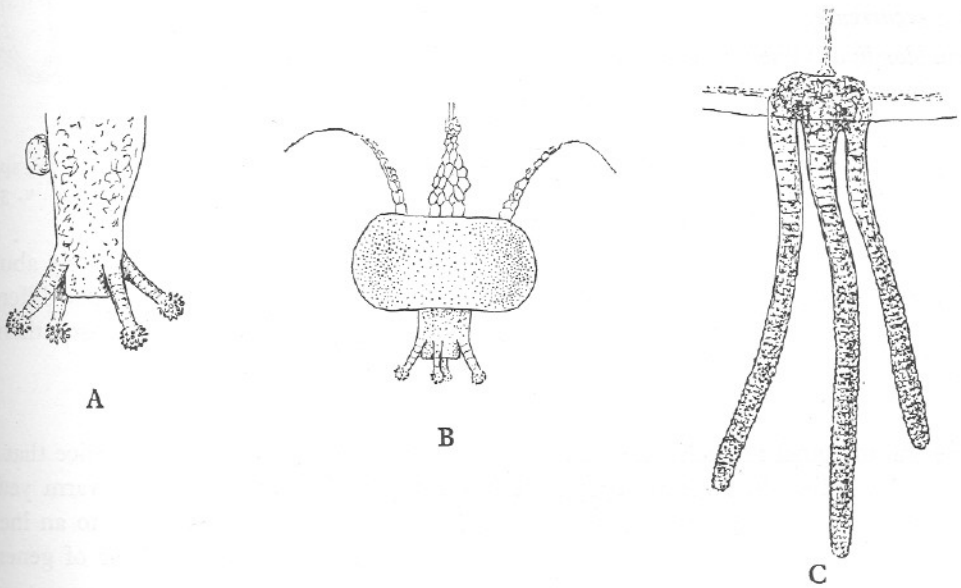
* Forbes (1848) gives a 4 mm. scale in his plate.

and in each series there are four interradial buds approximately at right-angles. The proximal series, nearest the base of the stomach, is the first to develop and the buds in each series show a graded order of development in that the two oldest buds stand opposite one another. When



Text-fig. 69. *Lizzia blondina*. Semi-diagrammatic illustration of three stages of development, seen from above.

viewed from the aboral pole, with the oldest bud lying uppermost, the third oldest is on the left side. Chun records an exception to this rule in which the third oldest was on the right side when the medusa was orientated as thus mentioned. There is a tendency for the two youngest buds in



Text-fig. 70. *Lizzia blondina*. Preserved specimens from Mounts Bay, Cornwall, 10. vi. 36. A, mouth; B, stomach with ripe male gonad; C, perradial marginal tentacle group.

a series to lie on a plane slightly more distal than that of the two oldest. The budded medusae are liberated with eight marginal bulbs, some or all of which may have a single tentacle. Chun states that as in *Rathkea* the buds are ectodermal in origin (see also Braem, 1908 and Kramp, 1926*a*).

The gonads start to ripen towards the termination of asexual reproduction and ripe sexual cells may be present while some buds still remain unliberated. When fully sexually mature the gonads completely surround the stomach in the form of a ring-shaped cushion (Text-fig. 70B).

Sexually mature specimens may be found in all stages of development, even at the earliest stage at which all eight marginal bulbs have not yet developed their single tentacles.

The eggs measure 0·08–0·12 mm. in diameter, and the heads of the spermatozoa not more than 0·001 mm. (Chun, 1895).

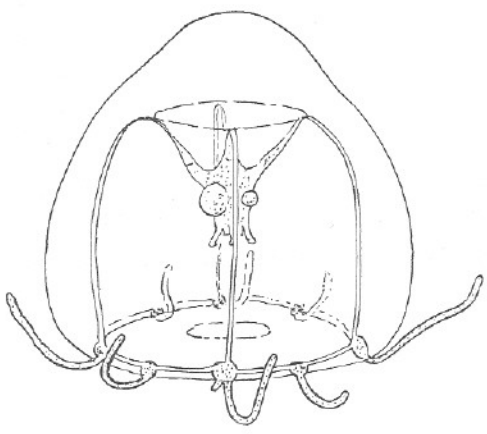
Since medusae may be found mature at any stage of development the identity of the species was not at first certain and three separate species were described, one for each of the following stages:

First stage	One tentacle on each perradial marginal bulb . .	'*Dysmorphosa minima*'
Second stage	Two tentacles on each perradial marginal bulb . .	'*Lizzia claparedei*'
Third stage	Three tentacles on each perradial marginal bulb . .	'*Lizzia blondina*'

Browne (1896*a*) records an abnormal specimen from Plymouth which was completely trimerous, having three radial canals, three oral tentacles and six marginal bulbs. It was about 1 mm. in diameter and had two tentacles on each of the three perradial marginal bulbs and three single interradial tentacles.

Hartlaub (1911) records specimens from Concarneau with radial streaks of exumbrellar nematocysts.

NEMATOCYSTS. Microbasic euryteles and desmonemes (Russell, 1938*b*).



Text-fig. 71. *Lizzia blondina*. Living specimen 0·9 mm. high, Plymouth, 20. v. 37.

Seasonal occurrence

Lizzia blondina is likely to occur abundantly in the plankton in any month from May to October; it may occasionally be found as late as November and has been seen at Plymouth at the end of March and fairly abundant in April. It has once been recorded as early as 14 February at Valencia (M. & C. Delap, 1905). Owing to rapid proliferation by budding this species may at times be exceedingly abundant. Both sexual and asexual individuals may be found together at any time. *Lizzia* thus differs from *Rathkea* and *Hybocodon* of which sexually mature species appear later in the season than those reproducing by asexual budding.

Habits

In life the marginal tentacles are capable of extending to a length of about twice that of the umbrella. According to Kramp (1927), from a study in Danish waters, in warm years the medusae disappear quicker than in cold years. This he suggests as being due to an increased rate of gemmation at higher temperatures and an indication that the number of generations is limited.

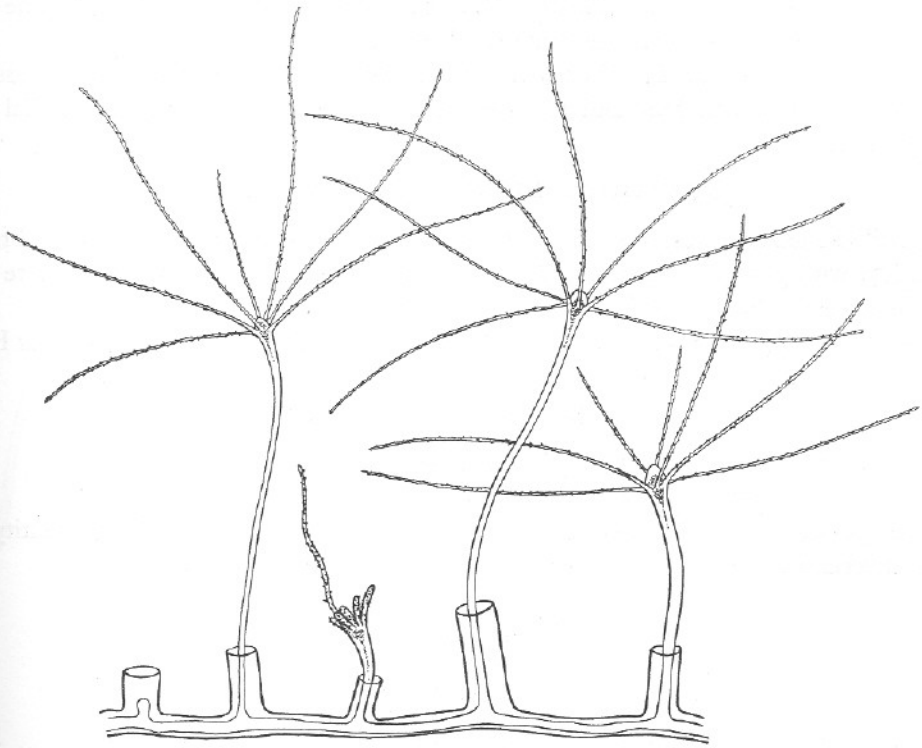
As an instance of their occasional great abundance Fowler (1898) mentions that in the Faeroe-Shetland Channel they tinged the contents of the tow-nets. He found that over deep water they were epiplanktonic, living above a depth of 100 fathoms.

HYDROID. Not known. ? *Trichydra pudica*, see Strethill Wright (1862) and Rees (1941*c*, p. 138, figs. 4, 5).*

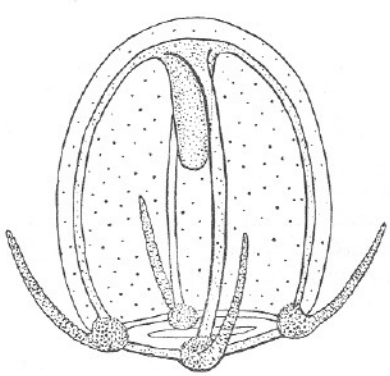
* In 1951 I reared medusae liberated from *Trichydra pudica* sent by Dr H. O. Bull from Cullercoats until they had eight marginal tentacles (Pl. XXXIV, figs. 3, 4). They looked very like *Lizzia* but had as yet no oral tentacles.

Historical

Lizzia blondina was first described by Forbes (1848) from specimens collected at the Shetland Isles in Brassay Sound and off Fitful Head in 1845. The specimens described were in the fully



A



B

Text-fig. 72. *Trichydra pudica*, possibly the hydroid of *Lizzia blondina*. A, four polyps from a colony, Millport, 12. iv. 40; B, newly liberated medusa, Millport, 15. iv. 40. (After Rees, 1941*c*, figs. 4, 5.)

developed stage with three tentacles on each perradial marginal bulb. Although Forbes saw other stages he did not describe them owing to fear of confusion on account of lack of knowledge of young stages of other medusae. The second stage with two tentacles on each perradial marginal bulb was described by Claparède in 1860 as *Lizzia* sp. ?, and subsequently named by Haeckel

L. claparedei. Finally Haeckel (1879) described the first stage with single marginal tentacles as *Dysmorphosa minima*.

Chun (1896) realized that *Lizzia claparedei* and *Dysmorphosa minima* were the same species and Browne (1895) suggested that *D. minima* was an early stage of *Lizzia blondina*. Browne (1896*a*) combined the three species under the name *L. blondina*.

The medusa described as *L. elizabethae* by Haeckel (1879) from Jersey was possibly an abnormal *L. blondina*, with four and two tentacles on each perradial and interradial margin bulbs respectively.

Subfamily THAMNOSTOMINAE

Bougainvilliid medusae with stomach without peduncle; with four dichotomously branching oral tentacles; with gonads interradially situated on stomach; with two, eight, or more solitary marginal tentacles; with (? or without) ocelli.

The Thamnostominae are represented in British waters by one genus, *Thamnostoma* Haeckel, and a single species.

Genus **Thamnostoma** Haeckel, 1879

MEDUSAE. Thamnostominae with eight or more marginal tentacles.

HYDROID. *Thamnostoma*, with perisarc investing tentacles.

Only one species of *Thamnostoma* has been recorded in British waters, and the identity of this species is uncertain since only two very young individuals have been seen.

Thamnostoma sp.

Text-fig. 73 A–E

Thamnitis n.sp.? Browne, 1905*a*, *Proc. Roy. Soc. Edinb.* vol. xxv, pt. ix, p. 758.

Browne (1905*a*) found two specimens of an early stage of this medusa in the Firth of Clyde in 1901, one on 21 September and the other on 8 October.

His descriptions of these two specimens were as follows:

Specimen of 8 *October*. The umbrella is bell-shaped, with thin walls; the ex-umbrella has a few nematocysts scattered over its surface. Velum very broad. The stomach is cone-shaped, with a quadrangular base, and is about half as long as the cavity of the umbrella. Four oral tentacles, which are fairly long and once dichotomously divided, and terminate with very small knobs containing nematocysts. The gonads have not yet begun to develop. Four perradial marginal tentacles, which are rather short and thin, and have cone-shaped basal bulbs. Ocelli are absent.

Colour. Stomach yellowish-brown. Basal bulbs of an orange colour.

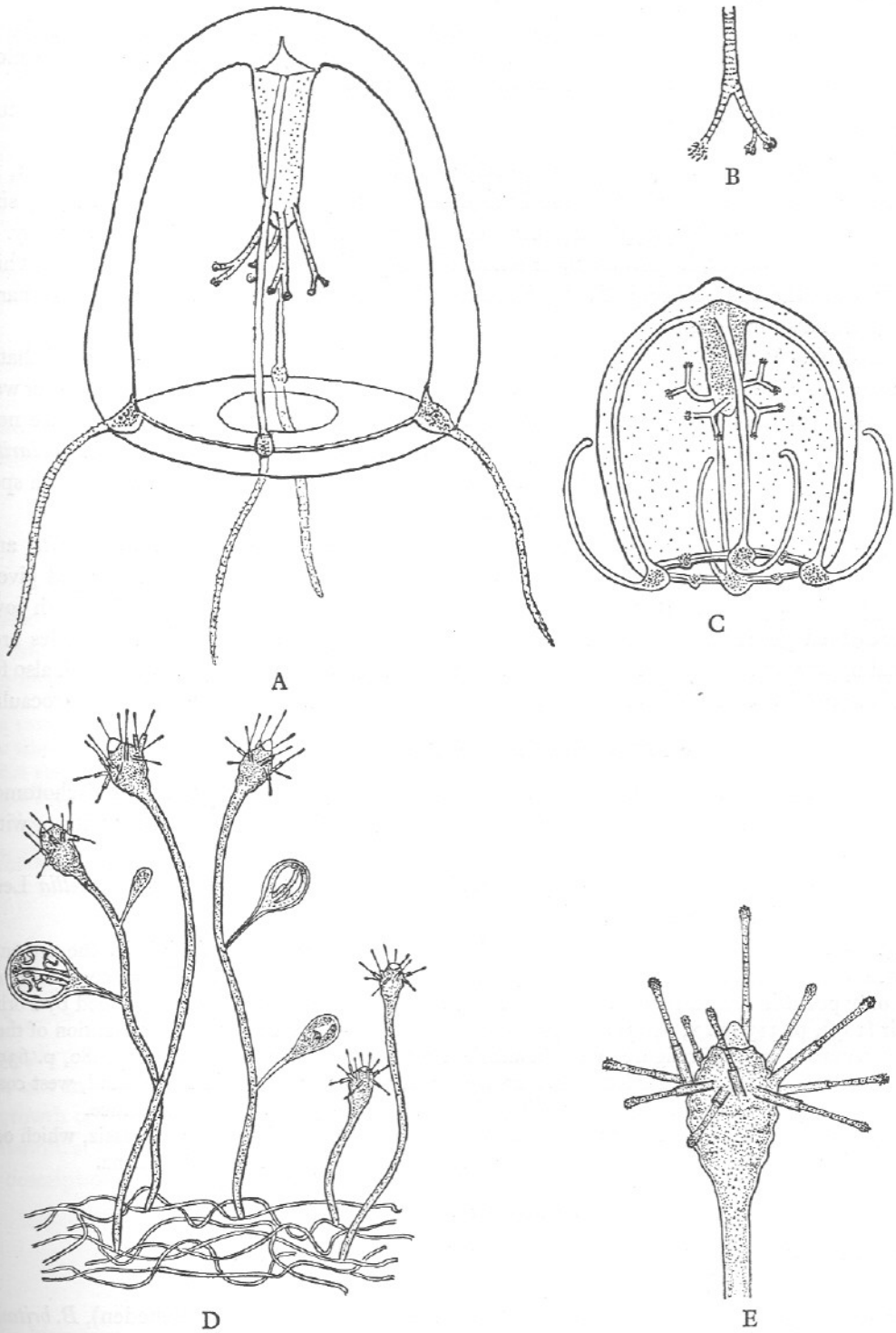
Size. Umbrella about 1 mm. in length and width.

The specimen is, without doubt, an early stage, as the gonads have not yet begun to develop. There is also an apical stalk over the base of the stomach. This stalk is the rudimentary remains of the canal by which the medusa was connected with its hydroid. It is frequently present in very early stages, but soon disappears by absorption.

The medusa was placed in a plunger bell-jar, kept there for six days, and then preserved. During the six days the oral tentacles developed another branch.

Tracing of drawings of this medusa made by Mr E. T. Browne are given in Text-fig. 73 A, B.

Specimen of 21 *September*. The stomach is cone-shaped. Four oral tentacles, which are two to three times dichotomously branched. Four radial canals. The gonads have not yet begun to develop. Four perradial marginal tentacles with large basal bulbs. Ocelli absent.



Text-fig. 73. *Thamnostoma* sp. Millport, 8. x. 01. A, *c.* 1 mm. high; B, oral tentacle (tracings of drawings by E. T. Browne). *Thamnostoma russelli:* C, newly liberated medusa, Herdla, Norway, 2. ix. 37; D, hydroid colony with medusa buds, Herdla, 6. ix. 37; E, single hydranth, Herdla, 1. ix. 37. (After Rees, 1938, fig. 7.)

Colour. By transmitted light, stomach bright yellowish-brown. The lower half of the basal bulbs bright yellow, the upper half (embedded in the jelly of the umbrella margin) yellowish brown. By reflected light, stomach and basal bulbs bright orange.

Size. Umbrella about 1·5 mm. in length. (This specimen was taken with its umbrella turned inside out.)

The above medusae are evidently very closely related to *Thamnostoma cidaritis* (Brückner, 1914) from the Mediterranean, which has also been described only in its young stages. A very similar species, *T. russelli* (Text-fig. 73C–E), has been described by Rees (1938) from Norway. This species differs, however, in possessing interradial marginal tentacles. Another species, which is only known in the adult stage, is *T. dibalia* (Busch).* This has a peculiar spur on the marginal tentacles and also has ocelli.

The hydroids of *T. cidaritis* and *T. russelli* are indistinguishable. Rees has suggested that they may be the same species and that the newly liberated medusa of *T. cidaritis*, living in warmer waters, is in a less advanced stage of development and consequently the interradial bulbs have not yet appeared. He also suggests the possibility that *T. dibalia* may be the adult stage of *T. cidaritis*.

Until more is known of the life histories of these medusae it is not possible to assign a specific name to the specimens described by Browne.

It seems likely, however, that its hydroid may closely resemble that of *T. cidaritis* and of *T. russelli*, and, in case it should be found, the diagnosis of a *Thamnostoma* hydroid given by Rees (1938) is supplied here: 'Stems rarely branched arising from a creeping stolon both covered by a brownish perisarc. Hydranths fusiform, with a single whorl of filiform tentacles around a conical hypostome, covered almost as far as the mouth by an investing perisarc which also forms a sheath around the base of each tentacle. Medusa buds, stalked, borne on the hydrocauli.'

Subfamily BOUGAINVILLIINAE

Bougainvilliid medusae with stomach with or without peduncle; with four dichotomously branching oral tentacles; with four, eight or sixteen groups of marginal tentacles; with or without ocelli.

The Bougainvilliinae are represented in British waters by one genus, *Bougainvillia* Lesson, of which six species are recorded.

Note. The genus *Nemopsis* L. Agassiz 1849 is distinguished from *Bougainvillia* by the presence of two kinds of tentacles on each marginal bulb, the median pairs having swollen club-shaped extremities.

The only possible British species, *Nemopsis crucifera* (Forbes & Goodsir), was described by Forbes & Goodsir (1851, p. 313, pl. x, fig. 5, as *Hippocrene*) from Tobermory. They made no mention of the two types of tentacles and their figures were insufficient for certain diagnosis. Haeckel (1880, p. 635) recorded a medusa which he regarded as this species from near Scourie, off Handa Island, west coast of Scotland. He mentions two types of tentacles. The medusa has not been recorded since.

Hartlaub (1911) suggested that it might have been a young *Nemopsis bachei* L. Agassiz, which occurs in the North Sea. I have not included it here as a certain member of the British fauna.

Genus **Bougainvillia** Lesson, 1830

MEDUSAE. Bougainvilliinae with four groups of marginal tentacles.

HYDROID. *Bougainvillia*.

Five species of *Bougainvillia* occur in British waters, *B. ramosa* (Van Beneden), *B. britannica* Forbes, *B. principis* (Steenstrup), *B. pyramidata* (Forbes & Goodsir), and *B. superciliaris*

* Haeckel (1879) thought the spelling should have been 'dibolia'; but Busch (1851) specifically mentions two pigment spots on each tentacle. (βᾶλιός, spotted).

(L. Agassiz). Only three specimens of *B. superciliaris* have, however, been recorded. There is a possibility that a sixth species, *B. macloviana* (Lesson), which has not been recorded, may be found, since it is common in the southern North Sea. A brief description and figures of the species have therefore been included.

The medusae of this genus are at first very confusing to identify, but if the following points are examined identification of the adults is fairly easy.

The species may first be divided into two groups according to the development of a peduncle.

1. Peduncle absent or weakly developed — *ramosa*, *britannica*, *principis*
2. Peduncle well developed . . . — *pyramidata*, *superciliaris*, *macloviana*

Taking the first group we then examine the number of times the oral tentacles branch dichotomously and the number of tentacles on each marginal bulb.

	No. of times oral tentacles branch	No. of tentacles on each marginal bulb
ramosa	2–3	4–9
britannica	4–5	12–17
principis	5–6	20–30

B. ramosa is thus immediately separated by its few oral and marginal tentacles. The two species *britannica* and *principis* can also be separated on these characters, but it is as well to examine two other characters to make matters certain. These are:

Basal trunk of oral tentacle long	*britannica*
Basal trunk of oral tentacle short	*principis*
Ocellus elongated, on base of marginal tentacle	*britannica*
Ocellus round, on marginal bulb	*principis*

(See also p. 161)

The second group, with a well-developed peduncle, can be treated in the same way.

	No. of times oral tentacles branch	No. of tentacles on each marginal bulb
pyramidata	3–4	4– 8
superciliaris	4–5	11–15
macloviana	5–7	35–65

These characters are alone sufficient to separate the three species, but complete confirmation is supplied by the appearance of the gonad. In *superciliaris* it is interradial on the stomach wall, but in *pyramidata* and *macloviana* it is adradial, and follows the course of the perradial outgrowth of the stomach over the peduncle.

Identification of the young stages is considerably harder and calls for a detailed comparison of the descriptions given in the following pages.

Bougainvillia ramosa (Van Beneden)

Plate VIII, fig. 1; Plate IX, figs. 4, 5; Text-fig. 74A–C

Eudendrium ramosum Van Beneden, 1844*a*, *Mém. Acad. R. Belg.* tome XVII, p. 57, pl. iv, figs. 10–13 (hydroid and medusa).

Van Beneden, 1866, ibid. tome XXXVI, p. 112, pls. vi, vii (hydroid and medusa).

Medusa ocilia (*octocilia*) Dalyell, 1847, *Remarkable Animals of Scotland*, vol. 1, p. 66, pl. xi.

Atractylis ramosa, Wright, 1858*b*, *Proc. Roy. Phys. Soc. Edinb.* vol. I, p. 449.
Wright, 1859*b*, *Edinb. New Philos. Journ.* vol. IX, p. 108, pl. i, figs. 1–3.
Allman, 1864*a*, *Ann. Mag. Nat. Hist.* ser. 3, vol. XIII, p. 366.
Bougainvillea britannica, Wright, 1858*b*, *Proc. Roy. Phys. Soc. Edinb.* vol. I, p. 449.
Wright, 1859*b*, *Edinb. New Philos. Journ.* vol. IX, p. 366.
Mayer, 1910, *Medusae of the World*, vol. I, p. 161 (in part).
Margelis ramosa, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 344 (in part).
Allman, 1864*a*, *Ann. Mag. Nat. Hist.* ser. 3, vol. XIII, p. 366.
Perigonymus muscus Allman, 1863, ibid. ser. 3, vol. XI, p. 12.
Bougainvillia ramosa, Allman, 1864*a*, ibid. ser. 3, vol. XII, p. 366.
Hincks, 1868, *Brit. Hydroid Zooph.* p. 108, pl. xix, fig. 2 (hydroid and medusa).
Allman, 1872, *Monogr. Gymnobl. Hydroids*, p. 311, pl. ix, figs. 5–7 (hydroid and medusa).
Böhm, 1878, *Jena Z. Naturw.* Bd. XII (N.F. Bd. V).
Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 183, figs. 161 (medusa), 162–7.
Neppi, 1921, *Pubb. Staz. Zool. Napoli*, vol. III, p. 2, pl. i, figs. 1, 2 (hydroid and medusa).
Sverdrup, 1921, *Skr. Vidensk. Kristiania*, Bd. I (1922), mat.-nat. Kl., p. 20, pl. iii, fig. 12.
Brink, 1925, *Tijdschr. ned. dierk. Ver. Leiden*, ser. 2, Deel XIX, p. 126, text-figs. A–C (hydroid).
Bougainvillia fruticosa Allman, 1864, *Ann. Mag. Nat. Hist.* ser. 3, vol. XIV, p. 58.
Hincks, 1868, *Brit. Hydroid Zooph.*, p. 110 (hydroid and medusa).
Allman, 1872, *Monogr. Gymnobl. Hydroids*, p. 314, pl. ix, figs. 1–4 (hydroid and medusa).
Brink, 1925, *Tijdschr. ned. dierk. Ver. Leiden*, ser. 2, Deel XIX, p. 126.
Bougainvillia muscus, Allman, 1864, *Ann. Mag. Nat. Hist.* ser. 3, vol. XIV, p. 58.
Hincks, 1868, *Brit. Hydroid Zooph.* p. 111, text-fig. 11, pl. ix, fig. 3 (hydroid and medusa).
Allman, 1872, *Monogr. Gymnobl. Hydroids*, p. 317, pl. x, figs. 1–3 (hydroid and medusa).
Graeffe, 1884, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Bd. V, Heft 3, p. 17 (medusa as *Margelis* forms I–IV).
Brink, 1925, *Tijdschr. ned. dierk. Ver. Leiden*, ser. 2, Deel XIX, p. 126.
Lizusa octocilia Haeckel, 1879, *System der Medusen*, p. 80.
Bougainvillia autumnalis Hartlaub, 1897, *Wiss. Meeresuntersuch.* N.F., Bd. II, Abt. Helgoland, p. 465, pl. xv, figs. 11–13.
Mayer, 1910, *Medusae of the World*, vol. I, p. 169; pl. xvi, figs. 4, 5; pl. xvii, figs. 3, 4.
Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. XX, p. 51, pl. ii, figs. 17–21.
Bougainvillia benedenii Bonnevie, 1898, *Z. wiss. Zool. Leipzig*, Bd. LXIII, p. 484, pl. xxvi, figs. 34–5 (hydroid and medusa).
Brink, 1925, *Tijdschr. ned. dierk. Ver. Leiden*, ser. 2, Deel XIX, p. 126, pl. vi (hydroid and medusa).
Lizusa octociliata Aurivillius, 1898, *K. Svenska VetenskAkad. Handl.* N.F., Bd. XXX, no. 3.
Bougainvillia gibbsi Mayer, 1900*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, no. 1, p. 5, pl. iv, figs. 14, 15.
Hargitt, 1901, *Biol. Bull. Woods Hole*, vol. II, p. 228, figs. 2–7 (abnormal specimens as *Margelis*).
Margelis autumnalis, Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. V, p. 708.
Browne, 1906*a*, *Trans. Linn. Soc. (Zool.) London*, ser. 2, vol. X, p. 170.
Bougainvillia ramosa var. *nana* Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 189.
Bougainvillia ramosa var. *minima* Kramp & Damas, 1925, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. LXXX, p. 189.

Specific Characters

Jelly thick. Sometimes with a very slight peduncle. Oral tentacles branching dichotomously two or three times. Four to nine tentacles on each marginal bulb. Ocelli situated on marginal bulbs at bases of tentacles, round.

Description of Adult

Umbrella semi-globular, about as high as wide with thick jelly, especially in apical region. Velum narrow. Stomach short, sometimes with very slight peduncle. Four oral tentacles short, branching dichotomously twice, rarely three to four times, terminating in nematocyst clusters. Four radial canals and ring canal narrow. Gonads interradial or adradial?; egg capsules with nematocysts. Four perradial marginal bulbs, small and oval in shape. Four to nine tentacles on

each marginal bulb. Ocelli adaxial, situated on the marginal bulbs at the base of each tentacle, round. Height when full grown 2·5–4·0 mm. Colour of marginal tentacle bulbs and stomach dark reddish brown, crimson or yellowish, sometimes with greenish tinge. Ocelli black.

Distribution

Owing to early confusion in its identification and to the apparent rarity of the medusa in the plankton *Bougainvillia ramosa* has not often been recorded from British waters. The distribution of the hydroid is, however, such that the medusa is likely to occur on all British coasts. The medusae have been recorded from Valencia, south-west Ireland; Scilly Isles; Plymouth; North Sea; Norway; Bay of Biscay; Mediterranean; Rhode Island, U.S.A. Its hydroid, with medusa buds, has been recorded from Iceland (Kramp, 1938*b*, 1939*b*). Hydroids possibly belonging to this species have in addition been found in South Africa, north-west of Cape Verde, Australia, Amboina and Japan, and ? China (Ling, 1937, *B. flavida*). Owing to the very variable form of the hydroid much confusion has arisen. It can probably be regarded as a rather southern species, perhaps commoner on the southern coasts of the British Isles.

Developmental Stages and Structural Details

When first liberated from its hydroid *Bougainvillia ramosa* the medusa is about 0·75 mm. in height (Pl. IX, fig. 4). The jelly is at first thin, but this soon swells up so that the diameter of the medusa becomes increased and the umbrella assumes a globular form. An umbilical canal is sometimes present. There are no scattered nematocysts on the exumbrella. The stomach is short, about one-third the height of the subumbrellar cavity. The four short oral tentacles are unbranched, and usually turned upwards. The four perradial marginal bulbs are small and round. There are two tentacles on each marginal bulb, one of which is usually slightly less developed than the other. There are two ocelli on each marginal bulb situated at the bases of the two tentacles. The colour of the marginal bulbs and stomach is pink or yellowish brown; the ocelli may be black or deep red.

During the course of its development the medusa alters little in form except for the branching of the oral tentacles and the further addition of tentacles to the marginal bulbs.

Six specimens examined from Plymouth in June 1898 gave the following results:

Height (mm.)	Width (mm.)	No. of tentacles on each marginal bulb	No. of times oral tentacles are branched
2·5	2·5	7	2
3	3	6–7	2
3	3·5	7–8	2
4	4	7–8	3
3	4	8–9	3–4

Another specimen taken at Plymouth on 8 September 1897 developed as follows:

	Size (mm.)	Marginal tentacles	Oral tentacle branches
8 September	4×2·5	5, 5, 5, 6	3
14 September	—	7, 7, 7, 6	4
20 September	5×4	7, 7, 7, 8	Fifth branch beginning

This medusa appears to show some variation in its degree of development at maturity. Specimens are found at times with ripe eggs while still at a small size, with the adult characters little developed. Kramp & Damas (1925), for instance, record a variety, var. *minima*, from Nordaasvand, south of Bergen, an almost enclosed basin with relatively high temperature. These were scarcely 1 mm. in height and had their oral tentacles unbranched, or at most once branched,

and had only two or three tentacles on each marginal bulb. Similar specimens are found in the Mediterranean, e.g. var. *nana* of Hartlaub (1911; see also Neppi & Stiasny, 1913*a*).

The gonads in large specimens are adradial in position and extend slightly on to the subumbrellar surface along the radial canals. This is well shown in the specimen figured by Strethill Wright (1859*b*) which he reared and regarded as *B. britannica*. Hartlaub (1897), however, in his description of *B. autumnalis*, showed that they were interradial. It is possible that the appearance of the gonads as interradial may be correlated with the limited area available on the stomach in individuals maturing at a small size. On the other hand, the possibility must not be overlooked that there are really two species which have not yet been separated.

Hartlaub (1911) mentions two abnormal specimens with three radial canals and three marginal bulbs. C. W. Hargitt (1901) has described a number of abnormalities in the American form of this medusa. He found after examining more than 500 specimens that generally they were constant in form, only about 2% being subject to variation. He records completely trimerous and pentamerous forms. The latter had only single tentacles on two of the marginal bulbs and four oral tentacles. Amongst other abnormalities he describes one with four extra incipient radial canals, and another which was twinned, one half being normal and the other trimerous.

Robson (1914*a*) records two abnormalities: (i) three oral tentacles and five marginal bulbs, one with only one tentacle, and another with three ocelli; (ii) four oral tentacles, one branched, only one tentacle on each marginal bulb, but two spots on each bulb.

Goette (1907) states that the ova do not originate in the outer epithelium of the manubrium, but wander there from the endoderm; but the sperm originate in the outer epithelium.

NEMATOCYSTS. Microbasic euryteles and desmonemes (Russell, 1938*b*).

Seasonal occurrence

Bougainvillia ramosa medusae have been recorded from the plankton in May, June, August and September at Plymouth, and August and November at Valencia.

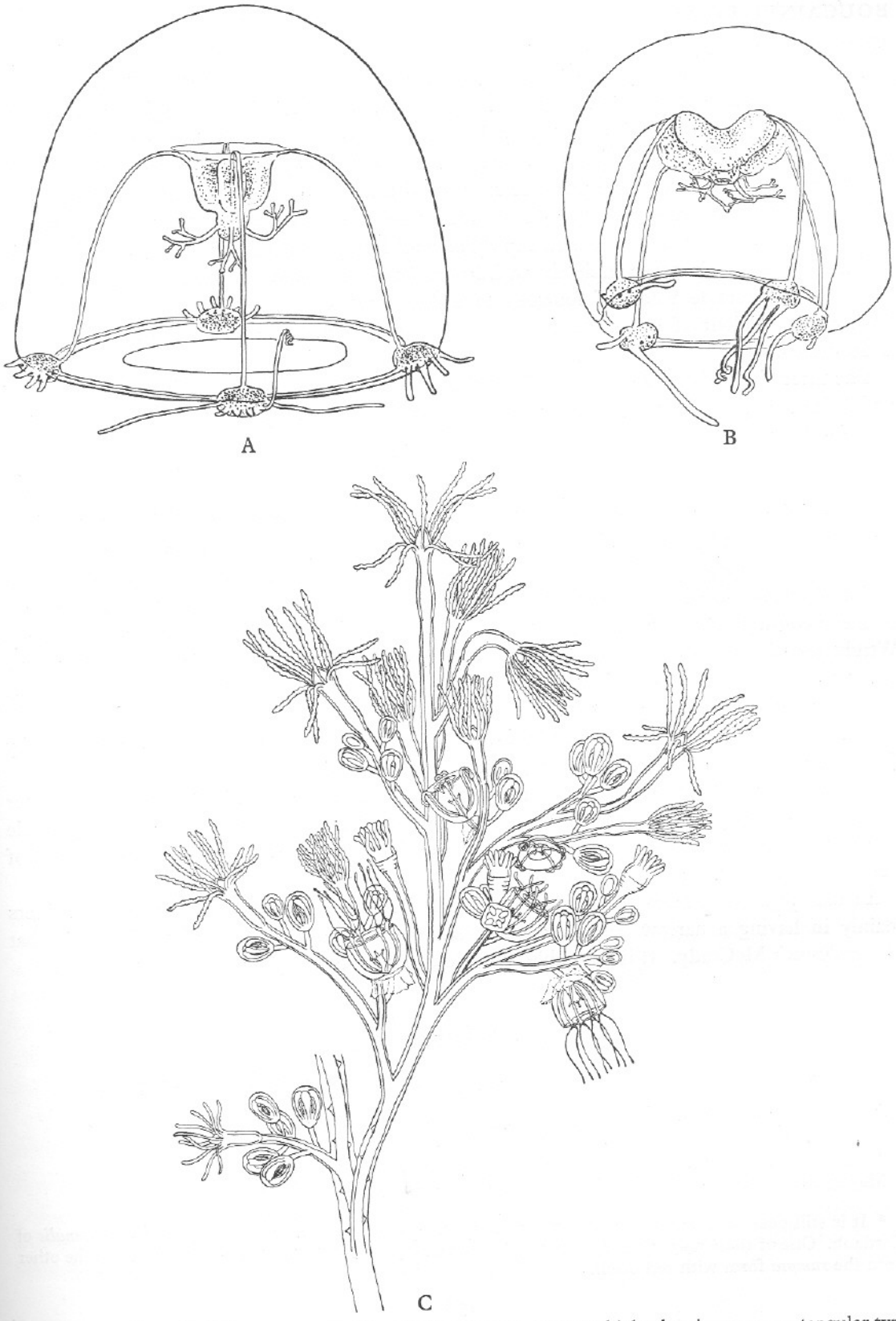
Considering the abundance of the hydroid the medusa seems to be remarkably scarce in the plankton, and it is probably likely to occur during any month in the summer and autumn. Orton (1920) records the hydroid as producing medusae at Plymouth during April, May, August, September and October.

In the North Sea Hartlaub gives the occurrence of the medusa as August to December; Robson (1914*a*) records the liberation of medusae from the hydroid on the Northumberland coast from July to October.

Habits

Bougainvillia ramosa is one of the easiest medusae to obtain in the laboratory from the hydroid (e.g. Browne, 1907*a*), but it is very difficult to rear. The smallest fragment of the hydroid if given suitable conditions will quickly spread over the surface of the vessel in which it is kept and innumerable medusae will be produced. Browne (1898*a*) records placing a colony of this hydroid in an aquarium at Plymouth in October which in three days liberated not less than 4450 medusae, and still had a large number of buds. Orton (1914) found that the hydroid yielded medusae when not more than six weeks and a few days old.

The newly liberated medusae swim actively with their contracted tentacles curled upwards round the margin of the umbrella. When not swimming they remain poised in mid-water with their tentacles greatly extended horizontally.



Text-fig. 74. *Bougainvillia ramosa*. A, living male specimen 2·2 mm. high, showing more rectangular type of gonad, Plymouth, 29. x. 37; B, preserved specimen *c*. 1·8 mm. high, off Plymouth, 18. viii. 37; C, hydroid. (After Allman, 1871–2, pl. ix, fig. 1.)

BOUGAINVILLIIDAE

HYDROID (Text-fig. 74C).

Bougainvillia ramosa (Van Beneden). (= *B. muscus* Allman and *B. fruticosa* Allman.)

(For full description see Allman, 1872, *Monogr. Gymnobl. Hydroids*, p. 311, pl. ix, figs. 1, 5.)

Colonies of single, or little-branched polyps, erect, about 15 mm. in height, arising from a creeping stolon, perisarc slightly corrugated ('*muscus*' form); or hydrocaulus rising about 50 mm., much branched, main stem composed of aggregated tubes, perisarc slightly annulated or corrugated at origin of branches, and extending about to base of tentacles, which in extreme contraction appears as a membranous corrugated cup ('*fruticosa*' form); or with distinct cup into which the hydranth can be almost completely withdrawn ('*ramosa*' form). Hydranths cylindrical or fusiform, with single whorl of fourteen to eighteen tentacles held alternately upwards and downwards. Colour of hydranths pink or bright red. Medusa buds borne on peduncles on hydrocaulus.

The three kinds of growth can be derived from the simple '*muscus*' form (cf. e.g. Hallez, 1905*a*, and Brink, 1925). Hallez (1905*b*) records the parasitization of the hydroid by the Pycnogon, *Phoxichilidium*.

Historical

Bougainvillia ramosa was first described under the hydroid form with its newly liberated medusa by Van Beneden (1844*a*) as *Eudendrium ramosum*, believing it to be the hydroid described by that name by Ehrenberg. Strethill Wright showed that Van Beneden's species was not a true *Eudendrium* and placed it in the genus *Atractylis*, whence Allman on the strength of the likeness of the medusa to *Bougainvillia britannica* transferred it to the genus *Bougainvillia*. Strethill Wright reared the medusa to the adult stage and thought that it was *B. britannica*. The hydroid and young medusa were also described by Dalyell (1847) as *Tubularia* (*Sertularia*) *ramosa* and *Medusa ocilia* (*octocilia*) respectively.

The synonymy of species has been in doubt* owing to the production of similar medusae by the three hydroid growth forms, *muscus*, *fruticosa*, and *ramosa*.

Hartlaub (1897) described the medusa from the plankton as *Bougainvillia autumnalis* and later (1911) combined this species with *B. ramosa*. As mentioned above, however, there is still a possible doubt as to the correct identification of the species. Kramp (1926*a*) has given a good account of the history of this species.

A small species was described by Hartlaub (1911) from the Adriatic as *B. triestina*. This differs mainly in having a narrow base to the stomach and in this respect it resembles somewhat *B. carolinensis* McCrady. It is advisable, however, to keep these species distinct at present.

Bougainvillia britannica Forbes

Plate VIII, figs. 2, 3; Plate IX, figs. 1–3; Text-figs. 75A, B, 77A, B, 78A, 79A

?*Hippocrene britannica* Forbes, 1841, *Ann. Mag. Nat. Hist.* vol. VII, p. 84, pl. i, fig. 2*a*.
Bougainvillia britannica Lesson, 1843, *Acalèphes*, p. 291.
Allman, 1872, *Monogr. Gymnobl. Hydroids*, p. 313, pl. ix, fig. 8.
Mayer, 1910, *Medusae of the World*, vol. I, p. 161 (in part); pl. xvii, fig. 8.

* It is still possible that there are two species: (1) *B. ramosa* as reared by Wright; (2) *B. autumnalis* of Hartlaub. One of these may come from the hydroid *muscus-fruticosa* form with black ocelli, and the other from the *ramosa* form with red ocelli.

Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 162, figs. 142, 143, 145–9 (?figs. 150 and 151, hydroid).
Sverdrup, 1921, *Skr. Vidensk. Kristiania*, Bd. I (1922), mat.-nat. Kl. p. 19, pl. iii, fig. 11.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. V, pt. x, p. 43.
Bougainvillea britannica, Forbes, 1848, *Monogr. Brit. Medusae*, p. 62, pl. xii, fig. 1.
?*Bougainvillea nigritella* Forbes, 1848, ibid. p. 63, pl. xii, fig. 2.
Medusa duodecilia Dalyell, 1848, *Remarkable Animals of Scotland*, pl. xi, figs. 11, 12.
?*Hippocrene simplex* Forbes & Goodsir, 1851, *Trans. R. Soc. Edinb.* vol. XX, p. 313, pl. x, fig. 6.
Bougainvillea dinema Green, 1857, *Nat. Hist. Review*, vol. IV, p. 26, pl. v, fig. 6.
Margelis ramosa, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 344 (in part).
Haeckel, 1879, *System der Medusen*, p. 88 (in part).
Hartlaub, 1894, *Wiss. Meeresuntersuch.* N.F., Bd. I, Abt. Helgoland, p. 191.
Margelis nigritella, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 345.
Browne, 1905*a*, *Proc. Roy. Soc. Edinb.* vol. XXV, pt. ix, p. 759.
Margelis zygonema Haeckel, 1879, *System der Medusen*, p. 635.
Thamnitis nigritella, Haeckel, 1879, ibid. p. 84.
Margelis britannica, Browne, 1895, *Trans. Liverpool Biol. Soc.* vol. IX, p. 267 (in part).
Browne, 1905*a*, *Proc. Roy. Soc. Edinb.* vol. XXV, pt. ix, p. 754.
?*Bougainvillia flavida* Hartlaub, 1897, *Wiss. Meeresuntersuch.* N.F., Bd. II, Abt. Helgoland, p. 456, pl. xiv, figs. 1–4, 7–10, *not* 5 and 6 (hydroid and medusa, in part).
Bougainvillia xantha Hartlaub, 1897, ibid. p. 461, pl. xv, figs. 2, 3; pl. xvi, fig. 3; pl. xvi*b*, fig. 19.
Mayer, 1910, *Medusae of the World*, vol. I, p. 165.
Bougainvillia bella Hartlaub, 1897, *Wiss. Meeresuntersuch.* N.F., Bd. II, Abt. Helgoland, p. 470, pl. xv, fig. 7.
Margelis bella, Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. V, no. 5, p. 708.
?*Bougainvillia nigritella*, Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 169, fig. 152.
?*Bougainvillia simplex*, Hartlaub, 1911, ibid. p. 181, fig. 160.
?*Bougainvillea charcoti* Le Danois, 1913, *Bull. Soc. Zool. Fr.* tome XXXVIII, p. 15, figs. 1–3.

Specific Characters

Jelly very thick. No peduncle. Oral tentacles branching dichotomously usually four to five times. Usually twelve to seventeen tentacles on each marginal bulb. Ocelli situated on bases of marginal tentacles, elongated.

Description of Adult

Umbrella usually slightly higher than wide, with very thick jelly; umbrella margin square. Velum moderately broad. Stomach short, with broad base, cross-shaped in section; no peduncle. Four oral tentacles fairly long, not reaching beyond umbrella margin, branching dichotomously usually four to five times, terminating in nematocyst clusters. Four radial canals broad; ring canal narrow. Gonads adradial, sometimes spreading over interradial region of stomach wall. Four perradial marginal bulbs, broad triangular, somewhat variable in shape, about half as wide as interradial space. Up to thirty tentacles on each marginal bulb, usually twelve to seventeen, with elongated clavate ends. Ocelli adaxial, situated one on base of each marginal tentacle, usually elongated in shape, lying across width of tentacle. Height when full grown 6–7 mm., rarely 8 mm. Colour of marginal bulbs bright orange yellow; marginal tentacles pale yellow; stomach yellow; ocelli black.

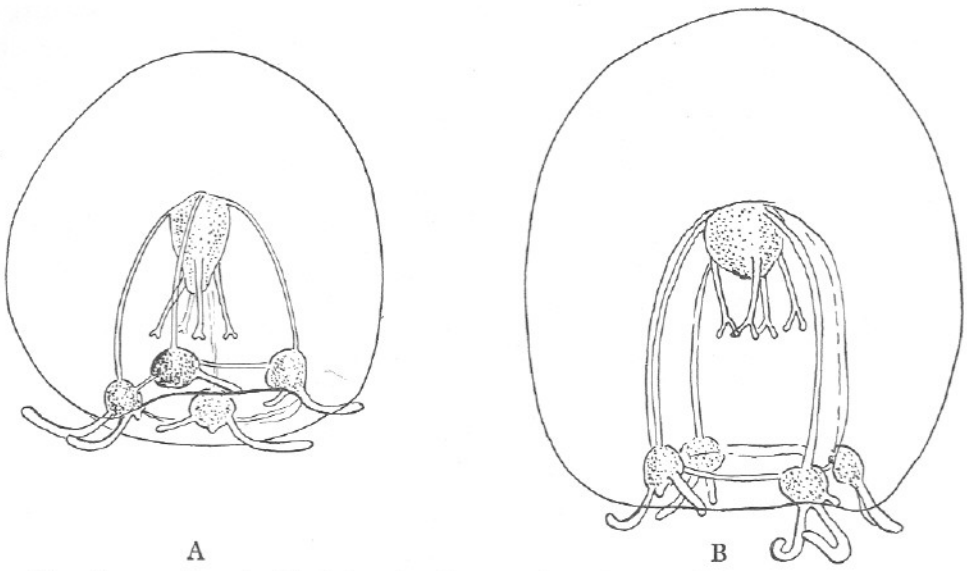
Distribution

All coasts of British Isles; Shetland Islands; Bergen and Oslofjord, Norway; North Sea; Kattegat; English Channel; Eastport, Maine, U.S.A.

Developmental Stages and Structural Details

Soon after liberation from its hydroid (? *Bougainvillia flavida*) the medusa is almost spherical, with very thick jelly, and a small subumbrellar cavity. It is about 0·75 mm. in diameter. There are nematocysts on the exumbrella. The margin of the umbrella is square in outline, a character

that persists somewhat even in the adults. The radial canals are broad. The velum is very broad. The four short oral tentacles are unbranched, and there is only one tentacle on each marginal bulb. The colour of the marginal bulbs is bright yellow and there are no ocelli. Hartlaub (1897) mentions that on liberation the jelly is thin but it very quickly swells up to assume its spherical form. At a size of about 1 mm. (Text-fig. 75 A) there are two tentacles on each marginal bulb and the oral tentacles are beginning to branch, though they may still remain unbranched at the three marginal tentacle stage. The first ocelli usually appear on the perradial marginal tentacles



Text-fig. 75. *Bougainvillia britannica*. Preserved specimens, off Plymouth, 20. iv. 34. A, *c.* 1·4 mm. high; B, *c.* 2 mm. high.

at the three marginal tentacle stage (Text-fig. 77 A) or sometimes later; they may be crimson. They are on the marginal tentacles and appear after the tentacle is budded out.

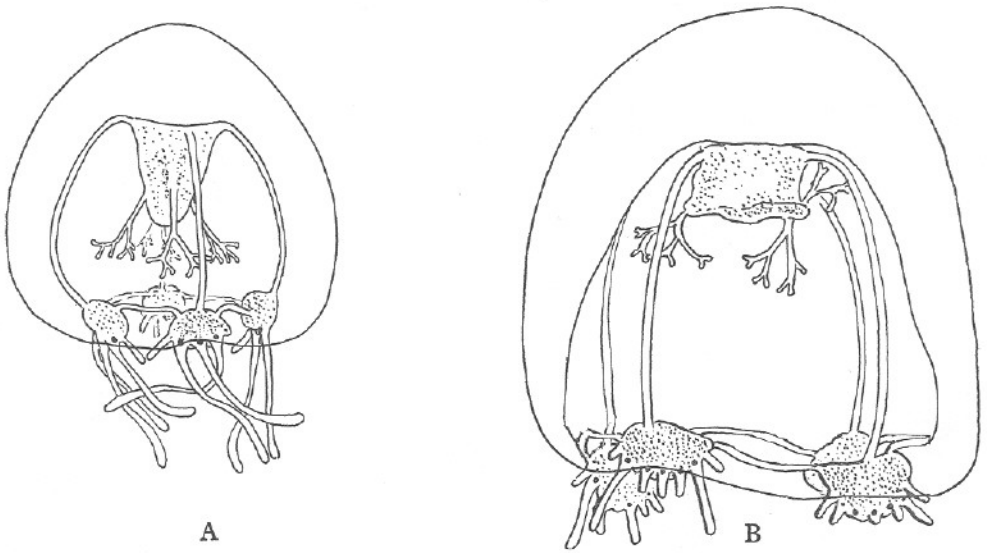
The further development of the medusa (Pl. IX, figs. 1–3) as it increases in size involves the addition of new tentacles successively on the outer sides of the marginal bulbs and the further branching dichotomously of the oral tentacles. The examination of 140 specimens at Plymouth gave the following results, which show the degree of development of the oral tentacles and number of tentacles on each marginal bulb in medusae of different sizes.

Diameter (mm.)	No. of tentacles on each marginal bulb	No. of times oral tentacles are branched
1·5	3	1–1(+)
1·75	3– 4	1–2
2·0	4– 5	1–2(+)
2·25	4– 5	(1)–2
2·5	4– 6	(1)–2–2(+)
2·75	5– 6	2
3·0	5– 7	2
3·25	5	2
3·5	8– 9	3
4·0	9–11	3–3(+)
4·5	10–11	3(+)–4
5·0	10–12	3(+)–4
6·0	11–13	4–4(+)
7·0	14–15	4
7·5	16–17	5(+)

NOTE. (+) implies that some of the branches are just starting to subdivide. Numbers in brackets are exceptional occurrences.

It is evident from this table that full grown medusae will have about eleven to seventeen tentacles on each marginal bulb, and the oral tentacles will be dichotomously branched four or five times. This agrees with observations by Hartlaub (1911) on a swarm in the North Sea. The specimens had well developed gonads and averaged 5–7 mm. in height and the number of tentacles on each marginal bulb averaged twelve to sixteen.

Hartlaub (1911) gives as the largest size 12 mm. in height, tentacles on each marginal bulb up to thirty in number, and oral tentacles branching at most seven times. Such individuals must be exceptional. The adult medusa shows variation in a number of characters. The thickness of



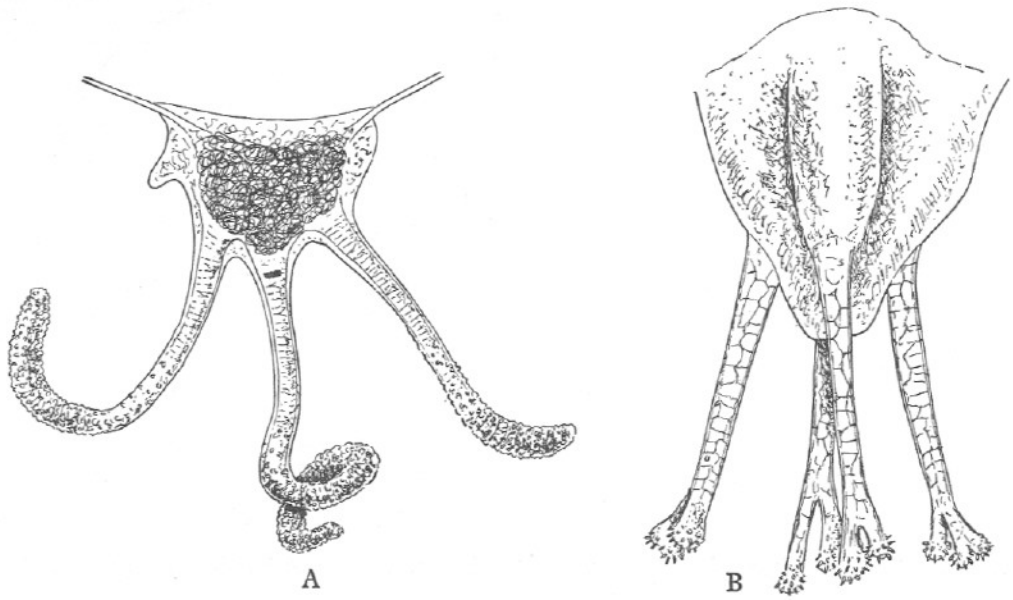
Text-fig. 76. *Bougainvillia principis*. Preserved specimens. A, *c.* 1·3 mm. high; B, *c.* 2 mm. high.

the jelly varies considerably; in some specimens the jelly of the umbrella apex is little thicker than that of the sides, in others it is very much thickened and gives the medusa a somewhat oblong appearance. The stomach varies in length and when very short the oral tentacles are three times as long as the stomach. The oral tentacles have long basal trunks and the branches themselves tend to be rather long (Text-figs. 77B, 78A). The breadth of the radial canals is variable. The shape of the marginal bulbs also varies somewhat from triangular to crescent or kidney-shaped, and this is probably conditioned by the number of tentacles. The jelly of the umbrella overhangs the margin of the subumbrellar cavity and the marginal tentacles emerge from funnel-shaped depressions in this jelly.

The gonads form cushion-like pads on the adradial surfaces of the stomach, which may, especially in the females, spread over the interradial region.

Bougainvillia britannica is at first rather difficult to distinguish from *B. principis*; the following are the characters by which the two species may be differentiated. In *britannica* the jelly is usually much thicker and hence the subumbrellar cavity is smaller than in *principis* medusae of the same size. The broad basal attachment of the stomach is usually quite horizontal in *britannica* whereas in *principis* there is at times a distinct tendency towards the formation of a shallow cone-shaped peduncle. In fully mature specimens of *britannica* the gonads tend to spread over the interradial walls of the stomach; in *principis* they are much more distinctly adradial cushions. The basal trunks and the branches of the oral tentacles (Text-fig. 78A, B) are longer and narrower in

britannica than in *principis*, though in preserved specimens this may not be very marked owing to contraction; even then, however, the basal trunks in *principis* are broader, and the tentacles are more branched in *principis*. This latter character is very obvious when two specimens are seen side by side. The marginal bulbs (Text-figs. 79 A, B) are narrower in *britannica* on the whole than in *principis* and there are fewer tentacles in fully grown specimens. In *britannica* the ocelli are situated at the tentacle bases on the tentacles themselves, and they are generally elongated in shape lying across the width of the tentacles (Text-fig. 79 A). In *principis* the ocelli are situated at the junctions of the tentacles with the bulb, on the bulbs themselves, and they tend to be round



Text-fig. 77. *Bougainvillia britannica*. Details of living specimen 2·3 mm. diameter, Plymouth, 21. iv. 39. A, marginal tentacular bulb; B, stomach and oral tentacles.

(Text-fig. 79 B). In *principis* there is also a mass of dark pigment in the centre of the bulb with elongations directed towards the bases of the tentacles; this persists in specimens preserved in formalin. In the younger stages the oral tentacles are more branched and the tentacles on the marginal bulbs more numerous in *principis* (cf. tables for the two species, pp. 160, 166).

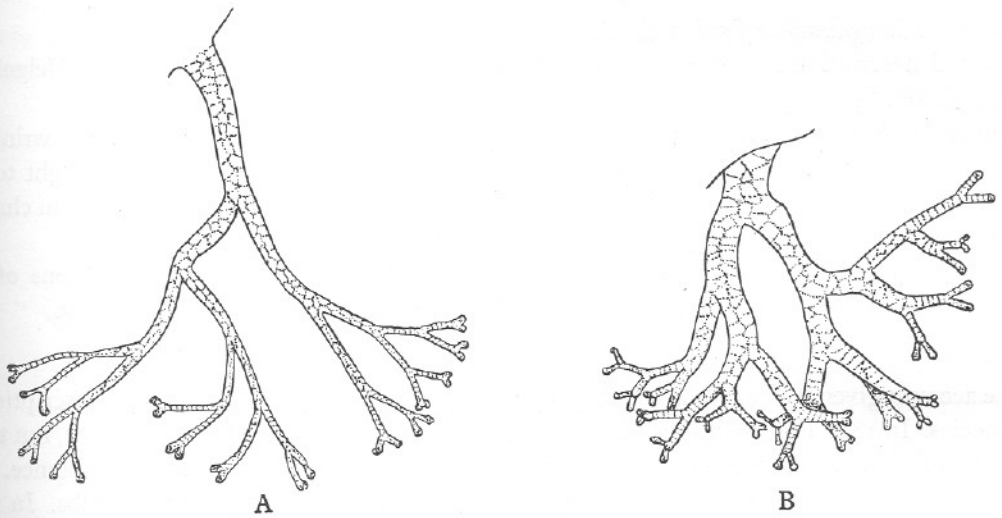
In very many specimens of *B. britannica* a large number of the tentacles often seem to be missing, appearing merely as small finger-like stumps. It is not quite certain whether in these the tentacles are actually broken off or whether they are in a state of extreme contraction. The following observation of Mr Browne would tend to support the latter view. A specimen taken at Valencia 6 mm. in height had apparently only two tentacles on each marginal bulb. On the next day there was a complete series of ten to thirteen tentacles on each bulb not fully expanded; these had become fully expanded by the evening. If the tentacles had actually been lost, this would appear to have been too rapid for their complete regeneration.

Browne (1905*a*, p. 760) has also said:

When a *Margelis* is just taken out of a tow-net it usually has its tentacles more or less contracted. Occasionally a specimen is found with all its tentacles rigidly contracted, forming mere stumps or lobes round the margin of the compound basal bulb. When a specimen in this condition is

placed in a glass of sea water, the tentacles, within a few hours, begin to expand, and nearly always those at the corners of the basal bulbs are the first to expand. At this stage the medusa may have one or two tentacles expanded on each of the four bulbs. Now Forbes's figure of *Bougainvillea nigritella* (Monograph, pl. xii, fig. 2) shows basal bulbs with only one tentacle, and the tentacle is not in the middle of the bulb, but at one end.... It is clear from Forbes's description that he was describing a *Margelis* which had four out of five tentacles in a state of contraction....

Hartlaub (1911) has recorded a number of abnormalities in *B. britannica*. Some specimens had two, three or five radial canals. Two specimens were observed which had four radial canals but seven marginal bulbs, and another with six bulbs. One was seen in which two marginal bulbs



Text-fig. 78. A, oral tentacle of *Bougainvillia britannica*, adult specimen, Plymouth, 24. v. 34; B, fully branched oral tentacle of *Bougainvillia principis*, Valencia, 1895. (E. T. Browne collection.)

ran together so as to form a continuous series of marginal tentacles. In another specimen there were three radial canals one of which branched and had a marginal bulb at the termination of each branch, the two bulbs running together so as to form a continuous series of forty-three marginal tentacles.

The eggs are *c.* 0·14–0·15 mm. in diameter.

Planulae have been reared from ripe specimens at Plymouth; these were 0·36 mm. in length and were colourless. Two very small polyps were developed which had four tentacles. Hartlaub (1911) mentions the rearing of young polyps from planulae; these began with three tentacles.

NEMATOCYSTS. Microbasic euryteles and desmonemes (Russell, 1938*b*).

Seasonal occurrence

Round the southern British coasts *Bougainvillia britannica* occurs usually in April, May, or June. Specimens may, however, be found as late as August. On the northern coasts its period of maximum abundance is probably slightly later, being recorded from the Northumberland coast in September and October, and as common in June and July (Sanderson, 1930; Watson, 1930).

Habits

Observations made on large numbers of *Bougainvillia britannica* taken at Plymouth in 1934 (Russell, 1938*a*) show that the life of the medusa is probably not more than two months in those

waters. Data are also given on the growth in size of the medusa. While on 20 April the average size of the medusae was just over 2 mm., this had increased to 3·5 mm. on 16 May, and to 5·5 mm. on 24 May. In the daytime this species lives in the deeper water layers, being rarely caught above 18 m. (Russell, 1927); on two days in June and July the region of maximum abundance was at 25–30 m. Observations on the vertical migration of the medusae (Russell, 1928, 1931) showed that on the two occasions on which collections were made they must have been living very deep in the water in the daytime, but their numbers increased in the intermediate depths at night, and once they reached the surface layers.

Kramp (1927) has shown their value as indicators of water movements in Danish waters.

HYDROID. ? *Bougainvillia flavida* Hartlaub. (Text-figs. 80, 81.)

(For full description see Hartlaub, 1897, *Wiss. Meeresuntersuch.*, N.F., Bd. II, Abt. Helgoland, p. 456, pl. xiv, figs. 1–4.)

Simple or slightly branched colonies 5–7 mm. in height. Thin perisarc, slightly wrinkled, expanding into membranous cup at base of hydranth, reaching to the tentacles. Eight to ten filiform tentacles arranged in a single whorl; low hypostome. Medusae borne singly or in clusters on branching stalks immediately below the hydranth.

This hydroid has only been found by Hartlaub at Helgoland, but his descriptions of the medusae tend to support the suggestion that this is the hydroid form of *B. britannica*.

Historical

The account given by Forbes in his 1848 monograph is here regarded as the type description of this species. In 1841 Forbes described a medusa under the name *Hippocrene britannica*, but there are certain differences between this and the 1848 description to which he made no reference. The 1841 species was described as being an inch in length and as having red marginal bulbs. In 1848 Forbes remarks that it occurred in the 'Kyles of Bute, whence it was first described', but this locality was not mentioned by him in 1841.

Owing to the difficulties of assigning specific characters to *Bougainvillia* species and their changes in marginal and oral tentacles with growth, *B. britannica* was described by Hartlaub (1897) as three species *flavida*, *xantha* and *bella*. While there can be little doubt of the identity of *xantha* and *bella*, that of *flavida* is less certain, and must be regarded with some reservation until the hydroid is re-discovered. The adults from the plankton with which Hartlaub connected his *flavida* are certainly not *britannica*, and he later (1911) thought that his *flavida* was *ramosa*.

In 1847 Dalyell described this species under the name *Medusa duodecilia*. If Forbes's 1848 description is regarded as the type, Dalyell's name should strictly speaking have priority. It is, however, advisable in view of the doubt of the early history of the species to keep the name *Bougainvillia britannica* which is now in general use. (See also Kramp, 1926*a*.)

Bougainvillia principis (Steenstrup)

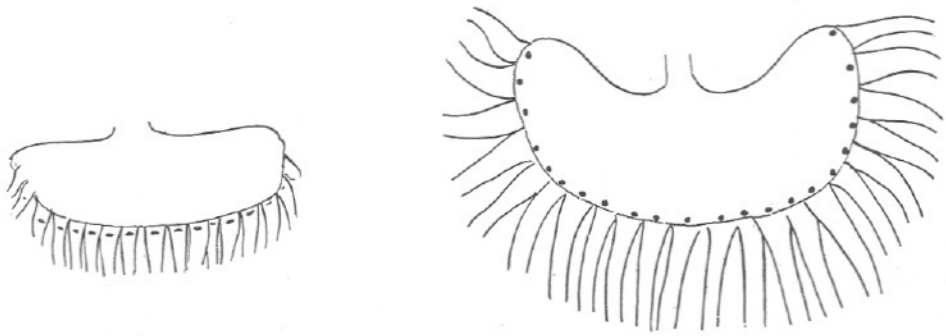
Plate VIII, fig. 4; Text-figs. 76A, B, 78B, 79B

Margelis principis Steenstrup, in Lütken, 1850, *Vidensk. Medd. naturh. Foren. Kbh.* p. 35.
L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 344.
Haeckel, 1879, *System der Medusen*, p. 88, pl. vi, figs. 14–16.
?Hartlaub, 1897, *Wiss. Meeresuntersuch.* N.F., Bd. II, Abt. Helgoland, p. 472, pl. xvi*a*, figs. 2, 4, 10.
Browne, 1895, *Trans. Liverpool Biol. Soc.* vol. IX, p. 266.
Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. V, p. 708.

Bougainvillea fruticosa, Romanes, 1876*a*, *J. Linn. Soc. London, Zool.* vol. XII, p. 526.
Bougainvillea allmanii Romanes, 1877*a*, ibid. vol. XIII, p. 190.
Nemopsis heteronema Haeckel, 1879, *System der Medusen*, p. 93 (in part).
Margelis britannica, Browne, 1896*b*, *Irish Naturalist*, p. 180.
Hippocrene aurea Linko, 1904*b*, *Zool. Anz., Leipzig*, p. 216.
Bougainvillia principis, Mayer, 1910, *Medusae of the World*, vol. I, p. 160.
Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 177, fig. 158.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. V, pt. x, p. 48, chart VIII.

Specific Characters

Jelly only moderately thick. No or slight peduncle. Oral tentacles branching dichotomously usually five to six times. Usually twenty to thirty tentacles on each marginal bulb. Ocelli situated on marginal bulbs at bases of tentacles, round.



Text-fig. 79. A, *Bougainvillia britannica*, marginal tentacular bulb, adult, Plymouth, 24. v. 34; B, *Bougainvillia principis*, marginal tentacular bulb, specimen from Valencia, 1895. (E. T. Browne collection.)

Description of Adult

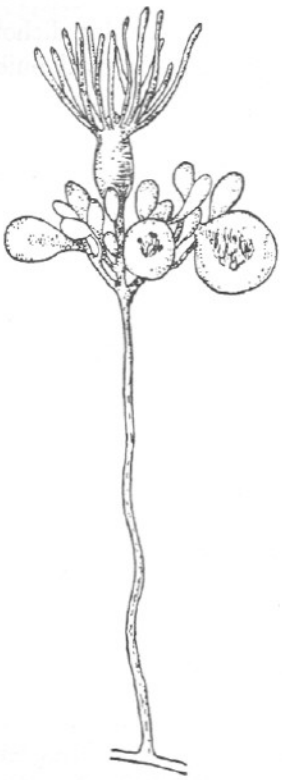
Umbrella globular, sometimes wider than high, with jelly of moderate thickness. Velum fairly broad. Stomach short, with broad base, cross-shaped in section; often with a slight broad-based peduncle. Four oral tentacles short, branching dichotomously usually five to six times, terminating in small nematocyst clusters. Four radial canals broad, ring canal narrow. Gonads adradial. Four perradial marginal bulbs, broad epaulette-shaped, about same width as interradial space. Up to forty tentacles on each marginal bulb, usually twenty to thirty. Ocelli adaxial, situated on the marginal bulbs at the base of each tentacle, round. Height when full grown 10–11 mm., usually 7–8 mm. in British waters. Colour of marginal bulbs wine red, dark reddish brown, brown or orange, with central mass of dark pigment with rays radiating towards the tentacles; stomach wine-red or golden yellow; ocelli black.

Distribution

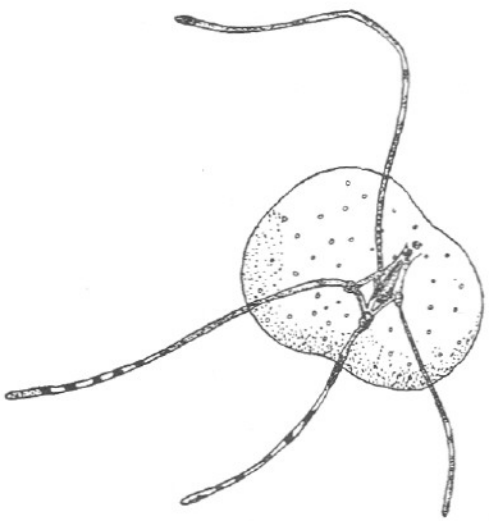
Round the British Isles *Bougainvillia principis* has been recorded from the Shetland Islands; the Hebrides; Cromarty Firth; off north-east Scotland; Port Erin, Isle of Man; Valencia, south-west Ireland; and Plymouth. Elsewhere the species has been recorded from Rockall, Iceland, west Greenland, Faeroe Islands, Norwegian coast, Barents Sea, North Sea, Skagerak, west coast of Jutland, and Helgoland. It is a northern boreal species which is commoner on the northern and outer western coasts of the British Isles than in the English Channel area.

Developmental Stages and Structural Details

The first stage of the medusa *Bougainvillia principis* has not yet been described because its hydroid is not known. The smallest specimen so far recorded (Browne, 1900) was 1·5 mm. in height. The oral tentacles were twice dichotomously branched and there were four tentacles on each marginal bulb (Text-fig. 76A). A smaller specimen has been seen at Valencia only 1 mm. in height in which the oral tentacles were once branched and there were three tentacles on each marginal bulb with ocelli already present.



Text-fig. 80. *Bougainvillia flavida*, possibly the hydroid of *Bougainvillia britannica*. (After Hartlaub, 1911, fig. 150.)



Text-fig. 81. Medusa liberated from *Bougainvillia flavida*, possibly *B. britannica*. (After Hartlaub, 1911, fig. 151.)

During the growth of the medusa the oral tentacles continue to branch dichotomously and the marginal tentacles increase in number. Below are given the results of the examination of a number of specimens mostly from Valencia showing the number of tentacles on each marginal bulb, and the number of times the oral tentacles are branched in medusae of different sizes.

Height (mm.)	No. of tentacles on each marginal bulb	No. of times oral tentacles are branched
1	3	1
1·5	4	2
2	4– 7	2–3
3	8–12	3–4
4	8–25	3–5
5	12–23	5–6
7	24–26	5

It appears from these figures that full-grown specimens in British waters probably have between twenty and thirty tentacles on each marginal bulb and their oral tentacles branched dichotomously five to six times.

In adult specimens the width of the umbrella is often greater than its height and the usual maximum size in British waters is probably somewhere about 7–9 mm. in width. Kramp (1926*a*) has recorded specimens up to 11 mm. in width in more northern waters. Hartlaub gives the number of tentacles on each marginal bulb as thirty to forty and the oral tentacles with 150–200 endings; this would imply that some branches have become divided five times and others six.

The shape of the marginal bulbs varies somewhat with the growth of the medusa, being rather triangular in shape in young specimens, but becoming very broad and epaulette-shaped in the later stages. On the abaxial surface are a number of dark pigment masses radiating out towards the bases of the tentacles. The ocelli appear on the margins of the bulbs before the tentacles develop.

The gonads form distinct cushion-like bean-shaped pads on the adradial sides of the stomach and rarely spread over the interradial regions. Viewed from the apical surface they form a distinct cross.

The main characteristics by which this species can be distinguished from *B. britannica* are given under that species on p. 161.

Seasonal occurrence

Bougainvillia principis has been recorded in April and May at Valencia, south-west Ireland; May at Plymouth; May at Port Erin; May to August in the Cromarty Firth; May in the Hebrides, and June east of north Scotland (Kramp, 1926*a*). Being a northern boreal species it evidently tends to appear earlier in southern British waters than in the far north.

HYDROID. Not known.

Historical

Bougainvillia principis was first briefly described by Steenstrup under the name *Margelis principis* from specimens from the Faeroe Islands in a communication to Lütken (1850). The specimens were kept in the Copenhagen museum and subsequently examined and described more fully by Haeckel (1879).

Bougainvillia pyramidata (Forbes & Goodsir)

Text-fig. 82A–C

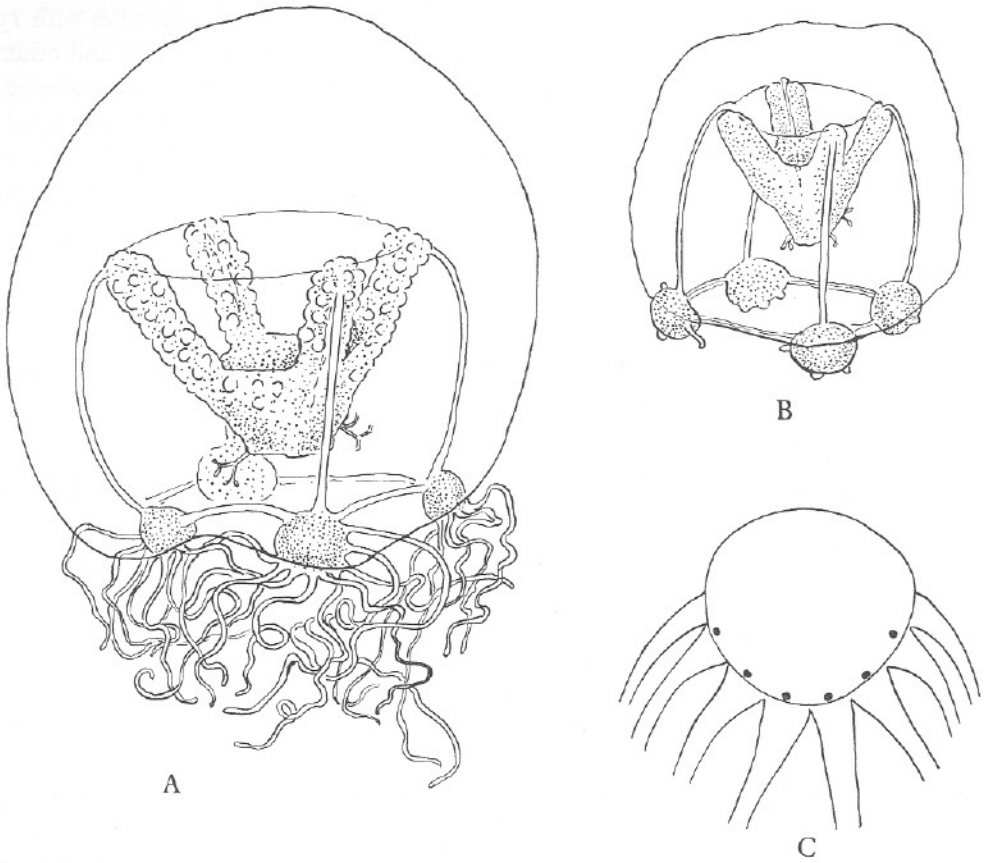
Hippocrene pyramidata Forbes & Goodsir, 1851, *Trans. Roy. Soc. Edinb.* vol. XX, p. 312, pl. x, fig. 4.
Haeckel, 1879, *System der Medusen*, p. 635.
Browne, 1905*a*, *Proc. Roy. Soc. Edinb.* vol. XXV, pt. ix, p. 751.
Margelis pyramidata, Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. V, p. 709.
Bougainvillia pyramidata, Mayer, 1910, *Medusae of the World*, vol. I, p. 168.
Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 180, fig. 159.

Specific Characters

Jelly moderately thick. Cone-shaped peduncle. Oral tentacles branching dichotomously three to four times. Elongated adradial gonads. Up to eight tentacles on each marginal bulb.

Description of Adult

Umbrella globular, about as high as wide; jelly thick, especially in upper half of umbrella. Velum narrow. Stomach on broad cone-shaped peduncle, with four perradial lobes extending along whole of peduncle. Four oral tentacles short, branching dichotomously three to four times, terminating in nematocyst clusters. Four radial canals and ring canal narrow. Gonads adradial



Text-fig. 82. *Bougainvillia pyramidata*. Preserved specimens from Valencia, 1897. (E. T. Browne collection.) A, adult female, 2·5 mm. high; B, young male, 1·3 mm. high; C, marginal tentacular bulb of specimen 2·75 mm. high.

lying along the basal margin of the stomach and its lobes. Four perradial marginal bulbs, small and oval in shape. Usually six to nine tentacles on each marginal bulb. Ocelli adaxial, situated on the marginal bulbs at the base of each tentacle, round. Height when full grown up to 8 mm., usually about 3–5 mm. Colour of marginal bulbs reddish brown or yellow; stomach yellowish brown; ocelli black.

Distribution

Bougainvillia pyramidata appears to be limited to oceanic Atlantic water on the western coasts of the British Isles. It has so far only been recorded from Loch Laigh, Mull; Handa Island, west coast of Scotland; Millport, Firth of Clyde; Port Erin, Isle of Man; and Valencia, south-west Ireland.

Developmental Stages and Structural Details

The first stage of *Bougainvillia pyramidata* has not yet been described because its hydroid is not known. The smallest living specimens seen at Valencia were about 2 mm. high by 1·5 mm. wide; these had five tentacles on each marginal bulb and the oral tentacles were twice dichotomously branched. Below are given the results of the examination of a number of specimens from Valencia Harbour in 1897 showing the number of tentacles on each marginal bulb and the number of times the oral tentacles are branched in medusae of different sizes and sexes.

Height (mm.)	No. of tentacles in each marginal bulb	No. of times oral tentacles are branched	Sex
2	5	2	?
2·5	6	3	♂
3	6–9	2	♀ ripe ova
3	6–7	2–3	♂
3·5	7–8	—	♀ ripe ova
4	8–9	3–4	♂

The gonads are a characteristic feature of this species. Each forms a narrow band on one side of the stomach lobes extending along the peduncle up to the summit of the subumbrellar cavity, where it ends usually in a small, free, unattached curl. The width of the umbrella is sometimes slightly greater than its height. The marginal tentacles are very long and thin. The size of the peduncle increases with age, being quite small in the early stages.

Seasonal occurrence

Bougainvillia pyramidata has been recorded from Mull in August; Handa Island, autumn; Millport, July to November; Port Erin, September; and Valencia, June to August.

HYDROID. Not known.

Historical

This species was first described by Forbes & Goodsir (1851) from Loch Laigh in Mull as *Hippocrene pyramidata*; since then published records of its occurrence have been given only by Haeckel and Browne.

Bougainvillia superciliaris (L. Agassiz)

Text-figs. 83A, B, 84A, B, 85A–C

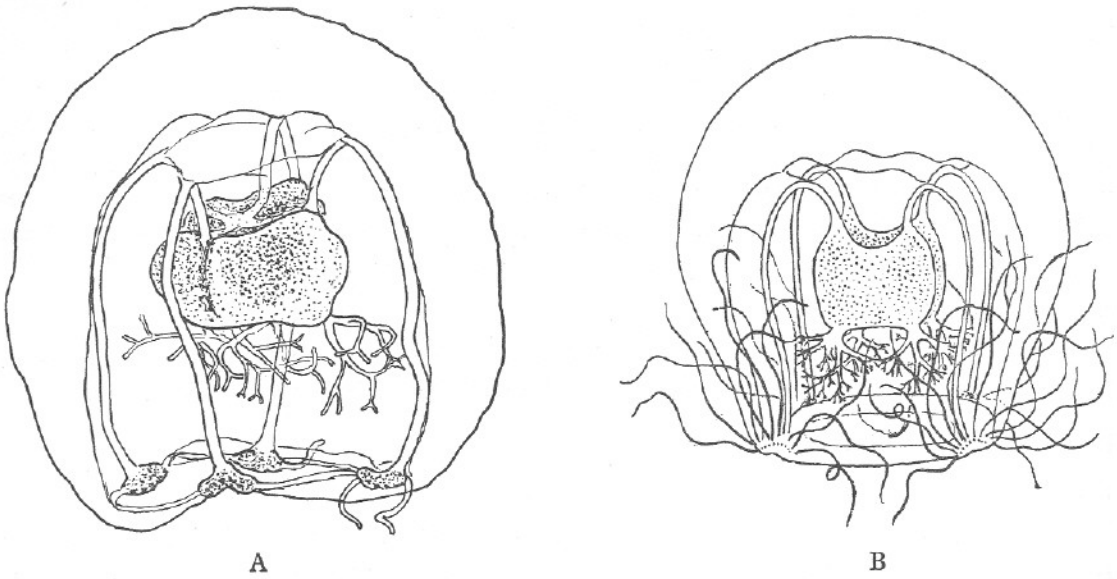
Hippocrene superciliaris L. Agassiz, 1849, *Contr. Nat. Hist. Acalephae N. America*, p. 273, pls. i–iii.
Haeckel, 1879, *System der Medusen*, p. 92.
Bougainvillia superciliaris, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 344.
Agassiz, A., 1865, *N. Amer. Acaleph.* p. 153, fig. 232 (*non* figs. 233–9).
Hartlaub, 1897, *Wiss. Meeresuntersuch.* N.F., Bd. II, Abt. Helgoland, Heft 1, x, p. 466, pl. xv, fig. 1; pl. xvi*a*, figs. 1, 5, 7–9, 12; pl. xvi*b*, fig. 3; pl. xvi*c*, figs. 3, 4.
Hartlaub, 1909*c*, *Crois. Océanogr. Belgica Mer du Grönland* 1905, p. 4.
Mayer, 1910, *Medusae of the World*, vol. I, p. 162, pl. xvii, fig. 1, text-figs. 87, 88 (*non* hydroid and young medusa).
Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 171, figs. 153–7 (hydroid and medusa).
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. V, pt. X, p. 44, chart VII.
Kramp, 1927, *K. danske vidensk. Selsk. Skr.* natur. og math. Afd., 8. Raekke, XII, pp. 22, 23, 56, 57, 173, and following pp.
Bougainvillea paradoxa Mereschowsky, 1879, *Ann. Mag. Nat. Hist.* ser. 5, vol. III, p. 177, pl. xx, figs. 1–5.
Bougainvillea superciliaris, Wagner, 1885, *Wirbellosen des Weissen Meeres*, Bd. I, p. 73, pl. ii, figs. 5–9.
Bigelow, 1909*b*, *Proc. U.S. Nat. Mus.* vol. XXXVII, no. 1706, p. 305, pl. xxi, fig. 2.
Hippocrene (*Bougainvillea*) *superciliaris*, Maas, 1904, *Rés. Camp. Sci. Monaco*, fasc. XXVIII, p. 9, pl. i, figs. 1, 2.

Specific Characters

Jelly moderately thick. Peduncle present. Oral tentacles branching dichotomously usually four to five times. Usually eleven to fifteen tentacles on each marginal bulb. Ocelli situated on bases of tentacles.

Description of Adult

Umbrella almost globular, or higher than wide; jelly moderately thick. Velum well developed. Stomach short, with broad base, cross-shaped in section; almost always with conspicuous peduncle. Four oral tentacles, not reaching beyond umbrella margin, branching dichotomously



Text-fig. 83. *Bougainvillia superciliaris*. A, preserved specimen *c.* 5 mm. high, Cap Linne, Spitsbergen, 12. viii. 48 (collected by P. S. B. Digby); B, after L. Agassiz, 1849, pl. i, fig. 1.

usually four to five times, each branch terminating in nematocyst cluster. Four broad radial canals; ring canal narrow. Gonads interradial; planulae developing *in situ* within capsules. Four perradial marginal bulbs, crescent-shaped, less than half as wide as interradial space. Up to twenty-two tentacles on each marginal bulb, usually eleven to fifteen. Ocelli adaxial, situated one on base of each tentacle. Height of umbrella up to 7–12 mm. Colour of stomach brown to reddish brown; marginal bulbs chestnut brown; ocelli black.

Distribution

Bougainvillia superciliaris has only been recorded twice in British waters. A single specimen in the museum at St Andrews was identified as such by Hartlaub (1911, p. 173), and Kramp (1930) recorded three specimens from near Deal Harbour.

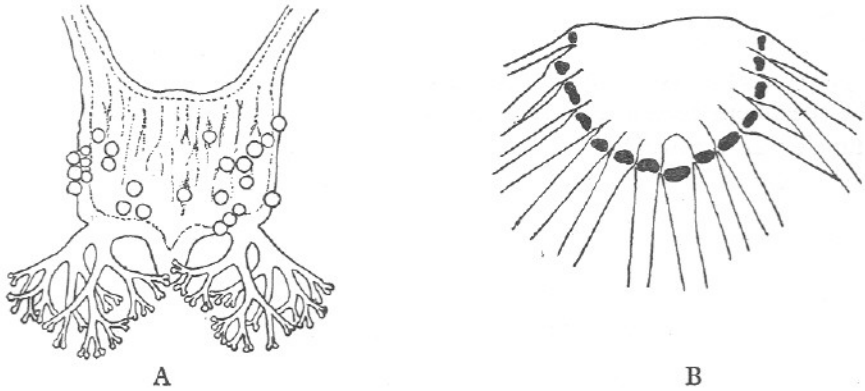
It is an arctic species, but it occurs southwards along the coasts of Norway, Denmark and Holland, in the Baltic and in the south-eastern North Sea at Helgoland. Its distribution is thus such that it might be expected to occur on the north-eastern coasts of the British Isles when the influence of the East Iceland arctic current is strong.

The species has been recorded from the White Sea, Barents Sea, Spitsbergen, Bear Island, Iceland, Greenland, Labrador, and along the American coast of the North Atlantic as far south as Woods Hole. It has also been recorded from the North Pacific (Bigelow, 1913).

Developmental Stages and Structural Details

The early development of *Bougainvillia superciliaris* has been described by Hartlaub (1897, 1911), who also described the hydroid with medusa buds from a small aquarium at Helgoland. The adult has been described and figured in great detail by L. Agassiz (1849).

While still attached to the hydroid the medusa already has three tentacles and three ocelli on each of the four marginal bulbs. Specimens caught in the plankton, 1 mm. in height, were still in the same stage of development (Text-fig. 85 A). The jelly of the umbrella is considerably thinner than in small *B. britannica*. The stomach is short and without a peduncle. The four oral tentacles are each branched dichotomously twice. The radial canals have brown pigment granules in them and the marginal bulbs are dark reddish brown. Hartlaub reared young specimens from the plankton. After five or six days the number of tentacles on each marginal bulb had increased to five, and the oral tentacles had continued to branch.



Text-fig. 84. *Bougainvillia superciliaris*. A, gonads, stomach and mouth-lips; B, marginal tentacular bulb. (After L. Agassiz, 1849, pl. ii, figs. 14, 18.)

The stomach peduncle began to appea rin medusae 3 mm. in height. Kramp (1926*a*) also states that the peduncle is distinctly seen in specimens not more than 2–3 mm. high.

In adult specimens the gonads cover the whole of the four interradial surfaces of the stomach, but they are separated perradially (Text-figs. 83 A, 84 A). A section shows that the ripe eggs form a single layer which lies directly on the mesogloea or supporting lamella; between them lie the younger egg cells, some of which are between the ripe eggs and the supporting lamella. The whole ovary is covered by a relatively thick ectodermal epithelium; which sinks in towards the mesogloea between the eggs. As the eggs become larger they become farther separated from the mesogloea and the ectodermal epithelium grows round them and eventually completely envelops them. This epithelium forms the capsule in which the planula develops, and it has a basal stalk.

The gonads and overlying epithelium are without nematocysts.

In sections of fully ripe ovaries Hartlaub found isolated young egg cells lying in the endoderm beneath the supporting lamella. In sections of quite young ovaries he only saw the supporting lamella in the radial corners of the stomach, but in older specimens it was developed everywhere and separated the ectoderm from the endoderm.

The usual number of times that the oral tentacles branch dichotomously is four or five (Text-fig. 84A), but Hartlaub has seen specimens branched as many as six and seven times, and Bigelow (1913) records up to eight times. The endoderm of the oral tentacles consists of several rows of cells (Kramp, 1930).

The usual number of tentacles on each marginal bulb is eleven to fourteen, but Hartlaub found as many as eighteen and twenty-two in specimens at Helgoland. Bigelow (1913) also records a specimen from the North Pacific with sixteen, eighteen, fifteen and fifteen tentacles on each bulb respectively. This specimen was 12 mm. high by 10 mm. wide and is probably the largest yet recorded.

The ocelli are round and on slight prominences, one on the base of each marginal tentacle (Text-fig. 84B). According to Agassiz (1849) they appear somewhat variable in shape, being either spherical, ovate, or crescent-shaped. This is probably due to their observation at different angles. Each ocellus has a lens and the histology has been described by Linko (1900*b*, p. 6). Mereschkowsky (1879) records the ocelli as red.

After a free-swimming existence, the planula, according to Hartlaub, attaches itself to the substratum along its whole length; after a further increase in length one end rises to form the primary polyp.

The segmentation of the egg has been described by Gerd (1892).

Mereschkowsky (1879) records abnormal specimens devoid of a stomach.

One of the specimens recorded by Kramp (1930) was not quite typical. It was 8 mm. high and the peduncle was unusually large, broad and conical; the ocelli appeared as transverse lines instead of being round.

Seasonal occurrence

The single specimen recorded by Hartlaub (1911) from the St Andrews museum was taken on 26 April 1899. Those from near Deal Harbour recorded by Kramp (1930) were taken in May 1907 and 1909.

The season of occurrence in the North Sea is from February to June.

Habits

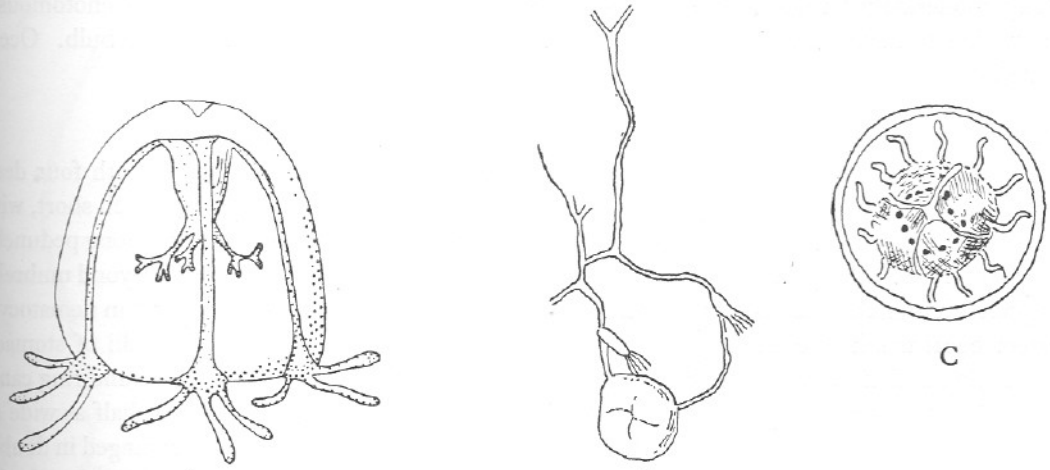
The swimming habits of the living medusa have been described by L. Agassiz (1849). It moves by 'repeated jerks and the whole animal seems rather to jump from place to place by its sudden contractions...'. When at rest it 'stands upright in the water, its tentacles more or less drawn out and stretched outside at various angles from the lower margin'. When fully extended the tentacles are longer than the diameter of the umbrella. When at rest, if the tentacles are contracted the medusa sinks slowly through the water; but it remains more or less poised in the water when the tentacles are outstretched. 'As soon as it contracts to move, the tentacles are reduced to a certain middle state of extension, and brought together in a backward direction; but when dilating, they are drawn in through the lower aperture in an inverted position. From its peculiar form, this animal turns easily every way, and moves with equal ease and elegance sideways or downwards, or obliquely in all possible directions. The arrangement of parts, however, is such that, during the most powerful contractions, the lower opening is brought into a square form, but when gradually relaxing passes again into a more rounded shape. When at rest it is perfectly circular and only the more straight course of the inferior chymiferous canal, extending from one sensitive bulb to the other, preserves some indication of the quadrangular outline.'

Hartlaub (1897) reared some young specimens from the plankton. He found that it was difficult to feed them in the earliest stages, and used chopped up *Sagitta*. Later, when the oral tentacles had increased in number, feeding was easier, and large specimens ate copepods. Out of ten specimens he only reared two to a large size; one of these lived for five weeks and the other for about two and a half months.

Hydroid. *Bougainvillia superciliaris* (Text-fig. 85 B, C).

(For full description see Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 174, fig. 156.)

Colonies of very small single hydranths rising from a creeping stolon. Hydranths sessile, with very delicate perisarc. Six(?) filiform tentacles arranged in a single whorl. Medusa buds borne singly on short stalks arising from creeping stolon; diameter of bud greater than length of hydranth.



Text-fig. 85. *Bougainvillia superciliaris*. A, young medusa 1 mm. high from Helgoland; B, hydroid with medusa bud; C, medusa bud (enlarged). (After Hartlaub, 1911, figs. 154, 156.)

This hydroid was discovered by John Hinrichs, Preparator at the Helgoland Biological Station, in a small aquarium at Helgoland containing stones covered with algae brought from Mandal in Norway.

Historical

Bougainvillia superciliaris was first described by L. Agassiz (1849) as *Hippocrene superciliaris*, from the north American coast of the Atlantic. The description is classical and was beautifully illustrated by A. Sonrel.

Agassiz gave the species the name *superciliaris* on account of the 'connection of the tentacles with the eye-specks'.

Bougainvillia macloviana Lesson

Text-figs. 86, 87, 88 A, B

Cyanaea bougainvillii Lesson, 1830, *Voyage . . . sur . . . 'La Coquille'*, p. 118, pl. xiv, fig. 3.
Bougainvillia macloviana Lesson, 1836, *Ann. Sci. nat. Paris*, sér. 2, tome v, p. 262.
Lesson, 1843, *Histoire Naturelle des Zoophytes*, p. 290.
L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 344.
Mayer, 1910, *Medusae of the World*, vol. I, p. 160.

Hartlaub, 1911, *Nordisches Plankton*, Lief. 15, XII, p. 156, fig. 139.
Kramp, 1928, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. LXXXV, p. 50.
Künne, 1933, *Zool. Anz. Leipzig*, Bd. CI, p. 249, fig. 1.
Browne & Kramp, 1939, *Discovery Rep.* vol. XVIII, p. 284, pl. xiv, fig. 6; pl. xv, figs. 7–14.

Hippocrene macloviana, Haeckel, 1879, *System der Medusen*, p. 90, pl. v, figs. 1, 2.
Browne, 1902, *Ann. Mag. Nat. Hist.*, ser. 7, vol. IX, p. 278.
Vanhöffen, 1912*a*, *Deutsche Südpolar-Expedit.* 1901–03, Bd. XIII, Zool. v, p. 359, pl. xxv, fig. 1.
Vanhöffen, 1912*b*, *Zoologica Stuttgart*, Heft 67, p. 11, pl. i, fig. 7; pl. ii, fig. 10.

Hippocrene, Benham, 1909, *Subantarctic Islands of New Zealand*, Art. XIV, p. 306, pl. xii, figs. 1, 2.

Perigonimus maclovianus, Vanhöffen, 1909, *Deutsche Südpolar-Expedit.* 1901–03, Bd. XI, Zool. III, p. 284, fig. 10 (hydroid and medusa buds).

Specific Characters

Jelly moderately thick. Large peduncle present. Oral tentacles branching dichotomously usually five to seven times. Thirty-five to sixty-five tentacles on each marginal bulb. Ocelli situated on marginal bulbs.

Description of Adult

Umbrella globular, or slightly higher than wide, with quadrangular margin, with four deep interradial longitudinal furrows; jelly fairly thick. Velum moderately broad. Stomach short, with well-developed cone-shaped peduncle, with four narrow perradial lobes extending along peduncle. Mouth with four short perradial lips; four perradial oral tentacles, not extending beyond umbrella margin, each branching dichotomously five to seven times, each branch terminating in nematocyst cluster; basal trunk of each oral tentacle very short. Gonads situated on interradii of stomach and hanging in folded bands along stomach lobes on peduncle. Four radial canals and ring canal fairly narrow. Four crescent- or V-shaped perradial marginal bulbs, each about half as wide as interradial space. Thirty-five to sixty-five solid tentacles on each marginal bulb, arranged in double row. Ocelli adaxial, situated on marginal bulb, one at base of each tentacle. Height of umbrella up to 15 mm. Colour of stomach, gonads, and marginal bulbs bright red, reddish brown, or orange; ocelli red or black.

Distribution

Bougainvillia macloviana has not been recorded from British waters. It has, however, been found in the south-eastern part of the North Sea from Helgoland and off the east Frisian coast in the region of Nordeney and Borkum (Künne, 1933). It is possible therefore that it might be found some time off the south-east coasts of England.

The medusa is an Antarctic species and has been recorded from the Falkland Islands, Kerguelen, the Auckland Islands, and the Campbell Islands, and other regions in the Antarctic (Kramp, 1948*b*). Its occurrence in the North Sea is presumably due to the transportation of the hydroid on ships coming from Antarctic waters.

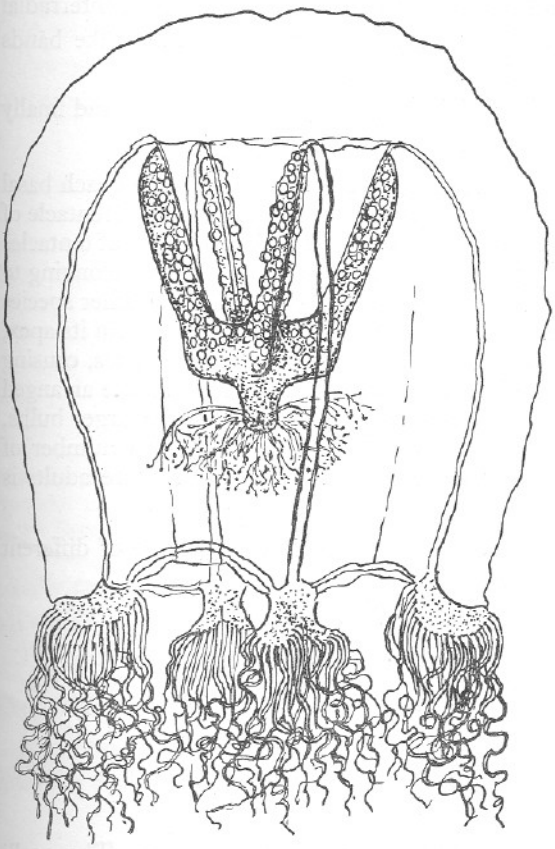
Developmental Stages and Structural Characters

The adult medusa has been well described by Künne (1933) and the development of the medusa has been given by Browne & Kramp (1939), from whom most of the following description is taken.

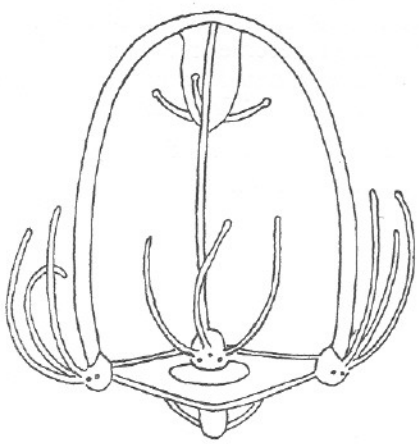
In the earliest stages, 0·5–0·75 mm. in height, the umbrella is bell-shaped or globular and the jelly thin (Text-fig. 87). An umbilical canal may be present. The velum is very broad. The stomach is small, cubical or cone-shaped, and has a quadrangular base. There is no peduncle.

The mouth is simple and the four oral tentacles are unbranched. There are no gonads. The marginal bulbs are globular or spherical, and there are two or three tentacles on each bulb. Vanhöffen (1909) records medusae with five tentacles and three ocelli on a bulb while still attached to the hydroid.

As the medusa grows the jelly of the umbrella increases considerably in thickness, especially in the apical region. When the medusa is about 2 mm. in diameter the stomach develops perradial lobes and the peduncle begins to appear.



Text-fig. 86. *Bougainvillia macloviana*. Preserved specimen *c.* 11 mm. high, Perseverance Harbour, Campbell Islands, 10. xii. 14. (Sent by P. L. Kramp from Th. Mortensen collection, Copenhagen Museum.)



Text-fig. 87. *Bougainvillia macloviana*. Early stage, Falkland Islands. (After Browne & Kramp, 1939, pl. xv, fig. 8.)

When the medusa is about 2–4 mm. in height the gonads start to develop on the stomach and its lobes. The marginal bulbs broaden and become heart-shaped; each now has five to ten tentacles arranged in a single row. Vanhöffen (1912*a*) mentions a medusa 1 mm. in diameter with eight or nine tentacles and four ocelli on a bulb.

With further growth four interradial longitudinal furrows appear on the exumbrella, and they become deep and conspicuous in the adult. Finally, less pronounced perradial furrows are developed. The umbrella margin, which is more or less quadrangular in all stages, becomes slightly embayed between the marginal bulbs.

The peduncle gradually increases in size, its base occupying the whole of the apex of the subumbrella. The stomach lobes extend along the whole length of the peduncle, but never beyond it. The oral tentacles (Text-fig. 88A) become considerably branched so that there may be as many as 400 terminal branches in all. According to Kramp (1928) and Künne (1933) all the branches of the oral tentacles have endodermal axes consisting of a single row of cells, except the basal trunk and first two branches.

The gonads are situated interradially on the stomach and spread out adradially along its lobes (Text-fig. 86); they are separated perradially and sometimes there appears to be an interradial division (Vanhöffen, 1912*b*, and Künne, 1933). When fully developed the ribbon-like bands along the stomach lobes hang down below the level of the mouth.

In their development the marginal bulbs (Text-fig. 88B) become at first U-shaped and finally V-shaped, the tentacles increasing in number meanwhile. Browne & Kramp say:

When the medusa is about 4–6 mm. high and has about ten to fifteen tentacles on each basal bulb, an inner series of tentacles begins to appear, starting at about the fourth or fifth tentacle of the outer series, away from the apex of the U or V; in this way a double alternating row of tentacles is formed. This inner series is formed partly by a pushing inwards of the tentacles belonging to the outer row, partly by addition of new tentacles in both of the two rows. In most other species of this genus new tentacles are only developed at both sides of the basal bulb away from its apex, but in *Bougainvillia macloviana* young tentacles may also develop among the older ones, causing an overcrowding which results in a displacement of the tentacles, so that they become arranged in two rows, both of which contain old as well as young tentacles. In some of the larger bulbs, the rows become irregular in places and the tentacles three deep. The maximum number of tentacles counted on one bulb was sixty-six, but the more usual number for mature adults is about forty to fifty-five.'

They give the maximum number of tentacles on one marginal bulb for medusae of different sizes as follows:

Height of umbrella (mm.)	No. of tentacles on one marginal bulb
6	16
9	32
10	35
11	40
12	45
12	47
13	61
15	55
15	65

The marginal tentacles have endodermal axes formed of single rows of cells. The ocelli which are situated on the bulb itself and not on the marginal tentacles are round or crescent-shaped. They are usually described as being black, though Benham (1909) stated that they were red. According to Künne (1933) in North Sea specimens there is a rusty brown zigzag band on each bulb. Vanhöffen (1912*a*) states that the gonads are redder in the males, and more yellow ochre coloured in the females.

While Antarctic specimens grow to a height of 15 mm., Künne gives the height of North Sea specimens as 8·5 mm. Vanhöffen (1912*a*) found numbers of planulae, 0·26 mm. long and 0·15 mm. broad, amongst his preserved specimens.

The egg capsules contain nematocysts.

Seasonal occurrence

In the south-eastern part of the North Sea *Bougainvillia macloviana* has been recorded in the months of April, May and June.

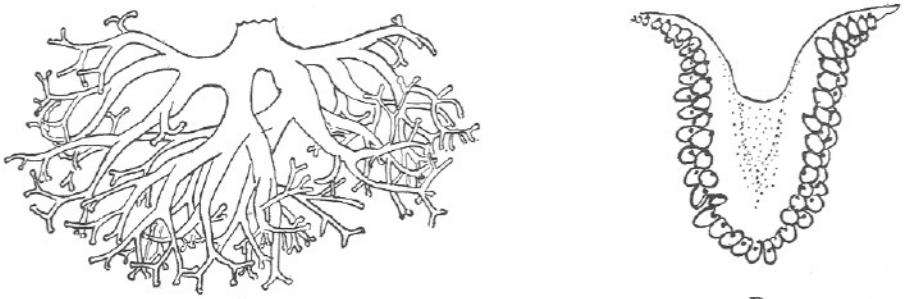
Habits

There are no observations on the habits of the living medusae. In the Antarctic the medusa is very abundant and appears to have a long breeding season (Browne & Kramp, 1939). Its appearance in the restricted part of the North Sea in small numbers only seems to indicate that the species is probably transported there by ships and is not truly indigenous.

Vanhöffen (1909) describes the settling of the hydroids on the bottom of the 'Gauss'.

Hydroid. (For full description see Vanhöffen, 1909, *Deutsche Südpolar-Expedit.* 1901–3, Bd. XI, Zool. III, p. 284, fig. 10.)

Colonies with long, thin, much-branched decumbent stems, with folded, but not clearly ringed, perisarc, which is continued as thin membrane over hydranth. Hydranths with up to sixteen,



A B

Text-fig. 88. *Bougainvillia macloviana.* Falkland Islands. A, oral tentacle of adult 12 mm. high; B, marginal tentacular bulb of full grown adult, with double row of much contracted tentacles, oral view. (After Browne & Kramp, 1939, pl. xv, figs. 11, 13.)

usually fewer, filiform tentacles arranged in a single whorl. Medusa buds borne singly on short annulated stalks. Size of medusa bud considerably greater than that of hydranth.

The hydroid has not yet been recorded in northern waters.

Historical

Bougainvillia macloviana was first described and figured very inadequately by Lesson (1830) from the Falkland Islands, as *Cyanaea bougainvillii.*

Family PANDEIDAE

Anthomedusae with umbrella with or without apical process; with or without exumbrellar nematocyst tracks; large stomach which may or may not extend beyond umbrella margin; with or without peduncle; mouth with four simple, or crenulated perradial lips, rarely with nematocyst clusters along margin; with four radial canals, rarely with centripetal canals or branching canals; with simple or folded gonads situated adradially or interradially on stomach wall, rarely on perradii on subumbrella; no asexual budding of medusae; with two, four or more hollow marginal tentacles with tapering conical basal bulbs often laterally compressed, or without basal swelling and with large terminal nematocyst cluster; with or without rudimentary marginal tentacles, marginal warts or tentaculae; with or without ocelli.

Hydroids with single whorl of filiform tentacles.

The Pandeidae are above all characterized by the form of the mouth-lips. These are almost invariably four perradial lips which may be simple or with folded or much crenulated margins.

Another feature which is characteristic of many species is the so-called 'mesentery'. In young medusae the radial canals enter the stomach at its base, but in some species growth occurs in the upper portion of the stomach so that its apex eventually lies well above the entrances to the radial canals. The stomach is attached to the subumbrella along the lines of a perradial cross, and with the upward growth of the stomach the arms of this cross curve over the dome of the stomach. The four lines of attachment thus separate the subumbrellar cavity into four pouches surrounding the stomach above the entrances of the radial canals. These lines of attachment have been somewhat falsely named 'mesenteries' and it seems perhaps better that the term should be dropped.

The radial canals are often very broad and ribbon-like, and often have jagged margins.

One of the chief characters on which the genera in the family are distinguished is the form of the gonads. These may be simple adradial swellings on the stomach wall, or they may be folded. The folding shows varying degrees of complexity, and on the form it takes the generic characters are largely based. In some genera, however, the form of the gonad is used as a specific character. The foldings, which are mostly horizontal, are really corrugations of the stomach wall; these corrugations may become so compressed that pits are formed between the folds. In some genera there are isolated pits as well as more or less continuous folds.

The marginal tentacles are also characteristic in most genera in that their basal bulbs are very elongated and tapering, almost carrot-shaped, and frequently laterally compressed. They may be continued slightly round the umbrella margin so as to clasp the margin and form exumbrellar spurs (Text-fig. 93 B). In one group of the Pandeidae, however, the marginal tentacles have no basal swellings, but they terminate in a large nematocyst cluster.

The Pandeidae can be conveniently divided into four subfamilies based on the form and numbers of marginal tentacles in the adult medusa. These are the Amphineminae, Protiarinae, Pandeinae, and Calycopsinae. Of these, the Protiarinae are not represented in the British fauna. The distinguishing characters of the four families are as follows:

Marginal tentacles with basal swellings:
- Not more than two in number . . . . **Amphineminae**
- Four in number and never more . . . . . **Protiarinae**
- Up to eight or more in number . . . . . **Pandeinae**

Marginal tentacles with terminal nematocyst cluster and without basal swellings . . . . . **Calycopsinae**

This seems to me a simpler classification than by using the characters of gonad form, or presence or absence of marginal tentaculae, because the variations in these characters are distributed throughout the four groups and they can best be used as generic or specific characters. In any event division into subfamilies is rather a matter of convenience than an attempt to show phylogenetic relationship. It is not possible with so few variable characters to decide which are of real phylogenetic significance.

In considering the marginal structures of the Pandeidae the use of the terms rudimentary marginal tentacles, marginal warts or swellings, and marginal tentaculae should be defined.

The rudimentary marginal tentacles appear as small elongated marginal bulbs, often with abaxial ocelli. They are regarded as rudimentary marginal tentacles on the grounds that fully developed marginal tentacles first appear in the same form. Thus it may be assumed that if the medusa could go on growing indefinitely all the rudimentary marginal tentacles would eventually grow into fully formed marginal tentacles. They are well exemplified in *Leuckartiara octona*.

The marginal warts or swellings are merely slight protuberances on the umbrella margin which never develop any further and are quite different from the early stages of development of a true marginal tentacle. They are found, for instance, in *Amphinema dinema*.

The marginal tentaculae are small marginal filiform appendages which differ from true marginal tentacles in that they have no basal swellings, and that they are solid, whereas the marginal tentacles in the Pandeidae are hollow. They are found, for instance, in *A. rugosum*.

In the British fauna there is one genus of Amphineminae with two species; three genera of Pandeinae with six species; and one genus of Calycopsinae with one species. Of these the Calycopsinae are deep-sea medusae and they differ from those of the other subfamilies in having radial canals which branch or in the presence of centripetal canals.

The classification of the Pandeidae was in great confusion until Hartlaub (1914) made a very thorough and satisfactory revision of the species in the family.

Subfamily AMPHINEMINAE

Pandeid medusae with umbrella with round or pointed apical process; without exumbrellar nematocyst tracks; with large stomach which may or may not extend beyond umbrella margin; with or without peduncle; with four simple perradial lips; with four unbranched radial canals; with simple or folded gonads situated on stomach wall, or rarely perradially on subumbrella; with two opposite perradial marginal tentacles with elongated conical basal bulbs; with no rudimentary marginal tentacles but with marginal warts or marginal tentaculae; with or without ocelli.

The Amphineminae are represented in British waters by one genus only, *Amphinema* Haeckel.

Genus **Amphinema** Haeckel, 1879*

MEDUSAE. Amphineminae with stomach not extending beyond umbrella margin; no peduncle; mouth with four simple upturned lips; gonads adradial or interradial, simple or folded; small marginal warts or marginal tentaculae present.

* The genus *Amphinema* was erected by Haeckel (1879). His type species was given under the name *A. titania*, which was the name given by Gosse (1853) for a medusa which was evidently *Oceania dinema* of Péron & Lesueur (1809). In his description Haeckel obviously confused two species, *A. dinema* Péron & Lesueur and *A. rugosum* (Mayer, 1900*a*). His synonymy, description and drawing show this, for while giving the folded gonads of *A. rugosum* his figure had the marginal swellings of *A. dinema*. The two species were correctly described by Mayer (1910) as *Stomotoca dinema* and *S. rugosum*. After pointing out this confusion Rees & Russell (1937) redefined the genus *Amphinema* and chose *A. dinema* (Péron & Lesueur) as the type species.

Haeckel's original definition of *Amphinema* gave folded gonads; Rees & Russell included smooth and folded gonads.

Hartlaub (1914) grouped the Pandeidae according to the form of the gonads. He erected the genera *Merga* and *Tiarula* for *Pandea violacea* Agassiz & Mayer (1899) and *Tiara tergestina* Neppi & Stiasny (1913*a*) respectively. In a footnote (1914, p. 261) he described a true *Amphinema dinema* as *Tiarula coeca*.

According to Hartlaub's definition of the genus *Tiarula* it should include *Amphinema dinema*. But if this were done we should have to erect a new genus for *A. rugosum*, since *A. dinema* is the type species of *Amphinema*.

The simplest course is to keep the genus *Amphinema* and use the gonad as a specific character. But this is complicated by an overlap in the generic descriptions of *Amphinema* and *Tiarula*, the former being medusae with two marginal tentacles and the latter with two to eight marginal tentacles. To overcome this complication I propose to redefine the genus *Amphinema* as having 'never more than two marginal tentacles' and sink the genus *Tiarula* as a synonym of *Merga*, whose definition must be changed from 'eight or more marginal tentacles' to 'two to eight or more marginal tentacles'.

PANDEIDAE

HYDROID. *Amphinema.*

There are two species of *Amphinema* in British waters, *A. dinema* (Péron & Lesueur) and *A. rugosum* (Mayer). They are easily distinguishable and are not likely to be confused with any other British medusae in their adult stages. In life the violet marginal tentacles of *A. dinema* are in striking contrast to the golden brown of *A. rugosum.*

The distinguishing characters are:

Gonads simple; with marginal warts	**A. dinema**
Gonads folded; with marginal tentaculae	**A. rugosum**

The hydroids of *A. dinema* and *A. rugosum* are bright red and that of the former used to be known as *Perigonimus serpens.*

Amphinema dinema (Péron & Lesueur)

Plate X, figs. 1, 2, 4; Plate XI, figs. 1, 3; Text-fig. 89

Oceania dinema Péron & Lesueur, 1809, *Ann. Mus. Hist. nat. Paris*, tome XIV, p. 346.
?Dianaea diadema Lamarck, 1817, *Anim. sans Vertèbr.* tome II, p. 506.
?Oceania diadema, Eschscholtz, 1829, *Syst. d. Acalephen*, p. 98.
Saphenia titania Gosse, 1853, *Devonshire Coast*, p. 387, pl. xxvi, figs. 7–9.
Saphenia apicata McCrady, 1858, *Proc. Elliott Soc. Nat. Hist.* vol. I, p. 129, pl. viii, figs. 2, 3.
Stomotoca dinema, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 347.
Mayer, 1910, *Medusae of the World*, vol. I, p. 109, text-fig. 60, pl. ix, figs. 8–10; pl. x, figs. 1–4.
Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien u. Stat. Zool. Triest*, Tom. XX, p. 40, pl. i, fig. 8.
Amphinema apicatum, Haeckel, 1879, *System der Medusen*, p. 50.
Amphinema titania, Haeckel, 1879, ibid. p. 50, pl. iv, figs. 8, 9 (in part).
Stomotoca apicata, Fewkes, 1881, *Bull. Mus. Comp. Zoöl. Harvard*, vol. VIII, p. 152, pl. ii, figs. 1, 4, 9.
Mayer, 1900*a*, ibid. vol. XXXVII, p. 3, pl. ii, figs. 3, 4.
Nutting, 1901, *Bull. U.S. Fish. Commiss. Washington*, vol. XIX (1899), p. 371, fig. 77.
Dinematella cavosa Fewkes, 1881, *Bull. Mus. Comp. Zoöl. Harvard*, vol. VIII, p. 151, pl. ii, figs. 2, 3; pl. iii, fig. 3.
Amphinema dinema, Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 475.
Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. V, p. 700.
Non Hartlaub, 1914, *Nordisches Plankton*, Lief. 17, XII, p. 259, figs. 214, 216, 217.
Rees & Russell, 1937, *Journ. Mar. Biol. Assoc.* vol. XXII, p. 62, figs. 1–4 (hydroid and medusa).
Tiarula coeca Hartlaub, 1914, *Nordisches Plankton*, Lief. 17, XII, p. 261, fig. 215.
Perigonimus serpens Allman, 1863, *Ann. Mag. Nat. Hist.* ser. 3, vol. XI, p. 10 (hydroid and medusa).
Allman, 1872, *Monogr. Gymnobl. Hydroid*, p. 327, pl. xi, figs. 7–9 (hydroid and medusa).
Hincks, 1868, *Brit. Hydroid Zooph.* p. 95, pl. xvi, fig. 3 (hydroid and medusa).

Specific Characters

Gonads simple, not folded, on each of eight adradial surfaces of stomach. Fourteen to twenty-four small or minute marginal warts.

Description of Adult

Umbrella bell-shaped, with large conical and often much elongated solid apical process; jelly moderately thick. Stomach cross-like in section, flask-shaped, in full extension nearly reaching umbrella margin. Mouth cruciform with four prominent, recurved, crenulated lips. Four radial canals and ring canal broad, with smooth or slightly jagged outlines. Gonads in form of simple pads on each of the eight adradial surfaces of the stomach. Two opposite perradial marginal tentacles, very extensile, smooth, with large hollow, elongated conical basal bulbs. Fourteen to twenty-four small or minute marginal warts. No ocelli. Height when fully grown 6 mm. Colour

of marginal tentacle bulbs bright violet; stomach emerald green, with an ochreish tinge in mature females; core of marginal tentacles yellow-ochre and small mass of ochreish pigment in each of two perradial marginal warts and at times on other marginal warts.

Distribution

Round the British Isles *Amphinema dinema* has been recorded from the coasts of Devon and Cornwall; the Scilly Isles; and Valencia, south-west Ireland. Elsewhere it occurs in the English Channel, the Adriatic, the American coasts of the Atlantic at Newport and the Tortugas; ? Madras (Menon, 1932); Pacific (Kramp, 1953).

Developmental Stages and Structural Details

The earliest stages of the medusa have been described by Rees & Russell (1937). On liberation from the hydroid, the medusa is about 0·7 mm. in height. The umbrella is bell-shaped, slightly higher than wide, broadest in its upper half and somewhat constricted near the margin. There is no apical process and the jelly is thickest near the umbrella margin. There are a few scattered exumbrellar nematocysts. The velum is broad. The stomach is cylindrical and about one-third the height of the subumbrellar cavity in length; the mouth is simple, without lips. The four radial canals are fairly broad and with smooth outlines. There are two opposite perradial marginal tentacles, with large basal bulbs, two small opposite perradial non-tentacular marginal swellings or warts, and traces of four interradial marginal warts. The colour of the marginal tentacle bulbs and stomach is bright orange red and the stomach has a greenish opalescence. Red pigment granules may be present in the radial canals.

When the medusa has reached a height of about 1·2 mm. the apical process appears. As development proceeds there is little change in the general form of the medusa beyond the increase in size of the apical process, the development of the mouth-lips, and the increase in number of marginal warts. In full-grown specimens these marginal warts may be as many as twenty-four in number. They are, however, exceedingly minute at times and liable to be overlooked. The two perradial marginal warts are generally the largest. The colour of the marginal tentacle bulbs changes from the orange red at the time of liberation through a reddish purple to a bright violet, and the stomach becomes at first greenish lemon in colour and eventually bright emerald green.

The gonads are in the form of eight simple plates on the adradial surfaces of the stomach. In females the eggs are usually round the periphery leaving a slit-like central region free of eggs; this tends to make the gonad appear longitudinally folded. In males the testes form continuous plates (Text-fig. 89).

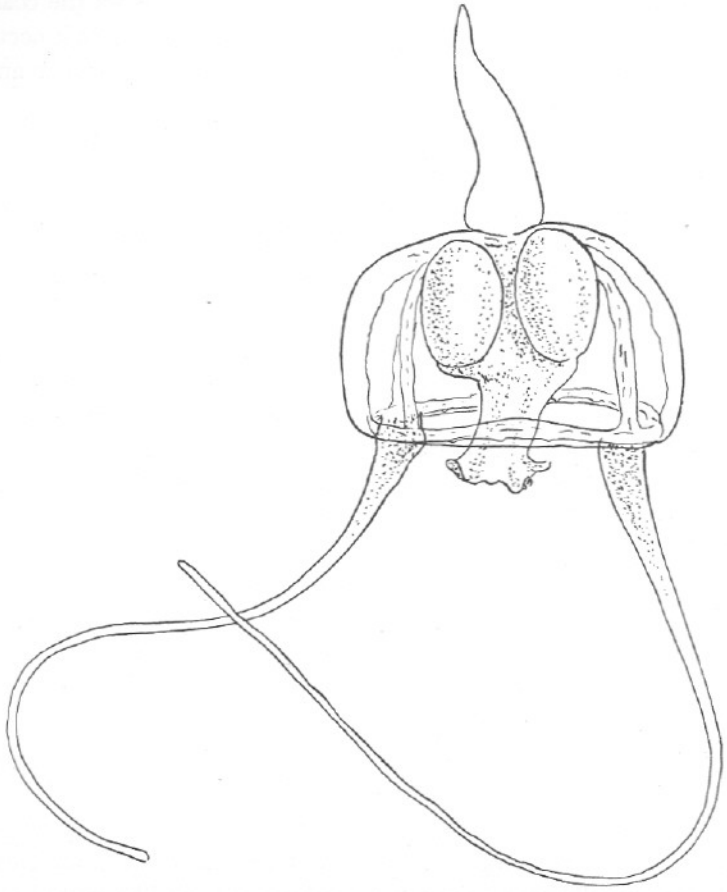
The development of the young hydroid from the egg has been followed by Rittenhouse (1910, as *Stomotoca apicata*) in America and also in the Plymouth Laboratory by Rees & Russell (1937). The eggs are opaque, spherical, 0·14–0·15 mm. in diameter. Segmentation is regular, but after the eight-cell stage the position of the blastomeres becomes very irregular. The free-swimming planula is *c.* 0·25 mm. long by 0·09 mm. broad. It fixes itself to the substratum along its whole length thus forming a hydrorhiza from the centre of which the first polyp arises. Rittenhouse attempted to cross the two species *Aphinema dinema* and *A. rugosum* without success. A colony of hydroids reared from the egg in the Plymouth Laboratory in October produced medusa buds in December (Rees & Russell, 1937).

NEMATOCYSTS. Microbasic euryteles only, in adult; desmonemes and microbasic euryteles in newly liberated medusa (Russell, 1938*b*).

PANDEIDAE

Seasonal occurrence

A. dinema appears in the plankton off the south-west coasts of the British Isles in late summer, being most abundant in September and October. Occasional specimens have been taken as late as January in the following year. It has been recorded as early as July at Valencia, south-west Ireland.



Text-fig. 89. *Amphinema dinema*. Preserved male, *c.* 3 mm. high, Plymouth, showing attitude commonly assumed.

Habits

A. dinema is a very actively swimming medusa whose marginal tentacles are capable of great extension, reaching ten times the height of the umbrella when fully stretched. The medusa has a curious habit of drawing the margin of its umbrella upwards and protruding its stomach. Lebour (1922) has shown that they will eat *Obelia*, *Calanus* and *Sagitta*, while one, 3·5 mm. across, ate an *Eutima*, *c.* 7 mm. in diameter, its two marginal tentacles being greatly extended and used for balancing while eating. The young medusa often keeps its marginal tentacles coiled in a tight spiral.

At Plymouth, medusae placed in bowls at 9.30 a.m. had shed no eggs at 5.10 p.m., but at 9 a.m. next morning eggs were present mostly in the first cleavage stage (Rees & Russell, 1937).

HYDROID. Originally named *Perigonimus serpens* Allman. (Pl. X, figs. 1, 4.)

(For description see Rees & Russell, 1937, *Journ. Mar. Biol. Assoc.* vol. XXII, p. 65, figs. 2, 4.)

Colonies of single hydranths 2–4 mm. in height arising from a creeping stolon. Perisarc surrounding base of hydranth delicate, smooth, transparent or pale horn-coloured, sometimes with membranous dilatation; with or without annulations at base of hydrocaulus. Hydranths with a single whorl of eight to fourteen filiform tentacles; not retractile. Colour of hydranth brilliant orange red. Medusae borne singly on short peduncles arising from the hydrorhiza.

Since our previous description (Rees & Russell, 1937) I have seen a colony of this hydroid in which the hydranths were fully as large as those described for *Amphinema rugosum* and in which the bases of the hydrocauli had two to four annulations (Pl. X, fig. 1). The colony liberated a young *A. dinema* medusa. It appears, therefore, that it may not be possible to distinguish the hydroids of *A. dinema* and *A. rugosum*, unless the production of medusa buds only on the stolon in the former and on both stolon and hydrocauli in the latter be a constant feature.

Historical

Amphinema dinema was first described by Péron & Lesueur in 1809 as *Oceania dinema*. It was subsequently described from the American coast by McCrady (1858) as *Saphenia apicata*. There has been confusion in the past between this species and *Amphinema rugosum* (see p. 179, n.). The medusa was first definitely linked to the hydroid *Perigonimus serpens* by Rees & Russell (1937).

Amphinema rugosum (Mayer)

Plate X, fig. 3; Plate XI, figs. 2, 4; Text-fig. 90A, B

Saphenia dinema, Forbes, 1848, *Monogr. Brit. Medusae*, p. 25, pl. ii, fig. 4.
Amphinema titania Haeckel, 1879, *System der Medusen*, p. 50, pl. iv, figs. 8, 9 (in part).
Stomotoca rugosa Mayer, 1900*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 4, pl. 2, fig. 5.
Mayer, 1900*b*, ibid. p. 32.
Mayer, 1910, *Medusae of the World*, vol. I, p. 112, pl. x, figs. 5, 6; pl. xi, figs. 1, 2.
Uchida, 1927*a*, *J. Fac. Sci. Univ. Tokyo, Zool.* vol. I, p. 202, fig. 32.
Amphinema n.sp. Browne & Vallentin, 1904, *Journ. Roy. Inst. Cornwall*, no. I, p. 124.
Amphinema dinema, Hartlaub, 1914, *Nordisches Plankton*, Lief. 17, XII, p. 259, figs. 214, 216, 217.
Amphinema rugosum, Rees & Russell, 1937, *Journ. Mar. Biol. Assoc.* vol. XXII, p. 67, figs. 5, 6 (hydroid and medusa).
Russell, 1938*a*, ibid. vol. XXII, p. 423.

Specific Characters

Gonads forming three or four folds sloping obliquely downwards towards the interradii on each of the eight adradial surfaces of the stomach. Sixteen to twenty-four small marginal tentaculae.

Description of Adult

Umbrella bell-shaped, with solid elongated-conical to hemispherical apical process; jelly moderately thick. Velum moderately broad. Stomach cross-like in section, flask-shaped, in full extension nearly reaching umbrella margin. Mouth cruciform, with four prominent, recurved, crenulated lips. Four radial canals and ring canal broad, with smooth or very slightly jagged outlines. Gonads forming three or four folds sloping obliquely downwards towards the interradii on each of the eight adradial surfaces of the stomach. Two opposite perradial marginal tentacles, very extensile, smooth, with large hollow, elongated, conical basal bulbs. Sixteen to twenty-four

small marginal tentaculae. No ocelli. Height when full grown 5–6 mm. Colour of marginal tentacle bulbs and stomach rich brownish yellow to orange, with central masses of deep purple-brown pigment; cores of the two marginal tentacles yellow ochre; marginal tentaculae colourless.

Distribution

Round the British Isles *Amphinema rugosum* has been recorded from the coasts of Devon and Cornwall; from Portland, the Scilly Isles, and Valencia, south-west Ireland. Its further distribution is North Sea, Shetland Islands and Fair Isle Channel; American coast of Atlantic at New England, Florida, Tortugas and Bahamas; Japan.

Developmental Stages and Structural Details

The earliest stage of the medusa has been described by Rees & Russell (1937). When first liberated from the hydroid the medusae are 0·42–0·65 mm. in height. The umbrella is bell-shaped, as high as wide. There is always a small apical process and usually the remains of an umbilical canal. There are scattered exumbrellar nematocysts. The velum is broad. The stomach is large and cylindrical, and about half the length of the subumbrellar cavity; it has rather a broad base. The mouth is simple. The four radial canals are fairly broad. There are two opposite perradial marginal tentacles with large basal bulbs; two small opposite perradial young marginal tentaculae, and four interradial marginal tentaculae developing, in all of which an endodermal core is present. The colour of the marginal tentacle bulbs is reddish orange, with a faint tinge of yellow along the adaxial side; the stomach is bright ochreish yellow with traces of the tentacular reddish orange pigment at its base.

There is no marked change in the general structure of the medusa during the course of its further development except that the marginal tentaculae develop in size and increase in number, and the apical process and mouth-lips become further developed. The marginal tentaculae arise from the lower edge of the umbrella margin beneath the ring canal and curl upwards round the margin in life. A specimen 2·4 mm. in height is shown in Pl. XI, fig. 2.

Examination of the numbers of the small marginal tentaculae in sixty-three specimens at Plymouth (Russell, 1938*a*) gave the following results:

Total no. of small marginal tentaculae	No. of individuals	Distribution of small tentaculae on either side of large tentacles	No. of individuals
11	1	5+ 6	1
12	2	5+ 7	1
13	6	5+ 8	1
14	14	6+ 6	1
15	10	6+ 7	5 (1 abnormal)
16	7	6+ 8	1
17	8	7+ 7	13
18	4	7+ 8	10
19	4	7+ 9	2 (1 abnormal)
20	1	8+ 8	5
21	3	8+ 9	8
22	3	8+11	1
—	—	9+ 9	4
—	—	9+10	3
—	—	9+12	1
—	—	10+10	1
—	—	10+11	2
—	—	11+11	3

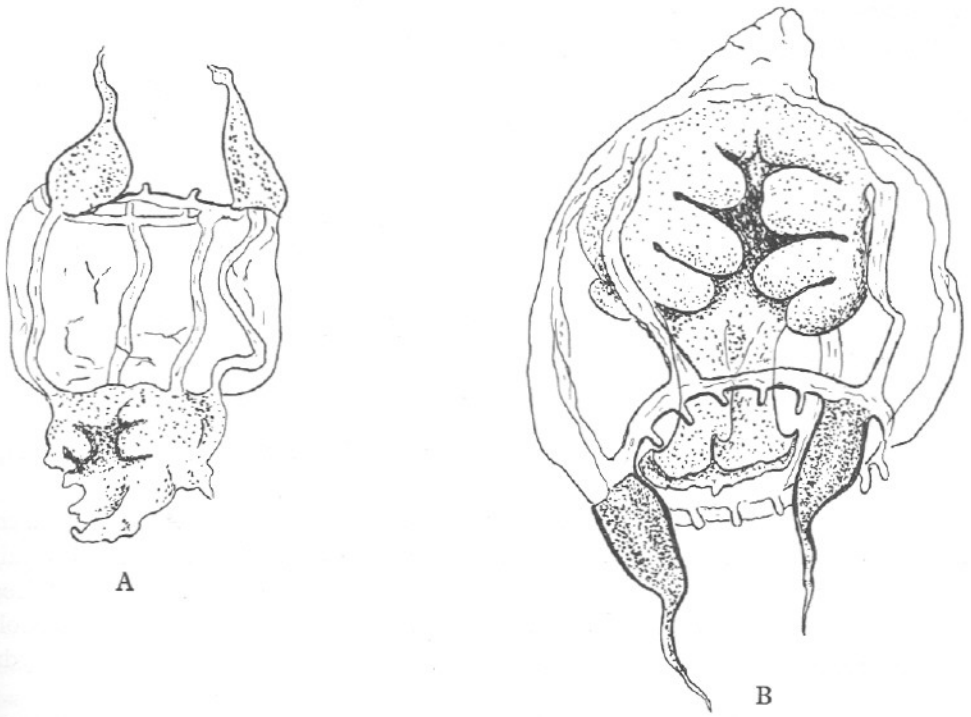
From these figures it is evident that there is considerable variation in the number of small marginal tentaculae, which have been recorded up to twenty-four in number, the most frequent

numbers here being fourteen to seventeen. The number must naturally vary with the age and size of the medusa.

An analysis of the distribution of the marginal tentaculae gives the following results:

Equal numbers on either side of two marginal tentacles	27
A difference of one on either side of two marginal tentacles	28
A difference of two on either side of two marginal tentacles	3
A difference of three on either side of two marginal tentacles	3

From these figures it appears that the normal increase in the number of marginal tentaculae is by the addition of one tentacula at a time alternately on either side of the medusa.



Text-fig. 90. *Amphinema rugosum*. Preserved specimens, Plymouth. A, young, inside out; B, adult male.

The radial canals may be connected with the stomach by a short 'mesentery' (see p. 178).

In adult specimens the gonads (Text-fig. 90B) form a continuous convoluted band which runs down the adradial surfaces of the stomach with three or four folds directed obliquely downwards towards each interradius, the gonads being continuous ventrally on the perradii and dorsally at the interradii. The eggs are opaque white. Rittenhouse (Brooks & Rittenhouse, 1907, p. 440) found that the eggs were deposited between 5.00 and 5.30 a.m. The development of the hydroid from the egg is probably very similar to that of *Amphinema dinema*.

A. rugosum appears to be rather prone to abnormality. Of the two abnormal specimens mentioned in the above table, one had the following arrangement: one marginal tentacle with single radial canal, eight marginal tentaculae with no radial canal, one marginal tentacle with radial canal which bifurcated near its origin from the stomach with the two branches rejoining at the

marginal tentacle bulb, one marginal tentacula, one half-size marginal tentacle with a radial canal, eight marginal tentaculae with the normal radial canal among them. In the other, one of the tentacular radial canals had bifurcated giving rise to a fully developed marginal tentacle at the end of each branch; its arrangement was one tentacle, two tentaculae, one tentacle, five tentaculae, one tentacle, seven tentaculae. I have seen other abnormal specimens: one in which there was only one marginal tentacle, the place of the missing tentacle being taken by a marginal tentacula; and two in which there were three marginal tentacles, in one of which the additional marginal tentacle was adradially situated and not opposite a radial canal.

NEMATOCYSTS. Microbasic euryteles (Russell, 1938*b*).

Seasonal occurrence

Amphinema rugosum occurs in the plankton at Plymouth usually in the spring and summer months, April to July, it has occasionally been seen as late as October. It has been seen in May at the Scilly Isles and Valencia; in June in the Shetlands and North Sea.

Habits

The marginal tentacles in this medusa are very extensile and when fully extended may reach ten times the height of the bell. When contracted they are carried coiled in a close spiral.

In the daytime the medusa lives generally in the deeper water layers below 20 m., but may migrate right to the surface at night (see Russell, 1925, 1927, 1928—recorded as *Stomotoca* or *Amphinema dinema*).

Apparently *A. rugosum* is an indicator of *Sagitta elegans* water (Russell, 1938*a*).

HYDROID. (For description see Rees & Russell, 1937, *Journ. Mar. Biol. Assoc.* vol. XXII, p. 67, fig. 5.)

Colonies of single, or slightly branched, hydranths 2–4 mm. in height arising from a creeping stolon. Perisarc surrounding base of hydranth firm, smooth, and horn-coloured, ending abruptly at its upper end without distinct dilatation; with two to five annulations at base of hydrocaulus. Hydranth with single whorl of eight to twelve filiform tentacles; not retractile. Colour of hydranths bright orange red. Medusae borne singly on short peduncles arising from hydrorhiza or hydrocaulus.

As stated on p. 183 it may not be possible to distinguish this hydroid from that of *Amphinema dinema* until medusa buds are produced or medusae liberated.

Historical

Amphinema rugosum was first described under its own specific name as *Stomotoca rugosa* by Mayer (1900*a*) from the American side of the Atlantic. Subsequent research has shown that a number of workers had in the past confused this species with *Amphinema dinema* (Pèron & Lesueur) and its American synonym *A. apicata* (McCrady). *A. rugosum* was well described and figured by Hartlaub (1914) as *A. dinema*; he suggested, however, that further research might show that there were two European species one of which would prove to be Mayer's *A. rugosum*. *A. titania* of Haeckel (1879) belongs partly to this species and partly to *A. dinema*; his description in so far as it applies to *A. rugosum* differs in having pigment spots on the marginal tentaculae.

The medusa was first linked to its hydroid by Rees & Russell (1937).

Subfamily PANDEINAE

Pandeid medusae with umbrella with or without round or pointed apical process; with or without exumbrellar nematocyst tracks; with mouth with much folded or crenulated lips; with four unbranched radial canals; with simple or folded gonads situated adradially or interradially on stomach wall; with two to eight or more marginal tentacles with tapering conical basal bulbs; with rudimentary marginal tentacles, and with or without marginal tentaculae; with or without ocelli.

The Pandeinae are represented in British waters by four genera, *Leuckartiara* Hartlaub, *Annatiara* Russell, *Neoturris* Hartlaub, and *Pandea* Lesson. The generic distinctions are based on the form of the gonads. The two first genera have no isolated pits in the interradial region, but only the gonadial folds; the third genus has folds and isolated pits; and the fourth has only isolated pits.

Gonads without isolated interradial pits:
- Horizontal folds directed towards perradii . . . . . **Leuckartiara**
- With irregular folds . . . . . **Annatiara**

Gonads with isolated interradial pits:
- Horizontal folds directed towards interradii . . . . . **Neoturris**
- Without folds . . . . . **Pandea**

Genus **Leuckartiara** Hartlaub, 1914

MEDUSAE. Pandeinae with umbrella with apical process varying much in shape and size; without exumbrellar nematocyst tracks; with large stomach not extending beyond umbrella margin, with perradial lines of attachment to subumbrella extending some way down sides; without peduncle; with mouth with four much folded or crenulated lips; with four broad and ribbon-like radial canals, often with jagged margins; with gonads covering interradial surfaces of stomach, horseshoe-shaped, with folds directed perradially; with numerous marginal tentacles with elongated laterally compressed conical bases often with well-developed exumbrellar spurs; often with rudimentary marginal tentacles; without marginal warts or marginal tentaculae; with or without abaxial ocelli.

HYDROID. *Leuckartiara.*

The structure of the gonad in *Leuckartiara* is characteristic. Typically it has the form of two vertical adradial folds from which a number of horizontal folds are directed perradially; the two vertical folds are connected by a single horizontal interradial fold. The whole gonad is thus somewhat horseshoe-shaped.

There are three species of *Leuckartiara* in British waters, *L. octona* (Fleming), *L. breviconis* (Murbach & Shearer), and *L. nobilis* Hartlaub. Of these *L. octona* is the most widespread round the British coasts, the other two being deeper water species.

The distinguishing characters of the adult medusae are:

Marginal tentacles:
- Sixteen to twenty-three; base with abaxial exumbrellar spur **L. octona**
- Forty or more; base with abaxial exumbrellar spur . . **L. nobilis**
- Up to 140; base without abaxial exumbrellar spur . **L. breviconis**

Another good character to look for in identifying the three species is the relative number of small and rudimentary marginal tentacles. In *L. octona* there are always one to three small

rudimentary marginal tentacles between every two well-developed marginal tentacles; in *L. nobilis* these are only few and irregularly scattered, and the number of smaller marginal tentacles usually exceeds that of the fully grown marginal tentacles; in *L. breviconis* the rudiments are even fewer in relation to the number of marginal tentacles which are very numerous.

Some difficulty may be experienced in identifying young stages.

The hydroid of *L. octona* has been well known under the name of *Perigonimus repens*; the hydroids of *Leuckartiara nobilis* and *L. breviconis* are not known. It should here be noted that the hydroid *L. abyssi* (M. Sars) (Text-fig. 98) may possibly belong to one of these species of medusae, or to *Neoturris pileata*. (See Rees, 1938.)

Leuckartiara octona (Fleming)

Plate XI, figs. 5, 6; Plate XII, fig. 3; Plate XXXI; Text-figs. 91, 92, 93 A, B, 94, 95, 96

Geryonia octona Fleming, 1823, *Edinb. Phil. Journ.* vol. VIII, p. 299.
Fleming, 1828, *British Animals*, p. 501.
Oceania pileata Ehrenberg, 1837, *Abh. K. Akad. Wiss. Berlin* (1835), pl. viii, figs. ii–iv.
Oceania octona, Forbes, 1848, *Monogr. British Medusae*, p. 27, pl. ii, fig. 3.
Oceania episcopalis Forbes, 1848, ibid. p. 27, pl. ii, fig. 1.
Oceania turrita Forbes, 1848, ibid. p. 28, pl. ii, fig. 2.
Eudendrium pusillum Wright, 1857, *Edinb. New Philos. Journ.* N.S. vol. VI, pl. ii, figs. 8, 9 (hydroid and medusa).
Eudendrium sessile Wright, 1857, ibid. p. 90, pl. iii, figs. 16, 17 (hydroid and medusa).
Atractylis repens Wright, 1859*b*, ibid. vol. IX, p. 108, pl. i, figs. 4, 5 (hydroid and medusa).
Atractylis sessilis, Wright, 1859*b*, ibid. vol. IX, p. 109.
Tiara octona, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 347.
Haeckel, 1879, *System der Medusen*, p. 57.
Tiara smaragdina Haeckel, 1864, *Z. Naturw. Jena*, Bd. I, p. 336.
Dinema slabberi Van Beneden, 1866, *Mém. Acad. R. Belg.* vol. XXXVI, p. 150, pl. ix, x (hydroid and medusa).
Haeckel, 1879, *System der Medusen*, p. 28.
?*Oceania gaedii* Van Beneden, 1866, *Mém. Acad. R. Belg.* vol. XXXVI, p. 95.
Perigonimus repens, Hincks, 1868, *Brit. Hydroid Zooph.* p. 90, pl. xvi, fig. 2 (hydroid and medusa).
Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 462.
Hartlaub, 1895, *Z. Wiss. Zool. Leipzig*, Bd. LXI, p. 157, pl. viii, figs. 5–7, 9–18 (hydroid and medusa).
Perigonimus sessilis, Hincks, 1868, *Brit. Hydroid Zooph.* p. 93, pl. xvii, fig. 1 (hydroid and medusa buds.)
Oceania coronata Allman, 1871, *Monogr. Gymnobl. Hydroids*, p. 33, fig. 8.
Oceania smaragdina, Spagnolini, 1871, *Atti Soc. ital. Sci. Nat.* vol. XIV, fasc. 3.
Tiara pileata, Haeckel, 1879, *System der Medusen*, p. 58 (in part), pl. iii, fig. 8.
Hartlaub, 1895, *Z. Wiss. Zool. Leipzig*, Bd. LXI, p. 157, pl. viii, figs. 5–7, 9–18 (hydroid and medusa).
Browne, 1895, *Trans. Liverpool Biol. Soc.* p. 258.
Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. V, p. 712, and tables (in part).
Browne, 1903, *Bergens Mus. Aarb.* no. 4, p. 11 (in part).
Turris episcopalis, Fewkes, 1881*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. VIII, p. 146, pl. iii, figs. 1–6.
?*Perigonimus jonesii* Nutting, 1901, *Bull. U.S. Fish. Commiss. Washington*, vol. XIX (1899), p. 372, fig. 80.
Tiara papua Maas, 1905, *Craspedoten Medusen, Siboga-Expedit.* Monogr. 10, p. 14.
Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 207, pl. xlii, figs. 1–4.
Turris vesicaria Mayer, 1910, *Medusae of the World*, p. 126, pl. xii, figs. 2, 3; pl. xiii, fig. 7.
Non Agassiz, 1865, *N. Amer. Aceleph.* p. 164, figs. 261–8.
Leuckartiara octona, Hartlaub, 1914, *Nordisches Plankton*, Lief. 17, XII, p. 285, figs. 238–52.
Bigelow, 1919, *Bull. U.S. Nat. Mus.* 100, vol. I, p. 282, pl. xxxix, figs. 5, 6.
Foerster, 1923, *Contr. Canad. Biol.* N.S., vol. I, p. 240, pl. i, figs. 4, 5.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. V, pt. x, p. 76, text-fig. 35, chart XIV; pl. ii, figs. 5–7.
Kramp, 1927, *K. danske vidensk. Selsk. Skr.* natur. og math. Afd., 8. Raekke, XII, p. 95, chart 12.
Rees, 1938, *Journ. Mar. Biol. Assoc.* vol. XXIII, no. 1, p. 12, text-figs. 3–5 (hydroid).

Specific Characters

Sixteen to twenty-three marginal tentacles, with always one to three club-shaped rudimentary marginal bulbs between adjacent marginal tentacles. Marginal tentacle bulbs with pronounced abaxial spur. Ocelli present.

Description of Adult

Umbrella bell-shaped, higher than wide, with conical or spherical, solid, apical process varying much in size; jelly thin. Velum narrow. Stomach flask-shaped, not extending beyond umbrella margin in full extension, with broad base. Mouth with four much crenulated lips. Four radial canals broad, with smooth or jagged outlines; ring canal broad, with smooth outlines. Radial canals joined to stomach by 'mesenteries'. Gonads situated interradially on folds of the stomach wall, horseshoe-shaped, with several folds directed outwards to each perradius. Sixteen to twenty-three marginal tentacles, hollow, smooth, with large, laterally compressed, elongated conical basal bulbs, clasping umbrella margin and forming pronounced abaxial spurs on exumbrellar surface. One to three club-shaped rudimentary marginal bulbs between adjacent marginal tentacles. One abaxial ocellus on each tentacular and rudimentary marginal bulb. Height when full grown 15 mm. or more. Colour of marginal tentacles and stomach a deep flesh-pink to crimson or yellowish brown; ocelli crimson.

Distribution

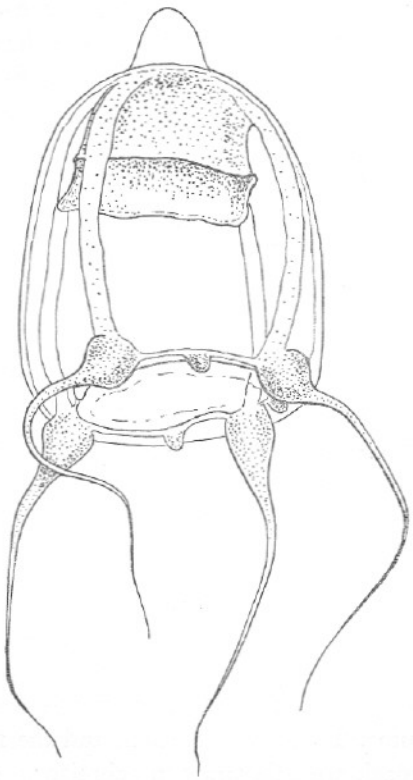
Leuckartiara octona is very common in British waters and is widely distributed on the north-western European coasts. Coasts of British Isles; west coast of Norway to Lofoten; Skagerak; Kattegat; south Iceland; Rockall; Mediterranean; east coast of North America from Newport to Labrador; Vancouver; Japan; ? Madras (Menon, 1932). A southern boreal species, which owing to its long span of life may be carried far off shore.

Developmental Stages and Structural Details

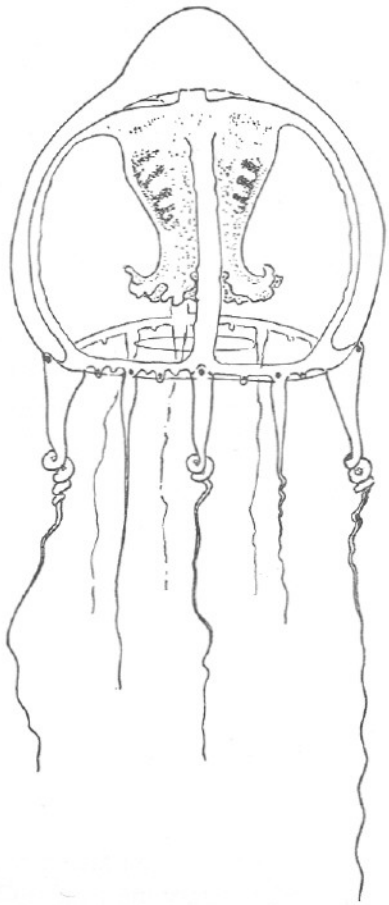
Growth. When first liberated from its hydroid the medusa is about 1·1 mm. in height. There may or may not be a slight apical process, and there are scattered nematocysts on the exumbrellar surface. The stomach is cylindrical and about one-third the height of subumbrellar cavity in length, the mouth is simple, without lips. There are two opposite perradial marginal tentacles and two opposite perradial rudimentary marginal bulbs. There are no ocelli, and the marginal tentacle bulbs, rudimentary marginal bulbs and stomach are pale straw to ochreish in colour.

The two perradial marginal bulbs then develop tentacles so that a four-tentacled stage is produced (Text-fig. 91). As this stage is developing two opposite interradial marginal bulbs appear, to be quickly followed by a further two interradial marginal bulbs. The mouth now has four distinct lips upturned at their corners and the radial canals are broadening and sometimes show signs of jagged outgrowths. There are now ocelli on the four marginal tentacle bulbs and on the four interradial marginal bulbs. According to Hartlaub the first ocelli appear after five days on the second pair of perradial marginal bulbs. The medusa is now about 2 mm. high. When the medusa is about 3·5 mm. high tentacles are beginning to develop on the interradial marginal bulbs and the rudiments of eight adradial marginal bulbs appear. In this way an eight-tentacled, or *octona*, stage is produced (Text-fig. 92). The mouth-lips are now considerably crenulated and the folds with developing gonads are beginning to form on the adradial surfaces of the stomach. All the tentacular marginal bulbs and the adradial marginal bulbs have abaxial ocelli. The medusa is now about 4 mm. in height.

Up to this eight-tentacled stage the sequence of development of the marginal tentacles usually proceeds in a fairly regular manner, though some marginal bulbs may lag slightly behind others in their rate of growth. From this stage onwards there is a tendency for the order of development of marginal tentacles to become more irregular, although typically the development of marginal tentacles on the adradial bulbs, each with new rudiments developing on its sides, will produce



Text-fig. 91. *Leuckartiara octona.* Preserved specimen 1·7 mm. high, Plymouth, 9. xi. 37.



Text-fig. 92. *Leuckartiara octona.* Young specimen 4 mm. high reared from the hydroid at Plymouth by W. J. Rees, 6. iii. 36.

a sixteen-tentacled stage. At this stage there may be one to three rudimentary marginal bulbs between adjacent marginal tentacles, each capable of producing a tentacle itself though rarely doing so. Old individuals with twenty marginal tentacles are frequently seen and specimens with as many as twenty-three occasionally; Hartlaub records up to twenty-eight marginal tentacles, though Kramp states that he has never seen individuals with more than twenty-three himself. Inequality in the rate of development may give rise to specimens with eleven, twelve, fourteen, or eighteen fully developed marginal tentacles. The sequence of marginal tentacle development has been fully described by Hartlaub (1914) and Kramp (1926*a*). Kramp has shown that the later development may apparently proceed in two ways, which he has termed the 'octagonal'

and 'duodecimal' methods respectively (Pl. XXXI). The octagonal development is that described above whereby a regular addition of marginal tentacles leads to four, eight and sixteen successively. The duodecimal development may proceed in one of two ways. Either there may be a retardation of the growth of one of the adradial marginal tentacles in each quadrant after the eight-tentacled stage, or after the four-tentacled stage two adradial marginal tentacles may develop in each quadrant instead of one interradial. Actually neither method can be said to be rigidly followed because of the various irregularities produced by retardation in the growth of some marginal tentacles, though perhaps the octagonal method may be regarded as the more typical. Also specimens may be found in which apparently octagonal development has proceeded in some quadrants and duodecimal development in the others.

Adult Characters

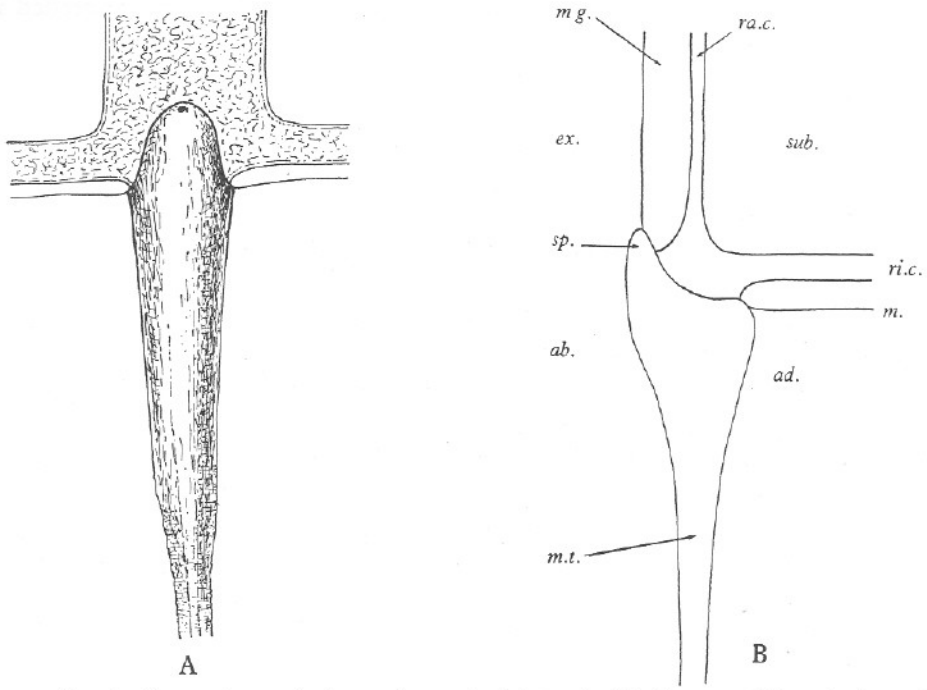
The solid apical process is very variable in shape and size. It is generally conspicuous and shorter than the height of the umbrella cavity. It may, however, be very slightly developed, and varies in shape from conical to hemispherical or even somewhat cylindrical. Sometimes its lower boundary is distinctly demarcated from the bell itself, while at other times its outlines merge into those of the bell without any distinction.

The margins of the mouth are very much crenulated, so much so that at times the distinction of four lips becomes impossible. The length of the mouth-lips also varies considerably, at times forming a definite elongation below the gonad region of the stomach and at others being so short as to appear as a mere fringe below the gonads.

The radial canals vary in width and have their margins thickened to give the appearance of a hemmed ribbon. The margins may be quite smooth or they may be jagged. At times these dentations of the radial canal outlines are wide and form small embayments stretching out into the surface of the bell. The ring canal generally has smooth outlines though a certain amount of jaggedness is apparent at times. The radial canals communicate with the stomach cavity by long slit-like openings. Along these openings the walls of the canals are connected both with the stomach wall and with the umbrella. These connexions are known as 'mesenteries' and they divide the upper portion of the subumbrellar cavity into four compartments. The mesenteries vary considerably in length and in some individuals are so short as to be hardly apparent.

The gonads (Pl. XXX, figs. 1–6) develop on the interradial regions of the stomach wall. Each has the appearance of a horseshoe whose arms are directed downwards on the adradii, and whose central portion connects these two arms high up on the stomach in the interradius. The horseshoe gives out six to ten projections on each outer side mostly directed horizontally towards the perradii, and a few near the upper end directed outwards and upwards. Some of these projections bifurcate. The shape and appearance of the gonads is produced by folding and pocketing of the walls of the stomach. There is a depressed interradial fold, the embayment of the horseshoe, and on either side of this central fold are a series of deep pouch-shaped depressions, between some of which are smaller depressions. The gonads develop on the non-depressed areas between each pocket, all over the surfaces of the pockets themselves and on either side of the central fold. They thus come to form a continuous horseshoe round the central fold and it is the raised portions of the gonad between the folds and pockets which give it its characteristic outline. The general outlines of the gonads vary considerably according to the irregularities of the foldings, and may be quite different in each quadrant.

The marginal tentacles, which coil spirally, are capable of great elongation. The base of the marginal tentacle is continued gradually into an elongated hollow bulb (Text-figs. 93, 94). This bulb is flattened laterally and very wide radially, being somewhat concave on its outer side so that it bends outwards. The base of the marginal tentacle bulb clasps the margin of the umbrella, being continued upwards over the exumbrellar surface as a large apical spur, on the abaxial point of which is the ocellus. The marginal tentacle itself is smooth but has a slight keel on its inner side and its nematocysts are arranged in the form of narrow clasps (see Kramp, 1926*a*). The presence of rudimentary marginal tentacle bulbs is a characteristic feature of this species;



Text-fig. 93. *Leuckartiara octona*. A, base of marginal tentacle; B, diagram of lateral view of marginal tentacle base to show abaxial spur. *ab.*, abaxial; *ad.*, adaxial; *ex.*, exumbrella; *m.*, umbrella margin; *mg.*, mesoglœa; *m.t.*, marginal tentacle; *ra.c.*, radial canal; *ri.c.*, ring canal; *sp.*, spur; *sub.*, subumbrella.

Kramp points out that these marginal bulbs are not rudimentary in the sense of being reduced tentacles, but that each would presumably be capable of developing into a marginal tentacle in time if the medusa were to live long enough. These small rudimentary marginal bulbs tend to be club-shaped. In young stages these rudimentary marginal bulbs develop fairly quickly after the neighbouring marginal tentacle is formed. As the medusa gets older, however, there is a general retardation in the growth of the rudimentary marginal bulbs, so that, while in young specimens only one rudimentary marginal bulb is found between adjacent marginal tentacles, in old specimens there are very commonly three, the centre one of which has not yet started to develop a tentacle. Kramp (1926*a*) points out that in this respect *Leuckartiara octona* differs somewhat from *L. breviconis* and *L. nobilis* in which the development of marginal tentacles proceeds more rapidly.

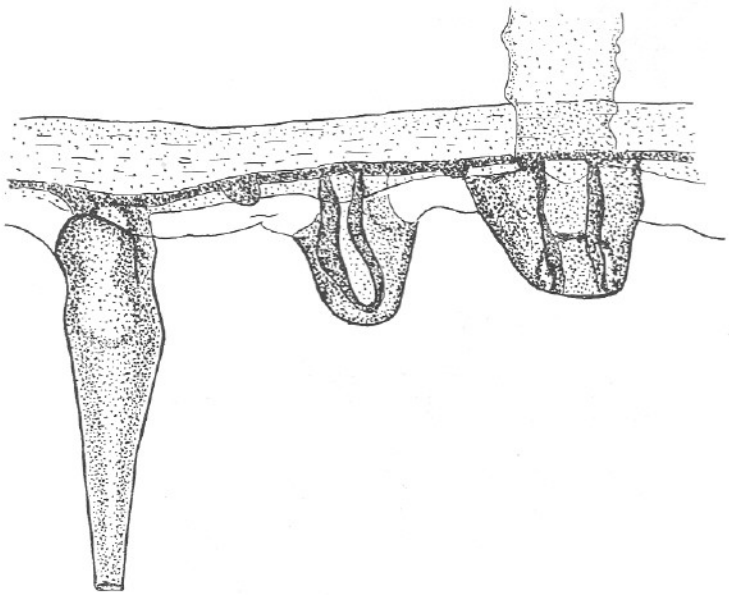
I have seen specimens in which the ocelli were broken up into horizontal rows of spots.

The full-grown medusa reaches a total height of a little over 15 mm. Specimens 10 mm. in height generally have fourteen to sixteen fully developed marginal tentacles. Hartlaub (1917)

however records two specimens, taken in the North Sea in February, 10 mm. in height with well-developed gonads, one of which had only four perradial marginal tentacles with three rudimentary marginal bulbs in each quadrant, while the other had six marginal tentacles only. These were no doubt medusae liberated unusually late in the season in which the cold conditions had retarded marginal tentacle development. Kramp (1930) states that in the Dover Straits and southern North Sea region these medusae do not surpass 10 mm. in diameter.

Hamman (1883) studied the development of the eggs at Helgoland and reared them to the planula stage. The eggs have no membrane and division is regular.

NEMATOCYSTS. Microbasic euryteles and microbasic mastigophores (Russell, 1938*b*).



Text-fig. 94. *Leuckartiara octona*. Showing the appearance of broken marginal tentacles in preserved specimens.

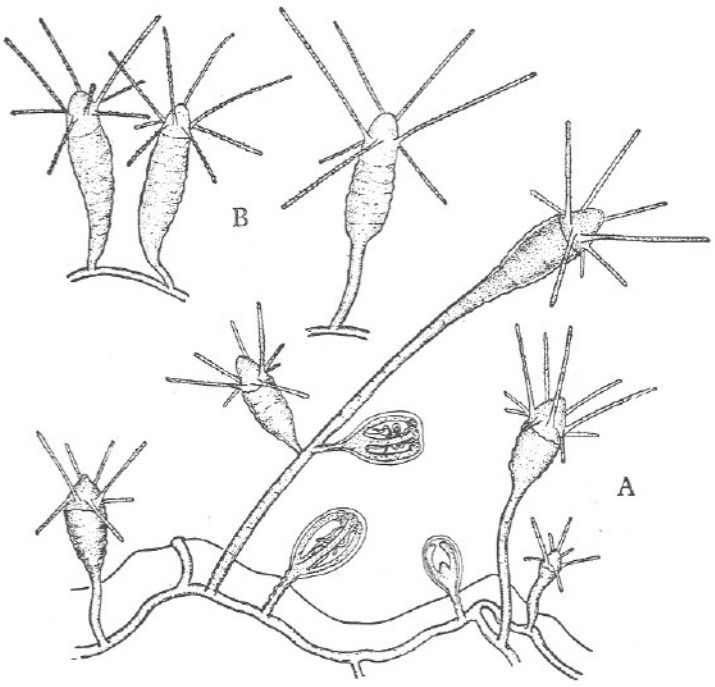
Seasonal occurrence

Leuckartiara octona occurs chiefly in the plankton during the months April to October. It is usually common and, as such, stray specimens may be met with in almost any month of the year. Kramp (1930) says that liberation of medusae from the hydroid seems normally to cease in August, though occasionally it may be continued somewhat later. In the north it seems to be most numerous towards the end of the summer. Robson (1914*a*) records the hydroid as liberating medusae from September to February on the Northumberland coast.

Habits

Leuckartiara octona is a very active medusa. If kept in an aquarium it shows intermittent periods of activity and quiescence. When the medusa is actively swimming its marginal tentacles are coiled into short tight spirals. When quiescent it sinks down through the water with marginal tentacles greatly elongated, in a fishing position. The feeding habits have been described by Lebour (1922, 1923). The medusae are highly voracious, eating almost anything given them, such as copepods, decapod larvae, *Podon*, *Poecilochaetus* larvae, young whiting, *Cottus* and *Callionymus*. One ate a young squid taking several days to digest it. Mayer (1910) records that they will feed on the siphonophore *Nanomia cara*.

The newly liberated medusae evince the same habits, swimming actively with the two marginal tentacles spirally coiled, and then resting and sinking, upper surface downwards, with the marginal tentacles streaming out many times the length of the umbrella. In the words of Strethill Wright: 'A jar of these lively creatures, some swimming rapidly like small frogs, with their half-coiled tentacles jerking backwards at each stroke, others descending headlong in flocks like the falling train of a rocket, and all glittering under oblique illumination in the dark water, forms one of not the least interesting of those scenes of beauty which are of daily occurrence to the naturalist.'



Text-fig. 95. *Leuckartiara octona*. A, hydroid colony growing on a *Turritella* shell inhabited by a hermit crab; B, transitional polyps of same. Plymouth, 16. iii. 36. (After Rees, 1938, fig. 4.)

These medusae are among the easiest to rear through the early stages after liberation from the hydroid, being unusually hardy and willingly taking food.

In the daytime the medusae generally live rather deep in the off-shore waters, with a tendency for the younger individuals to be nearer the surface. In the English Channel Russell (1927) has shown that their region of maximum abundance lies between 10 and 25 m. in the daytime from April to June, being somewhat higher in July. Being active swimmers they can undertake considerable vertical migrations and reach the surface in large numbers at dusk; they appear at times to show a secondary migration towards the surface at dawn (Russell, 1925, 1927, 1928, 1931).

Browne (1895) records these medusae as having been left by the tide on the sandy beach at Port Erin, Isle of Man.

Hartlaub (1914) states that they give a green phosphorescent light, which is limited to the gonads.

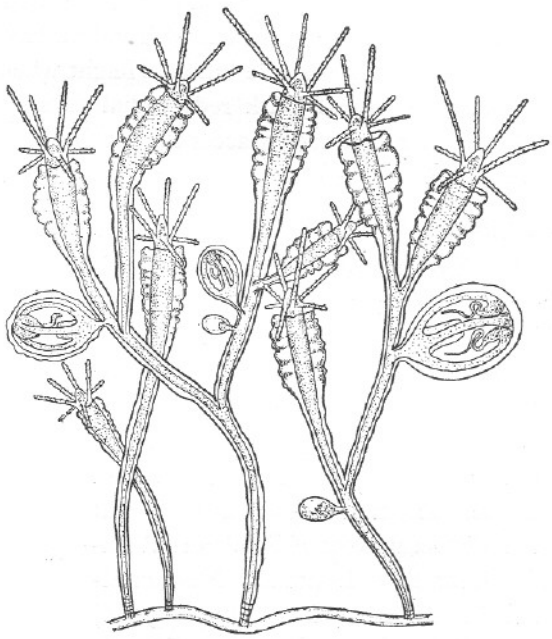
Leuckartiara octona is commonly parasitized by the metacercaria of the trematode *Pharyngora bacillaris* (Lebour, 1916*b*), and the larval stages of the pycnogon *Anaphia petiolata* may be found clinging to it (Lebour, 1916*a*).

HYDROID. *Leuckartiara octona* (= *Perigonimus repens* and *P. sessilis* of Wright). (Text-figs. 95, 96.)

(For full description see Rees, 1938, *Journ. Mar. Biol. Assoc.* vol. XXIII, p. 12, figs. 3–5.)

Colonies of single or slightly branched hydranths, 0·5–5·0 mm. in height arising from a creeping stolon. Perisarc surrounding base of hydranth, smooth or slightly corrugated, transparent or horn-coloured with a distinct membranous cup-shaped dilatation reaching to the base of the tentacles. Hydranths with a single whorl of six to twelve tentacles, white, partially retractile. Medusae borne on short peduncles arising from the hydrorhiza or the hydrocaulus.

The hydranths may be sessile or have long hydrocauli. Colonies are found in association with many species of crustacea and mollusca, and at times on other animals such as the polychaete *Aphrodite*, and the fish, *Agonus cataphractus*.



Text-fig. 96. *Leuckartiara octona*. Well-developed hydroid colony on *Corystes cassivelaunus*, Plymouth, 29. vi. 37. (After Rees, 1938, fig. 5.)

Historical

The first description of *Leuckartiara octona* was given by Fleming in 1823 as *Geryonia octona*. Since that date confusion has grown and a number of Tiarid species such as *Neoturris pileata*, and *Leuckartiara nobilis* have been mixed up with it. It remained for Hartlaub (1914) to straighten matters out and he has shown to the satisfaction of all what are the true species. He raised a new genus *Leuckartiara* to include those species with 'mesenteries' and horseshoe-shaped gonads.

Leuckartiara nobilis Hartlaub

Plate XII, fig. 4; Text-fig. 97

Tiara pileata var. *coccinea* Haeckel, 1879, *System der Medusen*, p. 58, pl. iii, fig. 6.
Tiara pileata, Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. v, p. 712, and tables (in part).
Leuckartiara nobilis Hartlaub, 1914, *Nordisches Plankton*, Lief. 17, XII, p. 308, figs. 257–60.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. v, pt. x, p. 83, text-fig. 36, chart XVI; pl. ii, fig. 9.

Specific Characters

Up to forty or more marginal tentacles, with only a few scattered rudimentary marginal bulbs. Marginal tentacular bulbs without well-developed abaxial spur. Ocelli present.

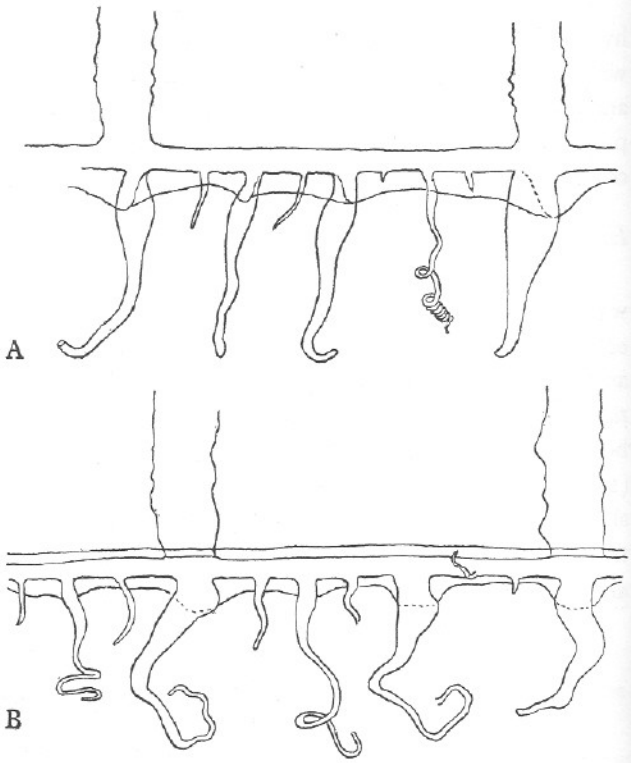
Description of Adult

Umbrella bell-shaped, higher than wide, with pointed or rounded solid apical process; jelly thin. Velum narrow. Stomach flask-shaped, constricted near mouth, not extending beyond umbrella margin in full extension, with broad base. Mouth with much crenulated lips. Four

radial canals very broad, with irregular and jagged outlines. Ring canal broad with smooth outlines. Radial canals joined to stomach by 'mesenteries'. Gonads interradial on folds of the stomach, horseshoe-shaped, with many folds directed outwards to each perradius. Up to forty or more marginal tentacles, hollow, smooth, with elongated, conical, laterally compressed basal bulbs which clasp the umbrella margin but do not form well-developed abaxial spurs. Marginal tentacles fairly widely spaced, with only a few scattered rudimentary marginal bulbs. Abaxial ocelli on marginal tentacle bulbs. Height when full grown 20–27 mm. Colour (after Haeckel): stomach, i.e. gonad, dark red; radial canals, ring canal and marginal tentacle bases bright yellow (the radial canals according to Hartlaub, by communication from Frl. Krasińska, are colourless).

Distribution

Leuckartiara nobilis has so far only been recorded in British waters from Valencia, south-west Ireland. It is likely, however, that it will be found on the western Irish, and western and northern Scottish coasts, where bathed by Atlantic oceanic water. Elsewhere this medusa has been recorded from south of Iceland; Atlantic Ocean west of Scotland; Rockall; Great Belt, Denmark; Newfoundland;* Mediterranean. Kramp (1926*a*) stated that in the northern Atlantic area, as far as was then known, the medusa is confined to regions of the Gulf Stream and Irminger Current. It is certainly an oceanic species and as such not likely to be found in the English Channel or southern North Sea. Kramp (1947) suggests that the medusa has a long life and can therefore drift far off shore.



Text-fig. 97. *Leuckartiara nobilis*. Portions of umbrella margin of two specimens from Monaco. A, from exumbrellar side; B, from subumbrellar side. (After Hartlaub, 1914, fig. 260.)

Developmental Stages and Structural Details

The first developmental stages of *Leuckartiara nobilis* have not yet been described. The smallest appears to be that recorded by Hartlaub (1914) which was 13 mm. in height, of which 7 mm. consisted of apical process. This had four well-developed perradial marginal tentacles; four considerably smaller interradial marginal tentacles, and eight still smaller adradial ones. Between these was a knob-shaped marginal tentacle rudiment. The mouth was much crenulated, and the radial canals very broad. The gonads were not fully developed, appearing only as a horseshoe with a deep central fold with the cross-foldings little pronounced.

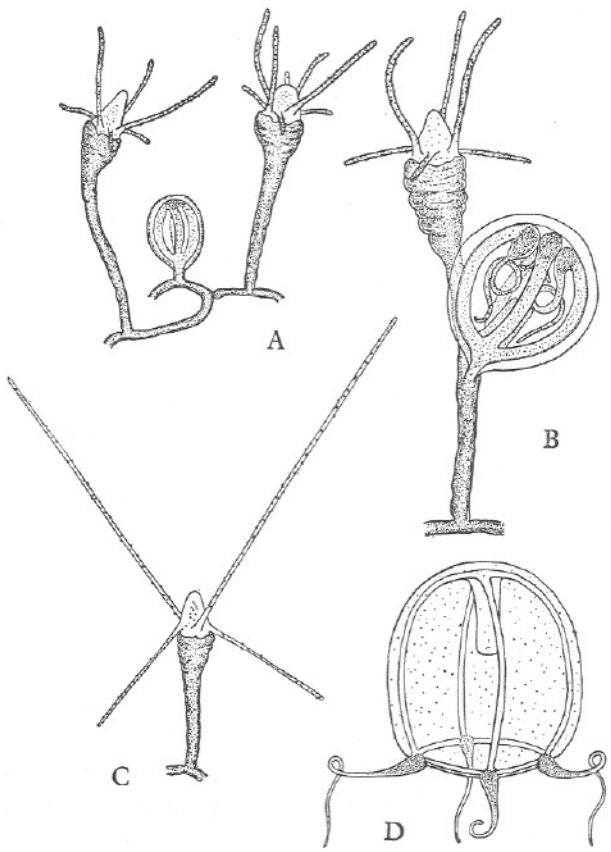
* Specimen sent to me by Miss Nancy Frost.

The marginal tentacle arrangement (Text-fig. 97) in a number of individuals of different sizes has been described and figured by Kramp (1926*a*). His data can be summarized as follows:

Height (mm.)	Diameter (mm.)	Marginal tentacles
Over 8	9	4 perrad. fully developed; 4 interrad. smaller; 17 small of different sizes; 11 rudiments
12	10	4 perrad.; 5 interrad.; 15 small of different sizes, 11 rudiments
c. 16	11	40 tentacles
19	15	16 fully developed alternating with 16 smaller
27	20	16 fully developed alternating with 16 smaller, 4 small tentacles and no rudiments (Had evidently attained maximal number of tentacles = 4+4+8+4+12+4=36)
?	20	12 fully developed, 22 smaller, and 8 rudiments = 42

The mode of development is sometimes octagonal and sometimes duodecimal, and either method may occur in different quadrants of the same specimen. Even in the largest individuals the number of fully developed marginal tentacles did not exceed twelve or sixteen, the remaining marginal tentacles being much smaller. Thus it is a characteristic of the species that in full-grown specimens the number of small marginal tentacles almost always exceeds those of the fully developed ones. In this respect *L. nobilis* differs from *L. breviconis*, while the absence of the regularly distributed one or three club-shaped marginal rudiments differentiates it at once from *L. octona*.

The longitudinal musculature of the marginal tentacles is very apparent and Hartlaub states that in stained material numerous closely lying nematocyst clasps can be seen crossing the longitudinal musculature at right angles. On the ad-axial side of the marginal tentacle there is a row of pit-shaped depressions, in the neighbourhood of which the nematocyst clasps are thickened. This row begins some distance from the basal bulb. The nematocyst clasps are relatively narrower than those of *L. octona*.



Text-fig. 98. *Leuckartiara abyssi*. A hydroid whose medusa is not known. A, portion of a colony with a gonophore developing from the stolon, Herdla, Norway, 6. viii. 37; B, polyp with a fully developed gonophore on the hydrocaulus, Herdla, 9. viii. 37; C, young polyp with its tentacles fully expanded, Herdla, 6. ix. 37; D, newly liberated medusa. (After Rees, 1938, fig. 6.)

The gonads agree in their essential structure and horseshoe-shape with those of *L. octona*. They differ from the latter, however, in that the folds are considerably more numerous, and more divided. The central deep fold may also have one or two pit-shaped depressions.

Seasonal occurrence

Little is known of the seasonal occurrence of *Leuckartiara nobilis*. The only records round British coasts are Valencia, May; and west of Scotland, May (Kramp, 1926*a*); it has been recorded from south of Iceland and near Rockall in July.

HYDROID. Not known. (See Text-fig. 98.)

Historical

Leuckartiara nobilis was first described in detail as a distinct species by Hartlaub in 1914. Previously this species had been confused in the synonymy of *Leuckartiara* and *Neoturris*, the only certain reference to the species being by Haeckel (1879) as *Tiara pileata* var. *coccinea*.

Leuckartiara breviconis (Murbach & Shearer)

Plate XII, fig. 2; Text-figs. 99, 100

Turris breviconis Murbach & Shearer, 1902, *Ann. Mag. Nat. Hist.* ser. 7, vol. IX, p. 73.
Murbach & Shearer, 1903, *Proc. Zool. Soc. London*, II (7), p. 170, pl. xviii, figs. 1, 2.
Mayer, 1910, *Medusae of the World*, vol. I, p. 127.
Leuckartiara brevicornis, Hartlaub, 1914, *Nordisches Plankton*, Lief. 17, XII, p. 304, figs. 254–6.
Hartlaub, 1917, ibid. Lief. 19, XII, p. 410.
Uchida, 1938*c*, *Sci. Rep. Tôhoku Univ.* ser. 4, Biol., vol. XIII, no. 1, p. 49, fig. 1.
Leuckartiara breviconis, Kramp & Damas, 1925, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. LXXX, p. 280.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. V, pt. x, p. 80, chart XV, pl. ii, fig. 8.

Specific Character

Marginal tentacles very numerous, up to 140 in number. Marginal tentacle bulbs without well-developed abaxial spur. No ocelli.

Description of Adult

Umbrella bell-shaped, higher than broad, with solid apical process of very variable size. Velum broad. Jelly thin. Stomach flask-shaped, not extending beyond umbrella margin in full extension, with broad base. Mouth with four crenulated lips. Four radial canals, broad, with jagged outlines; ring canal broad, with smooth outlines. Radial canals joined to stomach by 'mesenteries'. Gonads situated interradially on folds of the stomach wall, horseshoe-shaped, with horizontal folds. Marginal tentacles very numerous, up to 140 in number; hollow, smooth, with large, laterally compressed, elongated conical basal bulbs, clasping umbrella margin but not forming conspicuous abaxial spurs. No abaxial ocelli on marginal tentacle bulbs. Height when full grown up to 45 mm.; breadth up to 35 mm. Colour of umbrella bluish; marginal tentacles, gonads and stomach dark red or purple.

Distribution

In British waters *Leuckartiara breviconis* has only been recorded as yet from west of the Hebrides, and off the Orkney and Shetland Islands. Other localities are northern North Sea; southern part of west coast of Norway; Rockall; south Iceland; south and west Greenland; Pribyloff Islands, Alaska; Japan. Evidently an oceanic species with a distribution somewhat similar to that of *L. nobilis*.

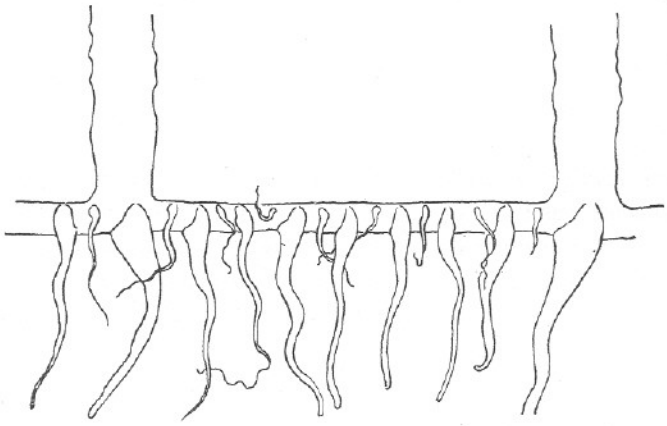
Developmental Stages and Structural Details

The youngest stages so far described (Hartlaub, 1914; Kramp & Damas, 1925) were about 5 mm. in height and 4 to 5 mm. in breadth. At this size they had twelve fully developed marginal tentacles, with twelve rudiments, one between every two fully developed marginal tentacles. Other specimens about this size had sixteen fully developed marginal tentacles. The sequence of development of the marginal tentacles in young medusae may thus be octagonal or duodecimal. With increasing growth in size the numbers of marginal tentacles may be very variable. Kramp (1926*a*) gives the following numbers of marginal tentacles for medusae of different sizes:

Diameter (mm.)	Marginal tentacles
4	16
5	12–32
7	16–46
10	40–68
11	38–65



Text-fig. 99. Possibly *Leuckartiara breviconis*. Young specimen from North Sea, 61° 15′ N.; 1° 30′ W., 24. iv. 05, 15 mm. high. (After Hartlaub, 1914, fig. 255.)



Text-fig. 100. *Leuckartiara breviconis*. Portion of umbrella margin of specimen from North Sea. (After Hartlaub, 1914, fig. 256.)

The largest specimen he saw was 34 mm. in height and 30 mm. broad, and had eighty-nine large and small marginal tentacles alternating, with only five marginal rudiments. The greatest number of marginal tentacles he observed was in a specimen 30 mm. high by 26 mm. broad which had 105, of which about every second one was fully developed, the remainder being much smaller and of different sizes; there were only a few tiny marginal rudiments. The type specimen described by Murbach & Shearer from the Pribyloff Islands was 45 mm. high and 35 mm. broad and had over 140 marginal tentacles. Hartlaub (1914) records a specimen 8 mm. high with thirty-six marginal tentacles; the gonads were already clearly formed and the radial canals broad and jagged.

The marginal tentacle bulbs (Text-fig. 100) are strongly laterally compressed and clasp the umbrella margin, but they do not form conspicuous abaxial spurs. Distally the marginal tentacle has a large number of deep transverse folds on the abaxial side, which according to Kramp (1926*a*) are on the adaxial sides, if present, in other Pandeids that he has examined.

The apical process may vary considerably in size and according to Kramp is always rounded and dome-shaped, though Hartlaub records a specimen 8 mm. in height with a 'spitzkuppelförmigen' process.

The adult gonads have the horseshoe-shape typical of other species of *Leuckartiara*. They are usually somewhat more irregularly folded than those of *L. octona* or *L. nobilis* (Kramp, 1926*a*).

Hartlaub records an abnormal specimen in which the radial canals were irregularly spaced; this was 15 mm. high and had a total number of fifty-three marginal tentacles including rudiments, which were distributed one between adjacent marginal tentacles. He also mentions a specimen from west Greenland which although 10 mm. in height (5 mm. of which was apical process) had only eight fully developed marginal tentacles; between every pair of these were three minute marginal rudiments of which the centre one was the largest.

Seasonal occurrence

Specimens have been taken off the Orkneys and Shetlands at the end of May (Kramp, 1926*a*); these were all young. Other records are northern North Sea, June; Aalesund, July, very large.

HYDROID. Not known.

Historical

Leuckartiara breviconis was first described by Murbach & Shearer (1902, 1903) as *Turris breviconis* from a specimen collected by Prof. Kincaid from St Paul Island, Pribyloff Islands. The species was transferred by Hartlaub (1914) to the genus *Leuckartiara*.

In the original description of the species the marginal tentacles are given as occurring mostly in two rows. This was an illusion produced by the unequal development of the marginal tentacles.

The specific name is frequently misspelt 'brevicornis', an error unfortunately introduced by Hartlaub (1914).

Genus **Annatiara** Russell, 1940

MEDUSAE. Pandeinae with umbrella without apical process; with exumbrellar nematocyst tracks; with large stomach, not extending beyond umbrella margin; with mouth with much crenulated lips; with radial canals at first narrow, then widening distally, with uneven outlines; with folded gonads on interradial surfaces of stomach; with marginal tentacles with elongated laterally compressed conical bases, without well-developed exumbrellar spurs; with rudimentary marginal tentacles; without marginal warts or marginal tentaculae; with abaxial ocelli.

HYDROID. Not known.

There is only one species in the genus, *Annatiara affinis* (Hartlaub). It is a deep-sea medusa which has not been recorded from British waters, but its distribution is such that it may be found.

Annatiara affinis (Hartlaub)

Text-figs. 101, 102, 103

Tiaranna affinis Hartlaub, 1914, *Nordisches Plankton*, Lief. 17, XII, p. 269, figs. 220, 221.
Kramp, 1920*a*, *Rep. Sci. Res.* '*Michael Sars*' *N. Atlantic Deep-Sea Expedit.* 1910, vol. III, pt. ii (1913–21), p. 6, pl. i, fig. 1 (1932).
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. v, pt. x, p. 68, pl. i, figs. 15–17, chart XI.
Ranson, 1934*d*, *Bull. Mus. Hist. Nat. Paris*, sér. 2, tome VI, no. 5, p. 436.
Annatiara affinis, Russell, 1940*a*, *Journ. Mar. Biol. Assoc.* vol. XXIV, p. 518.

Specific Characters. The only species of the genus.

Description of Adult

Umbrella bell-shaped, about as high as wide; jelly thick; no apical projection; exumbrella with numerous meridional nematocyst tracks. Velum ? . Stomach short, four-sided, with very broad base, attached to subumbrella along arms of horizontal perradial cross. Mouth with much crenulated margins. Four straight radial canals issuing from stomach at ends of arms of perradial cross, narrow at first, widening distally with uneven margins, entering by wide orifice into narrow ring canal. No centripetal canals. Gonads folded, on interradial walls of stomach, well developed adradially and regularly arranged along adradial sides of arms of perradial cross, irregularly arranged interradially. Up to forty-four large hollow smooth marginal tentacles, with elongated laterally compressed conical bases which clasp umbrella margin but do not form well-developed abaxial spurs. One very small or rudimentary marginal tentacle between adjacent large marginal tentacles. One abaxial ocellus on each large and rudimentary marginal tentacle base. Diameter of umbrella up to 23 mm. Colour of ocelli brown; remainder of medusa colourless in preserved material.



Text-fig. 101. *Annatiara affinis.* Specimen from North Atlantic, 46° 58′ N.; 19° 06′ W., 21. vii. 10. (After Kramp, 1920*a*, pl. i, fig. 1.)

Distribution

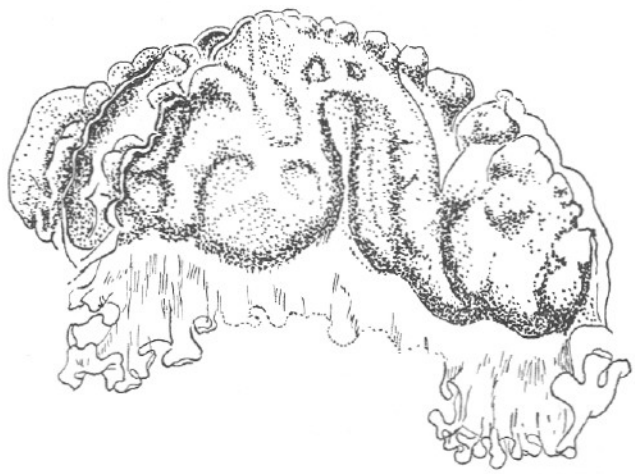
Annatiara affinis is a rare deep-sea oceanic medusa and it has not yet been recorded from the British area. Its distribution in the Atlantic is such, however, that it may be found over deep water off the western and northern coasts of the British Isles.

It has up to now only been recorded from the North Atlantic, in the following positions: 60° 00′ N., 10° 35′ W.; 48° 29′ N., 13° 55′ W.; 46° 58′ N., 19° 06′ W.; 44° 17′ N., 4° 44′ W.

Structural Details

The early development of *Annatiara affinis* has not been described nor is its hydroid known. Only eleven specimens have so far been recorded, none of which was in a perfect state of preservation.

The jelly of the umbrella, which is well developed, is thickest in the apical

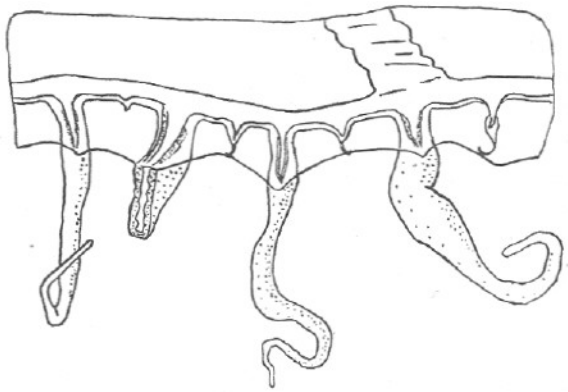


Text-fig. 102. *Annatiara affinis.* Stomach with gonad. (After Hartlaub, 1914, fig. 221.)

region, but it is noteworthy that it is thick also along the umbrella margin, being continued some way below the level of the ring canal. The subumbrellar cavity is very large. Ranson (1934*d*) is the only observer who has recorded the presence of exumbrellar nematocyst tracks. He states that each of these arises from the abaxial side of the base of each of the large and rudimentary marginal tentacles. Although the tracks were partly destroyed in his specimens Ranson was able to observe that those corresponding to the large marginal tentacles were broad and very long, reaching very high over the exumbrella. He thought that they were, without doubt, hollow.

The stomach is very broad and short, and Ranson explains this by the fact that it has passively followed the subumbrella in its growth in breadth.

Ranson states that the triangular interradial surfaces of the stomach are covered with gonads up to the apical angle at the top of the stomach. They are more dense adradially, but so weakly developed interradially that they give the impression of forming perradial stomach pouches, which is, however, not so. According to Kramp (1920*a*) each of the gonads forms eighteen to twenty folds.



Text-fig. 103. *Annatiara affinis*. Portion of the umbrella margin seen from the abaxial side, with four primary tentacles (one of which is broken off) and four secondary rudimentary tentacles. (After Kramp, 1926*a*, pl. i, fig. 17.)

The bases of the large marginal tentacles (Text-fig. 103) somewhat resemble those of *Leuckartiara nobilis*. The marginal tentacles themselves are probably of considerable length when fully extended (Kramp, 1926*a*). The rudimentary marginal tentacles were regarded by Kramp (1926*a*) as of a secondary nature, and differing from the large marginal tentacles in having narrow streaks of thickened ectoderm like abaxial spurs extending some way outwards over the exumbrella. These 'spurs' are, however, stated by Ranson (1934*d*) to be the exumbrellar nematocyst tracks.

The number of marginal tentacles probably increases with the growth of the medusa, as the following observations show:

Diameter of umbrella (mm.)	No. of large marginal tentacles	
14–15	*c.* 32	(Kramp, 1920*a*)
14	30	(Kramp, 1926*a*)
17	28	(Ranson, 1934*d*)
20	36	(Ranson, 1934*d*)
23	44	(Ranson, 1934*d*)

Ranson has noticed that some of these marginal tentacles are less developed than others. The marginal tentacles appear to be equally distributed between the four quadrants.

Seasonal occurrence

The months in which *Annatiara affinis* has been recorded are July, August and November.

Habits

Nothing is known of the habits of the living medusa except that it lives over deep water. It has been captured in nets with 300 m. of wire out.

HYDROID. Not known.

Historical

Annatiara affinis was first described and figured by Hartlaub (1914) from four imperfect specimens; he placed it in the genus *Tiaranna*. Kramp and Ranson have added to our knowledge of the species. The rudimentary marginal tentacles are in no way similar to the 'cordylus'-like tentacles of *T. rotunda* and Kramp (1926*a*) said in consequence that it was probably incorrect to refer them both to the same genus. Russell (1940*a*) erected a new genus, *Annatiara*, for the species.

Genus **Neoturris** Hartlaub, 1914

MEDUSAE. Pandeinae with umbrella with apical process varying much in shape and size; with or without exumbrellar nematocyst tracks; with large stomach not extending beyond umbrella margin; without peduncle; with mouth with four much folded and crenulated lips; with broad and ribbon-like radial canals, with jagged outlines; with gonads covering interradial surfaces of stomach, with adradial horizontal folds directed towards interradii and isolated pits situated interradially; with marginal tentacles with elongated laterally compressed bases, without conspicuous exumbrellar spurs; without rudimentary marginal tentacles; without marginal warts or marginal tentaculae; without ocelli.

HYDROID. Not known.

There is only one British species, *Neoturris pileata* (Forskål). It is one of our most handsome medusae and once seen is not likely to be confused with other species. It is at once identifiable by the structure of the gonad with its inwardly directed horizontal folds and isolated interradial pits. It is only likely to be found off the western and northern coasts of the British Isles where really deep water is not far away. Its hydroid has not been discovered (but see p. 188, *Leuckartiara abyssi*).

Neoturris pileata (Forskål)

Plate XII, fig. 1; Text-figs. 104, 105, 106

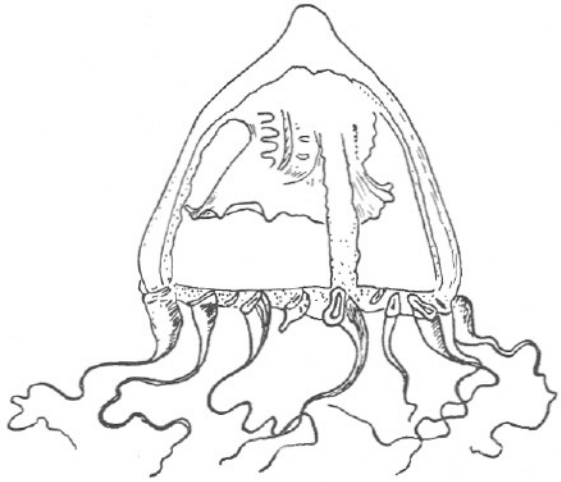
Medusa pileata Forskål, 1775, *Descriptiones Animalium*, p. 110, pl. xxxiii, fig. D.
Oceania lesueur Péron & Lesueur, 1809, *Ann. Mus. Hist. nat. Paris*, tome XIV, p. 345.
Océania pileata, Péron & Lesueur, 1809, ibid. p. 345.
Eschscholtz, 1829, *System der Acalephen*, p. 98.
Carybdea pisifera Oken, 1815, *Lehrbuch der Naturgeschichte*, Teil 3, Zool. vol. II, Jena.
Dianaea lesueur, Lamarck, 1817, *Hist. Nat. sans Vertèbres*, tome II, p. 506.
Dianaea pileata, Lamarck, 1817, ibid. p. 506.
Oceania Le Sueur, Eschscholtz, 1829, *System der Acalephen*, p. 98.
Oceania pileus Blainville, 1830, *Zoophytes* in *Dict. Sci. Nat.* vol. LX.
Tiara papalis Lesson, 1843, *Hist. Nat. Zooph. Acalèphes*, p. 287.
Turris digitale Forbes, 1846, *Ann. Mag. Nat. Hist.* ser. 1, vol. XVIII, p. 286.
Turris digitalis, Forbes, 1848, *Monogr. Brit. Medusae*, p. 21, pl. iii, fig. 1.
L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 346.
Haeckel, 1879, *System der Medusen*, p. 61, pl. iv, figs. 2, 3.
Mayer, 1910, *Medusae of the World*, vol. I, p. 129, fig. 68.
Oceania coccinea Leuckart, 1856, *Arch. Naturgesch. Berlin*, Jahrg. XXII, p. 20, pl. ii, fig. 3.
Turris constricta Patterson, 1859, *Proc. Dublin Univ. Zool. Bot. Assoc.* vol. I, p. 279, figs.
Oceania (Turris) pileata, Claus, 1877, *Denkschr. Akad. Wiss. Wien*, Bd. XXXVIII (1878), p. 64, pl. XI, figs. 46, 47.
Tiara pileata, Haeckel, 1879, *System der Medusen*, p. 58.
L. Agassiz, 1862, *Contrib. Nat. Hist. U.S.* vol. IV, p. 347 (in part).
Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. V, p. 712 (in part).
Browne, 1903, *Bergens Mus. Aarb.* no. 4, p. 11 (in part).

Turris coeca Hartlaub, 1892, *Nachr. Ges. Wiss. Göttingen*, p. 19, fig. 1.
Mayer, 1910, *Medusae of the World*, vol. I, p. 127.
Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. XX, p. 41.
Neoturris pileata, Hartlaub, 1914, *Nordisches Plankton*, Lief. 17, XII, p. 326, figs. 270, 273, 274–81.
?Bigelow, 1919, *U.S. Nat. Mus. Bull.* 100, p. 285, pl. xxxix, figs. 7, 8; pl. xl, fig. 1.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. V, pt. x, p. 92, text-fig. 37, chart XVIII, pl. ii, figs. 13, 14.
Kramp, 1927, *K. danske vidensk. Selsk. Skr.* natur. og math. Afd., 8. Raekke, XII, p. 101, chart 13.

Specific Characters. Marginal tentacles numerous, up to ninety in number.

Description of Adult

Umbrella bell-shaped, higher than wide, with solid apical process varying much in size; jelly thin. Velum narrow. Stomach flask-shaped, of very variable length, never extending beyond



Text-fig. 104. *Neoturris pileata.* Young specimen 4·5 mm. high, Trieste. (After Hartlaub, 1914, fig. 279.)



Text-fig. 105. *Neoturris pileata.* Preserved specimen 30 mm. high, Faeroe-Shetland Channel, 9. vii. 33. (Collected on Sir Edward Peel's yacht *St George.*)

umbrella margin in full extension, with broad base. Mouth with much crenulated lips. Four radial canals broad, with jagged outlines; ring canal broad, with smooth outlines. Radial canals joined to stomach by 'mesenteries'. Gonads interradial, each with two adradial series of folds directed inwards towards the interradius and a depressed interradial portion with round pits. Marginal tentacles numerous, sixty to ninety in number, hollow, smooth, with large, laterally compressed, elongated conical basal bulbs clasping the umbrella margin but not forming conspicuous abaxial spurs. No ocelli. Height when full grown 30–35 mm., width *c.* 15 mm. Colour of marginal tentacle bases yellow-ochre or orange; manubrium raisin-coloured (after Hartlaub, 1914).

Distribution

Neoturris pileata has been rarely recorded for certain off the British coasts, but the records show that the species is likely to be limited to those coasts bathed by Atlantic water. It has been recorded from the western mouth of the English Channel; Valencia, south-west Ireland; Port Erin, Isle of Man; Belfast; Shetland Islands; Moray Firth; Rockall Bank; Northumberland coast (Peacock, 1924, as *Turris digitalis*); North Sea; west coast of Norway to 64° N.; Skagerak and northern Kattegat; Iceland; Denmark Strait; Mediterranean; ? Philippines in Pacific. Kramp (1926*a*) states that in North Atlantic waters it appears to have its main occurrence within the areas of the Gulf Stream and Irminger Current, following the offshoots of these currents, but never penetrating into Arctic regions. He also stated that the species had not yet been found off the Atlantic coasts of Europe between the Straits of Gibraltar and the English Channel, but he recorded it in mid-Atlantic from 'Dana' collections (Kramp, 1947).

Developmental Stages and Structural Details

Development. The first stage of *Neoturris pileata* has not been described, the hydroid from which it is liberated not yet being known. The youngest stage described as yet (Text-fig. 104) was 4·5 mm. high and 5 mm. wide, from Trieste (Hartlaub, 1914). At this stage the medusa had sixteen marginal tentacles developed; the radial canals were very broad and with uneven outlines; the first traces of the gonads were already present; the mouth-lips were not yet strongly crenulated; the manubrium was 3 mm. long; and the apical process was weakly developed. Another stage, also described by Hartlaub from Trieste, was 8 mm. in height and 6·5 mm. in width; the number of marginal tentacles including rudiments was *c.* 40 and the apical process was quite pronounced. Kramp (1926*a*) has made observations on the numbers of marginal tentacles possessed by individuals of different sizes. He gives the following figures:

Diameter (mm.)	Marginal tentacles	Diameter (mm.)	Marginal tentacles
6	16, 16, 32	16	80
8	32, 40	18	80
9	64	19	60
10	48	22	60
12	50	23	64, 78
13	44, 56	25	80
14	51	—	—

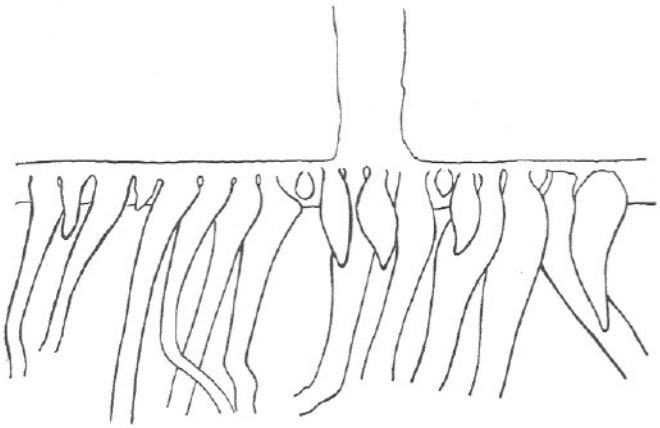
He states that at first the development of the marginal tentacles is fairly regular and that they may reach sixteen in number by octagonal or duodecimal development as in *Leuckartiara octona*. Further development, however, soon becomes irregular and after a certain size specimens appear to have as many marginal tentacles as available space will allow on the umbrella margin, new marginal tentacles appearing wherever there happens to be room.

Adult characters. The full-grown medusa shows considerable variation in certain characters. The apical process may vary very much in size; it may be a large almost spherical mass (Text-fig. 105) comprising over a third of the total height of the medusa, or it may be almost completely absent. The stomach also varies considerably in length, in some reaching almost to the umbrella margin while in others it is not even half the height of the subumbrellar cavity. The outlines of the radial canals are smooth at their lower ends.

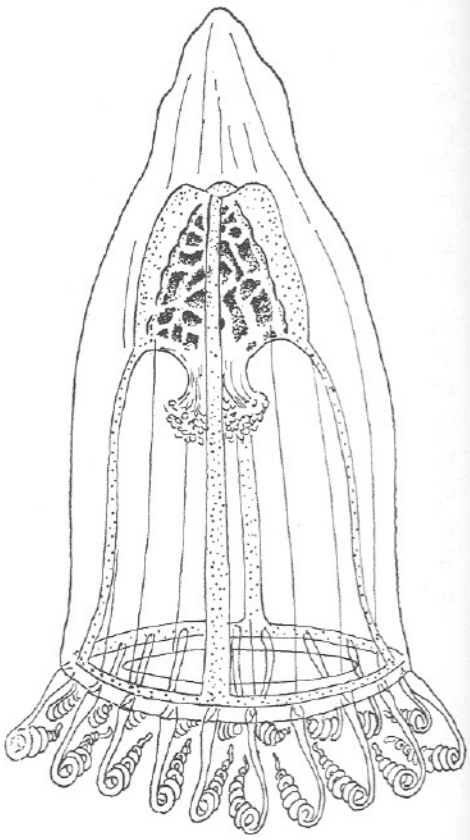
The gonads cover the stomach wall almost down to the mouth-lips. The general structure of each gonad appears as a central interradial field covered with a number of pit-like depressions bounded on either side by a series of adradial horizontal folds directed inwards towards the interradius. These adradially situated folds are produced by a series of depressions in the stomach

wall. The adradial series of folds are not connected interradially. While thus the general appearance of the gonad is produced by a number of depressions and folds as in *Leuckartiara* it differs fundamentally since in *Leuckartiara* the adradial folds are directed outwards and connected interradially, and the interradial field is more or less free of pits.

The marginal tentacles coil spirally. Their bases are continued into hollow elongated conical basal bulbs clasping the umbrella margin (Text-fig. 106). These bulbs are laterally compressed



Text-fig. 106. *Neoturris pileata*. Portion of umbrella margin. (After Hartlaub, 1914, fig. 278.)



Text-fig. 107. *Pandea conica*. Specimen from Naples. (After Hartlaub, 1914, fig. 286, from a coloured drawing by Merculiano.)

but have no well-developed abaxial spur. According to Kramp (1926*a*) the marginal tentacle is flattened on its abaxial side, and has a conspicuous longitudinal keel on its adaxial side; in the distal part of the tentacle this keel is interrupted by deep transverse grooves. The marginal tentacles are triangular in cross-section. The nematocysts are situated on transverse ridges forming rings or clasps, which are more numerous and crowded on the adaxial side. When tightly coiled the adaxial side of the marginal tentacles faces outwards, and thus that part most protected by nematocysts lies on the outside.

The histology of the musculature and nervous systems has been described by Krasińska (1914).

Seasonal occurrence

Owing to the scarcity of records of *Neoturris pileata* round the British coasts its seasonal occurrence cannot be given with certainty. The following general information given by Kramp

(1926*a*), however, will probably hold good for our own waters: 'At the north-western coasts of Europe the young individuals appear in May. Throughout the summer both young and fairly large specimens are found; old and very large specimens may be found from July to September, probably also later.'

Habits

Kramp (1927) states that in Danish waters this medusa keeps to the deeper, cold water, and that it does not grow to so large a size as in the Norwegian Sea and Atlantic Ocean.

HYDROID. Not known. (See p. 188 and Text-fig. 98.)

Historical

Neoturris pileata was first described by Forskål in 1775 as *Medusa pileata*. The species subsequently became confused with and buried in the synonymy of '*Tiara*' and '*Turris*'. It remained for Hartlaub (1914) to erect a new genus *Neoturris*, characterized mainly by the formation of the gonads and to re-describe Forskål's species.

Genus **Pandea** Lesson, 1843

MEDUSAE. Pandeinae with umbrella with or without conical apical thickening; with or without exumbrellar nematocyst tracks; with large stomach not extending beyond umbrella margin; without peduncle; with mouth with four folded and crenulated lips; with fairly broad and ribbon-like radial canals, with or without jagged outlines; with gonads covering interradial surfaces of stomach with irregular network of ridges with pits between; with marginal tentacles with elongated conical basal bulbs which may or may not be laterally compressed; with or without conspicuous exumbrellar spurs; without rudimentary marginal tentacles; without marginal warts or tentaculae; with or without ocelli.

HYDROID. Not known.

There are two species of the genus *Pandea** which are probably to be found in deep water off the western coasts of the British Isles, *P. conica* (Quoy & Gaimard) and *P. rubra* Bigelow. The two species can at once be distinguished from other Pandeid medusae by their gonads which form an irregular network of ridges and pits. The two species can easily be separated by a number of characters, e.g.:

With exumbrellar nematocyst ribs; gonad network coarse; marginal tentacle bulbs laterally compressed; ocelli present; subumbrella colourless . . . . . **P. conica**

Without exumbrellar nematocyst ribs; gonad network close meshed; marginal tentacle bulbs not laterally compressed; ?without ocelli; subumbrella deeply pigmented . . . . . **P. rubra**

Neither species is likely to be common, and of neither is the hydroid known.

Pandea conica (Quoy & Gaimard)

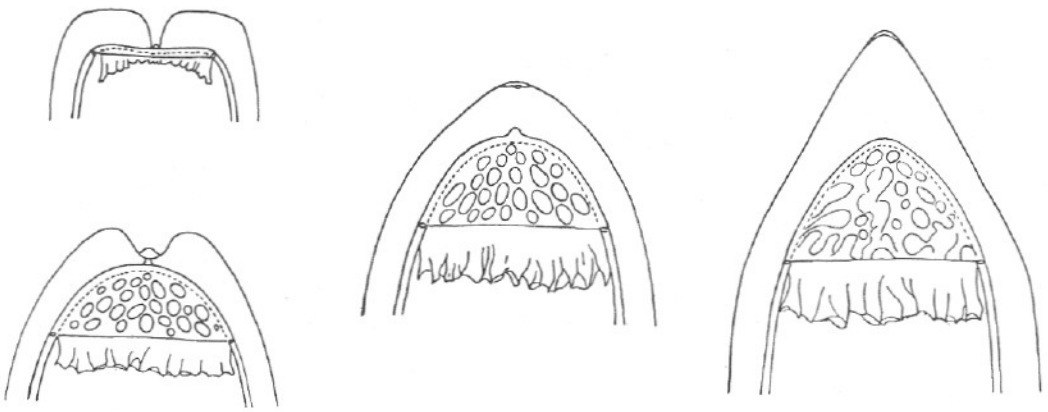
Text-figs. 107–10

Dianaea conica Quoy & Gaimard, 1827, *Ann. Sci. nat. Paris*, tome x, p. 182, pl. vi, figs. 3, 4.
Oceania conica, Eschscholtz, 1829, *System der Acalephen*, p. 99.
Gegenbaur, 1856, *Zeit. Wiss. Zool. Leipzig*, Bd. viii, p. 221, pl. vii, figs. 1–3.

* Lesson's original spelling was *Pandea*; Haeckel (1879) considered that the more correct spelling *Pandaea* should be used, but the former spelling is now generally adopted.

PANDEIDAE

Pandea conica, Lesson, 1843, *Histoire Naturelle des Zoophytes*, p. 288.
Mayer, 1910, *Medusae of the World*, vol. I, p. 118, fig. 63.
Hartlaub, 1914, *Nordisches Plankton*, Lief. 17, XII, p. 338, figs. 283, 286, 287.
Kramp, 1924, *Rep. Danish Oceanogr. Expedit.* vol. II, Biology, H. 1, p. 8, fig. 7, chart III.
Uchida, 1927*a*, *Journ. Fac. Sci. Imp. Univ. Tokyo*, vol. I, pt. iii, p. 214, fig. 38.
Kramp, 1928, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. LXXXV, p. 57.
Bigelow, 1938, *Zoologica, New York*, vol. XXIII, pt. ii, no. 5, p. 106.
Oceania sedecimcostata Kölliker, 1853, in Gegenbaur, Kölliker, & Müller, *Zeit. Wiss. Zool. Leipzig*, Bd. IV, Heft 3/4, p. 324.
Oceania pileata, Keferstein & Ehlers, 1861, *Zoologische Beiträge . . . in Neapel und Messina*, p. 81 (in part).
Tiara conica, L. Agassiz, 1862, *Cont. Nat. Hist. U.S.* vol. IV, p. 347.
Pandaea conica, Haeckel, 1879, *System der Medusen*, p. 54.
Hartlaub, 1892, *Nachr. Ges. Wiss. Göttingen*, p. 21, fig. 2.
Maas, 1904*a*, *Rés. Camp. Sci. Monaco*, Fasc. XXVIII, p. 16, pl. i, figs. 6, 7.
Ranson, 1936, ibid. Fasc. XCII, p. 84, pl. i, figs. 1–6.
Tiara reticulata Haeckel, 1879, *System der Medusen*, p. 60, pl. iii, fig. 11.
?*Tiara pileata* var. *ampullacea* Haeckel, 1879, ibid. pl. iii, fig. 7.



Text-fig. 108. *Pandea conica*. Diagrams to show the development of the apical process, stomach and gonads as the medusa grows. (After Ranson, 1936, pl. i, figs. 3–6.)

Specific Characters

Sixteen to twenty-four or more longitudinal exumbrellar nematocyst ribs; gonads forming coarse network of pits.

Description of Adult

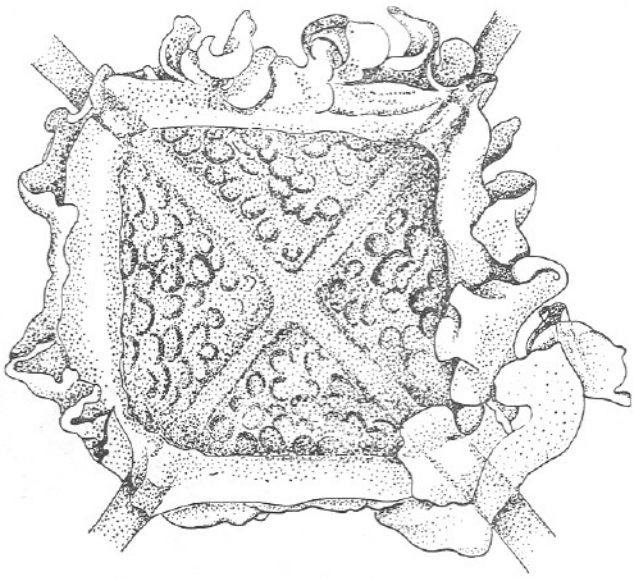
Umbrella bell-shaped, as high as or higher than wide, with rounded or conical summit with apical ectodermal thickening; with sixteen to twenty-four or more longitudinal exumbrellar nematocyst ribs, corresponding to number of marginal tentacles; jelly fairly thick. Velum narrow. Stomach large, pyramidal, almost filling upper half of subumbrellar cavity, about half of subumbrellar cavity in length; attached to subumbrella along perradii for about four-fifths of its length. Mouth with four perradial lips with folded or crenulated margins. Four radial canals fairly broad, with smooth or jagged outlines; ring canal narrower, with smooth outlines. Gonads situated on entire interradial walls of stomach, forming coarse-meshed network of ridges with pits between. Sixteen to twenty-four or more (sometimes as many as forty-four) smooth, hollow, marginal tentacles, each with conical, laterally compressed basal bulb, without well-developed

abaxial spur, each with one abaxial ocellus. No rudimentary marginal tentacles. Height 20–30 mm. Colour of stomach and gonads, reddish, brownish or yellowish; mouth-lips reddish or pink; tentacles milky yellow; ocelli red or reddish brown; subumbrella colourless.

Distribution

The only record of *Pandea conica* from British waters is possibly that of a specimen figured by Haeckel (1879), as *Tiara pileata* var. *ampullacea*, from the Scottish coast. It seems probable that this specimen was *Pandea conica*, although the species has not been recorded since in the eastern North Atlantic.*

The species appears to have a wide distribution. It is common in the Mediterranean, and has been recorded off Bermuda (Bigelow, 1938), in the South Atlantic (Haeckel, 1879; Vanhöffen, 1910), and in the Pacific off Japan and the Philippine Islands (Uchida, 1927*a*, and Kramp, 1928).



Text-fig. 109. *Pandea conica*. Looking through the mouth into the stomach of a specimen 2 mm. high. (After Ranson, 1936, pl. i, fig. 1.)

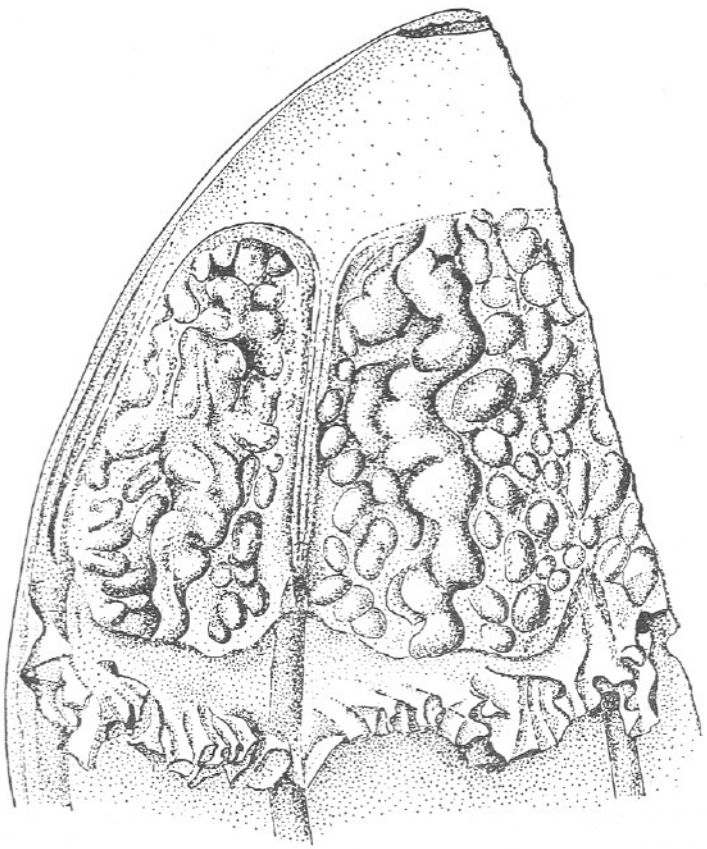
Developmental Stages and Structural Characters

The earliest stage of *Pandea conica* immediately after liberation from the hydroid has not been described for certain, since its hydroid is not known. The smallest specimen described in detail from the plankton was 1 mm. high and 1 mm. wide (Ranson, 1936). Its shape was that of the trunk of a four-sided pyramid, the four angles corresponding to the four radial canals. The summit of the umbrella was flattened and had a slight depression in its centre. The stomach was large and broad, and covered the quadrangular summit of the subumbrella. It was quite horizontal and attached to the subumbrella along the four arms of a perradial cross. The mouth had folded lips, slightly elongated in the four perradial corners. There were four perradial marginal tentacles, of which two were larger and two smaller. In each of three of the interradial quadrants there were two rudimentary tentacular marginal bulbs, and in the remaining quadrant there was one.

The growth and development of the medusa has been described by Ranson (1936). In young specimens the summit of the umbrella is flat and in its centre there is a depression in which the ectoderm and endoderm are in contact, there being no mesogloea (Text-fig. 108). This is, in fact, probably the remnant of the umbilical junction between the hydroid and the medusa. As the medusa grows this depression becomes filled up by the development of the mesogloea between the two cell layers. Finally, it assumes the rounded or conical shape of the adult, in which there is an ectodermal thickening right at the apex.

* The specimens recorded by Hartlaub (1914) from the Bay of Biscay were in fact from the Straits of Gibraltar (see Kramp, 1920*a*).

The exumbrellar nematocyst ribs appear at an early stage, and in specimens 3–4 mm. high they are already as numerous as the large marginal tentacles, and run from the umbrella margin to the centre of the apical depression of the umbrella. The nematocyst ribs corresponding to the developing marginal tentacular bulbs do not run for the whole length of the umbrella; they run up for shorter or longer distances according to the degree of development of the bulb. In preserved specimens these nematocyst ribs appear as longitudinal ridges. According to Ranson (1937) they are ectodermal thickenings and have no underlying axis of endoderm cells.



Text-fig. 110. *Pandea conica*. Stomach of a specimen 10 mm. high seen from inside. (After Ranson, 1936, pl. i, fig. 2.)

As the medusa grows the stomach increases in height, and its growth is mostly upwards towards the umbrella apex. In this way the four lines of attachment to the subumbrella, which are at first horizontal, become nearly vertical, and the subumbrellar cavity becomes divided into four upper compartments.

The gonads are already apparent in medusae 4 mm. in height, in the form of a few isolated pits. These pits increase in number and in size as the interradial walls of the stomach grow in height and width. As the pits increase in size some of them may coalesce, so that sometimes the appearance of a central longitudinal fold or furrow is produced.

The above observations on the development of the medusae are illustrated in Text-fig. 108.

The development of the marginal tentacles in medusae of different sizes has been followed by Ranson and his observations may be summarized as follows:

Height (mm.)	Width (mm.)	No. of marginal tentacles or bulbs in each interradial quadrant	Total Tentacles	Total Bulbs
1	1	2 b., 2 b., 2 b., 1 b.	4	7
2	2·5	1 t., 4 b., −2 t., 3 b., −3 t., 2 b., −2 t., 3 b.	12	12
3	3	3 t., 2 b., −2 t., 3 b., −3 t., 2 b., −3 t., 2 b.	15	9
4	4	3 t., 2 b., −2 t., 2 b., −3 t., 3 b., −4 t., 1 b.	16	8
6	5	3 t., 2 b., −3 t., 2 b., −4 t., 1 b., −4 t., 1 b.	18	6
7	5	4 t., 2 b., −3 t., 3 b., −4 t., 1 b., −5 t., 1 b.	20	7
8	7	4 t., 2 b., −4 t., 2 b., −4 t., 1 b., −4 t., 2 b.	20	7
10	8	4 t., 2 b., −6 t., −6 t., −4 t., 2 b.	24	4

Thus it is apparent that the marginal tentacles are quite numerous while the medusa is small. The maximum number recorded is forty-four in a specimen from Japan (Uchida, 1927*a*). Specimens with thirty-four or thirty-five tentacles have also been recorded by Bigelow (1938) from Bermuda, and by Kramp (1928) from Japan.

Seasonal occurrence

In the Mediterranean *Pandea conica* has been recorded in all months from January to September inclusive (see Kramp, 1924).

Habits

Little is known of the habits of the living medusa. Gegenbaur (1856) remarked on its active swimming movements and the fact that it might swim with its marginal tentacles held extended or spirally coiled (Text-fig. 107).

The medusa may apparently live in the upper water layers, but the depth to which it descends is not known since all captures over deep water have been made with open nets (see Kramp, 1924).

HYDROID. Not known.

Historical

Pandea conica was first described and figured by Quoy & Gaimard (1827) from Gibraltar, as *Dianaea conica*.

Pandea rubra Bigelow

Text-figs. 111, 112

Pandea rubra Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, no. 1946, p. 14, pl. ii, figs. 1–7.
Hartlaub, 1914, *Nordisches Plankton*, Lief. 17, XII, p. 340, fig. 288.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. V, pt. x, p. 96, pl. ii, fig. 15, chart XVII.
Bigelow, 1938, *Zoologica, New York*, vol. XXIII, pt. ii, no. 5, p. 107.

Specific Characters

No exumbrellar nematocyst tracks; gonads forming very fine meshed network of pits.

Description of Adult

Umbrella bell-shaped, as high as or slightly higher than wide; with rounded summit without marked apical process; without exumbrellar nematocyst tracks; jelly thin. ? Velum narrow. Stomach large, with broad base, about half height of subumbrellar cavity in length; attached to subumbrella along perradii for about four-fifths of its length. Mouth with four lips with much folded and crenulated margins. Four radial canals, broad, with wavy or jagged outlines; ring

canal broad, with smooth outlines. Gonads situated interradially on stomach, forming very close-meshed irregular network of ridges with pits between. Twelve to ? twenty-four marginal tentacles of varying sizes, hollow, smooth, each with large conical basal bulb, not laterally compressed, with distinct abaxial spur, and clasping margin of exumbrella. No rudimentary marginal tentacles. ? No ocelli. Height 30–40 mm., up to *c.* 75 mm. Colour of subumbrella, stomach, mouth, gonads and marginal tentacles deep brownish red or chocolate.

Distribution

Pandea rubra has not yet been recorded in British waters. It has, however, been taken far out in the North Atlantic west of the British Isles in 54° 04′ N., 26° 08′ W., and in the deep channel east of Rockall (Kramp, 1920*b*, 1926*a*). It is, therefore, likely to occur in deep water off the western coasts of Ireland and Scotland.

Elsewhere it has been recorded from the neighbourhood of Bermuda (Bigelow, 1938) and from the north-west Pacific and the Bering Sea (Bigelow, 1913).

Structural Characters

The young stages of *Pandea rubra* have not been described nor is its hydroid known; indeed, altogether only twelve specimens of this medusa have so far been recorded.

The smallest specimen, described by Bigelow (1913) from the Pacific, was *c.* 18 mm. wide; in each of the two quadrants which were entire it had two interradial marginal tentacles. If complete it might, therefore, have had twelve marginal tentacles in all. The next smallest specimen was 27 mm. high and 25 mm. wide; it had two, three, two, three interradial marginal tentacles in each quadrant respectively, making fourteen in all.

These small specimens were similar in general appearance to the older medusae, but the gonads were less developed and their pits shallower. They occupied the entire interradial areas. The margins of the four radial canals were slightly wavy, and those of the ring canal smooth. The pigmentation was limited to the stomach, mouth, and gonads, which were deep brownish red.

The details of the four remaining specimens recorded by Bigelow were as follows:

Height (mm.)	Width (mm.)	No. of interradial marginal tentacles in each quadrant
35	37	4, 2, 2, 2
40	38	3, 3, 4, ?
47	38	4, 3, 3, 4
c. 75	?	5, 4, ? ?

Thus, five was the greatest number of interradial marginal tentacles found in a quadrant. If this number were to occur in all four quadrants, it might be assumed that the maximal total number of marginal tentacles may be twenty-four.

The two specimens recorded by Kramp (1926*a*) were 30 mm. high by 40 mm. wide, and *c.* 30 mm. wide, respectively; of these the former had twelve marginal tentacles and the latter eight. Specimens 38–40 mm. high recorded by Bigelow (1938) from Bermuda had twelve to fourteen marginal tentacles.

According to Kramp the radial canals are very narrow proximally, but their width is more than doubled in the distal region; the ring canal is somewhat expanded on both sides of each marginal tentacular bulb.

The structure of the gonads is apparently characteristic of the species, the network of ridges and pits being much closer and more complex than in *P. conica* (Text-fig. 111).

Kramp states that the abaxial spur of the marginal tentacle base (Text-fig. 112) is deeply pigmented, though frequently its extreme end is transparent and colourless and embedded in the jelly of the exumbrella. No true ocelli, however, have as yet been seen in *P. rubra* and this may be a further distinction between this species and *P. conica*, which according to most descriptions has ocelli.

Kramp gives the length of the marginal tentacles as about 20 mm.; they have smooth surfaces without wrinkles, but there are weakly developed transverse grooves on the abaxial side.

The colour of *P. rubra* appears to be characteristic. Bigelow states that the entire subumbrella is so densely pigmented, except near its margin, that the stomach is entirely hidden, and the more lightly coloured radial canals show as pale bands. The complete pigmentation of the subumbrella appears to be an adult character, for in small specimens, although the stomach,



Text-fig. 111. *Pandea rubra*. Stomach and gonads. (From Hartlaub, 1914, fig. 288, after Bigelow, 1913, pl. ii, fig. 2.)



Text-fig. 112. *Pandea rubra*. Base of marginal tentacle showing large abaxial spur; specimen from North Atlantic. (After Kramp, 1926*a*, pl. ii, fig. 15.) *ex.*, exumbrella; *sp.*, spur.

gonads and marginal tentacles are densely pigmented, the deep pigmentation of the subumbrella only occurs in the immediate vicinity of the base of the stomach. In such specimens the pigmented radial and ring canals show up distally as dark bands.

Kramp says that the pigment of the marginal tentacles is exclusively endodermal, the ectoderm being transparent and colourless. It is not known whether the subumbrellar pigmentation is ectodermal or endodermal.

Seasonal occurrence

The two specimens recorded from the North Atlantic were taken in July, and those from near Bermuda in May and July.

Habits

Nothing is known of the habits of living *P. rubra*. It is probably a bathypelagic species as its coloration implies, living at intermediate depths in the open ocean. The specimens recorded

in the Pacific were taken in depths between 300 fathoms and the surface, those in the North Atlantic in hauls with 1000 m. of wire out, and those off Bermuda from between 914–1463 m. and the surface.

HYDROID. Not known.

Historical

Pandea rubra was first described and figured by Bigelow (1913) from the Pacific. While keeping *P. rubra* and *P. conica* as separate species, Ranson (1936) suggested the possibility that they might be two races of the same species. There are, however, good grounds for regarding the two species as quite distinct (see Bigelow, 1938).

SUBFAMILY CALYCOPSINAE

Pandeid medusae with umbrella without apical process; without exumbrellar nematocyst tracks; stomach not extending beyond umbrella margin; no peduncle; mouth with simple or slightly folded lips, or with margins much crenulated and armed with stalked nematocyst clusters; with four unbranched or branched radial canals, with or without centripetal canals; with folded gonads situated adradially or interradially; with eight or more marginal tentacles without basal swellings, but each terminating in large nematocyst cluster; with or without rudimentary or dwarf marginal tentacles; with or without ocelli.

The Calycopsinae contain a number of deep-sea species of medusae only one of which, *Bythotiara murrayi* Günther, has so far been recorded in British waters. *Bythotiara* Günther is thus the only genus represented, but owing to the wide distribution of deep-sea medusae in general it seems likely that other genera may eventually be found in deep water west or north of the British Isles. It is thus possible that *Heterotiara anonyma* Maas and *H. minor* Vanhöffen may eventually be found as both are of rather widespread distribution. Similarly *Calycopsis typa* Fewkes and *C. simplex* Kramp & Damas might be expected.

It will therefore be useful to give the characters by which these genera of the Calycopsinae may be distinguished.

Four unbranched radial canals:	
No centripetal canals	**Heterotiara**
Four branching radial canals:	
No centripetal canals	**Bythotiara**
Four unbranched radial canals:	
With centripetal canals	**Calycopsis**

Genus **Bythotiara** Günther, 1903

MEDUSAE. Calycopsinae with mouth with four simple lips; with four branching radial canals; without centripetal canals; with folded interradial gonads; with rudimentary or dwarf marginal tentacles; without ocelli.

HYDROID. Not known.

There is only one British representative of the genus, *Bythotiara murrayi* Günther. It will only be found rarely in deep water and cannot be confused with any other British species.

Bythotiara murrayi Günther

Plate XIII, fig. 1; Text-figs. 113A, B, 114A, B, 115, 116

Bythotiara murrayi Günther, 1903*a*, *Ann. Mag. Nat. Hist.* ser. 7, vol. XI, p. 424, pl. X, figs. 4, 5.
Maas, 1910, *Bull. Inst. Océanogr. Monaco*, no. 183, p. 1.
Mayer, 1910, *Medusae of the World*, vol. I, p. 185, figs. 97, 98.
Vanhöffen, 1911, *Wiss. Ergebn. Deutsch. Tiefsee-Expedit. Valdivia* 1898–1899, Bd. XIX (1925), Heft 5, p. 213, figs. 9*a–c*.
Hartlaub, 1914, *Nordisches Plankton*, Lief. 17, XII, p. 355, figs. 304–6.
Kramp, 1924, *Rep. Danish Oceanogr. Expedit.* 1908–10, vol. II, H. 1, p. 12, figs. 8–11, chart IV.
Kramp & Damas, 1925, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. LXXX, p. 281.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. V, pt. X, p. 97.
Ranson, 1936, *Rés. Camp. Sci. Monaco*, fasc. XCII, p. 98, pl. I, fig. 12.

Specific Characters

Four primary radial canals each bifurcating once; gonads with horizontal folds not divided longitudinally.

Description of Adult

Umbrella hemispherical or somewhat bell-shaped, about as high as or slightly higher than wide, with rounded apex; jelly thick. Stomach small, somewhat rhomboid in shape; without peduncle. Mouth with four short simple lips. Four primary radial canals, each bifurcating near point of origin from stomach to form eight straight narrow smooth canals joining narrow ring canal; each primary canal leaves stomach as short narrow vertical funnel (='mesentery'). Four gonads, one covering each interradial wall of stomach, with transverse folds. Eight large smooth hollow primary marginal tentacles, with no basal swellings, each terminating in large hemispherical nematocyst cluster; situated one opposite each radial canal. One to five small hollow secondary marginal tentacles between every two primary marginal tentacles. No ocelli. Height and diameter of umbrella up to 20 mm. Colour of umbrella faint violet; gonadial part of stomach brick red; remainder of medusa colourless. (In long-preserved specimens the stomach and gonads are flesh-coloured.)

Distribution

Bythotiara murrayi is a deep-sea oceanic medusa which has only been recorded off the British Isles far out from the west and south-west coasts of Ireland.

Elsewhere its distribution is wide, although it has only been recorded in small numbers. It has been taken in the Norwegian fjords; the Skagerak; the north Atlantic Ocean; the Mediterranean; off the mouth of the Congo River, in the South Atlantic; and off Sumatra, in the Indian Ocean.

Since it is a deep-sea species it is unlikely to be found anywhere close inshore on the British coasts except where very deep water is fairly near at hand.

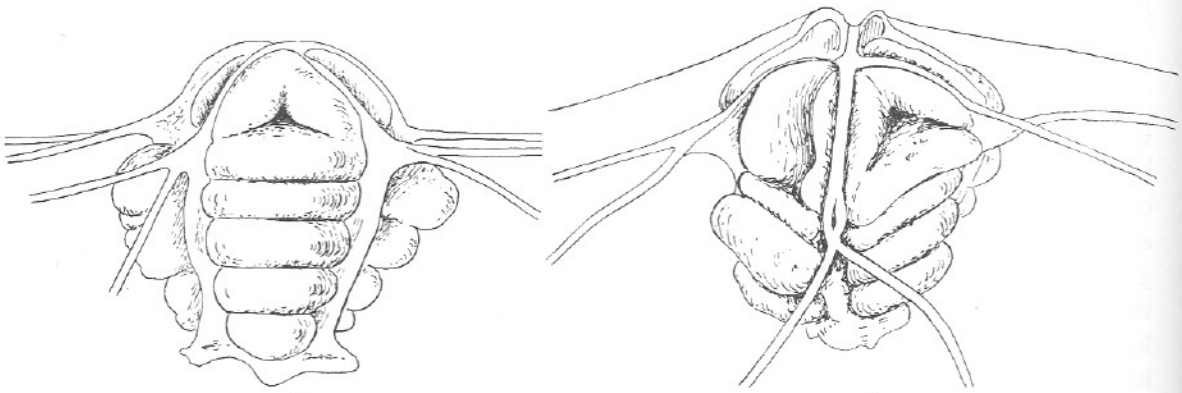
Structural Details

The hydroid of *Bythotiara murrayi* is not known and no early stages of the medusa have been described. All the specimens so far recorded have been between 5 and 21 mm. in height. Structurally these medusae were all fully developed, having typically eight radial canals and eight primary marginal tentacles. The smallest specimen, 5 mm. in height, recorded by Kramp (1924) from the Mediterranean was already mature with the eggs lying on the outer side of the stomach from which they are easily dropped.

PANDEIDAE

In well-preserved specimens the upper part of the stomach (Text-fig. 113A, B) projects upwards for about one-third of its length as a rounded dome. Over this the cross-shaped lines of attachment of the stomach to the subumbrella appear as two grooves crossing one another approximately at right angles. The lower two-thirds of the stomach is four-sided and tapers slightly towards the mouth.

The four primary radial canals are fairly broad and each leaves the stomach at a point about one-third of the distance from its summit as a small vertical funnel-shaped slit or 'mesentery', after which it immediately bifurcates to form two slightly narrower canals. Considerable abnormality may be shown in the numbers of radial canals and in their branching. Most authors have recorded abnormalities and examples of some found by Kramp (1924) in specimens from the Mediterranean are given in Text-fig. 114A. I have also figured two abnormalities found among six specimens in a collection of medusae taken from the west coast of Ireland 50 miles west-north-west of Tearaght (Text-fig. 114B). Specimens may be found in which there are three or five primary radial canals.



Text-fig. 113. *Bythotiara murrayi*. Stomach and gonads. A, lateral interradial view; B, perradial oblique view from above.

Normally each primary radial canal bifurcates once, but sometimes a primary radial canal may join the ring canal without branching at all. The branches formed by bifurcation often give off supernumerary branches, and there may be anastomosis between the branches. Branches from one series of canals may also anastomose with neighbouring branches from another series. Sometimes a branch will bifurcate and the resulting branches will join together again, thus forming an island. Specimens may be found in which supernumerary branches end blindly, not yet having grown as far as the ring canal.

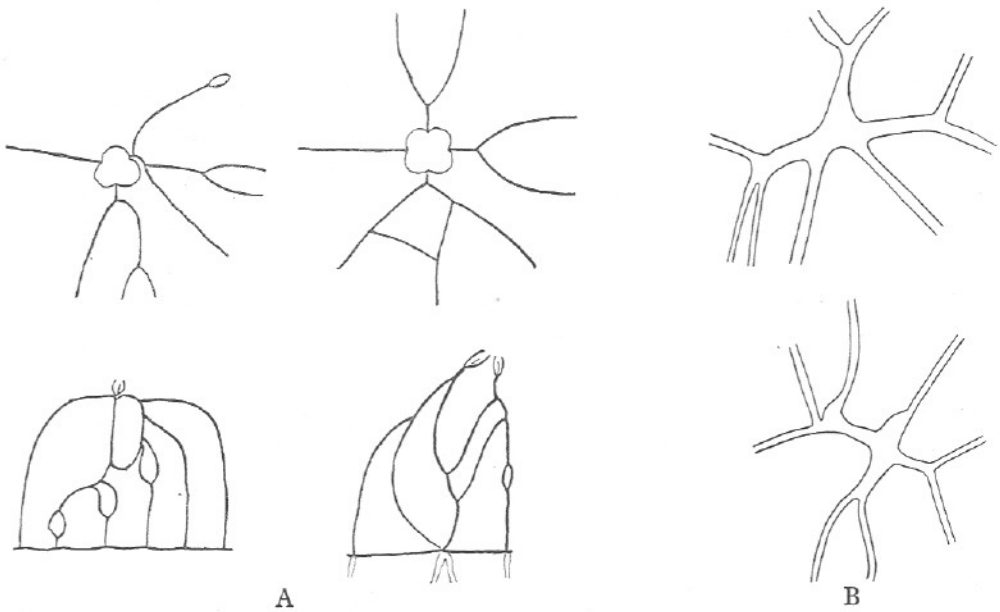
While normally all the canals are centrifugal, an instance has been recorded by Kramp (1926*a*, p. 97) in which one centripetal canal running blindly upwards from the ring canal was seen.

In normal branching eight radial canals join the ring canal, but it is quite easy to realize that this number may be greater in abnormal specimens. Even when the branching is abnormal the symmetry at the umbrella margin may be maintained; this is so, for instance, when one primary canal does not bifurcate but another gives rise to three branches, or when supernumerary branches rejoin and run to the margin as a single canal. The greatest number of canals joining the ring canal is that recorded by Vanhöffen (1911) in which each of the original bifurcations from the primary canals bifurcated again to produce sixteen canals. Kramp (1924, p. 15, no. 3)

recorded a specimen in which ten canals joined the ring canal although there were only three primary canals present.

Kramp remarks that supernumerary canals may be formed in two different ways; either by bifurcation during the growth of the canal towards the umbrella margin before the ring canal is reached, or by the development of side branches either during the growth of the canal or after it has reached the ring canal.

The gonads are entirely interradial. A normal gonad is shown in Text-fig. 113A, B. In the lower two-thirds of the stomach, below the points of departure of the primary radial canals, the gonads are folded transversely to form three or four horizontal cushion-like folds. The triangular



Text-fig. 114. *Bythotiara murrayi*. A, abnormal branching of radial canals in four specimens from the Mediterranean (after Kramp, 1924, fig. 11); B, abnormal arrangement of radial canals in two specimens caught 50 miles W.N.W. of Tearaght, Ireland.

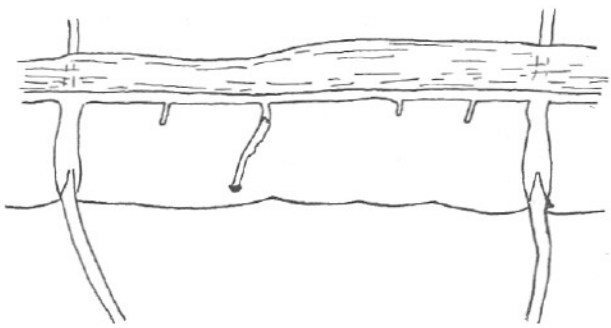
mass fitting between the two arms of the cross-shaped lines of attachment of the upper dome-shaped portion of the stomach to the subumbrella is depressed in its centre, so that a lower horizontal cushion and two upper lateral vertical cushions are formed. Sometimes the horizontal folding is not so regular as that figured. Irregularity is also naturally more marked when the numbers and branching of the primary radial canals are abnormal. When there are five primary canals the stomach may be five-sided and there are then five gonads.

The primary marginal tentacles are normally eight in number, and these are situated one opposite each junction of a radial canal with a ring canal. In specimens with abnormal branching of the radial canals the number of primary marginal tentacles is still usually eight, although nine may sometimes occur. Kramp (1924, p. 15, no. 4) records a specimen in which there are only eight radial canals joining the ring canal but nine primary marginal tentacles, two of which are practically contiguous.

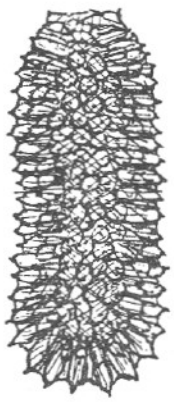
The primary marginal tentacles leave the umbrella margin some distance from the ring canal, but their unswollen bases run inwards through the lower exumbrellar side of the jelly to the ring canal (Text-fig. 115).

The primary marginal tentacles are of a very delicate transparent nature and of uniform thickness throughout their length. They have no nematocysts except in the terminal cluster. Near its extremity the primary marginal tentacle gradually widens to form a broad end on which there is a large opaque hemispherical cluster of nematocysts.

The small secondary marginal tentacles appear irregularly distributed, and there may be one to five between every two primary marginal tentacles. Possibly they have a normal sequence of development but some are lost in preserved specimens. These secondary marginal tentacles are reputed to be similar to the primary marginal tentacles except for their much smaller size. In the specimens I have seen, however, they differ in that they are covered with nematocysts



Text-fig. 115. *Bythotiara murrayi*. Portion of umbrella margin. (After Kramp, 1924, fig. 9.)



Text-fig. 116. *Bythotiara murrayi*. Tertiary marginal tentacle. (After Kramp, 1924, fig. 10.)

along their whole length, though in some the nematocysts may be rubbed off. In view of this I think it most probable that the even smaller tertiary marginal tentacles described by Kramp (1924) (Text-fig. 116) are merely developing secondary marginal tentacles.

The secondary marginal tentacles are attached to the umbrella margin immediately adjacent to the ring canal.

NEMATOCYSTS. ? Microbasic euryteles and desmonemes (Russell, 1940*a*).

Seasonal occurrence

Since *Bythotiara murrayi* is a deep-sea medusa it seems probable that it may be found at any time of the year. The records from the south-west and west of Ireland were in June and November. In other regions of its distribution it has been recorded in February, May, July, August and September.

Habits

Bythotiara murrayi is a deep-sea oceanic medusa, but there are no exact observations as to the shallowest depth at which it may be found. Usually the medusae have been taken in nets fishing with 1000 m. or more of wire out. The specimens taken 50 miles west of Tearaght were caught in a D-net at 350 fathoms.

HYDROID. Not known.

Historical

Bythotiara murrayi was first described by Günther (1903*a*) from a single incomplete specimen off the south-west coast of Ireland in 52° 18′ N., 15° 54′ W. All additional knowledge about the species has been given under the name Günther gave it.

Family TIARANNIDAE

Anthomedusae with umbrella without apical process and tending towards the hemispherical leptomedusan form; without exumbrellar nematocyst tracks; with large stomach not extending beyond umbrella margin, attached to subumbrella along four perradial furrows; mouth with four simple or slightly crenulated lips; with four simple radial canals and without centripetal canals; with folded gonads on interradial walls of stomach or forming adradial pouches in perradial extensions of stomach along course of radial canals on subumbrellar surface; no asexual budding of medusae; with numerous hollow marginal tentacles with conical basal bulbs; with hollow spindle-shaped marginal 'cordylus'-like structures with nematocysts at distal end; without ocelli.

HYDROID. Not known.

The Tiarannidae form an intermediate family between the Pandeidae and the Laodiceidae in the Leptomedusae. The family contains two genera, *Tiaranna* Hartlaub and *Chromatonema* Fewkes. Of these two, *Tiaranna* has previously been included in the Pandeidae and *Chromatonema* in the Laodiceidae. *Chromatonema* was, however, removed by Ranson (1936) to the Anthomedusae and placed in the family Williadae; the genus bears no relationship to the Williadae and is obviously much more closely related to *Tiaranna* (Russell, 1940*a*).

One of the chief characteristics of the Tiarannidae is the possession of marginal 'cordylus'-like structures with many terminal nematocysts. These differ from the true cordyli of the Laodiceidae in having many terminal nematocysts. It should, however, be noted that a few nematocysts are found in the cordyli of *Ptychogena crocea*, a fact which emphasizes the close affinities of the Tiarannidae with the Laodiceidae.

Genus **Tiaranna** Hartlaub, 1914

MEDUSAE. Tiarannidae with folded gonads on interradial walls of stomach.

HYDROID. Not known.

Only one species of *Tiaranna* has been recorded near the British Isles, *T. rotunda* Quoy & Gaimard. It is a deep-water species and is recognizable by the marginal 'cordylus'-like structures and by the form of the stomach, the upper portion of which is pushed up into the apical jelly of the umbrella in the form of a pyramid.

Tiaranna rotunda (Quoy & Gaimard)

Text-figs. 117, 118A, B, 119

Dianaea rotunda Quoy & Gaimard, 1827, *Ann. Sci. Nat.* tome X, p. 181, pl. viA, figs. 1, 2.
Oceania rotunda, Eschscholtz, 1829, *System der Acalephen*, p. 100.
Pandea rotunda, Lesson, 1843, *Hist. Nat. Zooph. Acalèphes*, p. 289.
Tiara rotunda, Haeckel, 1879, *System der Medusen*, p. 57, pl. iii, figs. 9, 10.
Maas, 1910, *Bull. Inst. Océanogr. Monaco*, no. 183, p. 8.

TIARANNIDAE

Turris rotunda, Mayer, 1910, *Medusae of the World*, vol. I, p. 124.
Tiaranna rotunda, Hartlaub, 1914, *Nordisches Plankton*, Lief. 17, XII, p. 266, figs. 218, 219.
Kramp, 1919, *Danish Ingolf-Expedit.* vol. V, pt. viii, p. 5, text-figs. 1, 2.
Kramp, 1920*a*, *Rep. Sci. Res.* '*Michael Sars*' *N. Atlantic Deep-Sea Expedit.* 1910, vol. III, pt. ii (1913–21), p. 6, pl. i, figs. 2–4 (1932).
Kramp & Damas, 1925, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. LXXX, p. 275, figs. 21, 22.
Kramp, 1926*a*, *Danish Ingolf-Expedit.* vol. V, pt. x, p. 68.
Ranson, 1936, *Rés. Camp. Sci. Monaco*, Fasc. XCII, p. 67, pl. i, figs. 10, 11.
Rotundula brochii Hartlaub, 1917, *Nordisches Plankton*, Lief. 19, XII p. 411, figs. 341–3.

Specific Characters

Sixteen to twenty-eight marginal tentacles.

Description of Adult

Umbrella hemispherical, about as wide as high or wider; jelly very thick; no apical process. Velum well developed. Stomach short and broad, in form of pyramid pushed up into apical jelly, attached to subumbrella along four boundaries of pyramidal faces. Mouth with slightly crenulated margins. Four straight narrow radial canals issuing from lower corners of stomach at junction with mouth. Ring canal narrow, widening opposite each marginal tentacle. Gonads transversely folded, on interradial walls of stomach, folds more prominent adradially. Marginal tentacles usually sixteen in number, reaching as many as twenty-eight, hollow, smooth, with conical basal bulbs. One to three, rarely four, spindle-shaped hollow marginal cordylus-like structures between adjacent marginal tentacles, terminating with abundant nematocysts. No ocelli seen. Diameter of umbrella up to 22 mm. Colour of stomach, canals, gonads and marginal tentacle bulbs, carmine red to violet.

Distribution

Tiaranna rotunda is a deep-sea oceanic medusa and it has not yet been recorded from the British area. Its distribution is such, however, that it may be found over deep water off the western and northern coasts of the British Isles. It has been recorded by Hartlaub from the northern North Sea.

Elsewhere it has been recorded from Norway, the Skagerak, Davis Strait, Irminger Sea, and the western end of the Mediterranean.

Structural Details

The early development of *Tiaranna rotunda* has not been described, nor is its hydroid known.

The umbrella is often wider than high and the subumbrellar cavity is very wide, and approaching the leptomedusan type. The apical jelly is very thick, its height being nearly that of the subumbrellar cavity. Some dimensions of the umbrella have been given as follows:

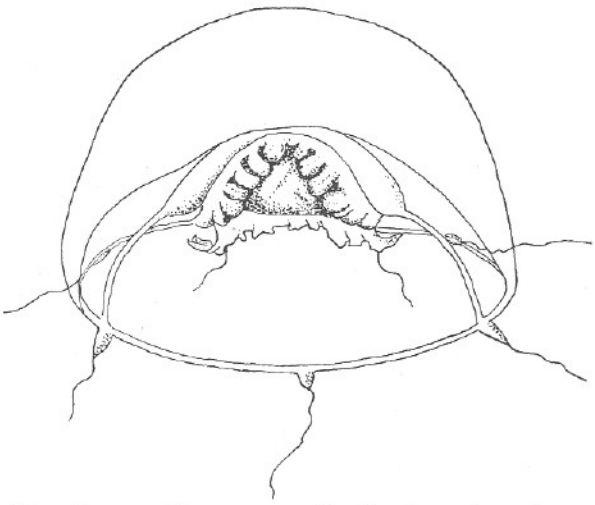
Umbrella		Height of subumbrellar cavity (mm.)	Thickness of jelly (mm.)	
Diameter (mm.)	Height (mm.)			
12	12	7	5	(Maas, 1910)
10–12	12	5	—	(Maas, 1910)
15	12	—	—	(Kramp, 1920*a*)
18	15	—	—	(Kramp, 1920*a*)
22	19	—	—	(Kramp & Damas, 1925)

The form of the stomach has been explained by Ranson (1936) on the principle that in young medusae the quadrangular base of the stomach is horizontal and attached to the subumbrella along the arms of a perradial cross. The base of the stomach is then pushed upwards into the

mesogloea by growth. It thus forms a pyramid and the boundaries of the four sides of the pyramid are the four arms of the original perradial cross along which the stomach is attached to the subumbrella. These four lines of attachment tend to become vertical and draw the mesogloea inwards to form four buttresses. In this way the points at which the radial canals issue from the stomach tend to be lowered and the radial canals consequently ascend a short distance at first before curving downwards towards the umbrella margin. The four triangular faces of the stomach bounded by the four mesogloeal buttresses are unattached, so that four pouches are formed in the apical part of the subumbrellar cavity.

According to Kramp (1920*a*) the mouth is faintly divided into four lips.

The gonads (Text-figs. 117, 118A) are stated by Hartlaub (1914) and Ranson (1936) to form adradial folds only, but Kramp (1920*a*) recorded folding also on the interradial region in the specimens he saw. In one specimen the gonads contained a number of comparatively large, whitish eggs, also in the interradial part. According to Kramp the folding is fairly regular, about twelve transverse folds being present in each gonad. Kramp & Damas (1925) also state that the interradial part is without gonads.



Text-fig. 117. *Tiaranna rotunda*. Specimen about 6 mm. high from the northern North Sea. (After Hartlaub, 1914, fig. 219.)

The conical basal bulbs of the marginal tentacles (Text-fig. 118B) have no exumbrellar spurs.

The marginal 'cordylus'-like structures (Text-fig. 119) are spindle-shaped and somewhat resemble those of *Chromatonema rubrum*. Their central part is swollen and they taper distally. They are inserted directly on the umbrella margin. According to Ranson (1936) they are only hollow in the middle portion, the endoderm cells fusing at the extremities. In the adult at any rate they do not communicate with the ring canal, but their endoderm is a prolongation of that of the canal.

The carmine to violet colour is fainter on the gonads and buccal region of the stomach. Kramp & Damas (1925) state that all the endodermal parts are coloured. In formalin the stomach and marginal tentacles are orange (Kramp, 1920*a*). Maas (1910) says that the canals and marginal tentacle bulbs may be yellow to rose.

Kramp & Damas (1925) described a specimen in which owing to the contraction of the jelly round the stomach the manubrium was, so to speak, buried in a niche completely isolated from the rest of the subumbrellar cavity. They conclude that *Rotundula brochii* described by Hartlaub (1917) was really a *Tiaranna rotunda* in a similar state of contraction.

Ranson (1936) describes and figures an abnormal specimen in which there were five radial canals and a corresponding number of gonads.

NEMATOCYSTS. Microbasic euryteles (Russell, 1940*a*).

Seasonal occurrence

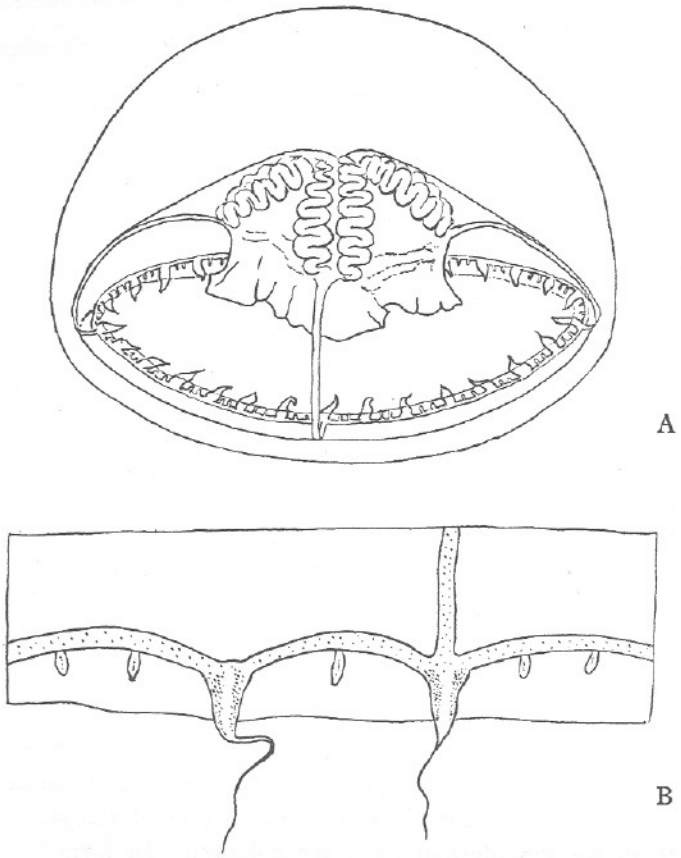
Tiaranna rotunda has been recorded in the months of May, June, August, September and October.

TIARANNIDAE

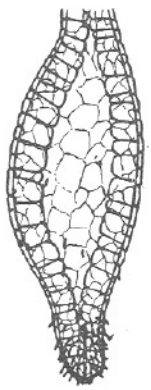
Habits

Nothing is known of the habits of the living medusa beyond that it normally lives in deep water. The shallowest record is that of Hartlaub (1917) from the northern North Sea where the bottom was at 130 m. As Hartlaub suggests, this specimen may have been carried in by water movements from a deeper region.

HYDROID. Not known.



Text-fig. 118. *Tiaranna rotunda*. A, adult medusa × 5; B, portion of umbrella margin × 30. (After Kramp, 1920*a*, pl. i, figs. 2, 3.)



Text-fig. 119. *Tiaranna rotunda*. Dwarf marginal tentacle. (After Kramp, 1919, fig. 2.)

Historical

Tiaranna rotunda was first described and very inadequately figured by Quoy & Gaimard (1827) as *Dianaea rotunda* from the Straits of Gibraltar. It was re-described rather insufficiently by Haeckel (1879) as *Tiara rotunda* in his new subgenus *Tiaranna*.

Genus **Chromatonema** Fewkes, 1882

MEDUSAE. Tiarannidae with gonads in form of series of pouches along proximal regions of radial canals.

HYDROID. Not known.

Only one species of the genus has been recorded near the British Isles, *Chromatonema rubrum* Fewkes. It is a deep-water species and is recognizable by the marginal 'cordylus'-like structures and the formation of the gonads as a series of pouches along the proximal regions of the radial canals.

Chromatonema rubrum Fewkes

Text-figs. 120, 121

Chromatonema rubrum Fewkes, 1882*b*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. IX, no. 8, p. 305, pl. i, fig. 41.
Kramp, 1919, *Danish Ingolf-Expedit.* vol. v, pt. viii, p. 7, pl. i, figs. 1–8; text-fig. 3; chart 1.
Kramp, 1920*a*, *Rep. Sci. Res.* '*Michael Sars*' *N. Atlantic Deep-Sea Expedit.* 1910, vol. III, pt. ii (1913–21), p. 8, pl. i, figs. 5, 6 (1932).
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 552, figs. 14, 15.
Ranson, 1936, *Rés. Camp. Sci. Monaco*, Fasc. XCII, p. 102, pl. ii, fig. 13.
Bigelow, 1938, *Zoologica, New York*, vol. XXIII, pt. ii, no. 5, p. 109.
Kramp, 1942, *Medd. Grønland*, Bd. LXXXI, no. 1, p. 51.
Thaumantias rubrum, Mayer, 1910, *Medusae of the World*, vol. I, p. 199.

Specific Characters

Umbrella up to 27 mm. in diameter; twenty to twenty-four marginal tentacles.

Description of Adult

Umbrella somewhat higher than a hemisphere, a little wider than high; jelly very thick, thinning towards umbrella margin. Velum narrow. Stomach short, quadrangular, and very broad, usually less than two-thirds the height of subumbrellar cavity; with broad quadrangular base attached to subumbrella along arms of perradial cross and continuing outwards to form four gonadial pouches running for half or two-thirds the distance towards umbrella margin; four triangular pouches between dorsal wall of base of stomach and subumbrella. Mouth with four short perradial lips with more or less crenulated margins. Four short straight radial canals and ring canal narrow. Eight rows of ten to sixteen sac-like gonads, one row on each side of each stomach pouch, each sac hanging down into cavity of stomach pouch being a pit in stomach wall immediately adradial to line of attachment with subumbrella; gonads sometimes extending on to central dorsal wall of stomach. Twenty to twenty-four marginal tentacles with hollow conical bulbs with heart-shaped bases; marginal tentacles all of same type. No ocelli. Two, rarely one, cylindrical or spindle-shaped 'cordylus'-like structures between adjacent marginal tentacles, with abundant nematocysts at distal ends. Diameter of umbrella up to 27 mm.; height up to 22 mm. Colour of stomach, radial canals, and ring canal light chocolate brown; marginal tentacles violet; gonads light chocolate brown with faint violet hue.*

Distribution

Chromatonema rubrum is a deep-sea oceanic species which has not been recorded for certain previously† from the British area. I have found one damaged specimen in Mr Browne's collection taken 50 miles north-west of Eagle Island off the west coast of Ireland.

* In preserved specimens stomach, canals and marginal tentacles bright orange or brick red; tentacular bulbs with brownish endodermal pigment.

† In March 1936 a young specimen, possibly of this species, was recorded off Plymouth (Russell, 1937, p. 680).

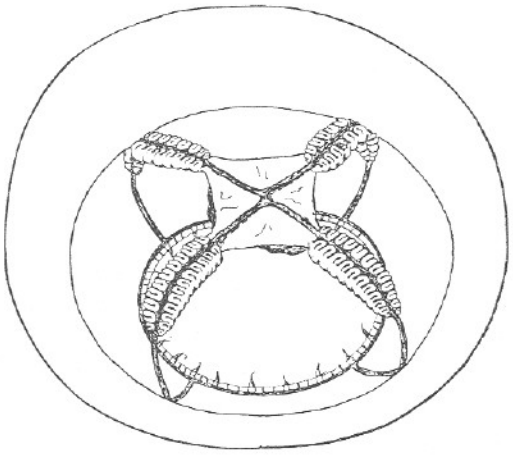
TIARANNIDAE

The medusa is apparently widely distributed in the North Atlantic, bounded in the north by a line between Norway, Faeroes, Iceland, Greenland and Baffin Land. It has been recorded as far south as the Azores and Bermuda. It has been recorded from Norway.

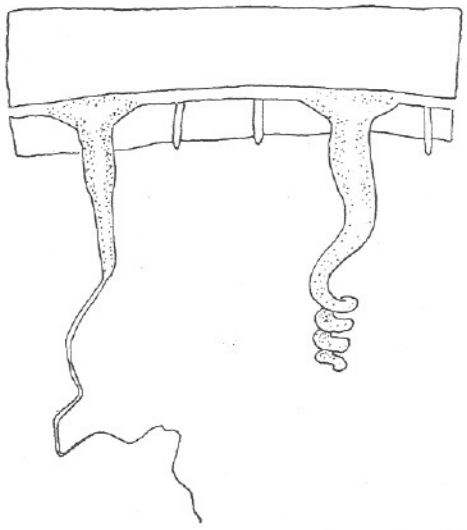
Structural Details

The early development of *Chromatonema rubrum* has not been described, nor is its hydroid known.

The structural details of the adult have been very fully described by Kramp (1919, 1920*a*). The most striking feature of this medusa is the structure of the gonads (Text-fig. 120) and their relation to the gastric system. On this latter point there has been disagreement. Kramp considered that the gonadial pouches should be regarded as the proximal regions of the radial



Text-fig. 120. *Chromatonema rubrum*. Adult medusa seen obliquely from above. (After Kramp, 1919, fig. 3.)



Text-fig. 121. *Chromatonema rubrum*. Portion of umbrella margin with marginal tentacles and 'cordyli'. (After Kramp, 1933*b*, fig. 15.)

canals. Ranson (1936), on the other hand, regards them as pouches from the stomach, and in this respect I think he is correct. The gonads are actually pits in the stomach wall in the immediate adradial region of its attachment to the subumbrella. The lower walls of the stomach pouch are formed from outgrowths from the buccal region of the stomach. This, however, does not in any way invalidate Kramp's detailed description of the structure of the gonads, if one substitutes 'stomach pouch' for his use of the words 'radial canal'. His description is as follows (Kramp, 1919, p. 8):

The line along which the gonadial part of the canal is attached to the subumbrella sends out a number of short lateral branches, so that the attachment of the dorsal wall of the canal has the shape of a pinnate figure. Occasionally this figure is somewhat irregular, or it may be more or less zigzag-shaped. Each of the radial canals contains two rows of sack-shaped gonads, attached to the dorsal wall of the canal in the spaces between the above-mentioned lateral branches of the line of attachment and hanging down into the cavity of the canal. The surface of a gonadial sack is covered with a thin entodermal epithelium, and each sack has a narrow ectodermal lumen communicating with the bell cavity through a fissure in the dorso-lateral wall of the canal. In view of the scarcity of room, the gonads of the two sides of the canal are more or less regularly

alternating. The number of gonads varies from 10 to 16 on either side of the canal. The side walls of the canal are, as a rule, tightly closed over the gonads so that the wall becomes faintly lobed or undulated. In the upper part of the lateral walls of the canal (outside the gonads) the entoderm consists of one layer of cubical or cylindrical cells. In the funnel-shaped part of the canal the lower parts of the lateral walls, which are not pressed by the gonads, are covered with a thicker entoderm, consisting of several layers of cells; evidently the digestion of the food takes place in this part of the radial canal. In larger specimens some of the proximal gonads are frequently developed in the dorsal wall of the stomach on either side of the cross arms.

A transverse section of the gonadial part of the radial canal is pear-shaped in the proximal part, nearly circular in the distal part.

Kramp (1919) states that the marginal tentacles (Text-fig. 121) may be spirally coiled, and that in their contracted state they are deeply and closely transversely wrinkled.

The small 'cordylus'-like structures between adjacent marginal tentacles are hollow. They have a thin ectodermal epithelium and a single layer of cubical endoderm cells surrounding the central lumen. Distally they are crowded with nematocysts. They are colourless and translucent. There is a small cushion on the umbrella margin to which each 'cordylus' is attached.

Kramp (1919) gives detailed dimensions of a male specimen from the Irminger Sea: diameter 14 mm., height 12 mm., length of gonadial pouch 3·5 mm., twelve pairs of gonads in each pouch.

Other dimensions given by Kramp (1919, 1920*a*) are:

Umbrella		
Diameter (mm.)	Height (mm.)	No. of marginal tentacles
9	8	16
11	10	15
11	10	—
13	11	18
14	13	15
15	13	—
17	14	18 (fully mature female)
27	22	*c.* 24 (*c.* 16 gonads on each side of each pouch)

The specimen in Mr Browne's collection must have been about 20 mm. in diameter, and had up to sixteen gonads in each series.

Kramp (1919) records two abnormal specimens. One had only three radial canals. In the other, a female, 22 mm. in diameter, one of the four stomach pouches bifurcated at its proximal end, forming two complete gonadial systems. The two branches reunited distally to form a single radial canal. Two of the other radial canals converged so much distally and joined the ring canal so close together that there was only room for one marginal tentacle between them.

Ranson (1936) also described a specimen with five gonadial pouches and four radial canals. Another specimen he figured was even more abnormal. While one arm of the perradial cross of attachment of the stomach continued normally along a gonadial pouch to the radial canal, the opposite one was short, without gonads, and ended blindly. Of the other two arms one bifurcated before reaching the gonadial part, while the other bifurcated half-way along the gonadial pouch.

The colour of the living medusa was described by Kramp (1942).

NEMATOCYSTS. Microbasic euryteles (Russell, 1940*a*).

Seasonal occurrence

The specimen recorded here from 50 miles north-west of Eagle Island was caught on 11 August 1904.

Other records of capture are in May, June, July, August and September.

TIARANNIDAE

Habits

Nothing is known of the habits of the living medusa beyond that it is a deep-sea species. All specimens so far obtained have been caught in nets with over 700 m. or usually 1000 m. or more of wire out. The only exception is one specimen recorded by Møller in 1843 from the surface off the west coast of Greenland (see also footnote on p. 223).

HYDROID. Not known.

Historical

Chromatonema rubrum was first described and figured by Fewkes (1882*b*) from several distorted specimens off the coast of New England, U.S.A. His description was rather inadequate. We owe to Kramp (1919) the first full and detailed description of the medusa. In his historical discussion Kramp gives an account of a specimen he found in the Zoological Museum of the University of Copenhagen collected by H. P. C. Møller off the west coast of Greenland in 1843. It appears that a drawing of this medusa was made by Møller under the name *Oceania cardinalis*, but after exhaustive search Kramp was unable to find any publication in which it appeared.

Two closely related species have been described, which are regarded by Ranson (1936) as synonymous with *Chromatonema rubrum*. They are *C. erythrogonon* (Bigelow, 1909*a*) from the Pacific and *C. hertwigi* (Vanhöffen, 1911) from the Indian Ocean. The differences are mainly a matter of size and numbers of marginal tentacles. *C. erythrogonon* reaches a size of 38 mm. in diameter and has up to *c.* sixty-four marginal tentacles, and *C. hertwigi* is as much as 50 mm. in diameter but has only twenty marginal tentacles. I agree with Kramp (1919) that we must await further investigations to show whether the three species are distinct or only local varieties of one and the same species.

ORDER

LEPTOMEDUSAE

(HYDROIDA THECATA)

Hydromedusae with hemispherical or flattened umbrella; with gonads confined to radial canals, or on radial canals but contiguous with stomach; marginal sense organs sometimes absent; when present, in form of cordyli, statocysts as open or closed marginal vesicles of ectodermal origin, or occasionally ocelli.

Hydroids thecate, very rarely with naked hydranths.

As with the Anthomedusae no hard and fast definition can be given. The Leptomedusae are consistent in that the gonads are always on the radial canals, but as already stated (p. 46) this condition may also be found in a few Anthomedusae. While the hydroids are as a rule thecate, that is with cup-like hydrothecae into which the polyp can be withdrawn, there are at any rate three genera, *Melicertum*, *Eutima*, and *Octorchis*, in which this is not so. It is possible that the absence of a hydrotheca in these hydroids is a result of secondary reduction from originally thecate forms.

The Leptomedusae have typically a much more flattened umbrella than have the Anthomedusae. Their stomachs also are small compared with those of the Anthomedusae, and the lack of space on the stomach walls possibly explains the position of the gonads on the radial canals.

In general form the Leptomedusae show much less diversity than do the Anthomedusae. For this reason their classification has been evolved very slowly, since they are now classified on small, though not insignificant, characters which were overlooked by earlier workers. One of the chief distinctions is based on the presence or absence of marginal sense organs and on their structure.

The marginal sense organs may be in the form of cordyli (p. 14), open or closed velar marginal vesicles of ectodermal origin (p. 12), or ocelli.

The following ten families of Leptomedusae are represented in British waters:

Laodiceidae, Melicertidae, Dipleurosomidae, Mitrocomidae, Campanulariidae, Lovenellidae, Phialellidae, Eirenidae, Aequoreidae, and Eutimidae.

Among these there are twenty-three British genera with twenty-eight British species.

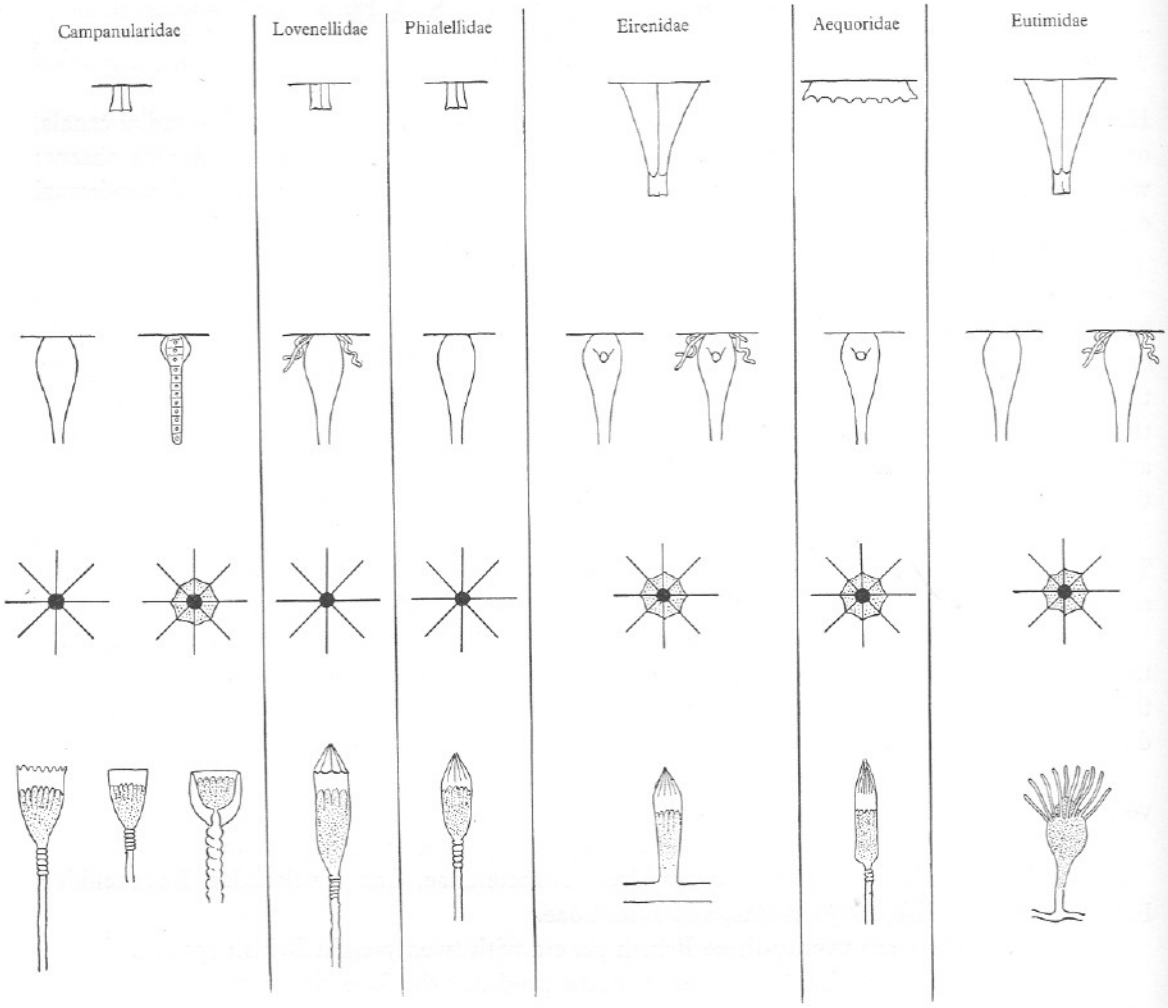
A classification of these families on sense organs produces the following grouping:

With no marginal sense organs	**Melicertidae**, **Dipleurosomidae**
With marginal cordyli	**Laodiceidae**
With open marginal vesicles	**Mitrocomidae**
With closed marginal vesicles	**Campanulariidae**, **Lovenellidae**, **Phialellidae**, **Eirenidae**, **Aequoreidae**, **Eutimidae**

It will be seen that the presence of marginal cordyli or of open marginal vesicles at once separates off the two families, Laodiceidae and Mitrocomidae respectively. These appear to form good natural families.

LEPTOMEDUSAE

The Leptomedusae with no marginal sense organs form rather a heterogeneous mixture and the Thaumantiadae has in the past been used as a repository for such forms.* It is obvious, however, that the two British representatives of the group, *Dipleurosoma* and *Melicertum*, cannot remain in the same family. The hydroid of the former is thecate and *Cuspidella*-like, and that of



Text-fig. 122. Diagram showing certain family characters of the Leptomedusae.

the latter is quite different in appearance and naked. On these grounds I have used the families Dipleurosomidae and Melicertidae.

But in the group with closed marginal vesicles it will be seen that no less than seven families are included. It is in this group of Leptomedusae that the difficulties of classification are greatest, since if the characters of the medusae alone are taken into consideration it is impossible to decide on any satisfactory classificatory character. As a result the majority of these medusae had been lumped together in one large family, the Eucopidae, which has for long been in need of revision.

* All authors are in agreement that the Thaumantiadae has now become an artificial family in need of revision. The name may eventually disappear.

A knowledge of the hydroids belonging to the medusae in this group shows that it is possible to split them into fairly well-defined families. By combining the medusa and hydroid characters a key to these seven families, in which the marginal vesicles are closed, becomes as follows:

Medusae without peduncle:
- Without excretory pores:
  - Hydrotheca without operculum . . . . . **Campanulariidae**
  - Hydrotheca with operculum:
    - Medusae with lateral cirri . . . . . **Lovenellidae**
    - Medusae without cirri . . . . . **Phialellidae**
- With excretory pores . . . . . **Aequoreidae**

Medusae with peduncle:
- Without excretory pores . . . . . **Eutimidae**
- With excretory pores . . . . . **Eirenidae**

Although the original grouping of these medusae was based on the characters of the hydroids this key shows that in fact they can be separated on the medusa characters alone except for the Phialellidae and Campanulariidae, both of which have no lateral cirri. A more detailed comparison of the characters of these families may be found on p. 284, and these characters are shown pictorially in Text-fig. 122.

Family LAODICEIDAE

Leptomedusae with base of stomach attached to subumbrella along edges of radial furrows; with quadratic four-lipped mouth, or, rarely, with very large cross-shaped mouth; with four to eight radial canals, simple or branched; with gonads on radial canals contiguous with stomach, simple or divided; with hollow marginal tentacles; with or without marginal cirri; with marginal cordyli; without marginal vesicles; with or without ocelli.

Hydroid *Cuspidella*-like, with single whorl of filiform tentacles; with hydrotheca without stalk and with folded operculum.

The distinctive character of the medusae of the family Laodiceidae is the marginal cordylus which is found in no other family, although a somewhat similar structure occurs in medusae of the Tiarannidae in the Anthomedusae. The first adequate description of a cordylus was given by Brooks (1895) and it is usually imagined that it serves as a sense organ, although its true function has never been shown. Two other characters of importance are the absence of marginal vesicles and the form of the gonad. Although the gonad is developed along the course of the radial canal, its proximal end is never distinctly separated from the stomach. In this respect it is possible that the Laodiceidae stand nearest to the Anthomedusae.

The Laodiceidae are represented in British waters by two genera, *Laodicea* Lesson and *Staurophora* Brandt. The two genera are at once distinguishable by the form of the mouth which is of the normal leptomedusan type in *Laodicea*, but which in *Staurophora* is in the form of a large cross, each lip being continued for a great distance along the course of the radial canal.

It is possible that a third genus, *Ptychogena* A. Agassiz, may some day be found to occur in deep water off the British Isles, but it has not yet been recorded. There are two north eastern Atlantic species, *P. lactea* A. Agassiz and *P. crocea* Kramp & Damas. The former is a purely arctic species, but *P. crocea* occurs on the Norwegian coast and has so far only been recorded from that region.

Genus **Laodicea** Lesson, 1843

MEDUSAE. Laodiceidae with small stomach; with four simple crenulated mouth-lips; with four radial canals; with simple wavy gonads; with marginal cirri; with adaxial ocelli.

HYDROID. Where known, *Cuspidella* with characters as family.

There is only one British species of the genus, *Laodicea undulata* (Forbes & Goodsir). There should be no difficulty in the identification of this medusa once the presence of marginal cordyli and ocelli has been ascertained. Indeed, it is the only British species of the Leptomedusae which has numerous black ocelli, except *Staurophora* which is easily distinguishable by the form of its mouth.

Laodicea undulata (Forbes & Goodsir)

Plate XIV, figs. 1–3; Text-figs. 123–31

Thaumantias undulata Forbes & Goodsir, 1851, *Trans. Roy. Soc. Edinb.* vol. xx, p. 313, pl. x, fig. 7.
Thaumantias confluens Forbes & Goodsir, 1851, ibid. p. 314, pl. x, fig. 8.
Thaumantias mediterranea Gegenbaur, 1856, *Z. Wiss. Zool. Leipzig*, Bd. viii, p. 237, pl. viii, figs. 1–3.
Laodicea calcarata L. Agassiz, 1862, *Contrib. Nat. Hist. U.S.* vol. iv, p. 350.
Cosmetira punctata Haeckel, 1864, *Jena Z. Naturw.* Bd. i, p. 334.
Lafoea calcarata, A. Agassiz, 1865, *N. Amer. Acaleph.* p. 122, figs. 184–9 (medusae only; *non* hydroid).
Laodice ulothrix Haeckel, 1879, *System der Medusen*, p. 133, pl. viii, figs. 5–7.
Browne, 1907*b*, *Ann. Mag. Nat. Hist.* ser. 7, vol. xx, p. 460.
Laodice calcarata, Haeckel, 1879, *System der Medusen*, p. 134.
Brooks, 1895, *J. Morph. Philadelphia*, vol. x, p. 287, pl. xvii.
Browne, 1897*a*, *Proc. Zool. Soc. London*, p. 823, pl. xlix, fig. 4.
Browne, 1907*b*, *Ann. Mag. Nat. Hist.* ser. 7, vol. xx, p. 460.
?*Ptychogena longigona* Maas, 1893, *Ergebn. Plankton Expedit. Humboldt-Stift.*, Bd. ii, K. c., p. 64, pl. vi, figs. 7–9.
Hebella calcarata, Nutting, 1901*a*, *Bull. U.S. Fish. Commiss. Washington*, vol. xix (1899), p. 378, fig. 94 (*non* hydroid).
Laodice undulata, Browne, 1907*b*, *Ann. Mag. Nat. Hist.* ser. 7, vol. xx, p. 460.
Laodicea cruciata, Mayer, 1910, *Medusae of the World*, vol. i, p. 201, pl. xxi, figs. 4, 5; pl. xxii, figs. 2–6; pl. xxiii, figs. 1–3; text-figs. 104, 105.
Laodicea bigelowi Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. xx, p. 60, pl. iii, figs. 30, 31.
Laodicea undulata, Kramp, 1919, *Danish Ingolf-Exped.* vol. v, pt. viii, p. 16, chart ii, pl. ii, figs. 1–8.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, xii, p. 554, figs. 16–18, and 9*a*.

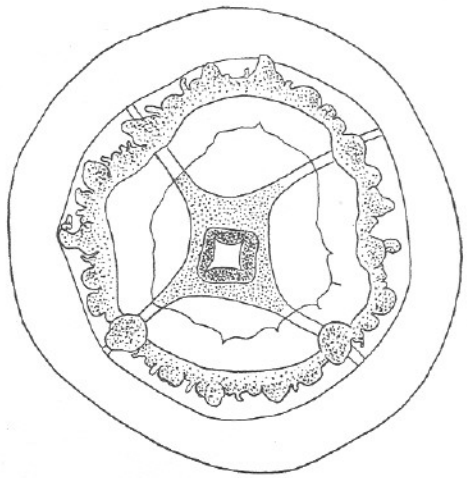
Specific Characters

Marginal tentacles, up to 300 or more in number, with basal endodermal spurs; usually one marginal cordylus between adjacent marginal tentacles; one or two marginal cirri between adjacent marginal tentacles, but sometimes absent or missing.

Description of Adult

Umbrella somewhat variable in shape, usually slightly flatter than a hemisphere; jelly fairly thin. Velum broad. Stomach quadratic, short; attached to subumbrella along arms of perradial cross. Mouth having four lips with folded margins; four straight radial canals and ring canal narrow. Gonads on upper parts of sides of four pouches formed by radial canals and lateral extensions of stomach tissue; extending to within short distance of umbrella margin; with five to eight pairs of lateral folds. Marginal tentacles hollow, 200–300 or more in number, with very

slight basal bulbs and abaxial spur-like endodermal processes on exumbrella; small single ocelli on adaxial sides of some marginal tentacle bases, variable in number. One to two small spiral cirri between adjacent marginal tentacles, sometimes missing. Usually one marginal cordylus between adjacent marginal tentacles; cordyli without nematocysts. Diameter up to 26 mm. (in British waters). Colour of stomach, gonads and marginal tentacle bases usually very delicate; sometimes colourless; gonads usually pinkish; bases of marginal tentacles slightly yellowish; colours vary from dark yellow, brown, pink to pale violet; ocelli black, dark violet or dark brown.



Text-fig. 123. *Laodicea undulata*. Preserved specimen 2·25 mm. in diameter, off Mount's Bay, Cornwall, 26. vii. 35. (Collected by C. F. Hickling.)

Distribution

Laodicea undulata is a medusa with a wide distribution. Off the British Isles it occurs most commonly on the northern, western and south-western coasts, although it has not been found at Millport. On the east coast it has not been recorded south of St Andrews. It has been recorded from Newhaven and the Dover Straits, but is probably scarce in the eastern part of the English Channel.

Elsewhere it has been recorded from the Belgian coast, the Skagerak, Atlantic waters between Iceland and Scotland, Iceland, the Portuguese coast, and the Mediterranean and Black Sea (see Thiel, 1935). It occurs on the North American coasts of the Atlantic from Massachusetts Bay to Cuba and the West Indies. It is possible that it may occur in the Pacific (see p. 239).

The medusa is evidently a coastal form in those regions bathed by oceanic water and may be found far out to sea; it seems to be an indicator of *Sagitta elegans* water.

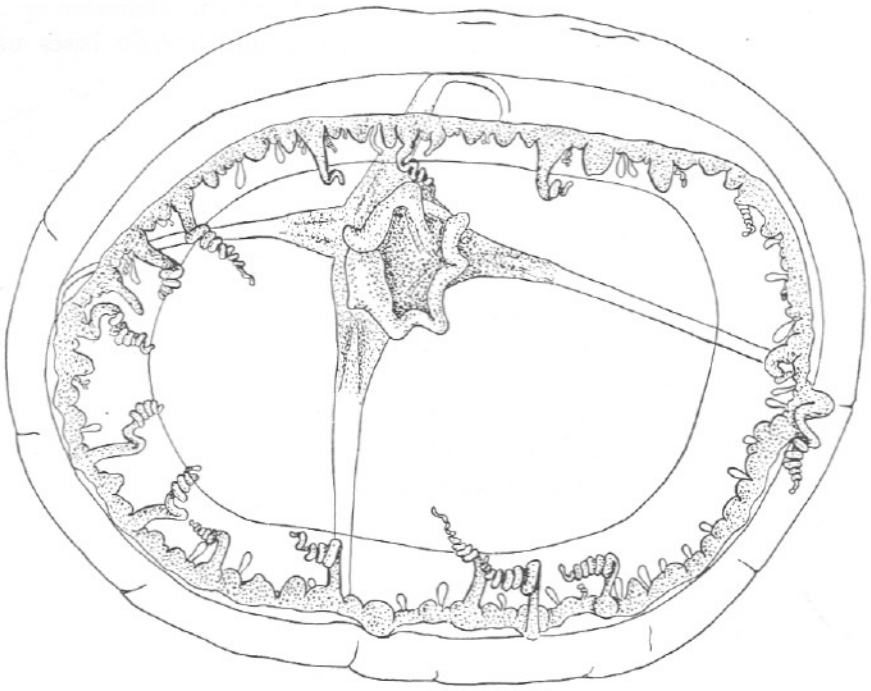
Developmental Stages and Structural Details

On liberation from its hydroid, a *Cuspidella* sp., the medusa *Laodicea undulata* is 0·7 mm. in height. The umbrella is bell-shaped, higher than wide, with uniformly thin jelly. There are numerous large nematocysts scattered on the exumbrellar surface. The velum is wide. The four radial canals and ring canal are narrow. The stomach is very short and the mouth is simple. There are two fully developed opposite perradial marginal tentacles and two opposite perradial developing marginal bulbs. There are four interradial spiral cirri on the umbrella margin and the rudiments of adradial cirri are situated one on one side of each of the two developing marginal bulbs. There are no marginal cordyli. There is a single black adaxial ocellus on each of the two tentacular and two developing marginal bulbs. The colour of the stomach and tentacular and developing marginal bulbs is very pale yellow.

As the medusa develops, the addition of new marginal tentacles and cirri is rapid, but the marginal cordyli do not appear until the medusa is about 2 mm. in diameter and has sixteen or more marginal tentacles.

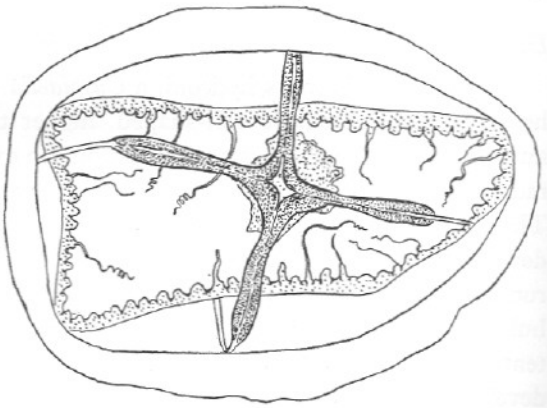
Stomach and gonads. The stomach soon develops to a quadratic form and is then only attached to the subumbrella along the arms of a narrow perradial cross; the arms of this cross do not always

meet at one point. By this method of attachment to the subumbrella four triangular pockets are formed, in both young and adult medusae, between the unattached dorsal wall of the stomach and the subumbrellar surface when the medusa is preserved with the mouth open (Text-fig. 128).



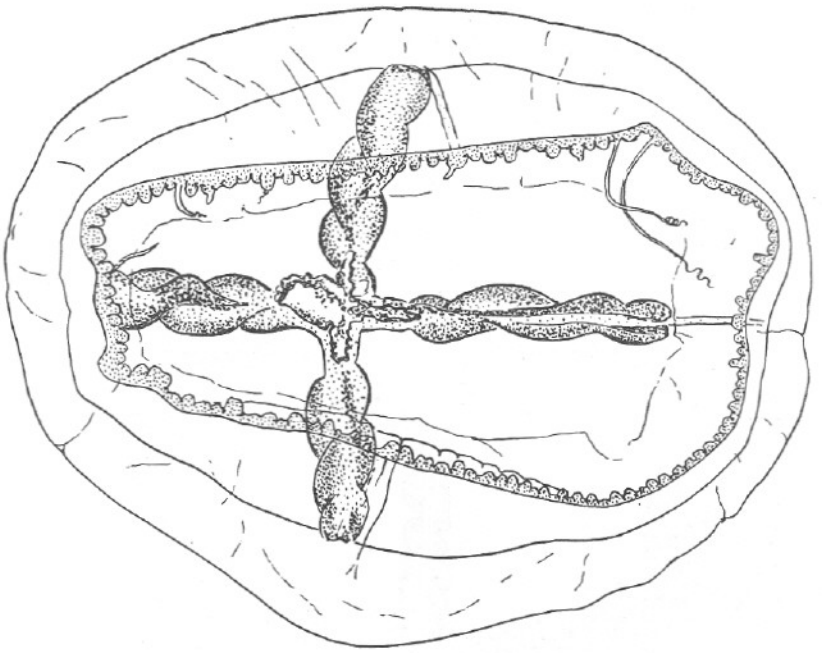
Text-fig. 124. *Laodicea undulata*. Preserved specimen *c.* 3·75 mm. in diameter, Plymouth, 25. vii. 34.

When the medusa is only about 3 mm. in diameter outgrowths develop from the stomach along the radial canals forming short folds which extend from the stomach and just arch over the top of the umbrella cavity (Text-fig. 124). They give the stomach the appearance of possessing four short lobes. These pouches grow eventually along the radial canals to within a short distance of the umbrella margin with the gonads developed on their sides (Text-figs. 125, 126, 127). They hang down like folds within the umbrella cavity and cross-sections show that when fully developed they are rather peculiar in structure. The upper parts of the sides of the pouches appear to be a downward development of radial canal tissue; it is on these portions that the gonads are developed. The lower portions of the pouch sides are gonad-free and appear as lateral extensions of large digestive cells from the stomach. The pouches are thus continuous cavities having as their dorsal walls the dorsal walls of the radial canals and serving the dual purpose of gonad production and digestion. Such a feature is



Text-fig. 125. *Laodicea undulata*. Preserved specimen *c.* 5 mm. in diameter seen from above, Plymouth, 11. ix. 35.

rather unusual among medusae so far as is known, and it was first brought to notice by Kramp (1919) in certain Laodiceids. The gonads themselves develop a series of five to eight swellings or pockets in the walls of the pouches on either side, often giving the whole a waved appearance. They are often slightly separated from the subumbrella distally.



Text-fig. 126. *Laodicea undulata*. Preserved specimen *c.* 10 mm. in diameter seen from below, Plymouth, 11. ix. 35.

The young egg cells are in the ectoderm and there is a fairly strong mesosarc which is only slightly pushed in towards the endoderm (Kramp, 1932, p. 325).

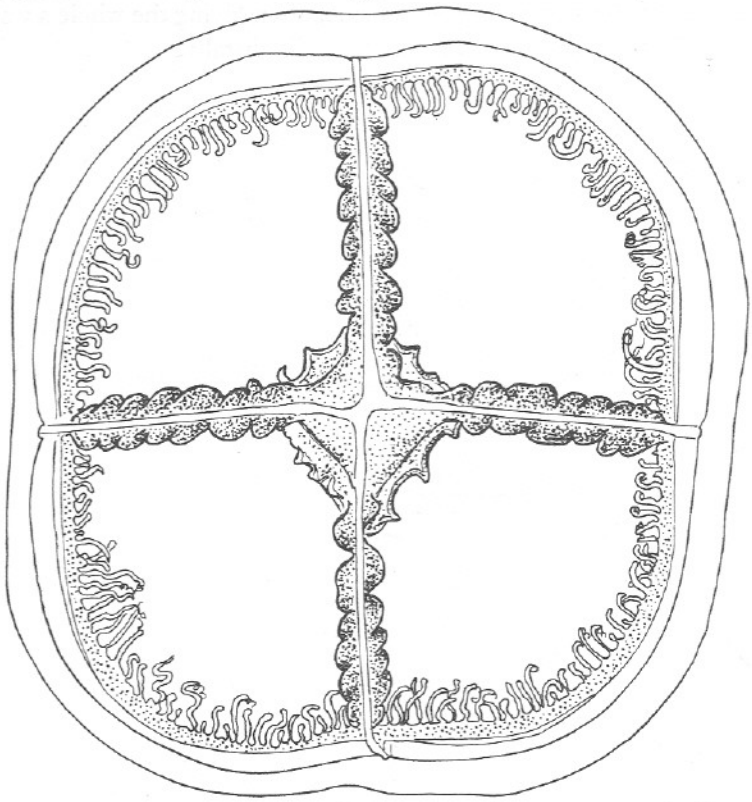
Marginal tentacles. The number of marginal tentacles is somewhat variable but depends naturally on the size of the medusa. Browne (1897*a*) gives the following numbers of marginal tentacles for specimens of different sizes from Valencia:

Diameter (mm.)	No. of marginal tentacles
3	*c.* 30
6	*c.* 60
9	*c.* 100
11	*c.* 120
17	*c.* 230
26	*c.* 300 or more

Kramp (1919) gives the following figures for medusae found in the waters round Scotland, the Faeroe Islands, Iceland, Norway and Denmark:

Diameter (mm.)	No. of marginal tentacles
5	48
7	100–140
8	160–180
11–15	230
16–20	290
21–25	390
26–30	440

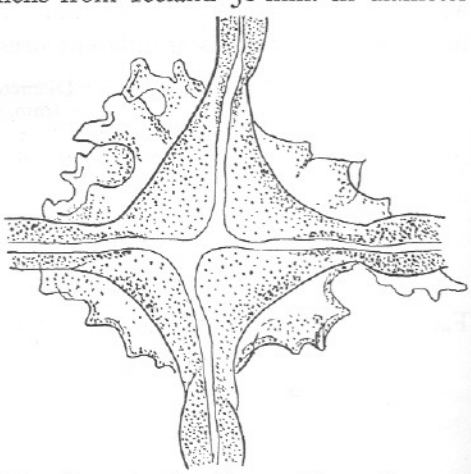
The largest specimens examined by Kramp were 37 mm. in diameter with *c.* 500 marginal tentacles from east of the Orkney Islands and 35 mm. with *c.* 620 marginal tentacles from south



Text-fig. 127. *Laodicea undulata*. Preserved specimen *c.* 15 mm. in diameter, Valencia, May 1899. (E. T. Browne collection.)

of Iceland. There appears possibly to be an increase in the number of marginal tentacles in more northerly waters. Kramp (1939*b*) records specimens from Iceland 50 mm. in diameter or more.

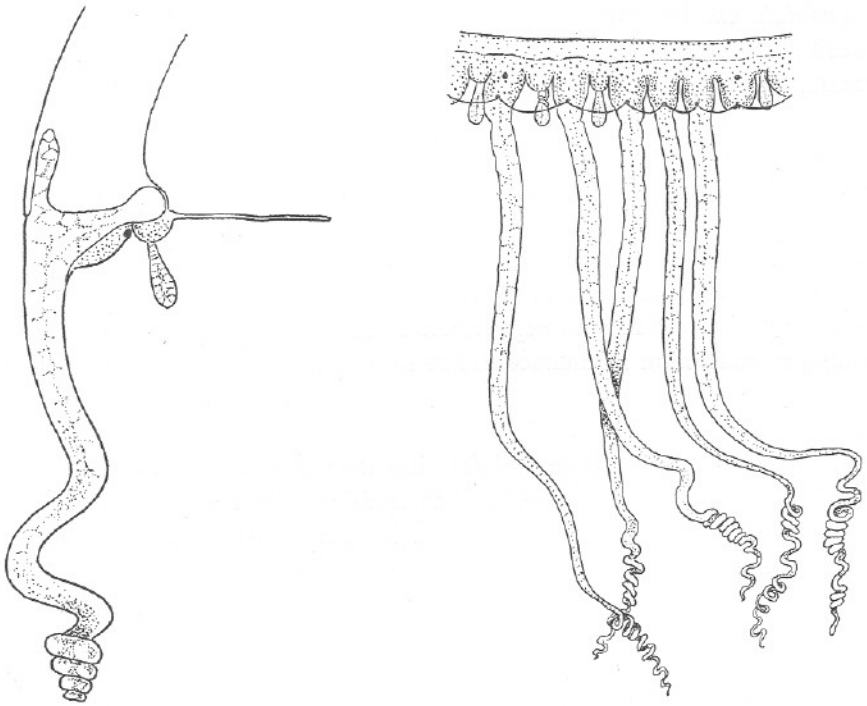
In preserved specimens the distal ends of the marginal tentacles are generally spirally coiled (Text-fig. 129B). The marginal tentacle bases are only slightly swollen. The histological details have been studied by Kramp (1919). The ectoderm of the basal bulb is thin, except on the adaxial side where it is partially thickened. The marginal tentacles are hollow, with a canal of rather uneven thickness running centrally except at the base where it is nearest the adaxial side. In young marginal tentacles there is an abaxial endodermal process or spur imbedded in the gelatinous substance of the exumbrella margin (Text-fig. 130A). The marginal tentacle first appears on the inner adaxial side of the umbrella margin but later it becomes carried by unequal growth of the bulb outwards on the



Text-fig. 128. *Laodicea undulata*. Stomach of preserved specimen with mouth open, drawn from above.

umbrella margin, thus the oldest marginal tentacles arise from the exumbrella a little above the margin itself.

The adaxial ocelli are very variable in number. There may be one on nearly every alternate marginal tentacle, or there may be several adjacent marginal tentacles with ocelli alternating with a number of adjacent marginal tentacles without ocelli. They may be very few in number compared with the number of marginal tentacles or they may be very nearly as numerous as the marginal tentacles; for instance Browne (1897*a*) observed eighty-eight ocelli on a specimen with 228 marginal tentacles, while in another large specimen nearly every marginal tentacle had an ocellus.



Text-fig. 129. *Laodicea undulata*. A, diagrammatic view of a section through the umbrella margin, with marginal tentacle and cordylus; B, portion of the umbrella margin of a specimen 10 mm. in diameter showing marginal tentacles, Plymouth, 11. ix. 35.

Spiral marginal cirri. The marginal cirri coil spirally and are thickly beset with nematocysts (Text-fig. 130C, E). They are very variable in number. Usually there are one or two between adjacent marginal tentacles. In preserved material there are often very few marginal cirri to be seen as they are easily lost; they may at times be entirely absent. A marginal cirrus is occasionally to be found on the outer side of a basal bulb of a marginal tentacle in the position of the spur.

Marginal cordyli. The marginal cordyli have been described in detail by Brooks (1895). They lie close to and below the velum and are usually directed inwards (Text-fig. 129A). They are typically club-shaped, having a thick distal portion and a narrow peduncle (Text-fig. 130D, E). The shape is, however, somewhat variable, as is also the size of the enclosed lumen. There is usually one marginal cordylus between adjacent marginal tentacles but their numbers are variable. Occasionally they number more than the marginal tentacles but as a general rule less. As Kramp (1919) has said, the number must depend on the development of the marginal tentacles, and

inequalities between the numbers of marginal cordyli and marginal tentacles may be due to the incomplete development of some tentacles.

Abnormalities. An abnormal female was taken at Valencia in August, 1899, which was 15 mm. in diameter and had five radial canals, five gonads and five mouth-lips.

The development of the hydroid from the egg has been followed by Metschnikoff (1886*a*, as *Laodice cruciata*) and the hydroid has been reared from the egg at Plymouth (Russell, 1936*a*).

The eggs are 0·18 mm. in diameter, and when fully developed the planula reaches a length of *c.* 0·4 mm.

Zoia (1895*b*) experimented on the development of isolated blastomeres.

Laodicea undulata can be distinguished at once from all other British Leptomedusae by its numerous ocelli. *Tiaropsis multicirrata* also has ocelli but never more than eight.

NEMATOCYSTS. Microbasic mastigophores and atrichous haplonemes (Russell, 1940*a*).

Seasonal occurrence

Laodicea undulata has been recorded from April to November inclusive at Valencia, where it was most abundant in May and in July, August and September and occasionally as late as November. At Plymouth it has been seen from February to November inclusive, with a period of maximum abundance in August and September. In other localities in the British Isles it has been recorded variously from May to September. The medusa is thus a spring and summer form usually reaching its maximum abundance in late summer.

Habits

When swimming actively *Laodicea undulata* has its marginal tentacles contracted with the basal regions held straight and the distal ends spirally coiled. When the medusa is poised motionless in the water the marginal tentacles are held in two positions. 'The basal portion of one tentacle points upwards, and that of the adjacent one slopes slightly downwards; the basal portion is stiff and straight, the outer portion gracefully curves over, with the free end hanging down and tapering out to an almost invisible thread.' (Browne, 1897*a*.)

Lebour (1922, 1923) has observed these medusae eating *Calanus*; one 10 mm. in diameter ate several young *Blennius pholis*, 'catching them quickly one after the other with its outstretched tentacles, until the stomach was full'.

Kramp (1919) states that the young specimens occur exclusively in the upper water layers near land; in deep waters large specimens have, however, been found as far down as 800 m.

Kramp (1930) and Russell (1938*a*) give indications that in the southern North Sea and English Channel the species only grows to a small size.

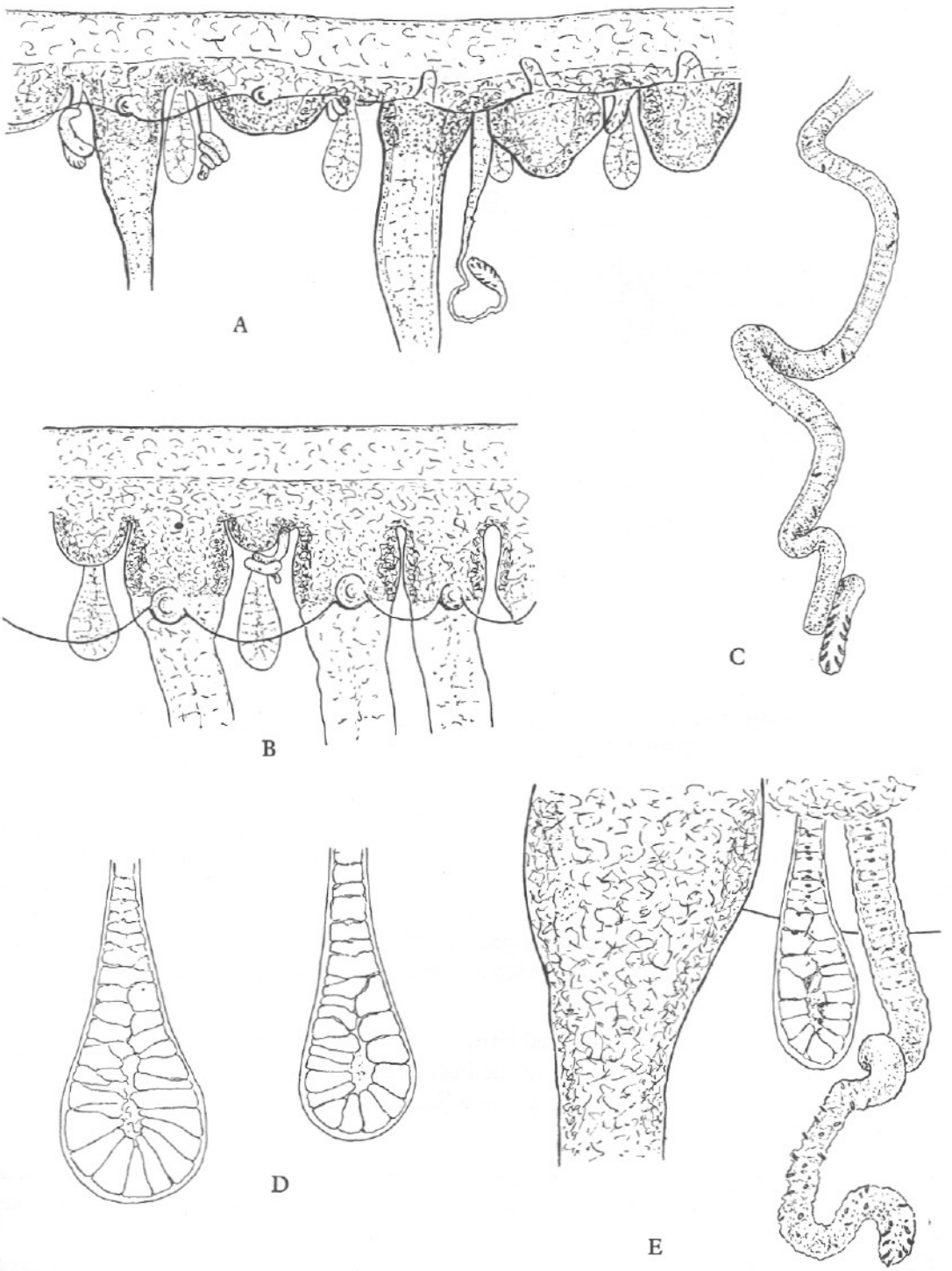
HYDROID. *Cuspidella* sp. (Text-fig. 131.)

(For full description see Russell, 1936*a*, *Journ. Mar. Biol. Assoc.* vol. xx, p. 581, figs. 1–7.)

Colonies of single hydranths rising from a creeping stolon. Hydrotheca cylindrical with terminal operculum bearing eight to ten teeth. Height of hydrotheca 0·3–1·0 mm.; width 0·09–0·16 mm. Old hydrothecae have transverse growth rings.

Hydranth very extensile, with a single whorl of ten to twelve filiform tentacles; completely retractile into hydrotheca. Hydranth colourless.

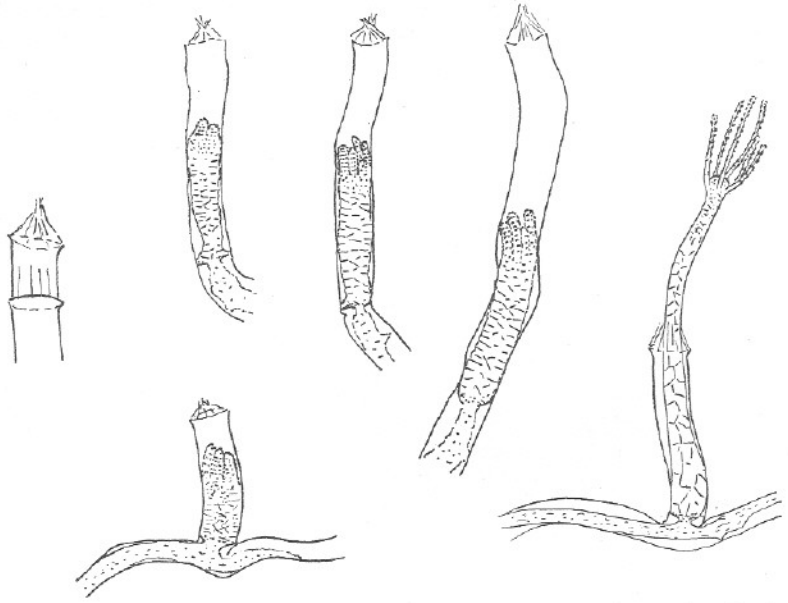
Gonotheca as hydrotheca but about twice as long.



Text-fig. 130. *Laodicea undulata*. Details of specimen 10 mm. in diameter, Plymouth, 11. ix. 35. A and B, portions of umbrella margin showing bases of marginal tentacles, marginal cirri, and cordyli; C, marginal cirrus; D, cordyli; E, base of marginal tentacle, marginal cirrus, and cordylus.

The specific identity of this hydroid is uncertain, though it resembles *Cuspidella costata* Hincks. It is, however, possibly indistinguishable from the hydroid of *Cosmetira pilosella* and it is known that a number of medusae arise from *Cuspidella*-like hydroids.

The medusae of *Laodicea undulata* have been seen in the Plymouth Laboratory liberated from *Cuspidella* collected off Plymouth.



Text-fig. 131. *Laodicea undulata*. Hydroids reared from the medusa in the Plymouth laboratory. (After Russell, 1936*a*, fig. 4.)

Historical

The specific name of *Laodicea undulata* is that given by Forbes & Goodsir (1851) in their description (as *Thaumantias*) of medusae collected in the Minch. At the same time they described a young specimen as *Th. confluens*. There can be little doubt that their species was *Laodicea undulata*, but the first adequate description of the species is that given by Gegenbaur (1856) as *Thaumantias mediterranea*. There has been great confusion in the synonymy of this species and this has been fully discussed by Browne (1897*a*, 1907*b*) and Kramp (1919). The characters used in the distinction of the species were:

1. The presence or absence of marginal cirri.
2. The presence or absence of a spur at the base of the marginal tentacles.
3. The number of marginal cordyli between adjacent marginal tentacles.
4. The shape of the gonads.

All of these characters are very variable and it now seems almost certain that the three species *Laodicea undulata* (Forbes & Goodsir), *L. calcarata* A. Agassiz, and *L. ulothrix* (Haeckel) kept distinct by Browne (1907*b*) are one and the same species.

Haeckel (1879) also identified the species with *Medusa cruciata* of Forskål (1775). However, Forskål's description is quite inadequate for identification, and Haeckel created worse confusion by including medusae from a number of other genera as synonyms. Kramp (1919) agreed with Browne's proposal to use *Laodicea undulata* as the name of the species.

A number of species of *Laodicea* have been described from the Pacific and Indian Oceans, namely *L. indica* (Browne, 1905*b*), *L. marama* (Agassiz & Mayer, 1899), *L. maasi* (Browne, 1907*b* and Vanhöffen, 1911), and *L. fijiana* (Agassiz & Mayer, 1899). Kramp (1919) was inclined to believe that these species might prove to be synonymous with *L. undulata*, but decision must be postponed until further detailed observations have been made.*

Genus **Staurophora** Brandt, 1834

MEDUSAE. Laodiceidae with unusual cross-shaped stomach with mouth-opening extending for considerable distance along course of each radial canal; with four radial canals; with gonads in branched diverticula in lateral walls of cross-shaped stomach; without marginal cirri; with adaxial ocelli.

HYDROID. Not known.

There is only one British species of the genus, *Staurophora mertensi* Brandt. The form of the stomach and presence of marginal cordyli make the species at once recognizable, and in addition the species is one of our largest Leptomedusae to which the species of *Aequorea* are alone comparable. *Aequorea* is immediately separable on account of its many radial canals. *Staurophora* is an arctic medusa and as such is only to be found in the north-eastern and eastern areas of the British Isles.

Staurophora mertensi Brandt

Text-figs. 132–7

Staurophora mertensii Brandt, 1838, *Mém. Acad. Imp. Sci. St.-Pétersb.* sér. 6, Sci. Nat. tome II, p. 400, pls. xxiv–xxv.
L. Agassiz, 1862, *Contrib. Nat. Hist. U.S.* vol. IV, p. 351.
Mayer, 1910, *Medusae of the World*, vol. II, p. 291; vol. I, pl. xxvi, figs. 4–9.
Kramp, 1919, *Danish Ingolf-Expedit.* vol. V, pt. viii, pp. 5, 39, pl. i, fig. 9; pl. ii, figs. 9, 10; pl. iii, fig. 7.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 599, figs. 22, 23.
Staurophora laciniata L. Agassiz, 1849, *Mem. Amer. Acad. Arts Sci. Boston*, vol. IV, IX, p. 300, pl. vii.
L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 351.
A. Agassiz, 1863, *Proc. Boston Soc. Nat. Hist.* vol. IX, p. 90, figs. 1–3.
A. Agassiz, 1865, *N. Amer. Acaleph.* p. 136, figs. 215*a*–219.
Wagner, 1885, *Wirbellosen des Weissen Meeres*, Bd. I, p. 80, pl. iv, figs. 14–20.
Hartlaub, 1897, *Wiss. Meeresuntersuch.* N.F., Bd. II, Abt. Helgoland, Heft 1, IX, p. 484, pl. xviC, figs. 5, 6, 9, 10; pl. xxii, fig. 2.
Browne, 1907*b*, *Ann. Mag. Nat. Hist.* ser. 7, vol. XX, p. 470.
Oceania multicirrata M. Sars, 1851, *Nyt Mag. f. Naturv.* Bd. VI, p. 158.
Staurophora vitrea M. Sars, 1863, ibid. vol. XII, p. 339.
Staurophora keithii Peach, 1867, *Journ. Roy. Inst. Cornwall*, vol. II, no. VIII, p. 358, pl. ii.
Staurostoma laciniata, Haeckel, 1879, *System der Medusen*, p. 130.
Staurostoma arctica Haeckel, 1879, ibid. p. 131.
Thaumantias melanops M'Intosh, 1890*b*, *Ann. Mag. Nat. Hist.* ser. 6, vol. V, p. 40, pl. viii, fig. 1.
?*Staurophora falklandica* Browne, 1907*b*, *Ann. Mag. Nat. Hist.* ser. 7, vol. XX, p. 472.
Browne, 1908, *Trans. Roy. Soc. Edinb.* vol. XLVI, pt. II (no. 10), p. 235, pl. i, figs. 1–7.
Staurophora discoidea Kishinouye, 1910, *Journ. Coll. Sci. Imp. Univ. Tokyo*, vol. XXVII, Art. 9, p. 29.

Specific Characters. This is probably the only species of the genus.

* Dr Kramp has since told me that after seeing some specimens from the Pacific he thinks that some may prove to be good species (see Kramp, 1953).

LAODICEIDAE

Description of Adult

Umbrella flatter than a hemisphere; jelly thick and smooth; exumbrella margin with numerous short centripetal furrows. Velum narrow. Stomach, mouth and four radial canals combined to form large perradial cross reaching nearly to umbrella margin. Four long slit-like arms of mouth with much folded marginal lips. Four open radial canals above mouth with numerous short lateral branched diverticula; very short closed portions of radial canals running to ring canal straight and narrow; ring canal narrow. Gonads on diverticula of four radial canals, more developed in middle region of each canal. Marginal tentacles short, hollow, extremely numerous, up to several thousands in large individuals; with elongated conical basal bulbs and well-developed pointed endodermal spurs. No marginal cirri. Adaxial ocellus on each marginal tentacle bulb. Many marginal cordyli, approximately alternating with marginal tentacles; marginal cordyli with narrow stems and without nematocysts. Diameter of umbrella reaching 200–300 mm.; height 30–50 mm. Colour of gonads, radial canals and ring canal milk-white; marginal tentacles light rosy; mouth-lips rosy or yellowish; remaining parts of glass-like transparency with bluish tinge.

Distribution

Off British coasts *Staurophora mertensi* has only been recorded from the following localities:* St Andrews (M'Intosh, 1890*a*, *b*); Peterhead (Peach, 1867); ? Cromarty Firth (Romanes, 1876*b*); east of the north point of Scotland (Kramp, 1919); and off Cullercoats on the Northumberland coast in June 1950 (letter from Dr H. O. Bull). It is a circumpolar boreal arctic species and is therefore only likely to occur in the far north of the British Isles and on the east coast when the influence of the arctic current in the North Sea is strong. If its identity with *S. falklandica* Browne should be proved, it is a bipolar species.

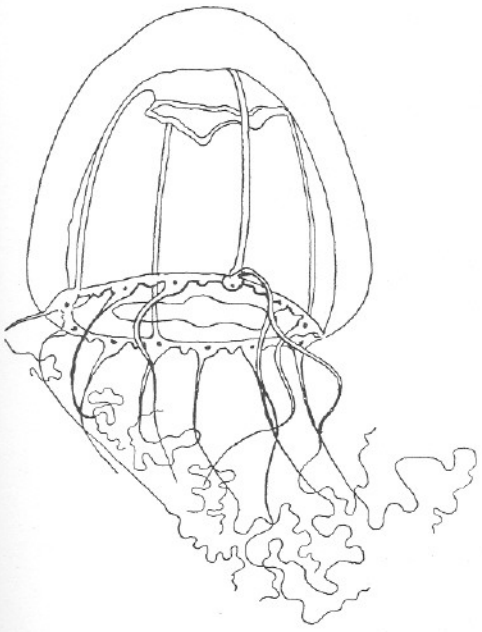
Developmental Stages and Structural Details

The first stage of *Staurophora mertensi* immediately after liberation from the hydroid has not been described as its hydroid is not known. The smallest stages as yet recorded from the plankton are about 2 mm. high (Hartlaub, 1897, p. 487; A. Agassiz, 1865, p. 136). The umbrella is bell-shaped. The velum is well developed. The stomach is short and has four simple lips; it has slit-like openings into the radial canals. The four straight radial canals and ring canal are narrow. There are no indications of gonads. There are eight marginal tentacles, each with a dark violet adaxial ocellus on its base. No mention was made by either author of the presence or absence of marginal cordyli. The colour of the umbrella is blue-blackish.

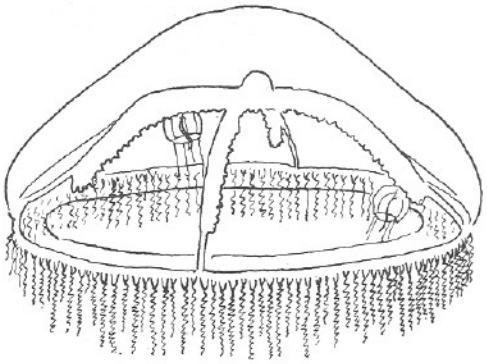
Hartlaub (1897) kept his specimens alive (see Text-fig. 132). After three weeks they had grown to a height of 10 mm. Some were still bell-shaped and others more hemispherical. The stomach had considerably increased in width without much growth in length; its diameter was 5 mm. The gonad rudiments were not yet apparent. The number of marginal tentacles had increased to fully one hundred, not counting rudiments of marginal tentacles. The bases of the larger marginal tentacles showed distinct spurs and on some of the bases there were two ocelli. Between every two marginal tentacles there was usually a cordylus. A. Agassiz (1865) gives two diagrams of stages with sixteen large marginal tentacles, the larger of which had apparently about forty smaller marginal tentacles.

* In the summer of 1951 it appeared in the Firth of Clyde (Gauld, 1952).

Stomach and mouth. The formation of the cross-like stomach and mouth is quite peculiar to this species of medusa (Text-fig. 134A, B). Its morphology has been clearly described by Browne (1907, p. 470). He likens it to the gonadial portion of the radial canal of a *Laodicea* which has been slit along its course ventrally, the cut edges becoming the mouth margins of *Staurophora*. He suggests that 'the mouth of *Staurophora* has arisen by the outgrowth of a central mouth along the enlarged portions of the radial canals of a *Laodice*-like medusa, and consequently those portions of the radial canals have been converted into a four-rayed stomach'.



Text-fig. 132. *Staurophora mertensi.* Young specimen. (After Hartlaub, 1897, pl. xvi c, fig. 6.)



Text-fig. 133. *Staurophora mertensi.* Adult medusa feeding on *Sarsia.* (After L. Agassiz, 1849, pl. vii, fig. 11.)

A. Agassiz (1865, p. 136) gives some figures showing the growth of the stomach and mouth.

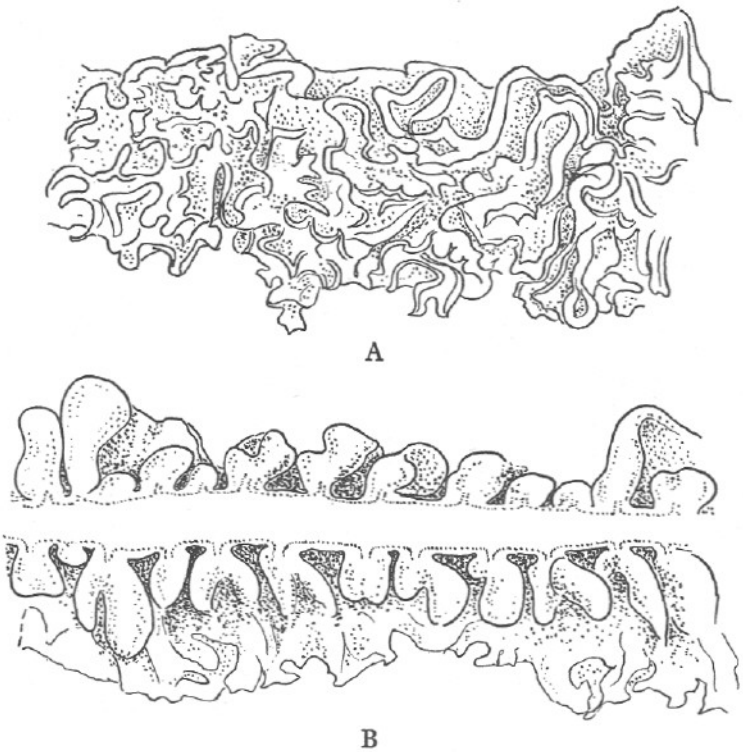
Kramp (1919, p. 42) gives the following data showing the width of the arms of the stomach and the length of the closed portions of the radial canals in specimens of different sizes from Greenland and Iceland:

Diameter of umbrella (cm.)	Largest breadth of cross-arms (mm.)	Length of narrow parts of radial canals (mm.)	No. of marginal tentacles
4·5	1·25	3·5	—
c. 5·0	1·25	4·0	—
5·5	2·0	4·0	—
7·0	—	5·0	*c.* 1000
8·0	3·0	5·0	> 1200
9·0	4·5	6·0	*c.* 1100
9·0	2·5	5·0	*c.* 1400
10·0	5·0	6·0	*c.* 1400
11·0	7·0	6·0	*c.* 1400
c. 12·0	8·0	9–10	*c.* 4400

Thus it is evident that already with a diameter of 45 mm. across the umbrella the arms of the stomach have extended well across the disk.

The *gonads* are developed on the lateral folds of the cross-like stomach and are more developed in the middle region than at the proximal and distal ends. Kramp (1919, p. 42) states that the primary lateral folds usually have four to six secondary folds, rarely seven or more. The lateral folds are flattened on their upper sides, but are only attached to the subumbrella surface along narrow branched lines.

According to Hargitt (1905, p. 44) 'the ova develop within the genital folds, the larvae being later discharged as actinulae'.



Text-fig. 134. *Staurophora mertensi*. Portion of mouth-lips: A, from below; B, from above. (Preserved specimen from 56° 08′ N.; 1° 52′ W., 27. vii. 37, sent by J. H. Fraser.)

The *marginal tentacles* are short. According to L. Agassiz (1849, pp. 304–5), even when fully expanded, they are less than half the diameter of the umbrella. The marginal tentacles usually form a graceful fringe about one-sixth of the diameter of the umbrella. He states that the marginal tentacles coil spirally, from right to left downwards, always coiling in the same direction all round the umbrella.

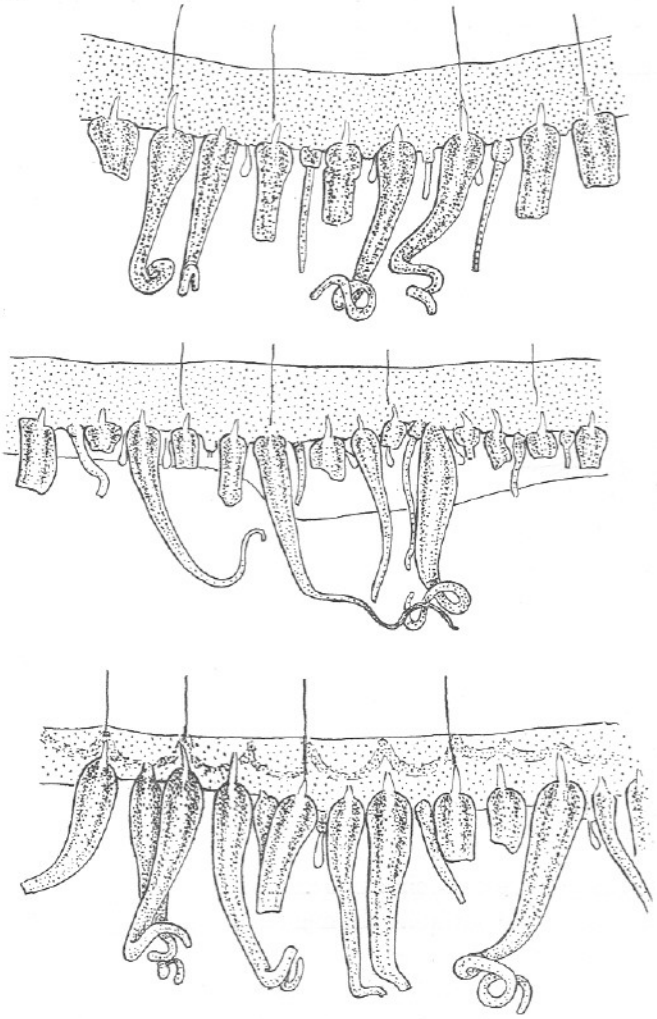
The ectoderm of the basal bulb of the marginal tentacle is somewhat thickened, particularly on the adaxial side (Kramp, 1919), and each marginal tentacle has a narrow, pointed endodermal spur, penetrating into the jelly close to the exumbrellar side (Text-fig. 136).

The marginal tentacles are very densely crowded (Text-fig. 135). While they arise in a regular sequence in young medusae, in the older individuals, after about sixty-four tentacles have developed, there appears to be little regularity.

The *ocelli*, which are adaxial, do not develop on the marginal tentacle bases until the marginal tentacles have grown to a fair size. Kramp (1919) mentions specimens with fewer ocelli than is

normal, but these may possibly have disappeared on preservation. The ocelli have been described by Linko (1900*b*, as *Staurostoma arctica*); each has a lens. Linko also described marginal vesicles, but Browne (1908) and Kramp (1919) failed to find any.

'In larger specimens the peripheral part of the exumbrella is provided with numerous deep, sharp, radiating furrows of very different length, though rarely more than 10 mm. long; the number of furrows is variable, one being found off every second or fourth of the tentacles.' (Kramp, 1919, p. 42.)



Text-fig. 135. *Staurophora mertensi*. Portions of umbrella margin of preserved specimen; lower figure shows puckering of ring canal; from 56° 08′ N.; 1° 52′ W., 27. vii. 37. (Sent by J. H. Fraser.)

Occasionally the marginal cordyli (Text-fig. 137) become transformed into marginal tentacles (Kramp, 1919, p. 5).

NEMATOCYSTS. Microbasic mastigophores (Russell, 1940*a*).

Seasonal occurrence

Among the British records the only dates given for the occurrence of *Staurophora mertensi* are May and June at Peterhead (Peach, 1867). (See also footnote on p. 240.)

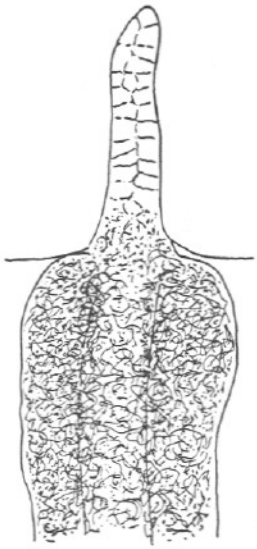
LAODICEIDAE

Habits

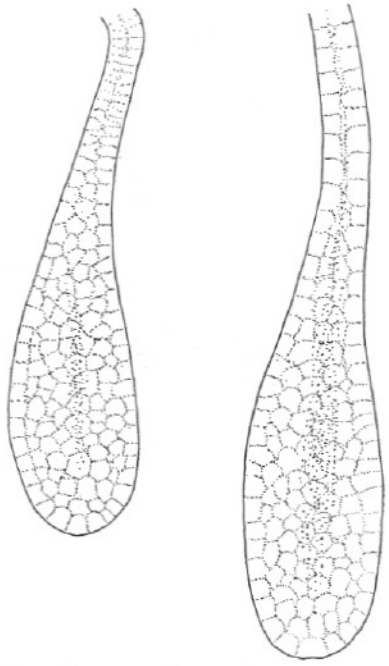
Staurophora mertensi is one of our largest species of Hydromedusae. The biology of the medusa on the American side of the Atlantic has been fully discussed by Bigelow (1926). Its rate of growth there is fast, e.g.:

Mid-May	*c.* 2 inches diameter
End of May	3–4 ,,
Early June	5–6 ,,
July	6–9 ,,

Specimens are often cast up on the beach in large numbers on the American coast.



Text-fig. 136. *Staurophora mertensi.* Base of marginal tentacle. (Same specimen as in Text-fig. 135.)



Text-fig. 137. *Staurophora mertensi.* Marginal cordyli. (Same specimen as in Text-fig. 135.)

Bigelow states that the youngest specimens swarm at the top of the water, the large adults being a metre or more below the surface. He mentions that these medusae must take a heavy toll of *Calanus* and smaller copepods.

The food is engulfed by the mouth-lips anywhere along its cruciform course. L. Agassiz (1849) gives a figure (Text-fig. 133) showing the medusa with a number of *Sarsia* in its mouth; he saw them feeding on *Sarsia*, tiaropsids, and young *Aurelia*.

The swimming motions of this medusa are very characteristic and have been described by L. Agassiz (1849, pp. 301, 304, 306), and Romanes (1885, p. 123). Briefly, while exhibiting the normal pulsating movements of medusae, an additional type of contraction occurs whereby the margin assumes the form of four distinct lobes or even a larger number of smaller lobes. Romanes describes this as spasmodic or persistent contraction. Romanes found that *Staurophora* resembled *Aurelia* in that the spasm wave was not easily blocked by section, whereas in the Hydromedusae generally the ordinary contraction wave is very easily blocked by this means. Further experi-

mental observations on this medusa are mentioned by Romanes (1876*b*, p. 285). He also states (1885, p. 27) that this species afforded an exception to the general rule that complete removal of the margin leads to permanent paralysis in Hydromedusae.

HYDROID. Not known.

Historical

Staurophora mertensi was first described by Brandt (1835) from drawings and notes made by Mertens of specimens he collected in the northern Pacific. The history of the synonymy of this species is fully discussed by Kramp (1919).

FAMILY MELICERTIDAE

Leptomedusae with base of stomach attached over its whole surface; with eight simple radial canals; with gonads on radial canals separated from stomach; with hollow marginal tentacles; without marginal cirri; without any kind of marginal sense organ.

HYDROID. Hydranths naked, with single whorl of filiform tentacles.

The family Melicertidae is represented in British waters by one genus, *Melicertum* L. Agassiz, the only genus of the family.

Genus **Melicertum** L. Agassiz, 1862

Characters as family.

There is one British species of *Melicertum*, possibly the only species of the genus, *M. octocostatum* (M. Sars). The medusa is sufficiently distinctive to be easily recognizable from its description.

Melicertum octocostatum (M. Sars)

Plate XIII, figs. 2–4; Text-figs. 138–42

Oceania octocostata M. Sars, 1835, *Beskriv. og Jagttagg*, p. 24, pl. iv, fig. 9.
Melicertum campanulatum Ehrenberg, 1837, *Abh. K. Akad. Wiss. Berlin* (1835), p. 255, pl. viii, figs. 5–7.
Aequorea octocostata, Lesson, 1843, *Hist. Nat. Zooph. Acalèphes*, p. 312.
Thaumantias milleri Landsborough, 1847, *Excursions to Arran*, p. 265.
Stomobrachium octocostatum, Forbes, 1848, *Monogr. Brit. Medusae*, p. 30, pl. iv, fig. 1.
Green, 1857, *Nat. Hist. Rev.* vol. IV, p. 244, pl. xiv, fig. 1.
Melicertum pusillum L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 349 (*non* Eschscholtz, 1829, p. 106).
Melicertidium octocostatum, Haeckel, 1879, *System der Medusen*, p. 138.
Browne, 1905*a*, *Proc. Roy. Soc. Edinb.* vol. XXV, pt. ix, p. 762, tables I–II.
Gemmill, 1921*a*, *Quart. Journ. Micr. Sci. London*, vol. LXV, no. 259, p. 339, pl. xvi (medusa and hydroid).
Melicertum octocostatum, Mayer, 1910, *Medusae of the World*, vol. I, p. 208.
Kramp, 1919, *Danish Ingolf.-Expedit.* vol. V, pt. viii, p. 52, pl. i, fig. 10; pl. iii, fig. 8.
Sverdrup, 1921, *Skrift. Vidensk. Kristiania*, I, Bd. I (1922), mat.-nat. Kl., p. 22, pl. iv, fig. 15 (?in part).
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 562, figs. 25, 26.
Kramp, 1942, *Medd. Grønland*, Bd. LXXXI, no. 1, p. 57.
'Gymnoblastic Hydroid', Robson, 1914*b*, *Rep. Dove Mar. Lab. Cullercoats*, N.S. III, p. 104, pls. i, ii (young medusa and hydroid).

Specific Characters

This may be the only species in the genus, if it proves to be identical with *Melicertum campanula* L. Agassiz; but at present differences have been recorded in the hydroids (see p. 251).

Description of Adult

Umbrella conical bell-shaped, slightly higher than wide; jelly moderately thin, thickened in apical region. Three to seven tracks of nematocysts on subumbrellar surface between every two

radial canals, extending upwards from umbrella margin, some reaching stomach, occasionally branched. Velum narrow. Stomach short, octagonal, with broad base; attached to subumbrella over whole dorsal surface. Mouth with eight simple or slightly folded lips. Eight broad radial canals, opening into stomach through vertical slits; ring canal narrow. Gonads in centre of broad vertical sides of radial canals, reaching nearly to umbrella margin; sinuous. About sixty-four to seventy-two large hollow marginal tentacles with laterally compressed bases, and about sixty-four to seventy-two smaller marginal tentacles alternating approximately with large marginal tentacles. No marginal cirri. No marginal sense organs. Umbrella height 11–13 mm.; width 10–14 mm. Colour of stomach, gonads, and marginal tentacle bases yellow or yellowish brown.

Distribution

On the coasts of the British Isles *Melicertum octocostatum* has been recorded from Dunbar Harbour, the Firth of Forth, St Andrews, Cromarty Firth, the Kyles of Bute, the Firth of Clyde, the north-west coast of Ireland, Valencia, the Dublin coast, Port Erin and Falmouth. The hydroid has been found off the Northumberland coast and in aquarium tanks at Millport.

It is a northerly species being more abundant on the north British coasts and rather scarce in the south-western area, although Cocks (1849) recorded it as abundant in Falmouth harbour.

Elsewhere it occurs on the Murman coast, Iceland, west Greenland, the Iceland-Faeroe Channel, the coasts of Norway, the Skagerak and Kattegat, Helgoland and Kiel, and in the Pacific on the Japanese coast.

Developmental Stages and Structural Details

Descriptions of the medusa *Melicertum octocostatum* when just liberated from its hydroid have been given by Robson (1914*b*) and Gemmill (1921*a*). The umbrella is slightly wider than high, being 1·3 mm. wide and 1·2 mm. in height. The jelly is thin, and there are, at first, traces of the umbilical attachment, but the apical region soon fills out and a slight apical process is formed. The subumbrellar nematocyst tracks are not developed, but there are a few scattered nematocysts on the exumbrellar surface. The stomach is very short and attached to the subumbrellar surface by a broad four-cornered base. The mouth has four perradial lips. There are four broad radial canals issuing from the four corners of the stomach base. Gemmill gives the interradial diameter of the stomach as 0·45 mm. and the width of the radial canals as 0·06 mm. The ring canal is narrow. There are four perradial marginal tentacles with slightly swollen hollow bases and there are four small interradial marginal tentacles or tentacle buds. The bases of the marginal tentacles are yellowish. Gemmill reared the medusae at Millport until they had sixteen marginal tentacles. A medusa has been reared slightly beyond this stage at Plymouth among specimens sent to me by Dr H. O. Bull from Cullercoats where they were liberated from the hydroid. The early development given below is based mainly on these Plymouth medusae (Pl. XIII, figs. 2–4). When the medusa is 1·5 mm. in diameter the four interradial marginal tentacles are further developed and the marginal tentacle bases and margin of the umbrella are bright yellow. When the four interradial marginal tentacles are nearly as fully formed as the four perradial, the rudiments of sixteen adradial marginal tentacles appear. At this stage four slight outgrowths develop from the stomach base, one on each interradius, which are destined to become the four interradial canals. Additional minute marginal tentacles now develop singly, on one side only of each of the four perradial and four interradial marginal tentacles. The interradial outgrowths from the stomach base gradually increase in length, their courses being preceded by fine indications which join them to the ring canal. At a stage where there are twenty-two marginal tentacles, including the

smallest rudiments, the four interradial canals have reached a point about half-way down the sides of the umbrella and have pointed ends. At this stage short nematocyst tracks are visible on the subumbrella running upwards for a short distance from the eight adradial marginal tentacles. The medusa is now about 2·25–2·6 mm. in diameter. When the medusa has grown to a diameter of 2·9 mm. the four interradial canals have joined the ring canal and the system of eight radial canals is complete. At this stage there are four large perradial and four large interradial marginal tentacles of equal size; there are sixteen small marginal tentacles, two between adjacent large marginal tentacles; and two small rudiments; that is twenty-six marginal tentacles in all. Subumbrellar nematocyst tracks run up from each of the sixteen small marginal tentacles, the longest reaching about half-way up the side of the umbrella. The colour of the stomach, marginal tentacle bases and umbrella margin is bright yellow, and this colour extends down the eight radial canals for a short distance from the stomach.

A summary of the development of the medusae at Plymouth is as follows:

Date	Age (days)	Umbrella diameter (mm.)	No. of marginal tentacles	Interradial canals	Nematocyst tracks
19. ii. 36	3	1·5	4+4	—	—
24. ii. 36	8	—	4+4+8 rud.	Beginning to develop	—
28. ii. 36	12	2·6	4+4+8+6	Half-way down umbrella	—
4. iii. 36	16	2·25	4+4+8+6	Half-way down umbrella	8, just beginning
18. iii. 36	28	2·9	4+4+8+8+2	Joined to ring canal	16, about half-way up subumbrella

The development of the medusae at Plymouth was somewhat quicker than that recorded by Gemmill, possibly because at Plymouth they were fed individually. Moreover the medusae reared in the laboratory have possibly not developed as fully as they do in the sea, for Browne (1905 *a*) recorded a specimen from the plankton only 2·5 mm. in height and width which was further developed. In this medusa the gonads were just beginning to appear, extending over the proximal half of the radial canals. It had about twenty large marginal tentacles, those opposite the eight radial canals being slightly larger than the others. There was also a minute marginal tentacle between every two large ones. Browne described a later stage 3·5 mm. in height and 4 mm. in diameter. In this specimen the gonads extended over the central third of the radial canals, forming two narrow bands along both sides of them. There were about forty large marginal tentacles and forty minute marginal tentacles alternating one with the other.

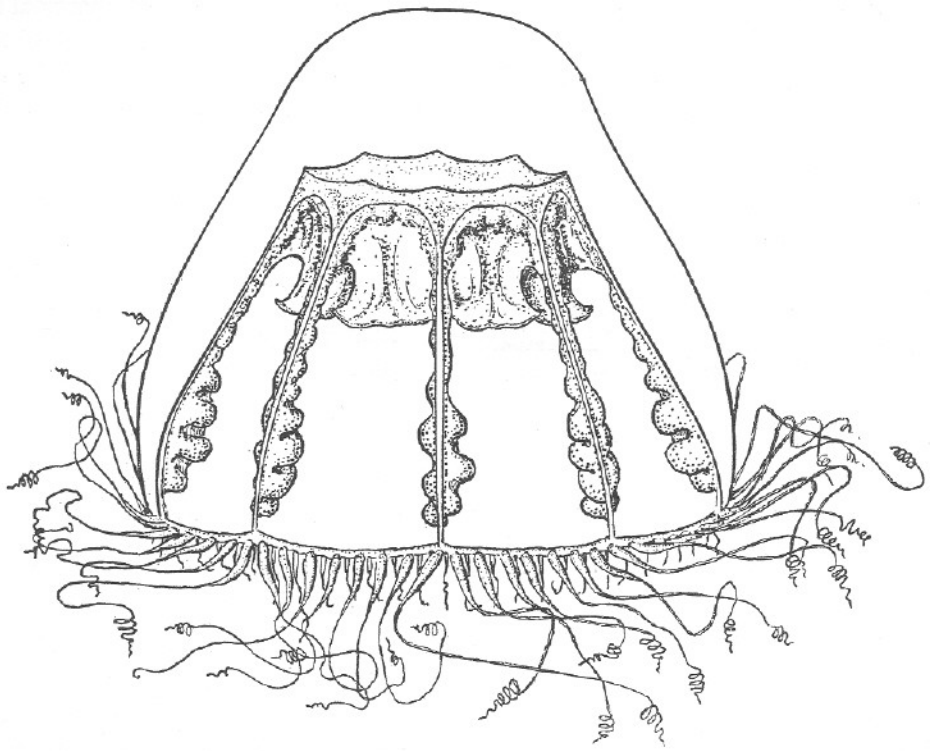
Kramp (1942) also gives details of the early stages of medusae caught off the west coast of Greenland very similar to the above. He says that the gonads were just appearing in specimens 3 mm. in diameter, and that they were well developed, though still immature in medusae 5 mm. in diameter. He gives the numbers of marginal tentacles on medusae of different sizes as follows:

Umbrella diameter (mm.)	No. of marginal tentacles
4–5	32+32=64
8	64+64=128
9	60+52=112
9	64+64=128
9	64+64=128
10	72+56=128
11	80+64=144
12	64+64=128
12	72+72=144

The largest specimen was 14 mm. in diameter with fifty-two large and fifty-eight small tentacles.

MELICERTIDAE

Details of the structure of the adult medusa are given by Kramp (1919). The stomach when contracted has eight longitudinal folds and the mouth eight short recurved lips. The stomach is, however, often dilated so that the mouth becomes large and more or less circular (Text-figs. 138, 139). The dorsal attachment of the radial canals to the subumbrella is straight, but the broad vertical lateral walls of the canals, on which the gonads are developed, are folded and sinuous. The gonads begin at a distance from the stomach of about one-quarter of the length of a radial canal, and they end about 1 mm. from the ring canal. They are more developed distally and are



Text-fig. 138. *Melicertum octocostatum*. Adult medusa. (After Kramp, 1933*b*, fig. 25.)

situated centrally on the lateral walls of the canals so as to leave a strip on each side below the subumbrella and the ventral region free of gonads. Romanes (1876*a*) stated that the external parts of the ovary were distinctly ciliated. The young egg cells are in the ectoderm, and the mesosarc is fairly strong and only slightly pushed in towards the endoderm (Kramp, 1932, p. 325).

The large and small marginal tentacles are not entirely regular in their alternation (Text-fig. 140). The small marginal tentacles are directed more adaxially than the large marginal tentacles.

In full development a subumbrellar nematocyst track runs from the umbrella margin to the stomach. But since the length of a track depends upon the age of the marginal tentacle opposite which it arises there are always a number of shorter tracks.

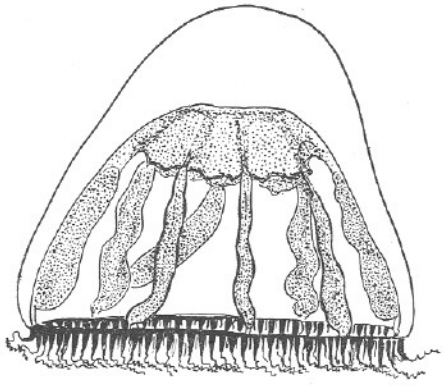
The hydroid has been reared from the egg at Millport by Gemmill (1921*a*). The eggs are 0·08 mm. in diameter, faintly yellowish in tinge, and with a delicate closely adherent membrane. No fertilization membrane is formed. Segmentation is total and equal.

The ciliation of the internal surfaces and of the subumbrella is described by Gemmill (1920).

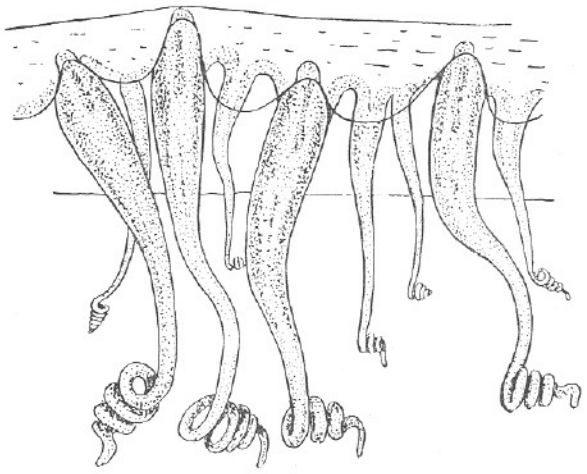
NEMATOCYSTS. Microbasic mastigophores and ? atrichous haplonemes (Russell, 1940*a*).

Seasonal occurrence

Melicertum octocostatum has been recorded in the plankton in the following months: October in Dunbar harbour; January, August, September, October and December at St Andrews; September, Isle of May; December, Firth of Forth; July in the Kyles of Bute; from May to October, and once as abundant in August, in the Firth of Clyde; May and June at Port Erin; May and July at Valencia; and in the summer at Falmouth.



Text-fig. 139. *Melicertum octocostatum.* Preserved specimen *c.* 10 mm. high, Arran, Scotland, 1897. (E. T. Browne collection.)



Text-fig. 140. *Melicertum octocostatum.* Portion of umbrella margin of preserved specimen *c.* 10 mm. high, Arran, Scotland, 1897. (E. T. Browne collection.)

Liberation of the medusae from the hydroid occurs from February to March in the tanks of the Millport Laboratory (Gemmill, 1921*a*) and from February to June at Cullercoats (Robson, 1914*b*). M'Intosh (1890*a*) states that the medusa is most plentiful at St Andrews in October, when large but unripe specimens are procured. In December some are 12·5 mm. in diameter and nearly ripe.

Habits

The behaviour of the living medusae has been described by Kramp & Damas (1925). They say that the marginal tentacles are extremely long and that the larger ones are carried curved back at first towards the summit and then trailing in the wake of the medusa; the smaller marginal tentacles are directed downwards. Figures of young medusae swimming are given in Plate XIII.

The young medusae reared at Plymouth were very voracious and were fed on larvae of the Polychaete *Polydora* and on copepods, two or three of which would be taken into the stomach at the same time.

Kramp & Damas state that *Melicertum octocostatum* is most frequent in the Norwegian fjords where there is much mixture of fresh water. The species may thus be somewhat estuarine and the fact that it has been recorded as abundant in the Firth of Clyde and in Falmouth harbour is in agreement with this. It is interesting also that the hydroid establishes itself in aquaria at Millport and Cullercoats.

MELICERTIDAE

HYDROID. *Melicertum octocostatum*. (Text-figs. 141, 142.)

(For full descriptions see Robson, 1914*b*, *Rep. Dove Mar. Lab. Cullercoats*, N.S., III, p. 104, pls. i, ii; and Gemmill, 1921*a*, *Quart. Journ. Micr. Sci. London*, vol. LXV, p. 339, pl. xvi.)

Colonies of single hydranths, 2·0–2·7 mm. in height, rising from a creeping stolon. Hydrocaulus with thin, smooth or slightly wrinkled perisarc reaching nearly to base of hydranth, where it thins away. Hydranth club-shaped with single whorl of ten to twenty delicate filiform tentacles. No web at base of tentacles. Hypostome conical. Hydranth not retractile, very flexible, colourless.



Text-fig. 141. *Melicertum octocostatum*. Hydroid. (After Robson, 1914*b*, pl. ii.)



Text-fig. 142. *Melicertum octocostatum*. Hydroid with medusa buds. (After Robson, 1914*b*, pl. i.)

Gonothecae borne on short stems on hydrocaulus well below base of hydranth; one to three medusae on each hydrocaulus, only one in each gonotheca; tentacle bases of attached medusae yellow.

This hydroid was first described as an unknown gymnoblastic hydroid by Miss Robson (1914*b*) from a position 40 miles north-east of Shields, in 45 fathoms, growing on an old shell of *Vulsella modiolus* (? *Modiolus*) and also on stones in the laboratory tanks at Cullercoats, where it has since been found by Dr H. O. Bull. Gemmill (1921*a*) described the same hydroid growing in the tanks at the Millport Laboratory where it had been noticed for several years. He reared medusae from the hydroid until the species was recognizable and also confirmed this by rearing hydroids from the eggs of ripe medusae from the plankton.

Historical

Melicertum octocostatum was first described by M. Sars (1835) as *Oceania octocostata* from Fløro, Norway. It was first seen in British waters by Forbes (1848) in the Kyles of Bute in 1839.

There is another species which occurs on the American side of the Atlantic, *Melicertum campanula* L. Agassiz. This species was kept distinct from *M. octocostatum* on account of its

larger size and the absence of subumbrellar nematocyst tracks, although several authors thought that they might eventually be proved to be identical. Kramp (1933*a*) examined some American specimens and found in fact that these nematocyst tracks were present and the specimens he saw appeared identical in every respect with the European medusae. He therefore decided that they were the same species. Apparently, however, Kramp was unaware of the publications by Robson (1914*b*) and Gemmill (1921*a*) on the hydroid of the European species; for A. Agassiz (1865) reared hydroids from the American *M. campanula* and these differ from those of *M. octocostatum*. In the hydroid of *M. campanula* the tentacles are webbed at their bases and there is a small theca; these are both absent in the European hydroid. Gemmill (1921*a*) pointed out that because of these differences in the hydroids the American and European species of medusae must be distinct. They must remain so unless Agassiz' observations should be proved to be mistaken by further rearing experiments.

Family DIPLEUROSOMIDAE

Leptomedusae with three, four, or more radial canals, simple or branched; with gonads on radial canals separated from stomach; with hollow marginal tentacles; without marginal cirri; without any kind of marginal sense organ.

HYDROID. Where known, *Cuspidella*-like, with single whorl of filiform tentacles; with hydrotheca without stalk and with folded operculum.

The family Dipleurosomidae is represented in British waters by the one genus, *Dipleurosoma* Boeck.

Genus **Dipleurosoma** Boeck, 1866

MEDUSAE. Characters as family.

HYDROID. *Dipleurosoma*, with characters as family.

There is only one British species of the genus, *Dipleurosoma typicum* Boeck. The species is at once distinguishable by the extraordinary irregularity in the numbers and branching of the radial canals. It is in fact impossible to describe a typical specimen.

Dipleurosoma typicum Boeck

Text-figs. 143–6

Dipleurosoma typica Boeck, 1866, *Vidensk. Medd. naturh. Foren. Kbh.* Nos. 10, 11, p. 131, figs. 1–3.
Dipleurosoma stuvitzii Boeck, 1866, ibid. p. 136, figs. 1–4.
Ametrangia hemisphaerica Allman, 1873*a*, *b*, *British Assoc. Rep.* p. 108; *Nature, London*, vol. IX, p. 73.
Dipleurosoma typicum, Haeckel, 1879, *System der Medusen*, p. 155.
Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. V, pp. 696, 715, pls. XX, XXI.
Maas, 1904*b*, *Sitzb. bayer. Akad. Wiss.* math.-phys. Kl., Bd. XXXIV, Jahrg. 1904, p. 441.
Mayer, 1910, *Medusae of the World*, vol. I, p. 224, fig. 117.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 562, fig. 24.
Dipleurosoma irregulare Haeckel, 1879, *System der Medusen*, p. 636.
Dipleurosoma hemispherica, Haddon, 1886, *Proc. R. Irish Acad.* vol. XIV (ser. 2, vol. IV), p. 526.
Dipleurosoma hemisphaericum, Browne, 1897*a*, *Proc. Zool. Soc. London*, p. 826, wood-cuts 10–12, pl. XLVIII, fig. 3.

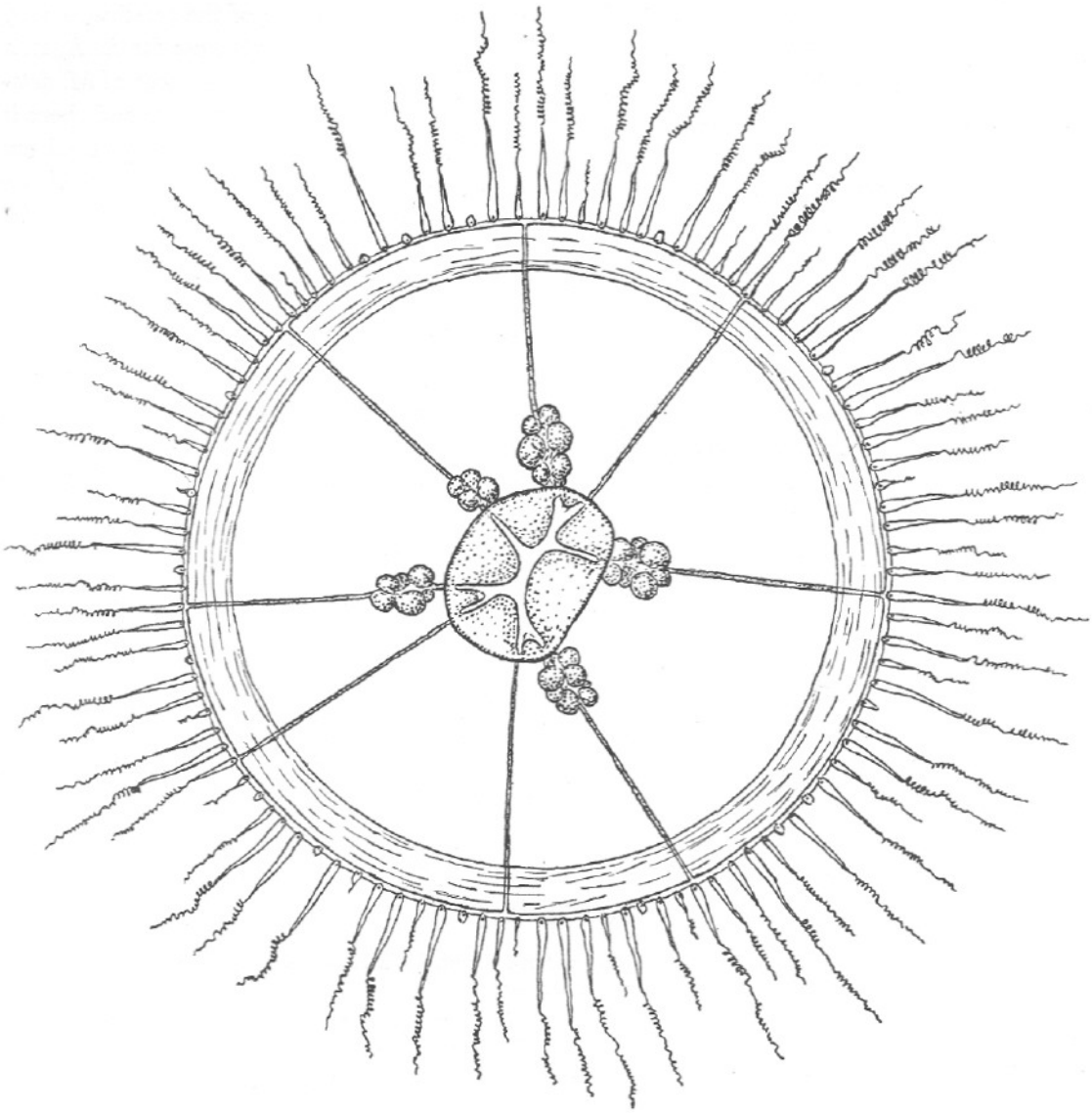
Specific Characters

This is the only certain species of the genus; radial canals branching between stomach and gonads.

DIPLEUROSOMIDAE

Description of Adult

Umbrella usually flatter than a hemisphere; jelly thin. Velum fairly broad. Stomach short, very variable in shape. Mouth with four simple lips. Radial canals narrow, very irregular in



Text-fig. 143. *Dipleurosoma typicum*. Adult medusa. (After Kramp, 1933*b*, fig. 24.)

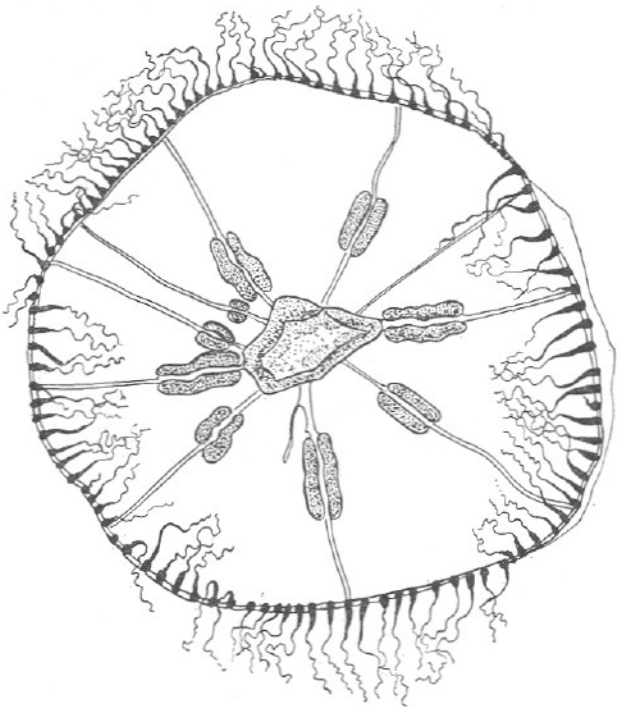
number, varying from five to eighteen, mostly about seven to thirteen; radial canals originate from outgrowths or lobes from stomach, and normally join narrow ring canal, some, however, never reaching it. Gonads from one to twelve in number, most usually five; situated along courses of radial canals and reaching usually about half-way to umbrella margin; formed as sacs in which eggs develop to planula stage which is unciliated. More than 100 marginal tentacles, each with

bulbous base and adaxial ocellus. No marginal cirri. No marginal sense organs. Diameter 8–12 mm. Colour of stomach and marginal tentacle bases pale yellowish brown, brown or reddish brown; ocelli black.

Distribution

Dipleurosoma typicum has only been recorded off British coasts from the south coast of Ireland (Allman, 1873*a*), Valencia (Browne, 1896*b*, 1897*a*, 1900; M. & C. Delap, 1905, 1906), Kingstown harbour (Haddon, 1886); Portobello, near Brighton (Haeckel, 1879, p. 636); and from Firth of Clyde (Browne, 1905*a*); I have myself collected specimens from Balta Sound, Shetlands, on 13 July 1933. Elsewhere it has been found only on the south-west coast of Norway (Boeck, 1866), and Newfoundland (Boeck, 1866).

In view of the abundance of this species in some years off Valencia its apparent rarity elsewhere is remarkable, as is its appearance near Brighton in the autumn of 1879.



Text-fig. 144. *Dipleurosoma typicum.* Preserved specimen *c.* 6·5 mm. in diameter, Valencia, 1898. (E. T. Browne collection.)

Developmental Stages and Structural Details

The earliest stages of development of *Dipleurosoma typicum* have not yet been described. The smallest specimens recorded by Browne (1900) were 3 mm. in diameter but details of the structure of these small individuals were not given.

The species is remarkable for the great diversity shown in its radial canal system which appears to differ in every specimen. The structure of the medusa has only been fully examined by Browne (1897*a*, 1900), using numerous specimens.

Stomach and radial canals. In the majority of the specimens examined by Browne (1900) the stomach was longer than it was wide, and this usual type is shown in Text-fig. 144; but it may be triangular, or nearly round, or very irregular (Text-fig. 145). The walls of the stomach meet above the centre and terminate in a mouth with four lips. In nearly all the specimens preserved in formalin the mouth was fully expanded, forming a simple ring.

The base of the stomach has the appearance of ground glass, divided by a number of clear lines which meet about the centre. These transparent lines correspond in position with some of the large radial canals. Browne considered that these lines mark the original position of the radial canals and that the stomach grows outwards, taking in a part of the canal. The radial canals are enlarged at their exits from the stomach and this is connected with the growth of the stomach whereby a portion of the canal is converted into a lobe of the stomach. Browne regarded this course of development as responsible for the irregular shape of the stomach.

After taking their origin from the stomach in the manner described above the radial canals do not branch.

From the irregular disposition of the radial canals even in specimens in which they are few, it seems doubtful whether they can be regular even in the first stages. Browne distinguished three types in the development of the radial canal system.

(i) A roundish stomach, with four or more canals about equal distances apart.

(ii) A triangular stomach, with three primary canals, one from each corner of the stomach, and the usual accessory canals, in different stages of development.

(iii) An elongated stomach, with a canal at each end and two canals on each side; also with accessory canals.

The number of radial canals leaving the stomach (including those which had not reached the ring canal) were counted in 217 specimens caught at Valencia in 1897. The results were as follows:

No. of canals leaving stomach	No. of specimens	No. of canals leaving stomach	No. of specimens
5	3	12	25
6	8	13	11
7	18	14	5
8	31	15	6
9	43	16	2
10	32	17	1
11	31	18	1

Browne considered that there is no tendency to produce permanent blind canals, but that the aim of every canal on leaving the stomach is to unite with the ring canal. He noticed in two specimens a short canal running out from the ring canal and directed towards the stomach.

Gonads. The generative elements are formed in oval sacs one of which develops on a radial canal at the point where it narrows after issuing from the stomach lobe. These sacs appear to be carried along the radial canals for they eventually come to lie about half-way between the stomach and the margin of the umbrella (Text-fig. 144). The disposition is thus very irregular according to the sizes of the gonads. Gonads may not be developed on all the radial canals; Browne found in 217 specimens from Valencia mentioned above that the number of gonads ranged from one to twelve, five being the most frequent number. He noticed that the females were in excess of the males in the proportion of about four to three.

The eggs develop as far as the planula stage in the gonadial sacs, after which the planula breaks out of the sac and remains attached to the outer wall for some time. The planula is nearly spherical in shape and possesses no cilia; it has little or no power of locomotion and the gastric cavity is fully formed.

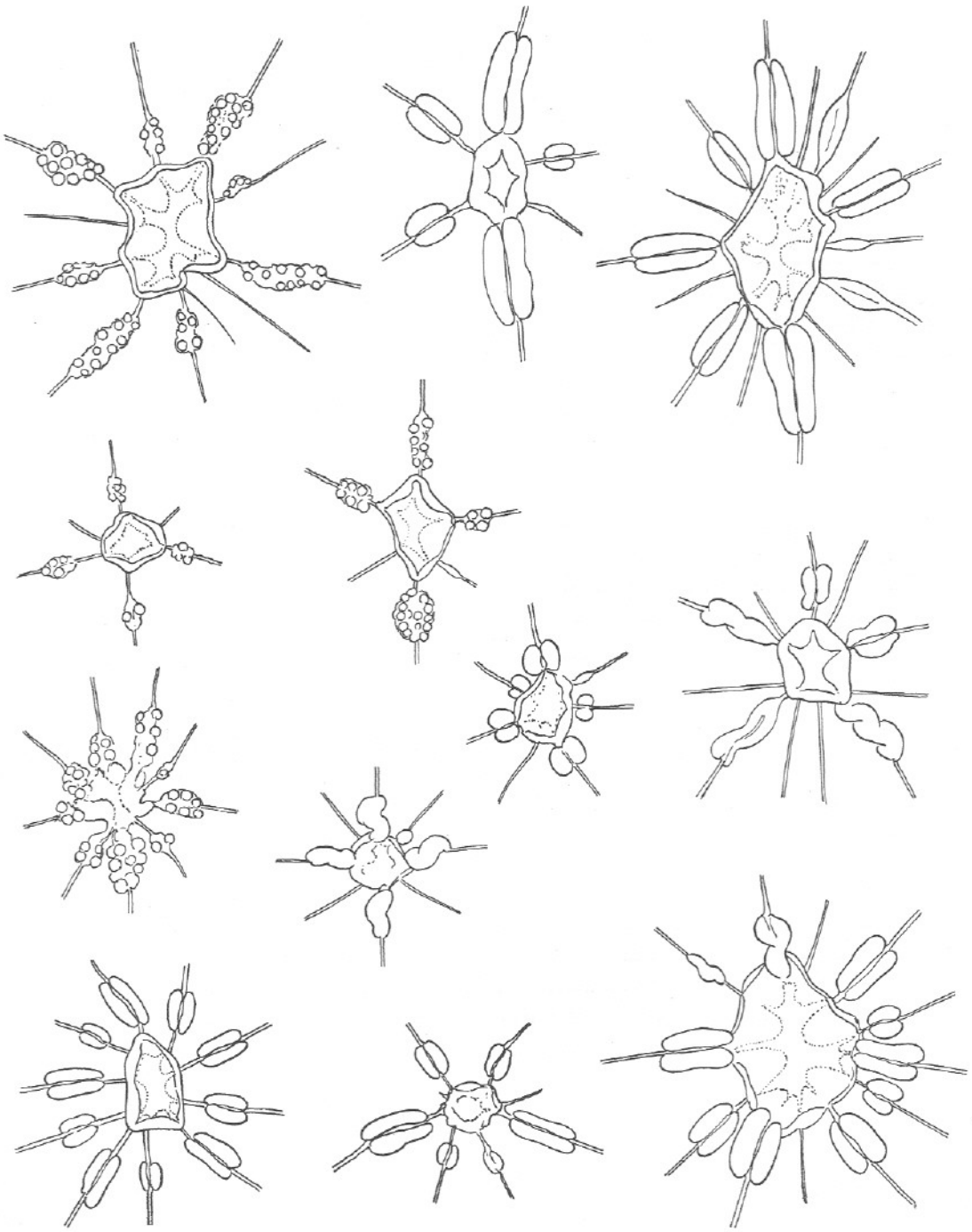
The marginal tentacles (Text-fig. 146) have slight basal thickenings on the adaxial side.

Haeckel gives the size of the adult medusa as up to 12 mm.; Browne, however, never saw a specimen exceeding 8 mm.

NEMATOCYSTS. ? Microbasic euryteles or mastigophores (Russell, 1940*a*).

Seasonal occurrence

Dipleurosoma typicum has been recorded in the plankton at Valencia from April until October inclusive. It varies in abundance considerably from year to year and in good years it has been recorded as most numerous in June, July, August and September. Haddon (1886) recorded it as very common in June 1885, in Kingston harbour, Ireland.



Text-fig. 145. *Dipleurosoma typicum*. Variation in numbers of radial canals in preserved specimens from Valencia, 1898. (E. T. Browne collection.)

DIPLEUROSOMIDAE

Habits

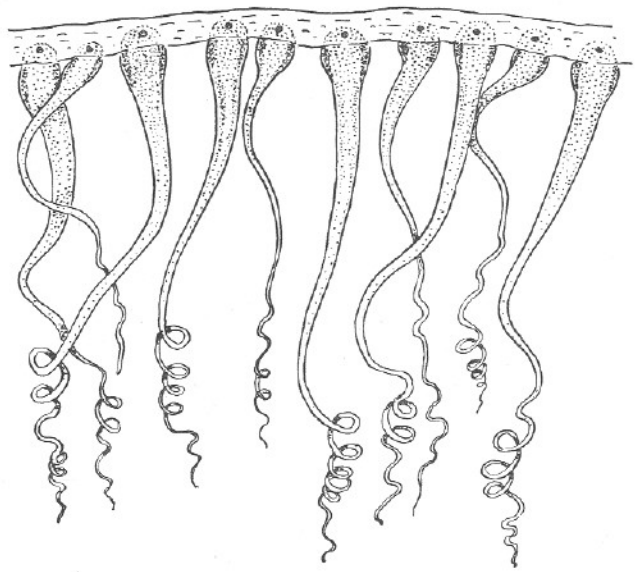
This medusa is very delicate and quickly dies in confinement. Its marginal tentacles are very extensile and can expand to a length of 7–10 cm.; when contracted they are spirally coiled.

At Valencia the species has been recorded as present in very large swarms in some years. For instance in 1897 Miss C. Delap wrote that it was more numerous than any other medusa and 'the water looked quite grey with them'.

I have seen specimens in Mr Browne's collection with Hemiurid parasites.

HYDROID. ? *Cuspidella* sp.

The hydroid of *Dipleurosoma typicum* has not yet been definitely identified. Young polyps have been reared by the Misses Delap (see Browne, 1900, p. 696) which appeared to belong to the genus *Cuspidella*. This observation needs confirmation.



Text-fig. 146. *Dipleurosoma typicum*. Portion of umbrella margin of preserved specimen, Valencia, 1898. (E. T. Browne collection.)

Historical

Dipleurosoma typicum was first described by Boeck (1866) as two species, *D. typica* from south-west Norway and *D. stuvitzii* from Newfoundland. It was subsequently described by Allman (1873 *a*, *b*) as *Ametrangia hemisphaerica* from south Ireland, and as *Dipleurosoma irregulare* by Haeckel (1879) from specimens collected off Brighton. The formation of these distinct species was due to the irregularity typical of the species and they were brought together as one species by Browne (1897 *a*, 1900).

Mayer (1910) and Kramp (1933 *b*) have included as a synonym Haeckel's species *D. amphithectum*. In that species the radial canals branch between the gonads and the umbrella margin. Browne (1900) pointed out that this formation could not be regarded as typical of the genus although Haeckel had based his generic characters on it. It is possible that *D. amphithectum* is an abnormality, or it may have been incorrectly described. In any case it is advisable to keep it distinct, or perhaps as a doubtful species until its existence is proved.

FAMILY MITROCOMIDAE

Leptomedusae with base of stomach attached to subumbrella along edges of radial furrows; with quadratic four-lipped, rarely eight-lipped, mouth; with four, eight, or more simple radial canals; with gonads on radial canals, oval or linear, separated from stomach; with hollow marginal tentacles; with or without marginal cirri; with open marginal vesicles; with or without ocelli.

HYDROID. *Cuspidella*-like, with single whorl of filiform tentacles; with hydrotheca without stalk and with folded operculum.

The distinctive character of the family Mitrocomidae is the open marginal vesicle. An excellent account of the morphology and classification of the family is given by Kramp (1932).

The Mitrocomidae are represented in British waters by four genera, *Mitrocomella* Haeckel, *Cosmetira* Forbes, *Halopsis* A. Agassiz, and *Tiaropsis* L. Agassiz. These genera can be distinguished on the following characters:

Without ocelli:
  With four radial canals:
    With spiral marginal cirri . . . . . **Mitrocomella**
    With flexile marginal cirri . . . . . **Cosmetira**
  With twelve to sixteen radial canals . . . . . **Halopsis**
With ocelli . . . . . **Tiaropsis**

Mention should here be made of the distinction between the marginal cirri of *Mitrocomella* and those of *Cosmetira*. In *Mitrocomella*, as in many other genera, these cirri coil spirally; they have a thickened stiffer basal region and a very extensile distal portion terminating in an elongated somewhat spiral nematocyst cluster. In adult *Cosmetira*, when preserved, the marginal cirri always appear as rather straight stiff structures and they have nematocysts arranged in rings along their whole length. But in very young specimens the cirri are of the same form as those of *Mitrocomella*. It seems most likely that the thin terminal portion breaks off and the thickened basal part continues to develop. As the medusa grows, new cirri appear only in the form found in the adult medusa.

Genus **Mitrocomella** Haeckel, 1879

MEDUSAE. Mitrocomidae with stomach with four simple lips; with four radial canals; with oval or linear gonads; with spiral marginal cirri; with eight to sixteen marginal vesicles; without ocelli.

HYDROID. *Cuspidella*-like.

There are two British species of the genus, *Mitrocomella polydiademata* (Romanes) and *M. brownei* Kramp. The two species can be distinguished by the numbers of marginal tentacles and of marginal vesicles.

Thirty-six to forty-eight marginal tentacles; sixteen marginal vesicles . **M. polydiademata**
Sixteen to twenty-four marginal tentacles; typically eight marginal vesicles . . **M. brownei**

The hydroid of *M. polydiademata* is not known.

Mitrocomella polydiademata (Romanes)

Text-figs. 147–9

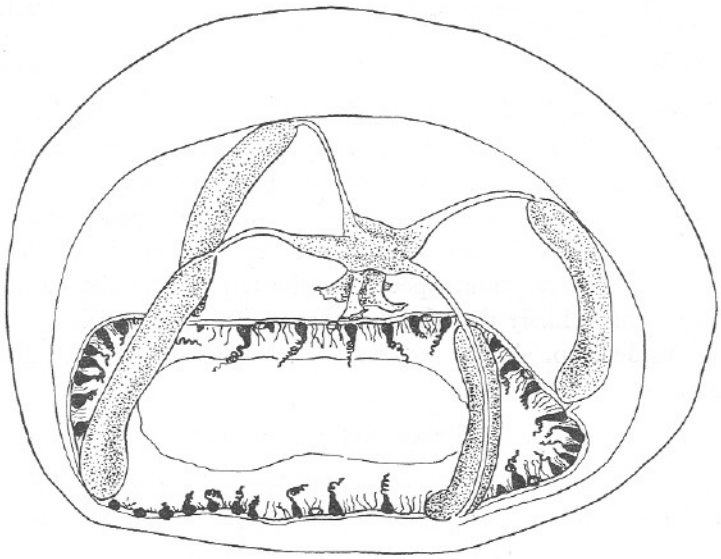
Tiaropsis polydiademata Romanes, 1876*b*, *Philos. Trans. Roy. Soc. London*, vol. CLVI, pt. i, p. 274.
Romanes, 1877*a*, *Journ. Linn. Soc. London, Zool.* vol. XIII, p. 194, pl. xv, fig. 3.
Tiarops polydiademata, Romanes, 1876*a*, ibid. vol. XII, pp. 525–6.
Mitrocomella polydiadema Haeckel, 1879, *System der Medusen*, p. 185.
Browne, 1895, *Trans. Liverpool Biol. Soc.* vol. IX, p. 279.
Browne, 1910, *Nat. Antarct. Expedit.* 1901–1904, *Nat. Hist.* vol. V, Zool. and Bot. p. 33.
Mitrocomella fulva Browne, 1903, *Bergens Mus. Aarb.* no. 4, p. 17, pl. i, fig. 3; pl. iii, figs. 1, 2 (in part).
Mitrocomella polydiademata, Browne, 1905, *Proc. Roy. Soc. Edinb.* vol. XXV, pt. ix, p. 767.
Kramp, 1932, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. XCII, p. 346, text-figs. 3, 5, 11, 18, 29, 30, 40; pl. x, figs. 3, 4.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 565, fig. 28.

MITROCOMIDAE

Mitrocoma polydiademata, Mayer, 1910, *Medusae of the World*, vol. II, p. 290, fig. 157.
Kramp, 1919, *Danish Ingolf-Expedit.* vol. V, pt. 8, p. 59, chart VI.
Mitrocoma cruciata Bigelow, 1915*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. LIX, no. 4, p. 320.
Bigelow, 1926, *Bull. U.S. Bur. Fish. Washington*, vol. XL (1924), pt. II, p. 348.

Specific Characters

Gonads linear, along distal half to four-fifths of radial canals; thirty-six to forty-eight marginal tentacles; sixteen marginal vesicles, each with twenty to thirty concretions.



Text-fig. 147. *Mitrocomella polydiademata*. Preserved specimen *c.* 10 mm. in diameter, male, Port Erin, 13. vi. 99. (E. T. Browne collection.)

Description of Adult

Umbrella hemispherical or somewhat higher than a hemisphere; jelly fairly thick. Velum well developed. Stomach short, quadratic, with small base; attached to subumbrella along arms of perradial cross, leaving small flat triangular pouches between dorsal wall of stomach and subumbrella. Mouth with four short lips, with slightly folded margins. Four straight radial canals and ring canal narrow. Gonads on four radial canals, linear, somewhat sinuous, with three or four bends on either side; occupying half to four-fifths of length of radial canal; median division distinct in male, indistinct in female. Marginal tentacles hollow, thirty-six to forty-eight in number (in European waters), with long tapering basal bulbs. No ocelli. Marginal cirri usually five to nine, sometimes more, in number between adjacent marginal tentacles; marginal cirri coil spirally. Marginal vesicles open, sixteen in number, each with fifteen to twenty concretions arranged in two rows or irregularly distributed. Diameter of umbrella 12–30 mm. Colour of stomach and marginal tentacle bases purplish or rosy; gonads yellowish brown, purplish or rosy.

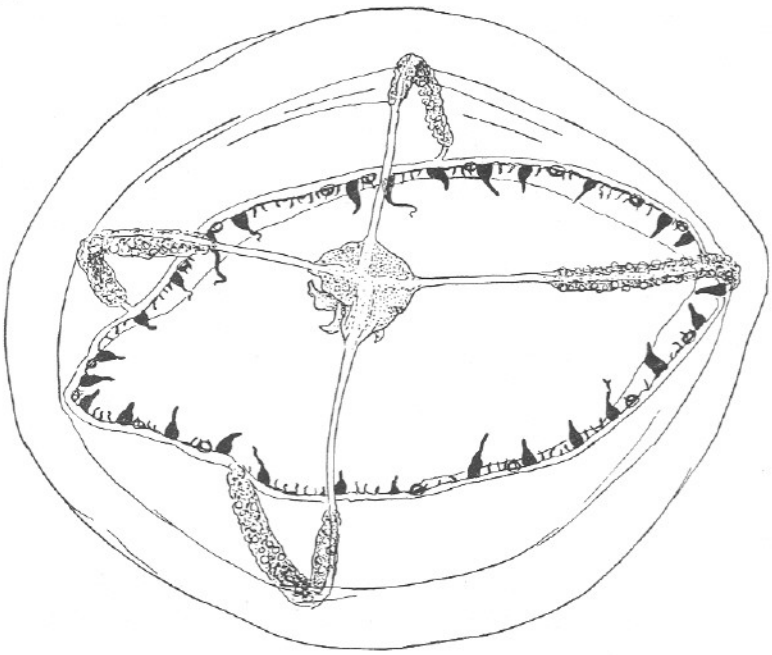
Distribution

In its distribution round the British coasts *Mitrocomella polydiademata* is a somewhat northerly species. It has been recorded from the Northumberland coast, Dunbar, Cromarty Firth, Shetlands, Firth of Clyde, and Port Erin, where Browne (1895) recorded it as abundant.

Elsewhere it has been found on the coast of Norway, in the Skagerak and Kattegat, off the Faeroe Islands and in the North Sea 90 miles off the Firth of Forth, and off the coast of Belgium; in Kara Sea and Barents Sea. It also occurs on the north-western side of the North Atlantic (Bigelow, 1915*a*, 1926, as *Mitrocoma cruciata* (see Kramp, 1932)); and off the coast of west Greenland.*

Developmental Stages and Structural Details

The first stage of the medusa *Mitrocomella polydiademata* has not been described since its hydroid is not yet known.



Text-fig. 148. *Mitrocomella polydiademata*. Preserved specimen *c.* 10 mm. in diameter, female, Port Erin, 13. vi. 99. (E. T. Browne collection.)

Kramp (1932) gives details of the development of the species as follows:

Diameter (mm.)	No. of fully developed marginal tentacles	No. of cirri between adjacent marginal tentacles
3	8–16	3–5
4–5	12–16	4–5
6–7	19–20	3–7
8	16–38	3–9
9	29–36	5–13
11–12	32–43	5–13

The numbers of marginal tentacles are thus somewhat variable at any one size, and 'the development of the tentacles, beyond the first sixteen, proceeds very irregularly, and they are not equidistant; the number of cirri between two successive tentacles is, therefore, variable, particularly so in older stages'. (Kramp, 1932, p. 347.)

* ?Consequent on climatic change (Jensen, 1939).

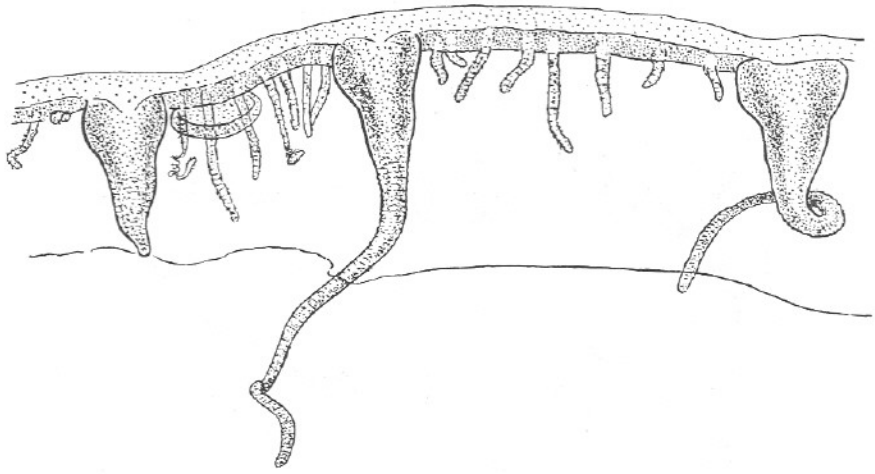
Kramp (1942) records a specimen from the west coast of Greenland 11 mm. in diameter which had fifty-eight marginal tentacles and twenty-two developing marginal bulbs.

In specimens 3–4 mm. in diameter the gonads are already fairly well developed along the distal half to two-thirds of the radial canal. This is in marked contrast with medusae of *Cosmetira pilosella* of the same size in which the gonads appear first at the proximal ends of the radial canals.

The marginal cirri (Text-fig. 149) can expand to a length of two or three times that of the marginal tentacle bulbs; they terminate in an elongated cluster of nematocysts.

Kramp states that even in the youngest specimens observed the sixteen marginal vesicles were all present.

Sanderson (1930, p. 226) recorded an abnormal specimen in which two adjacent radial canals were fused in the middle.



Text-fig. 149. *Mitrocomella polydiademata*. Portion of umbrella margin of preserved specimen in Text-fig. 147, showing a marginal vesicle without concretions.

Seasonal occurrence

On British coasts *Mitrocomella polydiademata* has been recorded from the plankton in the following months: June (Firth of Forth), between May and August (Cromarty Firth), July (Shetlands), June and July (Firth of Clyde), April, May, June and July (Port Erin). The species is thus evidently most likely to be found in the plankton in spring and early summer.

Habits

Observations on the reactions of *Mitrocomella polydiademata* to light and other stimuli were made by Romanes (1877*b*, pp. 683, 710, 731, 734).

In the dark the medusa is brilliantly luminous when stimulated (Romanes, 1876*a*).

Browne (1895) records that at Port Erin on 30 May 1893, 'many dozens were left by the tide upon the sandy beach, and amongst the weeds in the rock pools. The largest specimens were about 30 mm. in diameter'.

HYDROID

The hydroid of *Mitrocomella polydiademata* is not yet known. It will probably prove to be a *Cuspidella*.

Historical

Mitrocomella polydiademata was first named by Romanes (1876*b*) as *Tiaropsis polydiademata*; he (1876*a*) briefly described it as *Tiarops polydiademata* and later (1877*a*) figured it. Both his description and figure were somewhat inadequate but there can be little doubt about the identity of the species. He found it in the Cromarty Firth.

According to Kramp (1932) the medusae recorded by Bigelow (1915*a*, 1926) as *Mitrocoma cruciata* from the Gulf of Maine and Nova Scotia are exactly like *Mitrocomella polydiademata* in all essentials, except that they have more marginal tentacles, the numbers of which vary between forty-eight and sixty-four.

Mitrocomella brownei (Kramp)

Plate XV, fig. 4; Text-figs. 150–5

Euchilota n.sp. Browne & Vallentin, 1904, *Journ. Roy. Inst. Cornwall*, vol. L, p. 125.
Trissocoma brownei Kramp, 1930, *Mém. Mus. Roy. d'Hist. Nat. Belgique*, Mém. no. 45, p. 23, figs. 9–11.
Mitrocomella brownei, Kramp, 1932, *Vidensk. Medd. naturh. foren. Kbh.* Bd. XCII, p. 341, text-figs. 9, 37.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 566, fig. 29.
Rees & Russell, 1937, *Journ. Mar. Biol. Assoc.* vol. XXII, p. 75, figs. 9–11 (hydroid and medusa).

Specific Characters

Gonads oval, or short linear, near distal ends of radial canals; marginal tentacles normally sixteen; marginal vesicles eight to eleven, each with five to seven concretions.

Description of Adult

Umbrella usually flatter than a hemisphere; jelly uniformly thin. Velum fairly broad. Stomach short, quadratic, with very small base. Mouth with four simple perradial, slightly recurved lips. Four straight radial canals and ring canal very narrow. Four gonads on distal ends of radial canals, males oval, females somewhat elongated. Marginal tentacles solid, eleven to twenty-four in number, normally sixteen, with broad rounded bases. Marginal cirri six to eight in number between adjacent marginal tentacles; marginal cirri coil spirally. Marginal vesicles open, eight to eleven, typically eight, in number, each with five to seven concretions. Diameter of umbrella 4–7 mm. Colour of stomach, gonads and marginal tentacle bases bright pinkish or ochreish yellow; streaks of bluish black pigment on either side of marginal tentacle bases in large specimens.

Distribution

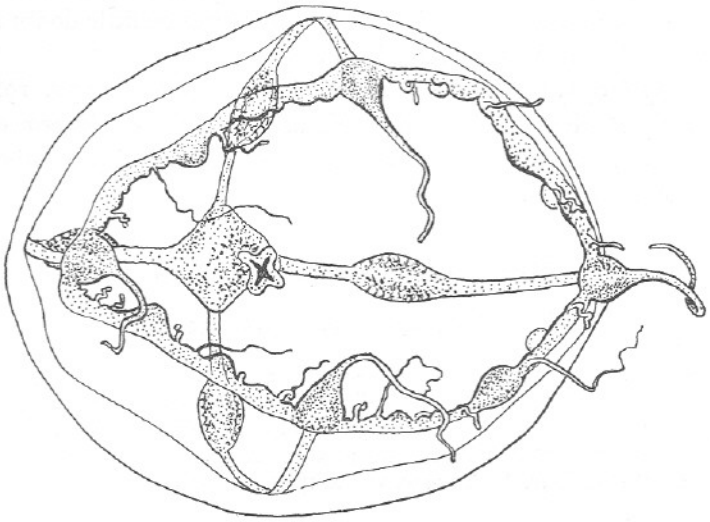
Mitrocomella brownei has only been recorded off British coasts from Plymouth, Salcombe, south of Start Point, Scilly Isles, Port Erin; and Valencia, south-west Ireland. It thus appears to be somewhat southern in its distribution.

It has also been recorded from the southern North Sea between Orford Ness and Zeebrugge.

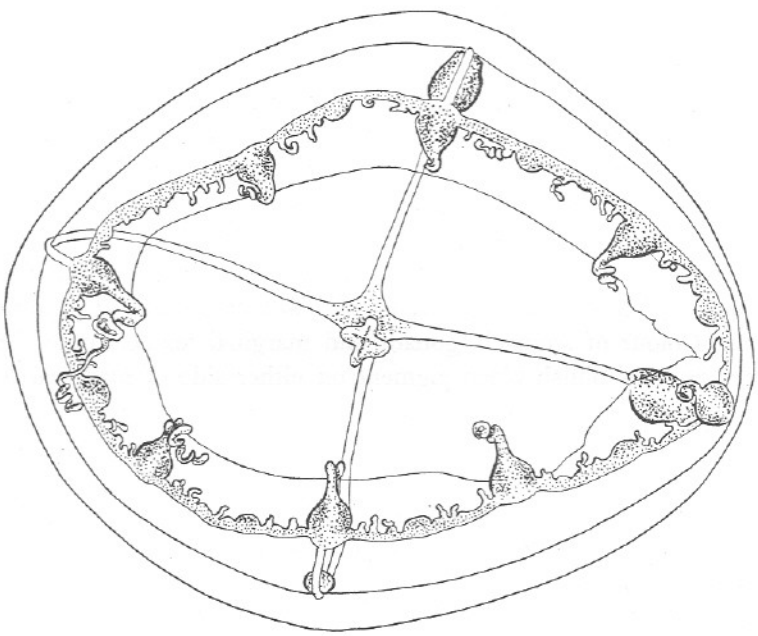
Developmental Stages and Structural Details

The medusa *Mitrocomella brownei* has not been seen immediately on liberation from its hydroid, which is a *Cuspidella*. Kramp (1930) has described medusae of different sizes, the smallest being 1·5 mm. in diameter. In this specimen the four perradial and four interradial marginal tentacles were already fully developed. The gonads were quite distinct, though very small, and situated

midway along the radial canals. The development of the adradial marginal tentacles appears to be slow. In small individuals 1·5–2·5 mm. in diameter (Text-figs. 150, 151) they show as tiny rudiments; in specimens 3 mm. wide some of the adradial bulbs may be somewhat pointed; but



Text-fig. 150. *Mitrocomella brownei.* Preserved specimen *c.* 1·5 mm. in diameter, Plymouth, 3. iii. 38.



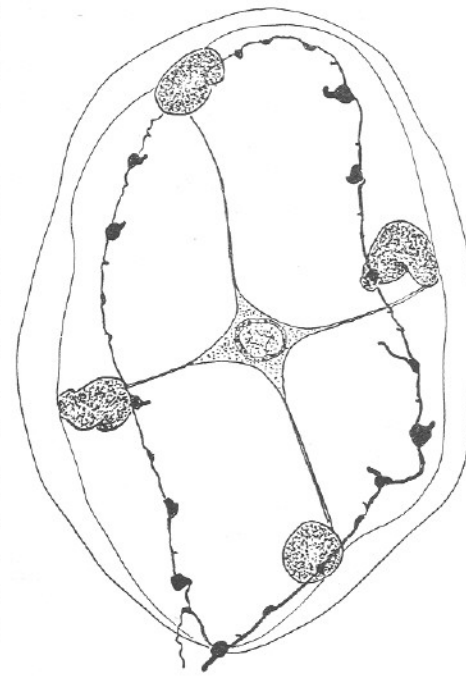
Text-fig. 151. *Mitrocomella brownei.* Preserved specimen *c.* 2 mm. in diameter, marginal vesicles not shown, Plymouth, 28. iv. 37.

the typical complete number of sixteen fully developed marginal tentacles is not seen in specimens less than 4 mm. in diameter and even then some of the marginal tentacles may not be fully developed.

The gonads, which first appear midway along the radial canals, reach their final positions on the distal portions of the radial canals when the medusae are about 3·5 mm. in diameter; they are then fairly large, much swollen, and sometimes fully developed. In larger specimens the ovaries are sometimes somewhat elongated. The gonads have a very thin mesosarc; the young eggs are in the ectoderm, and the larger eggs, enclosed in the mesosarc, push the mesosarc inwards into the endoderm (Kramp, 1932, p. 325).

The marginal tentacles can contract into a close spiral (Text-fig. 153). They are provided with small clusters of nematocysts forming incomplete rings, better developed on the adaxial than on the abaxial side of the tentacle. The endoderm of the marginal tentacles is solid, except in the basal bulbs; there is a thin and simple mesosarc (Kramp, 1932, p. 328). They may reach as many as twenty-four in number, but are typically sixteen.

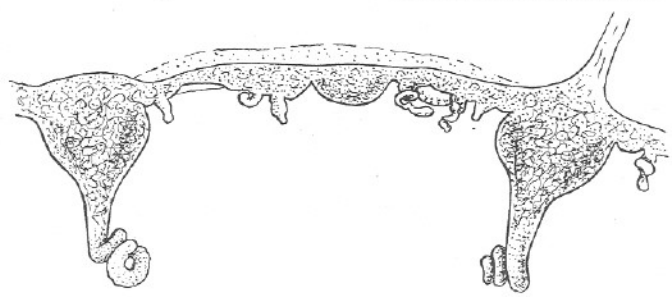
The marginal cirri (Text-fig. 154), which can coil spirally, can expand to a length of about two or three times that of the marginal tentacle bulbs and they terminate in an elongated cluster of nematocysts. The older cirri are usually situated a short distance above the margin of the umbrella.



Text-fig. 152. *Mitrocomella brownei*. Mature preserved specimen *c.* 5 mm. in diameter, Plymouth.

The number of marginal vesicles (Text-fig. 154B) is probably typically eight, but there may be as many as twelve (Rees & Russell, 1937). Kramp (1932, p. 342) found eight specimens with more than eight marginal vesicles among 175 examined. In specimens 1·5 mm. in diameter there are already eight marginal vesicles, each with two or three concretions.

NEMATOCYSTS. Basitrichous haplonemes and atrichous haplonemes (Russell, 1938*b*).



Text-fig. 153. *Mitrocomella brownei*. Portion of umbrella margin of specimen 2 mm. in diameter, Plymouth, 28. iv. 37.

Seasonal occurrence

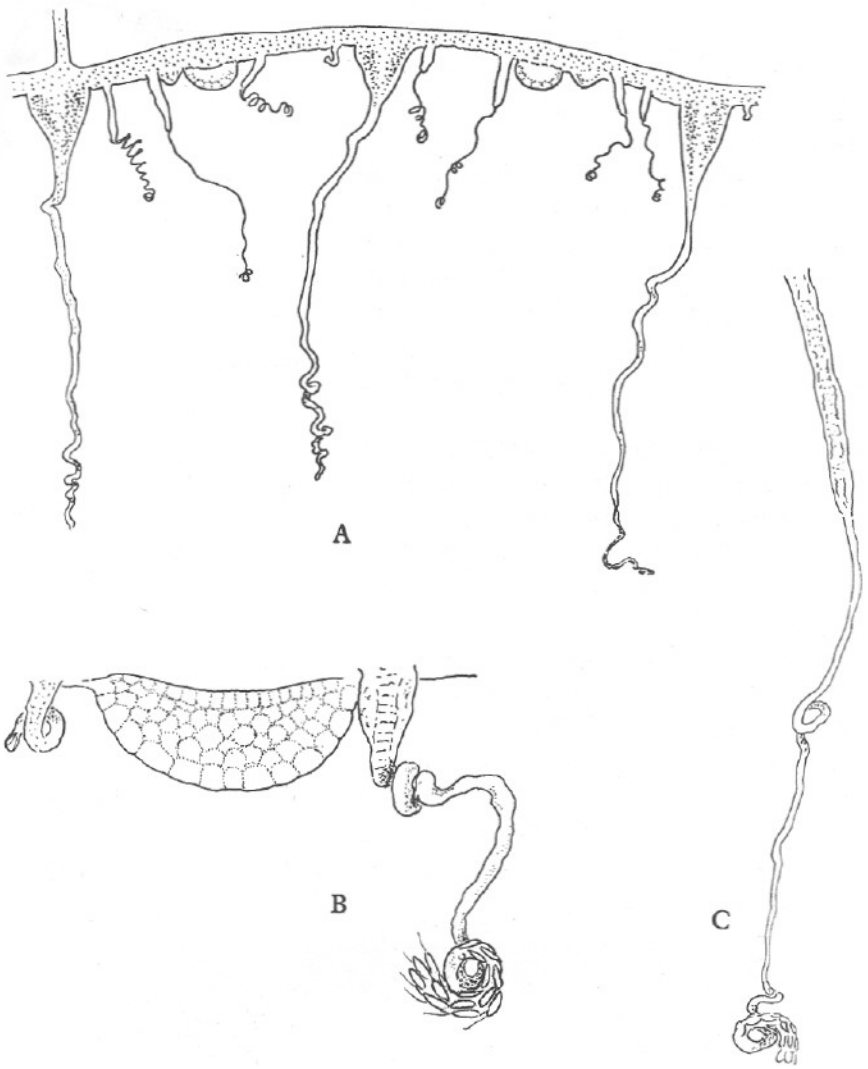
Mitrocomella brownei has been recorded from the plankton in British waters in the following months: April, May, August and September (Plymouth), September (Port Erin); October–November (Valencia), and August (southern North Sea).

MITROCOMIDAE

HYDROID. *Cuspidella* sp. (Text-fig. 155A, B.)

(For full description see Rees & Russell, 1937, *Journ. Mar. Biol. Assoc.* vol. XXII, p. 75, figs. 9–11.)

Colonies of single hydranths, up to 0·8 mm. in height when fully expanded, arising from



Text-fig. 154. *Mitrocomella brownei.* Details of preserved specimens. A, portion of umbrella margin showing marginal tentacle, cirri, and marginal vesicles; B, marginal vesicle with cirri, concretions not shown; C, marginal cirrus.

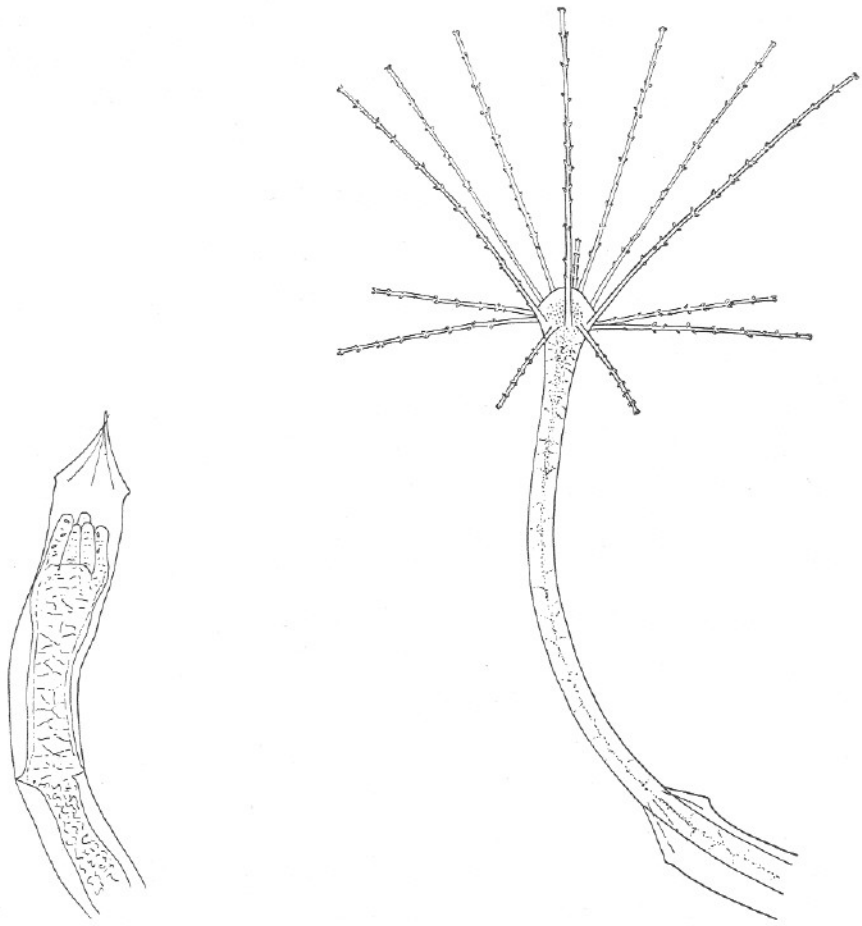
a creeping stolon. Hydrotheca cylindrical, with terminal operculum with about five to seven teeth. Height of hydrotheca 0·2–0·3 mm.; width 0·05–0·06 mm.

Hydranth very extensile, with a single whorl of eight to twelve filiform tentacles; completely retractile into hydrotheca; colourless. Gonotheca unknown.

The specific identity of this hydroid is uncertain. It agrees in dimensions with those given by Stechow (1923) for *Cuspidella humilis.* Since, however, Hincks gave no measure-

ments in his original description of the species it is impossible to decide whether it is indeed this species.

The hydroid of *Mitrocomella brownei* is about half the size of that of *Laodicea undulata*, and very delicate in appearance.



Text-fig. 155. *Mitrocomella brownei*. A, hydroid reared from the medusa in the Plymouth laboratory, 15. v. 37, width of hydrotheca 0·06 mm.; B, fully expanded hydranth of *Cuspidella* dredged from the Cattewater, Plymouth, 30. i. 36, width of hydrotheca 0·06 mm., possibly belonging to *Mitrocomella brownei*. (After Rees & Russell, 1937, figs. 10*a*, 11.)

Historical

Mitrocomella brownei was first described by Kramp (1930) as *Trissocoma brownei*. The species was first seen by Mr E. T. Browne, and Dr Kramp after seeing some of the specimens and drawings at Berkhamsted, subsequently found the medusa in the southern North Sea. He placed it first in a new genus *Trissocoma*, imagining that there were two kinds of marginal cirri present; later (1932), he realized that this was not so and transferred the species to *Mitrocomella*.

Genus **Cosmetira** Forbes, 1848

MEDUSAE. Mitrocomidae with stomach with four slightly folded lips; with four radial canals; with linear gonads; with flexile marginal cirri; with eight marginal vesicles; without ocelli.

HYDROID. *Cosmetira*, with characters as family.

There is one British species of *Cosmetira*, the only species of the genus, *C. pilosella* Forbes. The structure and appearance of the marginal cirri makes this species at once identifiable. Another characteristic feature is the presence of numerous marginal cirri well up over the surface of the exumbrella, giving the umbrella margin a distinctly pilose appearance in large specimens.

Cosmetira pilosella Forbes

Plate XV, figs. 1–3; Text-figs. 156–61

Thaumantias (*Cosmetira*) *pilosella* Forbes, 1848, *Monogr. Brit. Medusae*, p. 42, pl. viii, fig. 1.
Thaumantias pilosella, Gosse, 1853, *Devon Coast*, pp. 334, 344.
Euchilota pilosella, Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 484 (*non* pl. xvi, fig. 7).
Laodicea stauroglypha L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 350 (?in part).
Laodice cruciata Haeckel, 1879, *System der Medusen*, p. 132 (in part).
?*Halopsis megalotis* Maas, 1893, *Ergebn. Plankton Expedit.* Bd. II, K.c., p. 57, Taf. VI, figs. 3–6.
Cosmetira pilosella, Hartlaub, 1909*a*, *Zool. Anz. Leipzig*, Bd. XXXIV, p. 82, figs. 1–4.
Browne, 1910, *Nat. Antarct. Exped., Nat. Hist.* vol. V, p. 32.
Mayer, 1910, *Medusae of the World*, vol. II, p. 261, fig. 134*a*.
Kramp, 1919, *Danish Ingolf-Expedit.* vol. V, pt. viii, p. 61, chart VII.
Kramp, 1932, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. XCII, p. 356, text-figs. 7, 8, 10, 13, 16, 17, 25, 26, 27, 44.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 569, fig. 33.
Russell, 1938*a*, *Journ. Mar. Biol. Assoc.* vol. XXII, no. 2, p. 428.
Rees, 1941*b*, *Proc. Roy. Soc. Edinb.* Sect. B, vol. LXI, pt. i (no. 4), pp. 55–8, figs. 1, 2 (hydroid and medusa).
?*Cosmetira megalotis* Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 570, fig. 34.

Specific Characters

Possibly the only species of the genus (see p. 273).

Description of Adult

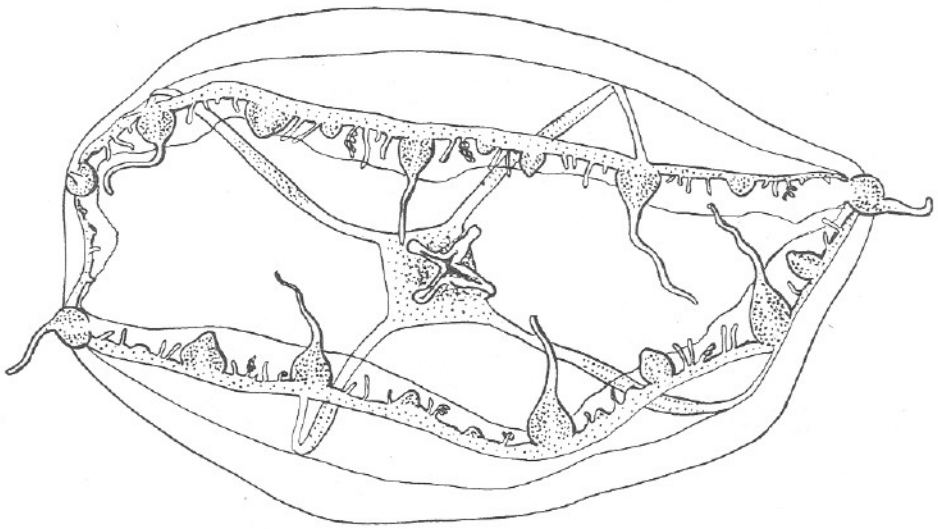
Umbrella hemispherical or usually somewhat flatter; jelly fairly thick in upper region, thinning towards umbrella margin. Velum well developed. Stomach short, quadratic, with very broad base; attached to subumbrella along arms of perradial cross, leaving four flat triangular pouches between dorsal wall of stomach and subumbrella. Mouth with four lips with crenulated margins. Four straight radial canals and ring canal narrow. Gonads on four radial canals, linear, slightly sinuous, half to three-quarters length of radial canal, slightly nearer ring canal than stomach, with median division in both sexes. Marginal tentacles hollow, *c.* sixty-five to one hundred in number, with large rounded basal bulbs. No ocelli. Six to ten marginal cirri between adjacent marginal tentacles, usually straight but may coil spirally; older marginal cirri extending well up surface of exumbrella. Marginal vesicles open, eight in number, each with twelve or more concretions, sometimes arranged in two rows. Diameter 20–48 mm. Colour of stomach and gonads reddish violet; marginal tentacle bases deep purple with reddish yellow centres.

Distribution

Cosmetira pilosella has been recorded from the following localities round the British coasts: Northumberland coast; Shetlands; Fair Isle Channel; Isle of Man; Bristol Channel; Ilfracombe;

Newquay (Cornwall); Valencia, south-west Ireland; Scillies; Falmouth; Plymouth; Salcombe; Newhaven; and Thames Estuary. It is thus likely to be found almost all round the British Isles. It is a species, however, whose normal habitat is round those west regions influenced by Atlantic oceanic water whence it is carried by water movements into other areas. Its occurrence in the English Channel and southern North Sea is thus normally a sign of the passage of mixed coastal and oceanic water into those regions.

Elsewhere the species has only been recorded from the English Channel, North Sea, Kattegat, Skagerak, and Norwegian coast near Bergen. It is thus apparently confined to north-west European waters.



Text-fig. 156. *Cosmetira pilosella*. Preserved specimen 3·3 mm. in diameter, Plymouth, 28. iv. 37.

Developmental Stages and Structural Details

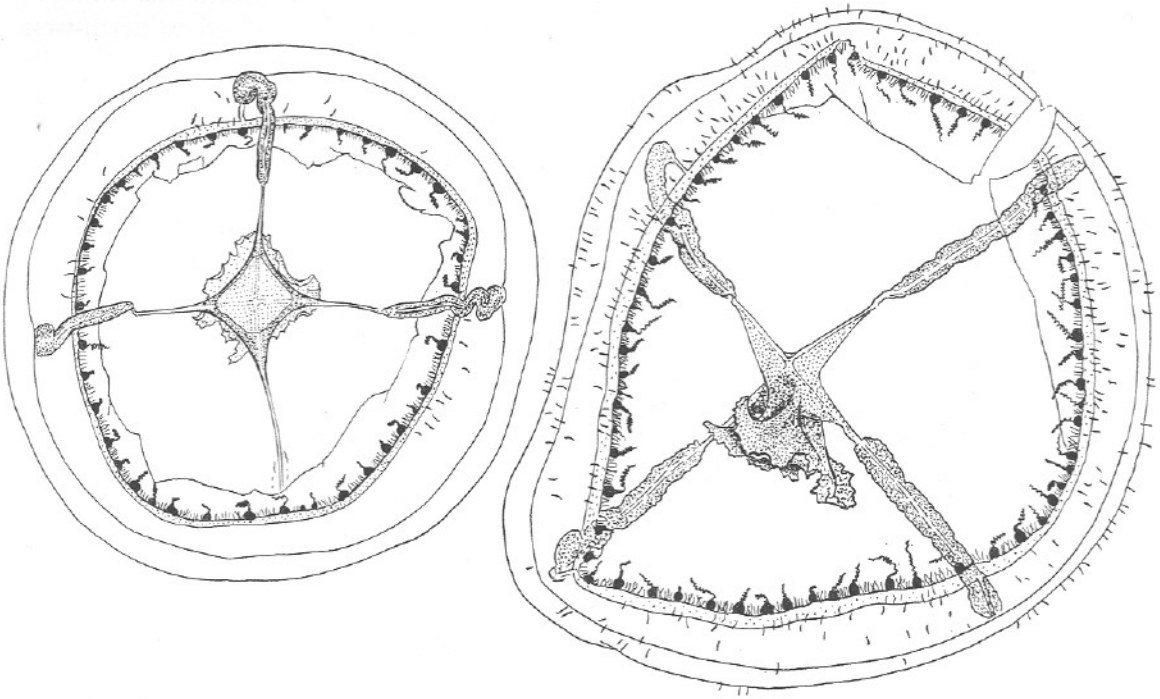
A medusa liberated from a *Cuspidella* hydroid at Plymouth on 28 March 1936 was reared until it could be connected with later stages caught in the plankton which were known to be the young of *Cosmetira pilosella*. The medusa, when first liberated from its hydroid, was 0·75 mm. in height. The umbrella was bell-shaped, higher than wide, with a slightly conical apex. There were scattered nematocysts on the exumbrella. The velum was broad. The stomach was very short and the mouth without lips. The four radial canals and ring canal were narrow. There were no signs of gonads. There were two opposite perradial marginal tentacles with large elongated basal bulbs. There were two small opposite perradial marginal bulbs without tentacles. There were eight spirally coiled marginal cirri, two in each interradius, with the rudiments of a third in one quadrant. There were no marginal vesicles. The colour of the stomach, marginal tentacle bases and marginal bulbs was reddish yellow.*

Three days later the medusa was 0·9 mm. high and 0·8 mm. wide. There were three spiral marginal cirri in each interradius and the rudiments of a fourth in two opposite quadrants. On 3 April the medusa was 1 mm. in diameter. The two perradial marginal bulbs without tentacles were more developed and four interradial marginal bulbs were appearing. There were as yet no signs of marginal vesicles. Four days later, with a diameter of 1·2 mm., the medusa had reached

* The above observations were subsequently confirmed by Rees (1941 *b*) at Millport in the Firth of Clyde.

the stage shown in Plate XV, fig. 1. There were still no signs of gonads, but eight marginal vesicles had developed, four of which had one concretion and the others two concretions. Not only were the marginal tentacle bases and developing marginal bulbs pinkish yellow, but this tinge was also present all round the umbrella margin.

Another specimen 1 mm. in diameter had two marginal vesicles on 7 April and two more appearing on the next day. This specimen was 1·2 mm. high on 9 April and had six marginal



Text-fig. 157. *Cosmetira pilosella*. Preserved specimens. Left, *c.* 16 mm. in diameter, Hoy, Orkney, June 1938 (collected by D. S. Falconer); right, *c.* 23 mm. in diameter, Valencia, 8. x. 97. (E. T. Browne collection.)

vesicles, five of which had one concretion, there being two concretions, a large and a small, in the other. On this same date, 9 April, the other specimen was still 1·2 mm. in diameter. It had two perradial marginal tentacles, two perradial marginal bulbs and four interradial marginal bulbs; there were two marginal cirri between adjacent marginal bulbs in each octant. There were still eight marginal vesicles, but the numbers of concretions had increased, there being three concretions each in four of the vesicles, and two each in the remaining four. The medusa could not be reared further.

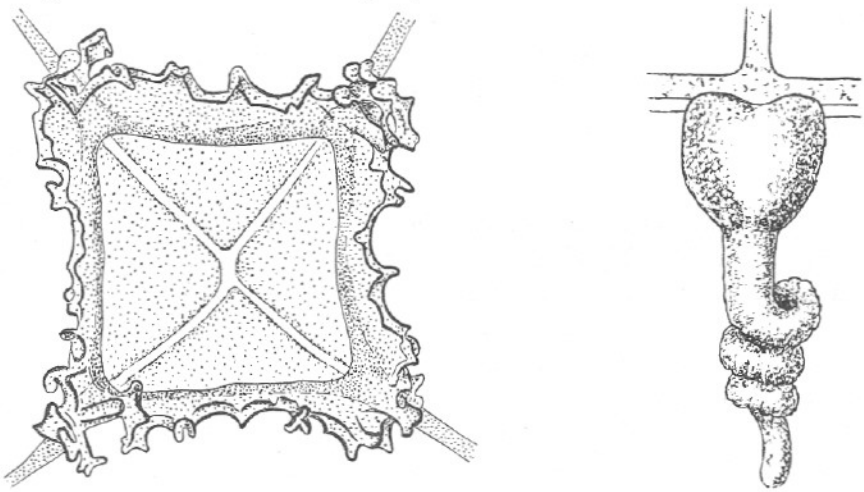
The next stage was found in the plankton. It was 1·5 mm. in diameter, and had four perradial marginal tentacles, and four interradial marginal bulbs; there were three marginal cirri in each octant. There were eight marginal vesicles, each with three to five concretions. The reddish yellow colour of the umbrella margin was very pronounced. There were no signs of gonads.

At this stage the medusa is about as high as it is wide and it soon begins to become more flattened. A specimen 1·7 mm. high and 1·8 mm. wide still had four marginal tentacles only, but the four interradial marginal bulbs were more developed and there were usually four or five

marginal cirri in each octant. One marginal vesicle had as many as six concretions. For the first time traces of the gonads are beginning to appear, high up on the radial canal near the stomach.

The next stage in development was shown by a specimen from the plankton 3·3 mm. in diameter (Text-fig. 156 and Pl. XV, fig. 2). The umbrella was now considerably flattened. There were four perradial and four interradial marginal tentacles and sixteen rudiments of marginal bulbs, one on either side of each of the eight marginal vesicles. The numbers of concretions in each marginal vesicle were now five to nine. The linear gonads were quite distinct and stretched from near the stomach for a distance of about one-third of the length of the radial canal. For the first time the typical violet colour of the adult was beginning to appear on some of the marginal tentacle bases and on the stomach.

At a diameter of 5 mm. it is quite easy to see by the elongated gonads and coloration that the medusa is a young *Cosmetira pilosella*. There are still only eight marginal tentacles, but the sixteen additional marginal bulbs are more developed; of the latter those nearest the radii develop first.



A B

Text-fig. 158. *Cosmetira pilosella*. A, stomach of preserved specimen looking through open mouth, caught off Plymouth, 17. viii. 32; B, marginal tentacle.

After this stage is passed the development and increase in number of the marginal tentacles must be rapid.

The *marginal tentacles* (Text-figs. 158B, 159) have large swollen bases; they are hollow and rather short. Their number is somewhat variable. Since observations have not been made on living specimens it is not possible to say how variable the numbers are according to the size of the medusa. In preserved material from Plymouth, in which contraction may have been very inconstant, the number of marginal tentacles varied from sixty-seven to ninety-nine in medusae 15–26 mm. in diameter (Russell, 1938*a*, p. 428). The marginal tentacles coil spirally.

The *marginal cirri* (Text-figs. 159, 160) vary in length according to their age; they are very extensile and when fully grown can extend to more than twice the length of a marginal tentacle base. They are armed with numerous nematocysts arranged approximately in rings. The marginal cirri can coil spirally and may also contract by shortening and remaining straight. In preserved material the marginal cirri almost without exception appear straight and stiff. As the margin of the umbrella grows, the older marginal cirri become carried upwards over the exumbrellar

surface, until they may lie as much as 3 mm. above the margin; an endodermal root runs down to the ring canal. In very young specimens the marginal cirri have the same structure as in *Mitrocomella*, terminating in an elongated cluster of nematocysts (Text-fig. 160A–C). Presumably the whip-like lash breaks off and the thickened basal portion develops nematocysts.

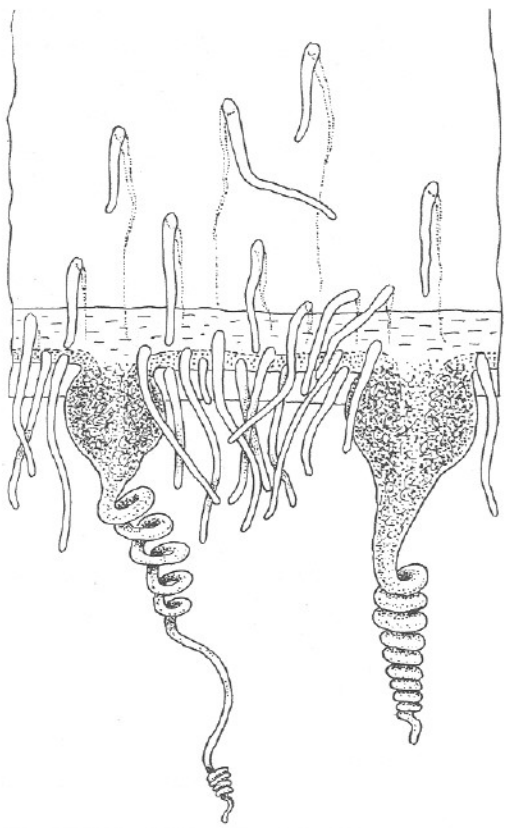
Kramp (1932, p. 325) states that the young eggs are found in the endoderm, the older eggs being enclosed in the mesosarc, bulging inwards among the endoderm cells. He also gives further histological details of the stomach and marginal tentacles.

Gosse (1853, p. 359) records an abnormal specimen in which one of the radial canals was divided into three branches at about one-third of its length from the ring canal, the ovary being correspondingly branched. The other radial canals were normal.

Occasional variation in the numbers of marginal vesicles also occurs, specimens being found with seven and ten vesicles (Russell, 1938*a*, p. 428).

Seasonal occurrence

Cosmetira pilosella has been recorded in the plankton off Plymouth from March to October inclusive and as most abundant from April to August. At Valencia it has been recorded from April to October. Although observations have not been so regularly made in other localities round the British Isles, where the species has been recorded, it is likely that it should be found at any time during the summer months. It must be realized however, that in certain areas such as the English Channel and North Sea the occurrence of this medusa is dependent on water movements and it is therefore likely only to be numerous under the appropriate hydrographic conditions.



Text-fig. 159. *Cosmetira pilosella*. Portion of umbrella margin of preserved specimen, Valencia, 8. x. 97. (E. T. Browne collection.)

Habits

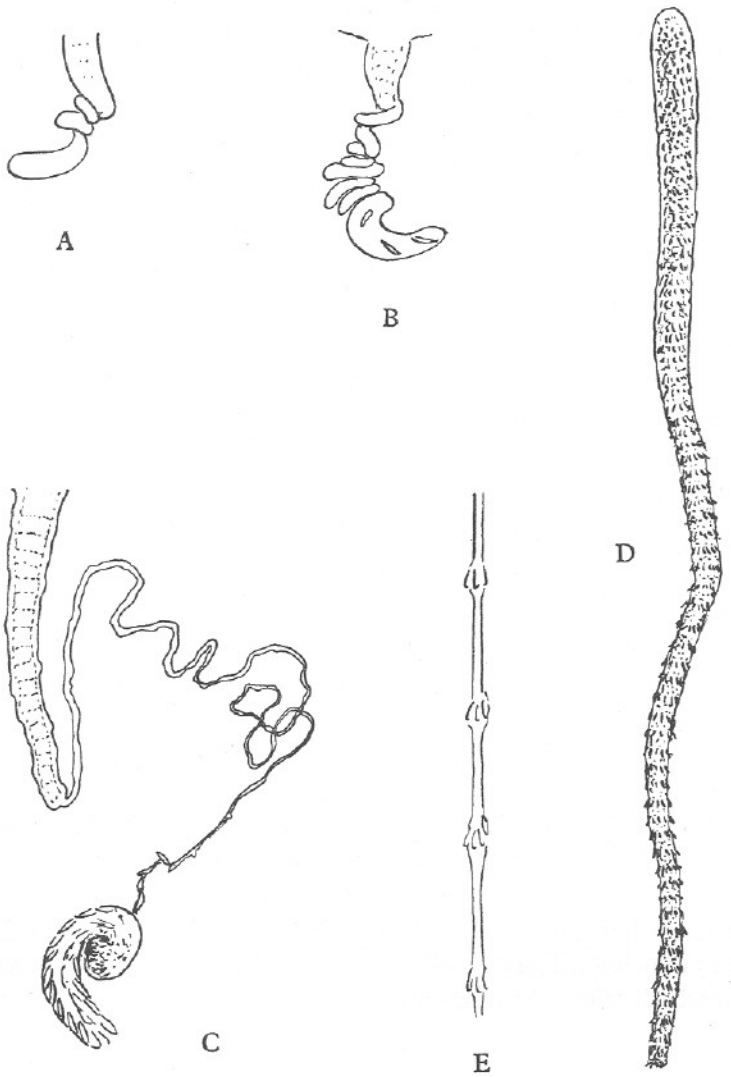
Lebour (1923) has recorded *Cosmetira pilosella* as eating young *Cottus*, and *Pleurobrachia*, 'when waiting for food the tentacles are widely outstretched and soon retracted when the food is caught'.

The medusa is usually restricted in the daytime to depths below 20 m. in off-shore waters, being almost completely absent above this level. At night it migrates upwards so that it may be caught at any depth (see Russell, 1925, 1927, 1928, 1931).

According to Gosse (1853) the marginal tentacle bases are capable of luminescence.

Mr Rupert Vallentin (1907), in a letter to Mr Browne, said that he saw in 1901 thousands of dead and dying specimens a mile and half from the shore off Newquay, Cornwall. Some of these specimens were examined by Mr Browne and he found that the gonads had been shed, some having

completely disappeared. The rupture of the gonads and their disappearance had produced a large opening and vacant space in the radial canals, so that the stomach was not in communication with the ring canal. The specimens were large in size, but had a contracted or shrunken appearance. Mr Vallentin said that these were all coming up Channel on the flood tide and so



Text-fig. 160. *Cosmetira pilosella*. Marginal cirri. A, B and C from young specimens; D and E, from old specimens, E being a portion of a fully extended cirrus.

were not damaged on the rocks. It is evident that this was an instance of the death of the medusae after the release of their sexual products and the completion of their free-swimming purpose.

Vallentin (1909) records similar dead and dying specimens in the Scillies.

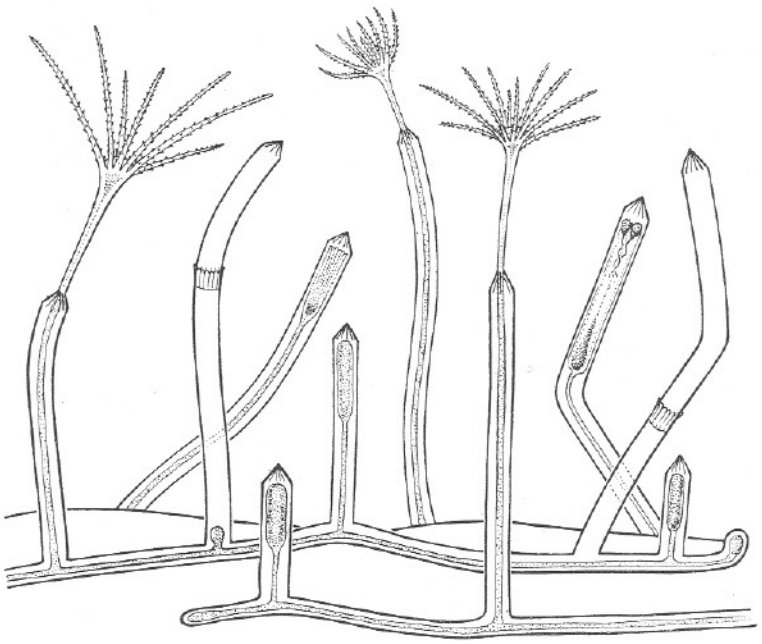
Gosse (1853) has recorded these medusae stranded in tidal pools.

Lebour (1916*a*) records that the larval stages of the pycnogon *Anaphia petiolata* may often be found clinging to the medusae.

HYDROID. *Cuspidella* sp. (Text-fig. 161.)

The Misses Delap (1905) reared hydroids from *Cosmetira pilosella* at Valencia; these hydroids were obviously a species of *Cuspidella*. Miss M. J. Delap's original drawings show a short cylindrical hydrotheca with a terminal operculum of about six to eight teeth, and an extensile hydranth with a single whorl of eight tentacles. These were young stages.

Later (Rees, 1941*b*) confirmed that the hydroid was a *Cuspidella* and he considered that it approached nearest to *C. grandis* Hincks in the form of the hydrotheca. The hydrothecae were up to 3·0 mm. in length with a diameter of 0·14–0·15 mm. They were long, smooth and tubular



Text-fig. 161. *Cuspidella*, the hydroid of *Cosmetira pilosella* showing hydrothecae and one gonotheca, Millport, 6. iv. 40. (After Rees, 1941*b*, fig. 1.)

and only a few had growth rings. The conical operculum had eight to twelve, usually ten, segments and it was 0·14–0·15 mm. high. The extensile hydranth had eight to ten filiform tentacles in a single whorl with irregularly distributed nematocysts.

Historical

Cosmetira pilosella was first described by Forbes (1848) from specimens collected in the Shetlands. Forbes states that Alder also found the species at Falmouth in 1847. Forbes placed the medusa in the genus *Thaumantias*, making for it a special subgenus *Cosmetira*. Although the medusa is quite distinctive, Haeckel (1879) caused confusion by including Forbes's species as a synonym of *Laodice cruciata*. The species was later re-described by Hartlaub (1909*a*).

The history of the species has been discussed in detail by Kramp (1919), who, however, erred in calling the marginal cirri 'dwarf tentacles'; later (1932) he corrected this, but maintained that the marginal cirri did not coil spirally. Examination of living specimens, however, showed that the marginal cirri can coil spirally (Rees & Russell, 1937).

Maas (1893, p. 57) described a species of medusa from the north-west coast of Scotland as *Halopsis megalotis*. This species has since been removed to the genus *Cosmetira*, and, indeed, there seems probably little ground left for regarding it as a separate species (Russell, 1938*a*, p. 429).

Genus **Halopsis** A. Agassiz, 1863

MEDUSAE. Mitrocomidae with stomach with four slightly folded lips; with more than eight radial canals; with linear gonads; with spiral marginal cirri; with numerous marginal vesicles; without ocelli.

HYDROID. Not known.

There is one British species of *Halopsis*, the only species of the genus, *H. ocellata* A. Agassiz. The species is immediately distinguishable from other species in the family by its large size and variable number of radial canals, twelve to sixteen.

A word of caution should, however, be given that it is just possible for the inexperienced to confuse the medusa with young *Aequorea*. The presence of marginal cirri is at once a distinguishing feature.

Halopsis ocellata A. Agassiz

Plate XIV, fig. 4; Text-figs. 162–6

Halopsis ocellata A. Agassiz, 1863, *Proc. Boston Soc. Nat. Hist.* vol. IX, p. 219.
A. Agassiz, 1865, *N. Amer. Acalephae*, p. 99, figs. 143–7, ?149, ?150.
Haeckel, 1879, *System der Medusen*, p. 217.
Fewkes, 1888*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. XIII, no. 7, p. 233, pl. iii, fig. 3.
Mayer, 1910, *Medusae of the World*, vol. II, p. 323.
Bigelow, 1914*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. LVIII, no. 2, p. 102.
Kramp, 1919, *Danish Ingolf-Expedit.* vol. V, pt. VIII, p. 65, pl. iv, figs. 1–5; text-figs. 6–9.
Kramp, 1920*a*, *Rep. Sci. Res. 'Michael Sars', N. Atlantic Expedit.* 1910, vol. III, pt. II (1913–21), p. 10, text-figs. 1–6.
Kramp & Damas, 1925, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. LXXX, p. 299, fig. 26.
Kramp, 1932, ibid. Bd. XCII, p. 353, text-figs. 6, 12, 19, 28, 32, 43.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 567, figs. 31, 32.

Specific Characters. This is the only species of the genus.

Description of Adult

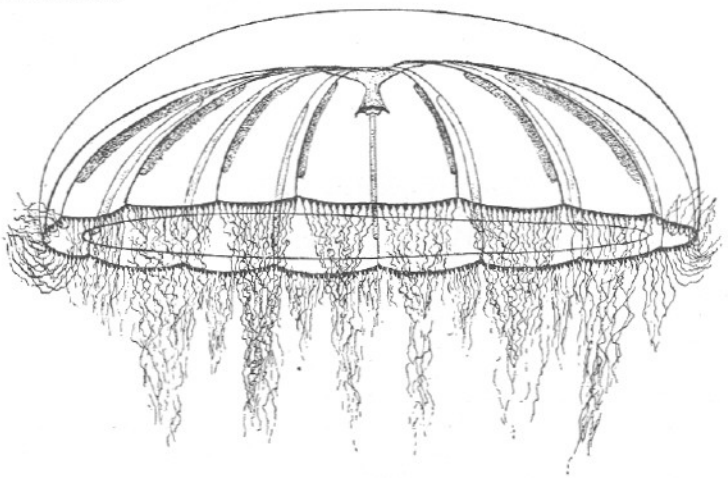
Umbrella watch-glass-shaped, about four times as broad as high; jelly fairly thick, especially in centre of disk, diminishing in thickness evenly towards margin. Velum fairly narrow. Stomach short, broad and flat, about one-fifth diameter of umbrella; circular or star-shaped in outline, with well-developed funnels; dorsal wall attached to subumbrella along continuations of radial canals, leaving numerous triangular pouches between upper stomach wall and subumbrellar surface. Mouth with four folded lips. Twelve to sixteen, rarely eleven or seventeen, straight radial canals and ring canal narrow; radial canals in four groups, originating as four canals which divide into three or four branches, branching usually occurring within periphery of stomach. Gonads linear, forming narrow, somewhat folded, bands along two-thirds of each radial canal, somewhat nearer umbrella margin than stomach; situated on side walls of radial canals, with median furrow in both sexes. Many hollow marginal tentacles, up to at least 450 in number, about one-third to one-half diameter of umbrella in length, with broad conical bases and nematocysts arranged in more or less complete rings. One, rarely two, long solid spiral marginal

cirrus between adjacent marginal tentacles. Usually five to six large open marginal vesicles between every two radial canals, making about eighty in all, each with large number of concretions. Diameter of umbrella 60–70 mm. Colour of whole medusa faint rose red; gonads greyish, pinkish or whitish.

Distribution

Although *Halopsis ocellata* has been known for many years from the American coast of the Atlantic it is only quite recently that Kramp (1919) showed that it occurred commonly in North European waters.

It appears to occur in deep or oceanic water near the coasts and has only been recorded in British waters well off-shore on the Atlantic coasts, off the west and south-west of Ireland and west and north of Scotland.



Text-fig. 162. *Halopsis ocellata*. Living specimen. (After Kramp & Damas, 1925; from Kramp, 1933*b*, fig. 32.)

Elsewhere it occurs as far north as the south coast of Iceland, the Faeroe-Shetland Channel, the Norwegian coast, and the North American Atlantic coast from Grand Manan to Cape Cod; west Greenland coast.*

Developmental Stages and Structural Details

The earliest stages of *Halopsis ocellata* have not been described and its hydroid is not known.

The smallest stage thought to belong to this species was described by A. Agassiz (1865) from the Atlantic coast of North America. It was not more than 5 mm. in height. The umbrella was deep bell-shaped. The stomach was short, its length being less than half the height of the subumbrellar cavity. There were only four straight narrow radial canals and a ring canal. There were no signs of gonads. There were four perradial and four interradial marginal tentacles, and the rudiments of the adradial marginal tentacles. There was one marginal cirrus on each side of a rudimentary marginal tentacle. There were sixteen marginal vesicles, each with two to three concretions.

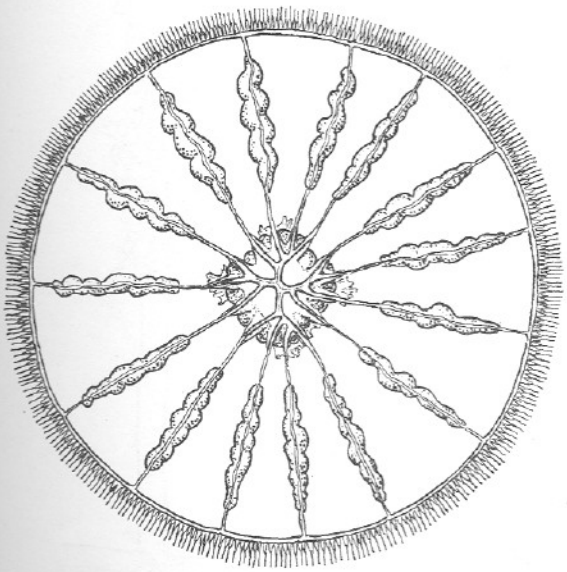
From the same area Agassiz (1865, fig. 148) also figures a specimen not more than 25 mm. in diameter in which there are still only four radial canals. In view of the following observations

* ?Consequent on climatic change (Jensen, 1939).

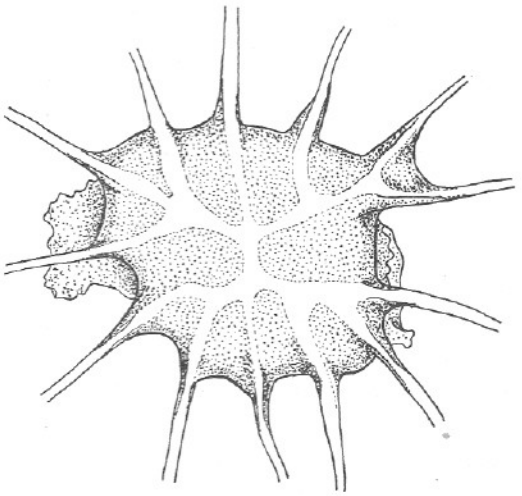
made by Kramp & Damas (1925) on young specimens from Norway it is improbable that Agassiz's specimen was *H. ocellata*.

Kramp & Damas give the following data on individuals less than 20 mm. in diameter:

Diameter of umbrella (mm.)	No. of radial canals
9	14
12	11
12	12
12	14
12	15
12	17
14	14
15	16
18	13



Text-fig. 163. *Halopsis ocellata*. (After Kramp, 1919; from Kramp, 1933*b*, fig. 31.)



Text-fig. 164. *Halopsis ocellata*. Stomach of preserved specimen *c.* 14 mm. in diameter. (Collected off mouth of English Channel by P. G. Corbin.)

It can be seen that in these specimens the numbers of radial canals varied between eleven and seventeen. It is thus evident that already at a size of about 10 mm. the complete number of radial canals is attained.

The following were the structural details of the smallest specimen obtained. Diameter of umbrella 9 mm.; gonads elongated and slightly developed, along all fourteen radial canals; thirty-five fully developed marginal tentacles and the same number, or more, of young marginal tentacles developing.

In larger specimens from west Greenland Kramp (1942) gives the numbers of radial canals as follows:

Diameter in mm.	32	38	47	65
Radial canals	19	17	14	15

Further detailed descriptions of specimens are given by Kramp (1919, 1920*a*, 1932).

The mesogloea of the stomach wall is fairly thick. The corners of the stomach are drawn out into short conical funnels which gradually merge into the radial canals (Text-fig. 164).

The average proportions of the diameter of the stomach for ten specimens of different sizes were as follows:

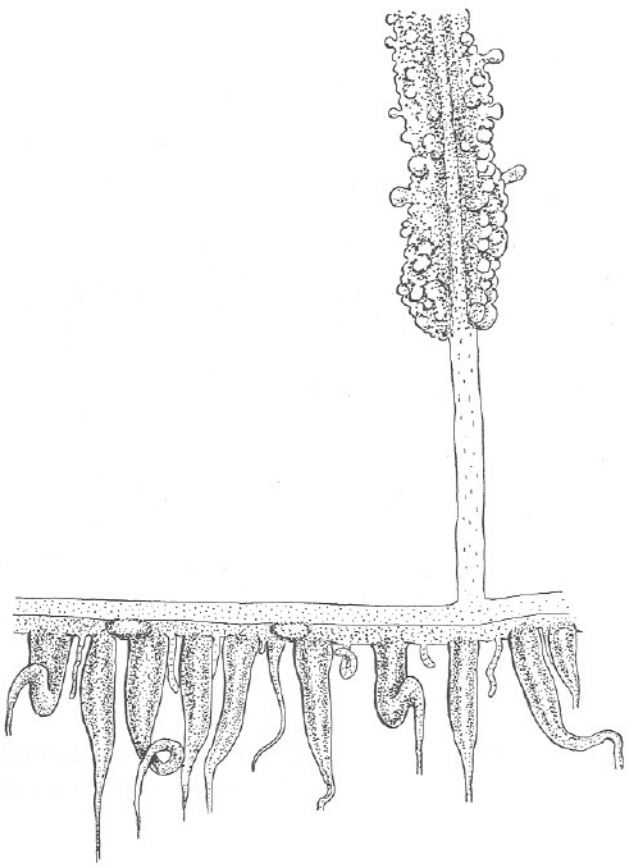
Diameter of umbrella (mm.)	Proportion of stomach diameter to umbrella diameter
20–25	0·31
26–30	0·29
31–35	0·26
36–40	0·21

The branching of the radial canals before their point of issue from the periphery of the stomach is often very irregular. Sometimes a branch may end blindly, not having reached the ring canal (Text-fig. 166).

The gonads are at first straight and later become sinuous. In the male gonads there may be as many as nine bends on either side, but the female gonads are never so thick or sinuous as the male. The gonads are mature when the medusa is about 35 mm. in diameter. The evacuation of the sexual products occurs first in the proximal part of the gonad. After spawning the radial canals become straight again. At the same time their walls break away from the subumbrella, so that only the narrow endodermal strip along which the canal was attached to the subumbrella remains. After the evacuation of the proximal part of the gonads the radial canals in this region thus hang downwards in a curve away from the subumbrella. After spawning the medusa continues to grow. Males 40–56 mm. in diameter and females of 44 mm. had spawned.

The young egg cells are ectodermal, and the mesogloea, being fairly strong, is only pushed slightly inwards towards the endoderm.

In two specimens examined the number of marginal tentacles between adjacent radial canals varied from nineteen to forty-nine and ten to thirty-six.



Text-fig. 165. *Halopsis ocellata.* Portion of umbrella margin showing distal end of radial canal and gonad of a specimen 30 mm. in diameter collected in the Faeroe-Shetland Channel from Sir Edward Peel's yacht *St George*, July 1933.

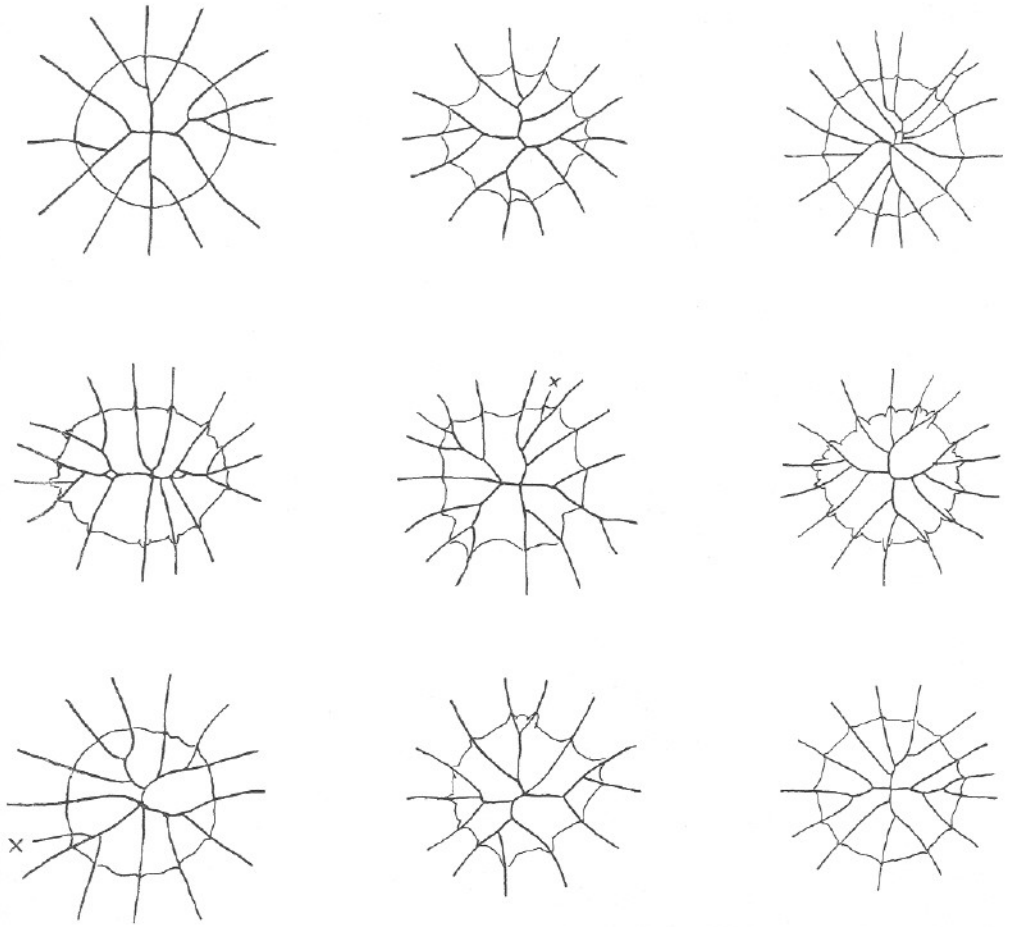
Similarly the number of marginal vesicles between adjacent radial canals showed variations of one to nine and three to ten.

Abnormalities occur in the branching of the radial canals, some of which may anastomose.

Kramp & Damas (1925) mentioned two abnormal specimens in which there was polygastry. One was 38 mm. in diameter and had three stomachs with fifteen radial canals in all (three, five and seven). The other was 33 mm. in diameter and had five stomachs and sixteen radial canals.

Kramp (1919) noticed a difference between specimens caught west of the British Isles and those from Iceland. In the Iceland specimens the average number of radial canals was higher, being 15·3 as against 12·6, and the diameter of the stomach was proportionately smaller when compared with that of the umbrella.

Fewkes (1888*a*) has recorded specimens up to 6 inches (15 cm.) in diameter.



Text-fig. 166. *Halopsis ocellata*. Diagrams of stomachs and proximal portions of radial canals seen from the apical side. (After Kramp, 1919, fig. 9.)

Seasonal occurrence

Halopsis ocellata has been recorded in the plankton in northern European waters from May to August inclusive.

Habits

A description of the living medusa has been given by Kramp & Damas (1925). Its movements are strong and it swims with much energy. The umbrella is extremely contractile. When at rest the umbrella is about four times as broad as high, and a slight waviness can be seen along the umbrella margin which is bayed opposite each radial canal.

HYDROID. Not known.

MITROCOMIDAE

Historical

Halopsis ocellata was first described by A. Agassiz (1863, 1865) from the Atlantic coast of North America. In his description he termed the marginal vesicles 'large compound eyes'.

The first fully detailed description was given by Kramp (1919), who also recorded it for the first time from the European side of the Atlantic.

Bigelow (1914*a*, p. 102) was the first to show that the marginal vesicles were open and that therefore *H. ocellata* should be included in the Mitrocomidae.

Genus **Tiaropsis** L. Agassiz, 1849

MEDUSAE. Mitrocomidae with stomach with four folded lips; with four radial canals; with linear gonads; with only one kind of marginal tentacle; without marginal cirri; with eight marginal vesicles, each with an ocellus.

HYDROID. Sessile '*Campanulina*'-like.

There is one British species of *Tiaropsis*, the only species of the genus, *T. multicirrata* (M. Sars). It is at once distinguishable from all other British Leptomedusae by the ocelli on the eight marginal vesicles.

The mention of one kind of marginal tentacle in the generic diagnosis given above is a distinguishing character from the genus *Tiaropsidium* Torrey; although present in the Mediterranean, medusae of that genus have not been recorded in British waters. Ranson (1925) recorded *T. mediterraneum* Metschnikoff from the English Channel, but Kramp (1932) shows that this was probably a young *Tiaropsis multicirrata*.

Tiaropsis multicirrata (M. Sars)

Plate XVII, fig. 1; Text-figs. 167–71

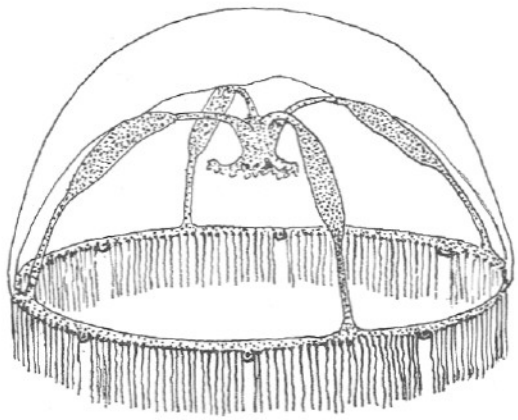
Thaumantias multicirrata M. Sars, 1835, *Beskriv. og Jagt.* p. 26, pl. v, fig. 12.
Thaumantias melanops Forbes, 1848, *Monogr. Brit. Medusae*, p. 45, pl. x, fig. 3.
Tiaropsis diademata L. Agassiz, 1849, *Mem. Amer. Acad. Arts Sci. Boston*, vol. IV, ix, p. 289, pl. vi.
L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, pp. 308, 355, text-figs. 45–8, pl. xxxi, figs. 9–15.
A. Agassiz, 1863, *Proc. Boston Soc. Nat. Hist.* vol. IX, p. 93, figs. 10–13.
A. Agassiz, 1865, *N. Amer. Acalephae*, p. 69, figs. 91–3.
Linko, 1900*a*, *Trav. Soc. Imp. Nat. St.-Pétersb.* tome XXIX, fasc. 4, p. 154, pl. figs. 3–5.
Mayer, 1910, *Medusae of the World*, vol. II, p. 258, pl. 31, fig. 11.
Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, p. 33.
Thaumantias pattersonii Green, 1857, *Nat. Hist. Rev.* vol. IV, p. 25, pl. iv, fig. 3.
Tiaropsis multicirrhata, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 355.
Tyaropsis scotica Allman, 1871, *Monogr. Gymnobl. Hydroids*, p. 140, fig. 57.
Tiaropsis scotica, Böhm, 1878, *Jena Z. Naturw.* Bd. XII (N.F. Bd. V), p. 183, pl. ii, figs. 15–30.
Thaumantias eschscholtzii Haeckel, 1879, *System der Medusen*, p. 129, pl. viii, fig. 4.
Tiaropsis multicirrata, Browne, 1895, *Trans. Liverpool Biol. Soc.* vol. IX, p. 278.
Browne, 1905*a*, *Proc. Roy. Soc. Edinb.* vol. XXV, pt. ix, p. 773.
Mayer, 1910, *Medusae of the World*, vol. II, p. 259.
Kramp, 1919, *Danish Ingolf-Expedit.* vol. V, pt. VIII, p. 77, text-figs. 11–14, chart X, pl. iv, figs. 6–10.
Kramp, 1932, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. XCII, p. 364, figs. 14, 15, 20, 35, 48.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 572, fig. 36.
Rees, 1941*c*, *Journ. Mar. Biol. Assoc.* vol. XXV, p. 138, figs. 6, 7 (hydroid and medusa).

Specific Characters

Gonads along middle half to two-thirds of radial canal, linear, somewhat sinuous. Marginal tentacles 200–300, or more, in number.

Description of Adult

Umbrella somewhat flatter than a hemisphere; jelly moderately thick. Velum well developed. Stomach short, with small base; attached to subumbrella along arms of perradial cross, leaving small flat triangular pouches between dorsal wall of stomach and subumbrella; situated on short broad peduncle. Mouth with four moderately long and broad lips with much folded margins. Four straight radial canals and ring canal narrow. Gonads along four radial canals, linear, somewhat sinuous; along middle half to two-thirds of radial canal, not reaching umbrella margin; median division present in both sexes. Marginal tentacles hollow, up to *c.* 200–300, or more, in number, with broad swollen bases without ocelli. No marginal cirri. Eight open marginal vesicles, each with *c.* twelve to thirteen concretions and one ocellus at base. Diameter *c.* 20 mm. Colour of stomach, gonads, and marginal tentacle bases, dull yellow; marginal tentacle bases with black pigment granules; sometimes black pigment granules in dorsal wall of ovary.



Text-fig. 167. *Tiaropsis multicirrata*. (After L. Agassiz, 1849, pl. vi, fig. 4.)

Distribution

Tiaropsis multicirrata has been recorded in British waters from the following localities: Northumberland coast; Dunbar harbour; Shetlands; Firth of Clyde; Port Erin; Falmouth; Plymouth; Belfast; Valencia; and Blacksod, Ireland. It is a northern boreal species and is probably normally scarce off southern British coasts, although Vallentin (1897) recorded it as very abundant in 1895 in Falmouth harbour.

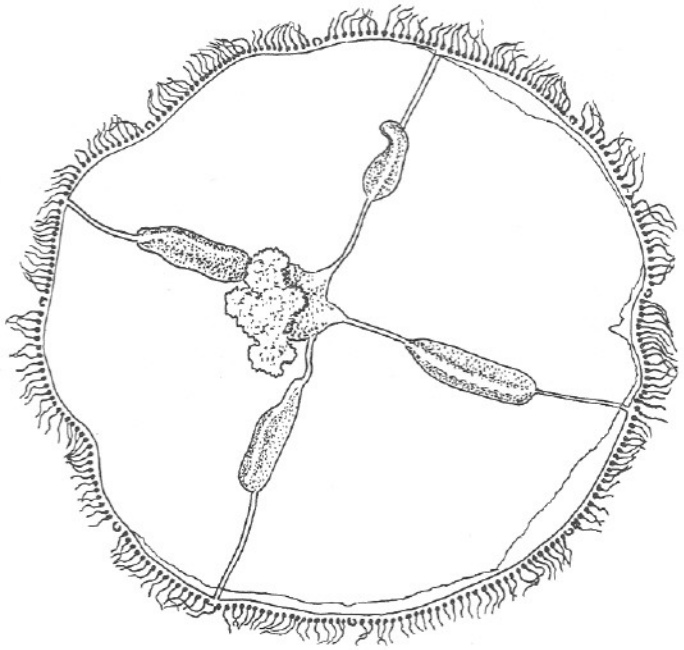
Elsewhere it has been recorded from Helgoland; Jutland; Kattegat; Little Belt; Norway coast; Barents Sea; Faeroe Isles; Iceland; west Greenland; Newfoundland; eastern North American coast at Massachusetts Bay, Boston, Woods Hole; Bering Sea in Pacific. It is a circumpolar species.

Developmental Stages and Structural Details

The newly liberated medusa (Text-fig. 170) has been described by Rees (1941*c*) and is 1·1 mm. high. This description is essentially similar to that of the smallest specimens recorded from the plankton which are about 0·75–1·0 mm. in height. The umbrella is bell-shaped and the jelly thin. There are many scattered nematocysts on the exumbrella. The velum is narrow. The stomach is very short and small, with a quadrangular base. There may be traces of an umbilical canal and a prolongation of the stomach into the mesogloea. The mouth has four well formed simple lips. The four radial canals and ring canal are narrow. The gonads are not yet apparent. There are twenty-three to twenty-four marginal tentacles, six in each quadrant. Of these the bases of the four perradial marginal tentacles and those of the interradial marginal tentacles are well developed,

those of the remaining marginal tentacles being smaller. There are eight adradial open marginal vesicles, each containing three to five concretions and having a black ocellus at its base. The colour of the stomach and bases of the marginal tentacles is yellow, or pale brown. (See Pl. XVII, fig. 1.)

The medusa soon changes in shape, for Browne (1905*a*, p. 774) recorded a specimen from the Firth of Clyde 1·5 mm. in height and 2·5 mm. in diameter, which was already bowl-shaped and had a moderately thick jelly. The stomach was short and flat, the mouth had four small lips. The gonads were just beginning to appear along the central portions of the four radial canals. The number of marginal tentacles had already increased to about seventy, and they were closely



Text-fig. 168. *Tiaropsis multicirrata*. Preserved specimen *c.* 12 mm. in diameter, Firth of Forth, 1909. (E. T. Browne collection, collected by W. Evans.)

packed round the margin of the umbrella. The bases of the marginal tentacles were spherical in shape, with a thick pad of nematocysts on the inner side. The marginal tentacles were small and slender, and covered with transverse, circular bands of nematocysts.

According to Kramp (1919) the stomach peduncle does not appear until some time after the medusa is about 2 mm. in diameter. The lips are also quite simple in the smallest specimens, only later becoming much folded. Kramp has given the order of development of the marginal tentacles in a specimen 1·5 mm. in diameter (see also A. Agassiz, 1862). This had forty-seven marginal tentacles and it appears that the sequence is probably as follows:

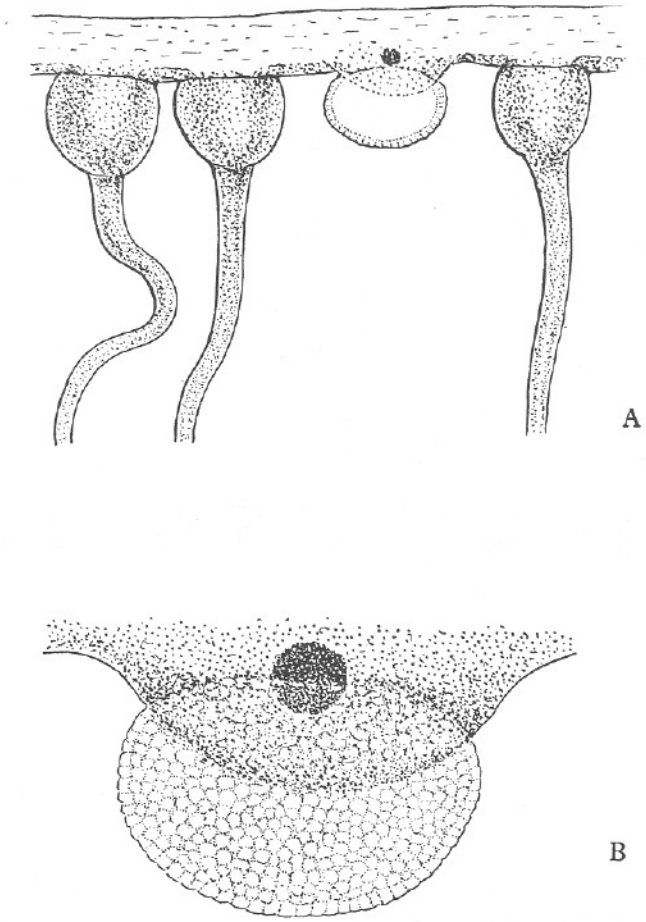
4 perradial + 4 interradial + 16 adradial + 16.

The position of the marginal vesicles is adradial.

The *gonads* have their proximal ends very near or at the base of the stomach peduncle (Text-fig. 167). In the female they are sinuous, with two or three bends on each side, but in the male they are thick and cylindrical with only a single constriction or bend near the middle. The medusae may be fully mature when only 10–12 mm. in diameter, but more usually at 14–15 mm.

The young eggs are found in the endoderm (Kramp, 1932), the older eggs being enclosed in a strongly developed mesosarc. As the eggs develop they move outwards, but the strong mesosarc forms an almost straight boundary against which the sides of the eggs become flattened.

The *marginal tentacles* (Text-fig. 169A). Kramp (1919, p. 84) gives observations on the numbers of marginal tentacles in medusae of different sizes from various localities. Although



Text-fig. 169. *Tiaropsis multicirrata*. A, portion of umbrella margin with marginal vesicle (concretions not shown) and ocellus; B, marginal vesicle enlarged.

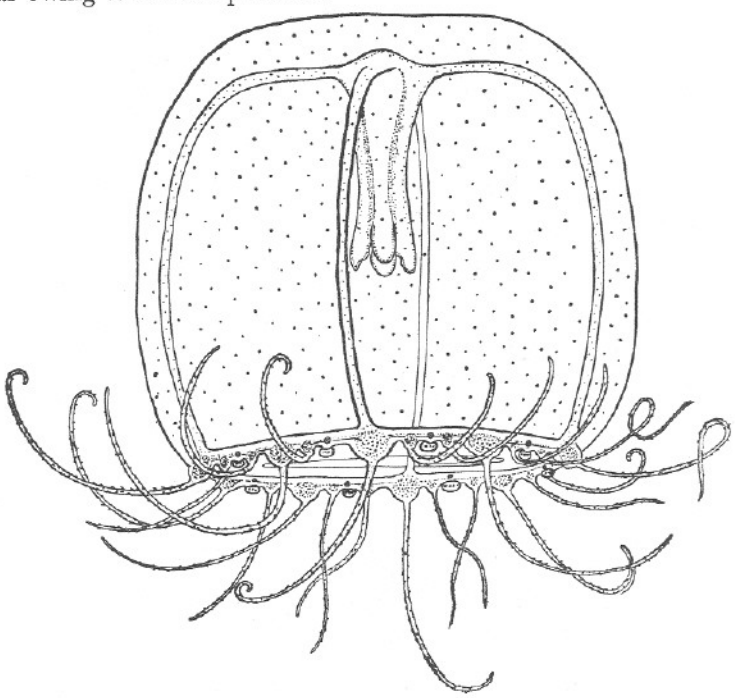
there is some variation from place to place, the variation at any one locality alone is so great that the following figures can be regarded as fairly representative:

Average diameter range (mm.)	Approximate no. of marginal tentacles
2·0	50
2·3–6·0	100
4·0–7·8	150
7·5–11·7	200
10·9–14·0	250

The greatest number of marginal tentacles observed by Kramp in any one medusa was 328, in a specimen 15 mm. in diameter from Iceland.

The *ocelli* (Text-fig. 169) (described by Agassiz & Mayer, 1899; Linko, 1900*a*; and Kramp, 1932, p. 337, fig. 35) have the form of cup-shaped masses of pigment in the endoderm of the circular canal. The cavity of the cup is filled with subepithelial cells of the ectodermal nerve layer on the adaxial side of the umbrella margin.

The open *marginal vesicles* (Text-fig. 169B) have been described by Böhm (1878) and Linko (1900*a*). The concretions are usually in a single bow-shaped row, but sometimes a number are pushed out of place so that two rows are formed. The concretions are large and globular, or somewhat angular owing to mutual pressure.



Text-fig. 170. *Tiaropsis multicirrata*. Medusa newly liberated from hydroid, Millport, 19. iv. 40. (After Rees, 1941*c*, fig. 7.)

Tiaropsis multicirrata is easily distinguishable from other medusae by the presence of the eight black ocelli beneath the marginal vesicles. These are still obvious in preserved material, although the black pigment in the marginal tentacle bases may disappear (see Bigelow, 1913, p. 33 and footnote).

Seasonal occurrence

Tiaropsis multicirrata has been recorded from the plankton off British coasts in the following months: April to July, Northumberland coast; June and July, Dunbar harbour; March and April, Firth of Clyde; March, April and May, Port Erin; April and May, Plymouth; May and June, Falmouth.

The medusa thus probably appears in the plankton in the spring and is mature by July.

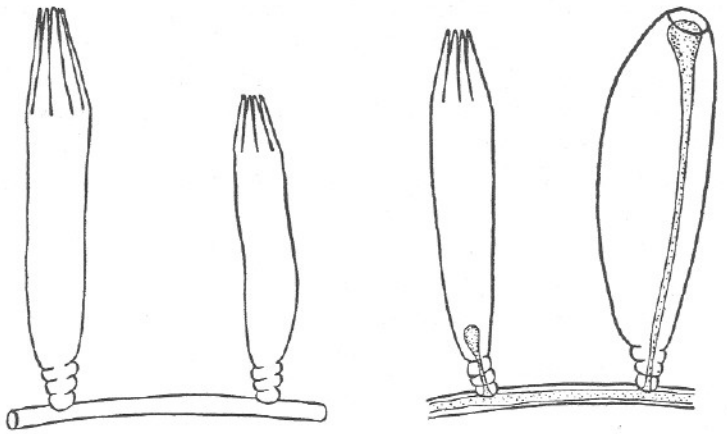
Habits

Drawings and a description of the pulsating movements of the umbrella of *Tiaropsis multicirrata* have been given by L. Agassiz (1849, as *T. diademata*). He records the movements as being graceful

and rather sustained. Agassiz states that they feed on small prey such as very young Ephyrae, and small particles of decaying animal matter; he also mentions that they are largely preyed upon by *Sarsia*.

Romanes (1876*b*, p. 274; 1877*b*, pp. 659, 710, 734, 736 et seq.; 1885) mentions this species as one of those on which he made his physiological observations.

Vallentin (1897) records the species as so abundant in Falmouth harbour during May and June, 1895, that 'the sea in certain protected places in the harbour was almost solid with examples'. In view of the usual more northerly distribution of this species this may indicate that hydrographical conditions in 1895 were somewhat abnormal. The specimens taken by Vallentin and sent to Mr Browne were heavily infested with a larval trematode (see also Greene, 1857).



Text-fig. 171. *Tiaropsis multicirrata*. Hydroid, Millport, 19. iv. 40. A, two hydrothecae; B, hydrotheca and gonotheca. (After Rees, 1941*c*, fig. 6.)

HYDROID. (Text-fig. 171 A, B.)

The hydroid of *Tiaropsis multicirrata* has been described by Rees (1941*c*) from a colony in which the polyps had died down after liberation of the medusae; they were living on a *Buccinum* shell dredged from 5 fathoms off Millport in April 1940.

Colonies of single hydranths up to 1 mm. in height rising from a creeping stolon, each with a very short, imperfectly ringed hydrocaulus. Hydrothecae deeply campanulate with perisarc at distal end folded to form a conical operculum with seven to eleven outer segments. Gonothecae ovate, smooth, with short imperfectly ringed stalk, arising singly from creeping stolon, about 1 mm. high.

Historical

Tiaropsis multicirrata was first described by M. Sars (1835) from Norway as *Thaumantias multicirrata*. For a long time the American form, described by L. Agassiz (1849) as *Tiaropsis diademata*, was kept distinct from the European medusa on the ground that it lacked the black pigment in the marginal tentacle bases. Bigelow (1913, p. 33 and footnote), however, showed that medusae from Massachusetts had this pigment, and Kramp (1919), after a careful comparison of specimens from both sides of the Atlantic, concluded that they were the same species.

Thaumantias eschscholtzi Haeckel, figures of which have often been reproduced as typical *Thaumantias*, were shown by Kramp (1919, p. 78) to be *Tiaropsis* after examination of Haeckel's original specimens.

Family CAMPANULARIIDAE

Leptomedusae with normal or reduced velum; with small stomach, without peduncle; with four simple radial canals; without excretory pores; with gonads on radial canals separated from stomach; with hollow, rarely solid, marginal tentacles; without marginal or lateral cirri; with closed marginal vesicles; without ocelli. In reduced medusae stomach and marginal tentacles may be absent.

HYDROID. *Campanularia*-like, with single whorl of filiform tentacles, with or without webs between their bases; with hydrotheca without operculum.

The Campanulariidae have no single distinctive character; they are only separable from certain other families by referring to a combination of characters in the medusae as well as the characters of the hydroid. They are at once separable from the Lovenellidae by the absence of lateral cirri, from the Eirenidae and Eutimidae by the absence of a peduncle, and from the Aequoreidae in having only four radial canals. There remains one other family with which the medusae might be confused, namely the Phialellidae, but in that family the hydroid, where known, has a hydrotheca with an operculum.

The Campanulariidae may be conveniently divided into three subfamilies based mainly on the characters of the medusae; these are the Campanularinae, the Obelinae, and the Orthopyxinae. Their distinguishing characters are as follows:

Medusa with normal velum; with hollow marginal tentacles	**Campanularinae**
Medusa with reduced velum; with solid marginal tentacles	**Obelinae**
Whole medusa reduced	**Orthopyxinae**

The Orthopyxinae also have a differentiating character in the hydroid which has a characteristic hydrotheca with very thick walls.

Subfamily CAMPANULARINAE

MEDUSAE. Campanulariidae with normal velum; with hollow marginal tentacles; with numerous marginal vesicles.

HYDROID. *Campanularia*-like, unbranched or branched colonies, with thin-walled hydrothecae.

The Campanularinae are represented in British waters by one genus, *Phialidium* Leuckart. In general appearance the medusae of this genus show the most simplified leptomedusan form, having no accessory marginal cirri and no peduncle.

Genus **Phialidium** Leuckart, 1856

Campanulariid medusae with characters as subfamily.

HYDROID. *Campanularia*-like.

There are two British species of the genus, *Phialidium hemisphaericum* (L.) and *P. islandicum* Kramp. Of the two species the hydroid of *P. hemisphaericum* is well known under the name *Clytia johnstoni* (Alder). The hydroid of *Phialidium islandicum* is not known, but the medusa must be placed provisionally in this genus.

The two species can usually be distinguished by the numbers of their marginal tentacles:

Sixteen to thirty-two marginal tentacles	**P. hemisphaericum**
Up to 200 marginal tentacles	**P. islandicum**

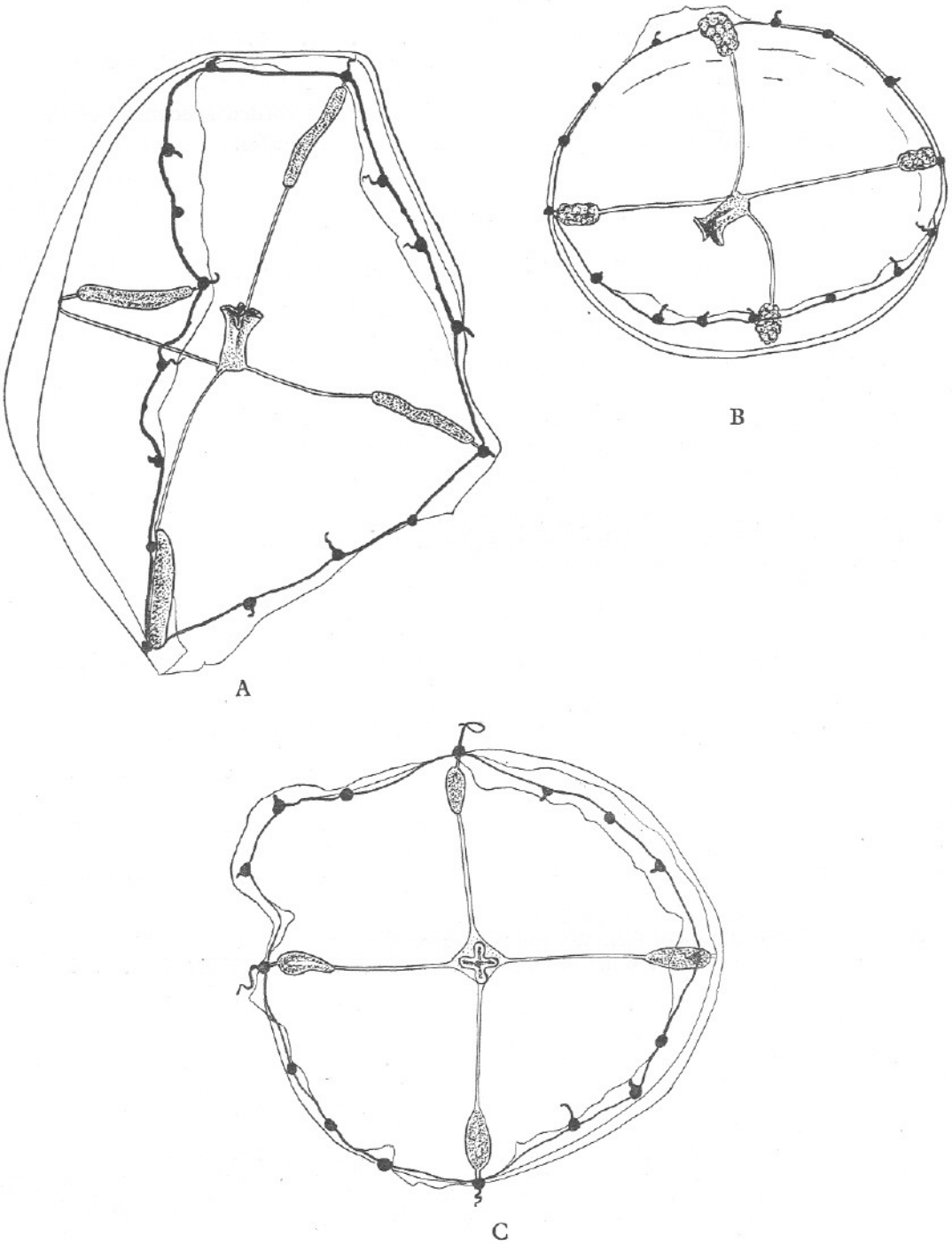
It should be mentioned, however, that Kramp (1919) has recorded specimens of *P. hemisphaericum* from Iceland with as many as fifty-eight marginal tentacles.

Phialidium hemisphaericum (L.)

Plate XVI, fig. 1; Plate XVII, fig. 6; Text-figs. 172–9

'*Medusa hemisphaerica* ...' Gronovius, 1760, *Acta Helvetica*, tome IV, p. 35, pl. iv.
Oceania hemisphaerica, Péron & Lesueur, 1809, *Ann. Mus. Hist. Nat. Paris*, tome XIV, p. 347.
Thaumantias pileata Forbes, 1841, *Ann. Nat. Hist.* vol. VII, p. 84, pl. i, fig. 3.
Forbes, 1848, *Monogr. Brit. Medusae*, p. 47, pl. xi, fig. 2.
Thaumantias sarnica Forbes, 1841, *Ann. Nat. Hist.* vol. VII, p. 85, pl. i, fig. 6.
Forbes, 1848, *Monogr. Brit. Medusae*, p. 48, pl. xi, fig. 4.
Thaumantias thompsoni Forbes, 1841, *Ann. Nat. Hist.* vol. VII, p. 84, pl. i, fig. 4.
Forbes, 1848, *Monogr. Brit. Medusae*, p. 49, pl. xi, fig. 5.
Thaumantias punctata Forbes, 1841, *Ann. Nat. Hist.* vol. VII, p. 85, pl. i, fig. 5.
Forbes, 1848, *Monogr. Brit. Medusae*, p. 53, pl. x, fig. 1.
Thaumantias lineata Forbes, 1848, ibid. p. 48, pl. xi, fig. 1.
Thaumantias hemisphaerica, Forbes, 1848, ibid. p. 49, pl. viii, fig. 2.
Thaumantias inconspicua Forbes, 1848, ibid. p. 52, pl. viii, fig. 3.
Hincks, 1868, *Brit. Hydroid Zooph.* p. 179, fig. 20.
Thaumantias buskiana Gosse, 1853, *Devonshire Coast*, p. 385, pl. xxii, figs. 5–11.
Eucope thaumantoides Gegenbaur, 1856, *Z. Wiss. Zool. Leipzig*, Bd. VIII, p. 243, pl. IX, figs. 9, 10.
Eucope campanulata Gegenbaur, 1856, ibid. p. 243, pl. ix, fig. 8.
Eucope affinis Gegenbaur, 1856, ibid. p. 244, pl. ix, figs. 12, 13.
Phialidium viridicans Leuckart, 1856, *Arch. Natur. Berlin*, Jahrg. XXII, p. 18, pl. i, fig. 12.
?*Thaumantias typica* Green, 1857, *Nat. Hist. Rev.* vol. IV, p. 26, pl. v, fig. 5.
Clytia johnstoni Hincks, 1868, *Brit. Hydroid Zooph.* p. 143, pl. xxiv, figs. 1, 1*a* (hydroid and young medusa).
Thaumantias leucostyla Spagnolini, 1876, *Catalogo Acalefi Medit.* p. 27.
Campanulina acuminata Boehm, 1878, *Jena Z. Naturw.* Bd. XII (N.F. Bd. v), p. 171, pl. ii, figs. 10–14.
Epenthesis cymbaloidea Haeckel, 1879, *System der Medusen*, p. 183 (in part).
Phialidium variabile Claus, 1881*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. IV, p. 111, pl. iv, figs. 34–8.
Haeckel, 1879, *System der Medusen*, p. 186 (in part).
Browne, 1895, *Trans. Liverpool Biol. Soc.* vol. IX, p. 280.
Clytia flavidula Metschnikoff, 1886*b*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. VI, p. 241, pl. figs. 9, 10, 15.
?*Clytia viridicans*, Metschnikoff, 1886*b*, ibid. p. 241, pl. i, figs. 11, 12, 13, 16.
Phialidium (*Clytia*) *flavidula*, Maas, 1893, *Ergeb. Plankton Exped.* Bd. II, K.c., p. 61.
Phialidium buskianum Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 488, pl. xvi, fig. 6.
Phialidium temporarium Browne, 1896*a*, *Proc. Zool Soc. London*, p. 489, pl. xvii, figs. 4–6.
Thaumantias forbesi Johansen & Levinsen, 1903, *K. danske vidensk. Selsk. Skr.* natur. og math. Afd., 6. Raekke, XII, p. 279.
Phialidium hemisphaericum, Mayer, 1910, *Medusae of the World*, vol. II, p. 266, figs. 140–4.
Kramp, 1919, *Danish Ingolf-Expedit.* vol. v, pt. viii, p. 91, pl. iv, fig. 14; pl. v, fig. 3; text-figs. 16, 17.
Kramp, 1927, *K. danske vidensk. Selsk. Skr.* natur. og math. Afd., 8. Raekke, XII, p. 114, fig. 2.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 579, figs. 42–4.
Russell, 1938*a*, *Journ. Mar. Biol. Assoc.* vol. XXII, p. 429, fig. 4.
Clytia volubilis, Sverdrup, 1921, *Skr. Vidensk Kristiania* 1922, I. mat.-nat. Kl., Bd. 1, p. 24, pl. iv, fig. 17.

Specific Characters. Sixteen to thirty-two marginal tentacles; usually two marginal vesicles between adjacent tentacles.



Text-fig. 172. *Phialidium hemisphaericum*. Preserved specimens, Plymouth, 3. iii. 38. A, male *c.* 8 mm. in diameter; B, female *c.* 5 mm. in diameter; C, male 5·5 mm. in diameter.

Description of Adult

Umbrella hemispherical or slightly flatter than a hemisphere; jelly fairly thin. Velum narrow. Stomach short, quadrate, with small base; no peduncle. Mouth with four short lips with slightly folded margins. Four straight radial canals and ring canal narrow. Gonads on four radial canals elongated or oval, situated on distal region of radial canal, not quite reaching ring canal; continuous over lower wall of radial canal without median furrow. Sixteen to thirty-two or more hollow marginal tentacles, smooth, with spherical bases; with a few partially developed marginal bulbs. No ocelli. No marginal nor lateral cirri. One to three, or more, closed marginal vesicles between every two marginal tentacles, each with one concretion, rarely two. Diameter of umbrella up to 20 mm. Colour of marginal tentacle bases and stomach very variable; yellowish, yellowish brown, reddish brown, greenish, or purple; gonads yellowish.

Distribution

Phialidium hemisphaericum is one of the commonest and most prevalent medusae in the plankton round the British coasts. It is to be found all round the British Isles.

Elsewhere it is widely distributed, occurring in European waters from the Mediterranean to as far north as the coasts of Iceland and Lofoten on the Norwegian coast.

Künne (1937*b*) states that it is an immigrant into the western Baltic; Pacific (Kramp, 1953).

Developmental Stages and Structural Details

When first liberated from its hydroid the medusa is 0·75 mm. in height (Pl. XVII, fig. 6). The umbrella is bell-shaped, as high as wide, and somewhat four-cornered in section near the margin. The jelly is thin. There are nematocysts scattered irregularly over the exumbrella. The velum is broad. The stomach is short and the mouth has four short lips. The four radial canals and ring canal are narrow. The four gonads are already apparent as small oval swellings situated on the middle of the course of each radial canal. There are four perradial marginal tentacles and four interradial rudimentary marginal swellings. There are eight adradial marginal vesicles, each with a single concretion. The colour of the stomach and marginal tentacle bases is yellowish brown or pale straw.

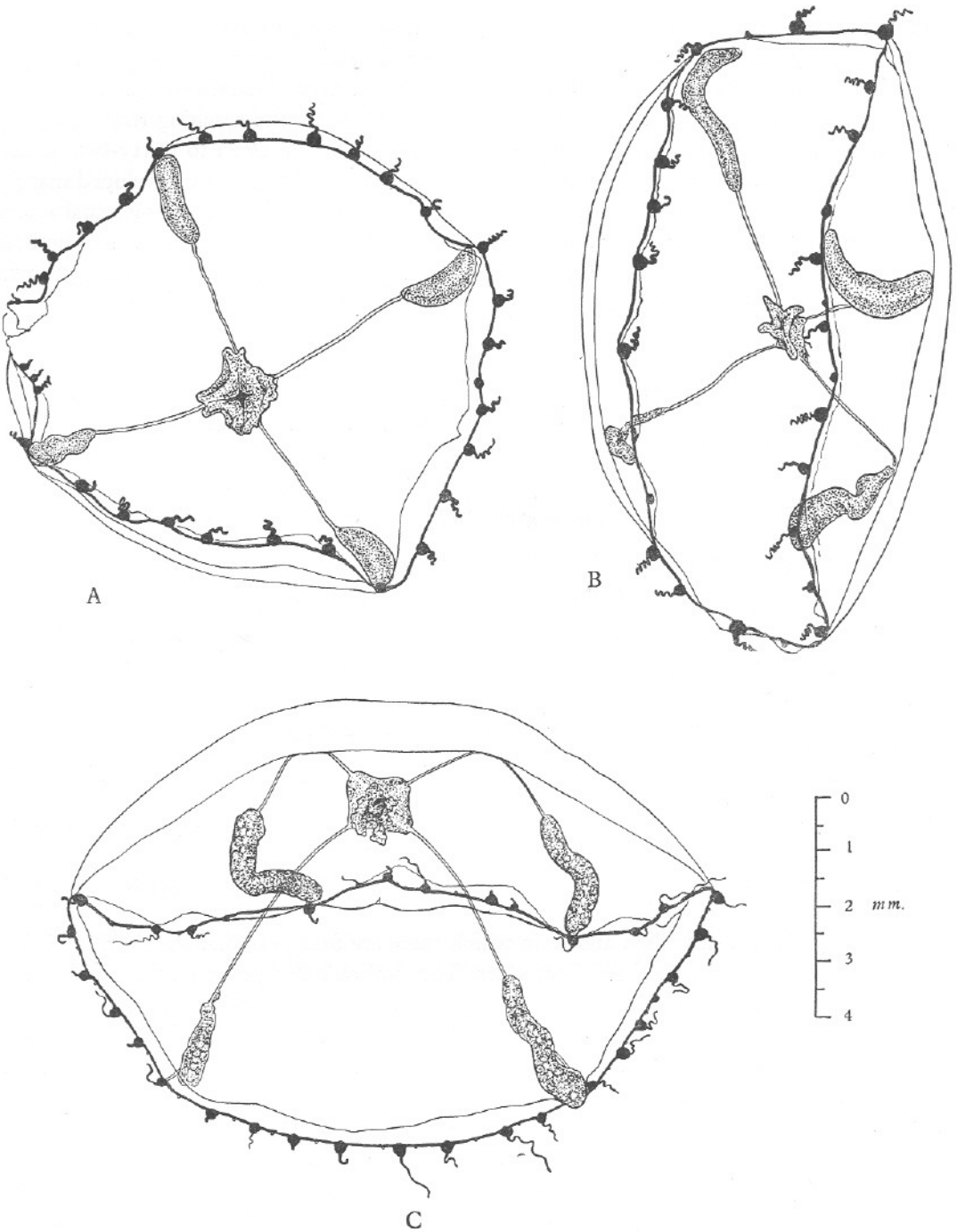
The further development of the medusa is fairly regular, and three stages may be distinguished before the final stage is reached.

The *first stage* is that described above, in which there are four perradial marginal tentacles.

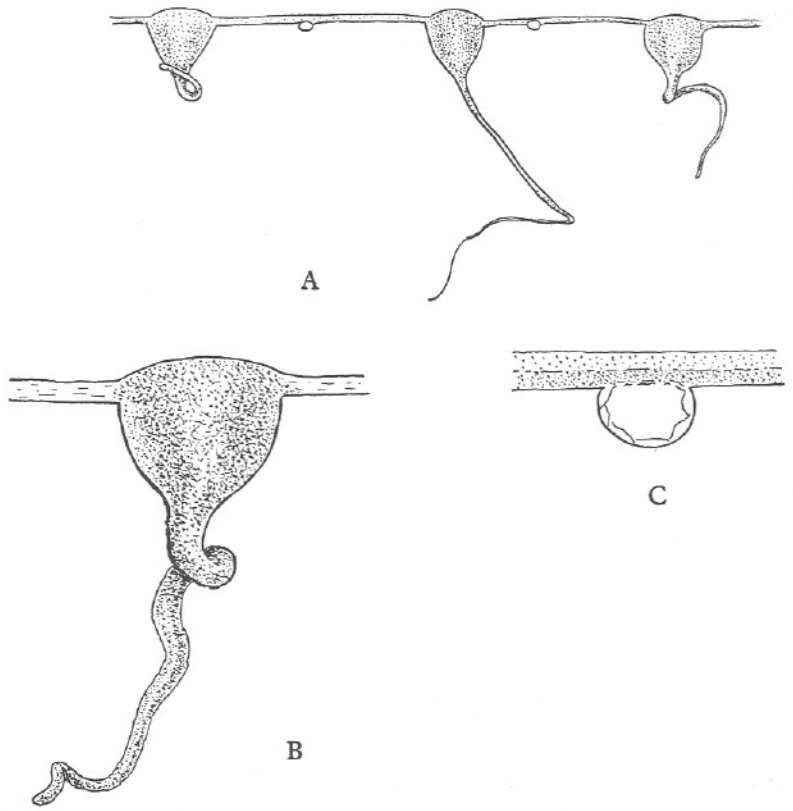
The *second stage* has eight marginal tentacles. The umbrella has become more flattened and is about 2–3 mm. in diameter. The four interradial marginal bulbs of the first stage have developed tentacles, bringing the total number up to eight. A few adradial marginal bulbs are beginning to appear. The eight marginal vesicles usually have each a single concretion, though occasionally two may be present in one vesicle.

The *third stage* has sixteen marginal tentacles. The adradial marginal tentacles do not appear in any definite order so that one quadrant may sometimes contain more marginal tentacles than another. The umbrella is considerably flattened, being about 6–7 mm. in diameter and 4–5 mm. high. The gonads are now situated more distally on the radial canals. The marginal vesicles have increased in number, there being always one between adjacent marginal tentacles, and sometimes two, so that their number is sixteen or more.

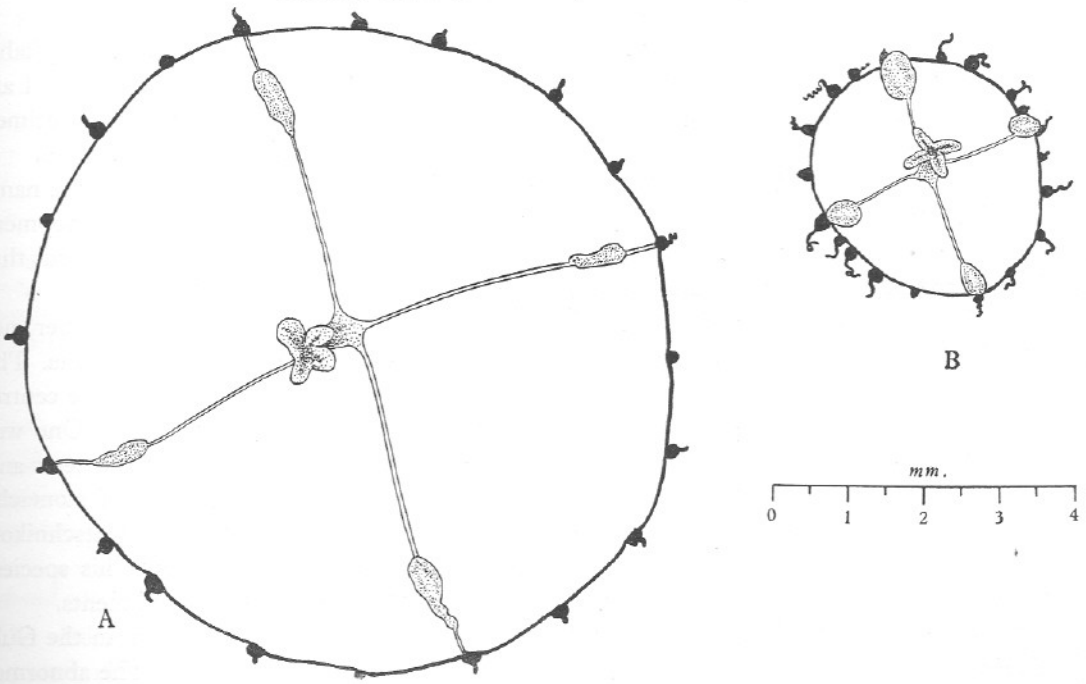
At this stage the medusa may be mature, but further growth leads to the production of thirty-two, or occasionally a few more, marginal tentacles. Thus *Phialidium hemisphaericum*



Text-fig. 173. *Phialidium hemisphaericum*. Preserved specimens. A and B, males, Plymouth, 11. iv. 34; C, female *c.* 10 mm. in diameter probably shrunk, Plymouth, 7. v. 34.



Text-fig. 174. *Phialidium hemisphaericum*. A, portion of umbrella margin; B, marginal tentacle; C, marginal vesicle, without concretion.



Text-fig. 175. *Phialidium hemisphaericum*. A specimen caught off Plymouth, 29. iv. 40, drawn to show shrinkage while moribund. A, alive 12 noon, 30. iv. 40 (from the appearance of the jelly the specimen had already shrunk a little; it showed creases and cracks); B, 9.15 a.m., 1. v. 40 (the marginal tentacles were still moving).

shows considerable variability as regards the degree of development of its structural characters at maturity, mature specimens being found with anything between sixteen and thirty-two marginal tentacles. In this respect there appears to be a tendency towards separation into two forms. In one of these, with thirty-two marginal tentacles, the gonads are large and considerably elongated. In the other, with sixteen marginal tentacles, the gonads are small and oval. It was at first thought that these two forms were specifically distinct, that with small oval gonads being identified with *P. buskianum* (Browne, 1896*a*). Although there is still a possibility that they may prove to be distinct species, the general opinion is that the difference between the two forms is seasonal in origin. In British waters the form with sixteen marginal tentacles and short oval gonads occurs mostly in the autumn (at Plymouth at any rate), the large medusae with elongated gonads being found in spring and summer.

Russell (1938*a*) gives a diagram showing the variations in the size of the umbrella and in the number of marginal tentacles found throughout the year in medusae from Plymouth. This agrees in essence with observations made by Kramp (1927) in Danish waters, except that the seasonal sequence in those waters was different, the smallest specimens being found in summer, and the largest in winter and spring.

Kramp (1919) gives some histological details. The marginal tentacle bases are somewhat spherical (Text-fig. 174A, B) and have the ectoderm well developed on the lateral and adaxial sides.

The marginal vesicles (Text-fig. 174C), which are spherical, are inserted up to their halves in the margin of the umbrella. The maximum number of vesicles is probably about ninety.

Kramp (1919) records specimens from Iceland in which the number of marginal tentacles might be as many as fifty-eight. This is considerably more than in medusae from British waters in which the maximum number of marginal tentacles recorded is thirty-eight.

Abnormalities. (Text-figs. 10A, B, 177.)

It appears that the medusa *Phialidium hemisphaericum* may at times be subject to a remarkable form of abnormality known as 'polygastry'. The only occurrence of this abnormality that I am aware of recorded from north European waters is that given by Maas (1893, p. 62) of a specimen with two stomachs, but it has been recorded on several occasions from the Mediterranean.

Davidoff (1881) recorded many specimens from Villefranche, in September, under the name *P. variabile*. These had two or three stomachs and Davidoff discovered that the development of two stomachs was followed by the complete transverse fission of the medusa. He records that specimens brought in from the plankton in this condition divided in one to two days.

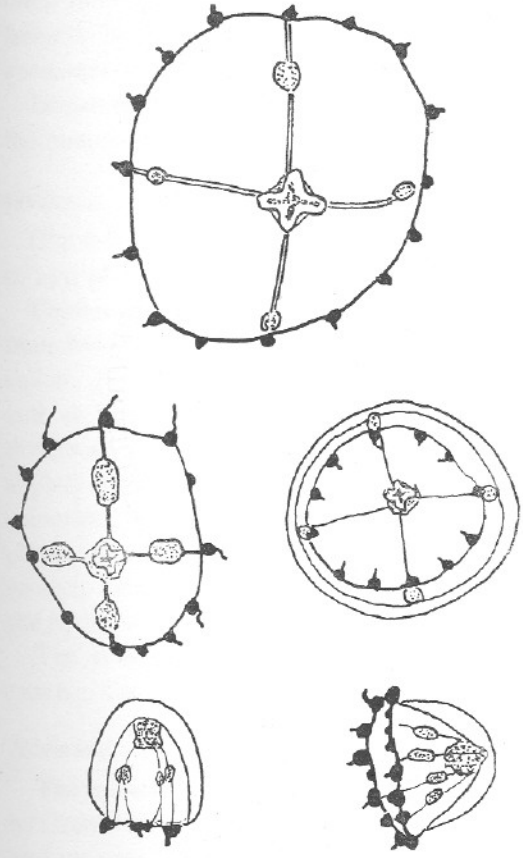
Lang (1886) recorded thousands of individuals from Naples, in August and September, not one of which was normal. Lang gave the name *Gastroblasta raffaeli* to these medusae. The specimens were all small, but had eight to twelve radial canals which radiated from the centre, but did not all reach the ring canal. These specimens each had several stomachs. One was oval in shape and had nine stomachs; the umbrella was 4 mm. across the greatest diameter and 2·7 mm. across the shortest. Lang also found that the increase in the number of stomachs was a prelude to the complete division of the medusa. He refers to a figure given by Metschnikoff (in a Russian paper) of *Eucope polygastrica*, which was apparently identical with his species. This had six radial canals, three fully developed stomachs, and three stomach rudiments.

Neppi & Stiasny (1913*b*) recorded a similar condition in *Phialidium variabile* from the Gulf of Trieste, in August. These specimens occurred among many normal medusae. The abnormal medusae were 0·6–2·6 mm. in diameter. The authors noted indentations in the margins of the

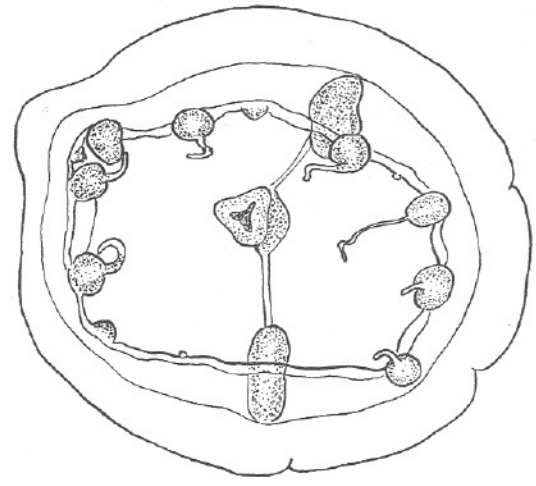
umbrellas as a preparation for division (Text-fig. 10A). The greatest number of stomachs seen was three, and there were, occasionally, centripetal canals.

They note that

(i) The form in question may occur in company with and at the same time as normal medusae.
(ii) The individual organs of both abnormal and normal medusae are identical.
(iii) The products of division are smaller than normal medusae.



Text-fig. 176. *Phialidium hemisphaericum*. Typical appearance of young and shrunken specimens, Plymouth, 3. iii. 38.



Text-fig. 177. *Phialidium hemisphaericum*. Abnormal specimen 2 mm. in diameter with only two radial canals, Plymouth, 3. iii. 38.

On these grounds Neppi & Stiasny considered that their medusae and those of Davidoff and Lang were identical and could be regarded as abnormal *P. variabile*. There seems little doubt that this is the same species as *P. hemisphaericum*.

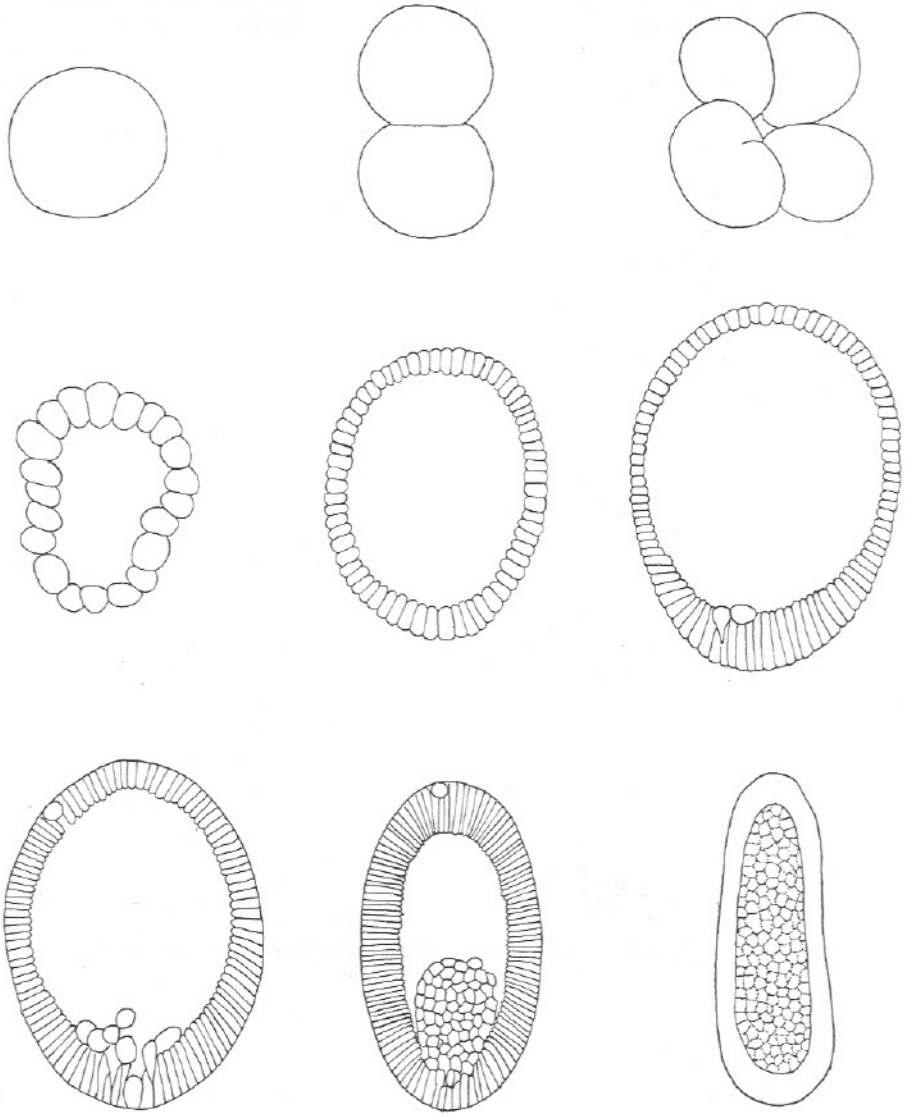
NEMATOCYSTS. ? Microbasic mastigophores and basitrichous haplonemes (Russell, 1938*b*).

Seasonal occurrence

The medusa *Phialidium hemisphaericum* may be found in the plankton off British coasts in any month in the year. There is, however, a pronounced decline in the production of medusae during the winter and they are most abundant from spring to autumn.

Habits

Lebour (1922) has given observations on the feeding of *Phialidium hemisphaericum*. *Sagit* was quickly eaten and young fish seemed to be preferred rather than copepods. Amongst t fish taken as food were species of *Cottus*, *Ammodytes*, *Agonus*, *Solea*, *Gobius* and *Blennius*. T



Text-fig. 178. *Phialidium hemisphaericum*. Development from egg to planula. (After Metschnikoff, 1886*a*, pl. ii, in the final stage the cilia have been omitted.)

young fish were caught and played on the marginal tentacles; sometimes this food would transferred without difficulty to the mouth in a few moments; at other times it took as long twenty minutes before the prey was finally taken into the mouth. Lebour notes that 'from a fe hours to half a day or, rarely, more was taken to digest the fish, sometimes the head part bei disgorged'.

The examination of the stomach contents of the medusae disclosed a large variety of food and most plankton animals were eaten.

Observations on the vertical distribution of this medusa have been made by Russell (1925, 1927, 1928, 1931). In the daytime the medusa appeared to be very irregularly distributed between the surface and the bottom. There were no marked indications of an upward migration at night.

The larval stages of the pycnogonid *Anaphia petiolata* are often found clinging to the medusae (Lebour, 1916*a*). Infestation by larval trematodes, and the attachment of young anemones are recorded by Browne (1896*a*).

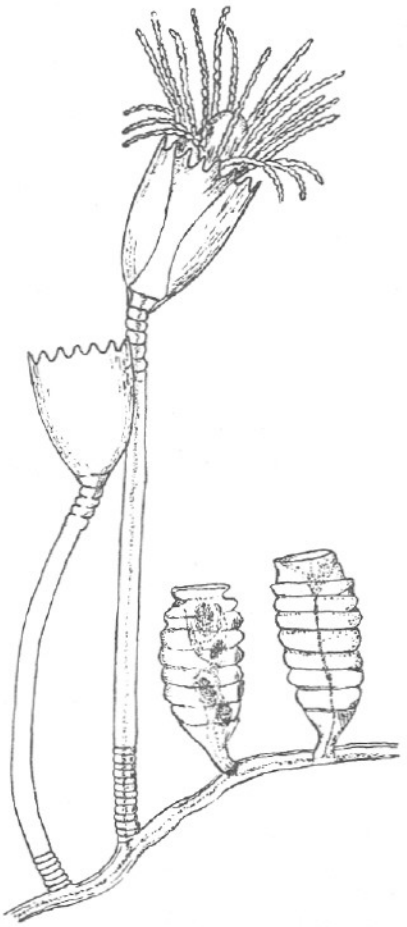
Drawings by Metschnikoff (1886*a*) of the development of the planula are reproduced in Text-fig. 178.

HYDROID. *Clytia johnstoni* (Alder). (Text-fig. 179.)

(For full description see Hincks, 1868, *Brit. Hydroid Zooph.* p. 143, pl. xxiv, figs. 1, 1*a*.)

Colonies of single hydranths, in rare instances slightly branched, reaching a height of 5 mm. rising from a creeping stolon. Hydrocaulus long, transparent, annulated at base and at top, intermediate portion generally smooth. Hydrothecae deeply campanulate, rather large, expanding slightly above, with ten to twelve triangular teeth. Hydranth colourless, with filiform tentacles in a single whorl. Gonothecae ovate, with strong transverse annulations, rarely smooth, arising from the creeping stolon, occasionally from the hydrocaulus; containing several medusa buds.

The young hydroid is very easy to rear from the medusa (see e.g. Str. Wright, 1858*a*).



Text-fig. 179. *Clytia johnstoni*, the hydroid of *Phialidium hemisphaericum*. (After Hincks, 1868, pl. xxiv, fig. 1.)

Historical

The medusa *Phialidium hemisphaericum* was first described by Gronovius (1760) and given the specific name *hemisphaerica* by Linnaeus. The medusa shows great variability both in the degree of development at maturity, in size and in coloration, and it has been recorded under many names. Forbes (1848), for instance, gives a number of colour varieties as different species. I have not attempted to give a complete synonymy list for this medusa. As one of the commonest it has been recorded in almost all works on medusae and on general plankton; nothing is to be gained by searching through all these references. The adoption of Gronovius's name prevents any likelihood of such a search introducing a new name for the species.

The possibility that there may be two species included in one (see p. 290) should, however, be mentioned here. Metschnikoff (1886*b*) described two species from the Mediterranean, *Clytia flavidula*, which is almost certainly *Phialidium hemisphaericum*, and *Clytia viridicans*. *C. flavidula* was the larger, and had sixteen to twenty-four marginal tentacles and thirty-three to seventy-one marginal vesicles in specimens 8–15 mm. in diameter. *C. viridicans* was smaller, but had more

marginal tentacles and fewer marginal vesicles proportionately, specimens 6–11 mm. in diameter having sixteen to thirty marginal tentacles and twenty-four to forty marginal vesicles. The jelly was also thinner and the swimming more energetic. It is to be noted that Metschnikoff (1886*a*) reared primary polyps from these two medusae which appear to be different. In *C. flavidula* the eggs were large, 0·25–0·27 mm. in diameter, and the primary polyp had a thick stem and rather wide-mouthed hydrotheca. In *C. viridicans* the eggs were 0·16 mm. in diameter and the primary polyp was much more slender.*

In any work on the genetics or physiology of this medusa, therefore, the possibility that there may be two distinct species confused as one should be borne in mind.

Phialidium islandicum Kramp

Text-figs. 180, 181

Phialidium islandicum, Kramp, 1919, *Danish Ingolf-Expedit.* vol. v, pt. viii, p. 95, pl. iv, figs. 11–13; pl. v, figs. 1, 2, chart xii.
Kramp & Damas, 1925, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. lxxx, p. 305.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, xii, p. 582, fig. 48.

Specific Characters

Diameter of umbrella up to 40 mm. About 200 marginal tentacles.

Description of Adult

Umbrella flatter than a hemisphere; jelly fairly thin. Velum fairly broad. Stomach very small, cross-shaped, perradial diameter only about one-tenth diameter of umbrella. Mouth with four pointed, more or less crenulated, lips. Four straight radial canals and ring canal narrow. Gonads on four radial canals very elongated, linear, extending from about 2 mm. from base of stomach to about 1 mm. from ring canal; continuous over lower wall of radial canal without median furrow. Up to about 200 hollow marginal tentacles, smooth, with swollen bases. No ocelli. No marginal nor lateral cirri. Small closed marginal vesicles of about same number as marginal tentacles; number of concretions in each vesicle not known. Diameter of umbrella up to 40 mm. Colour not known.

Distribution

Phialidium islandicum has not previously been recorded from the British area. It has, however, been recorded by Kramp & Damas (1925) from between the Shetland Islands and Norway in 60° 40′ N., 2° 23′ E. and 60° 40′ N., 0° 23′ W. The latter locality is very near the Shetland Islands. I have found a specimen in Mr Browne's collection caught at Valencia in May 1899.

Elsewhere the medusa has only been recorded round Iceland (Kramp, 1919).

Structural Details

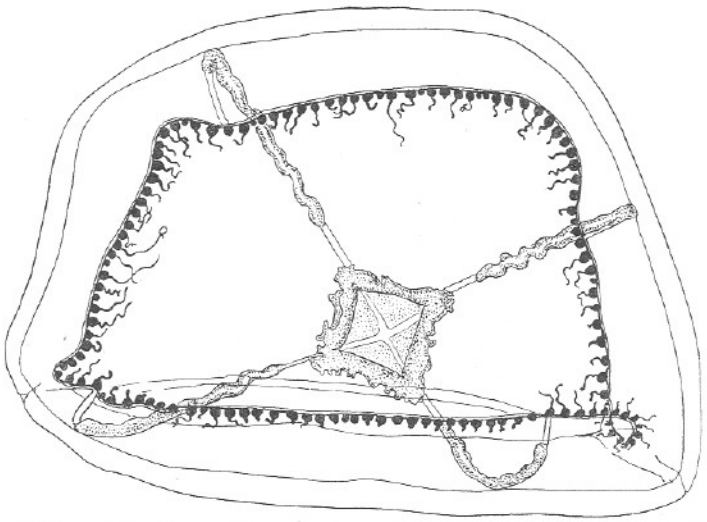
Nothing is known of the early development of *Phialidium islandicum*, nor is its hydroid known.

Our knowledge of the species is based on the description given by Kramp (1919):

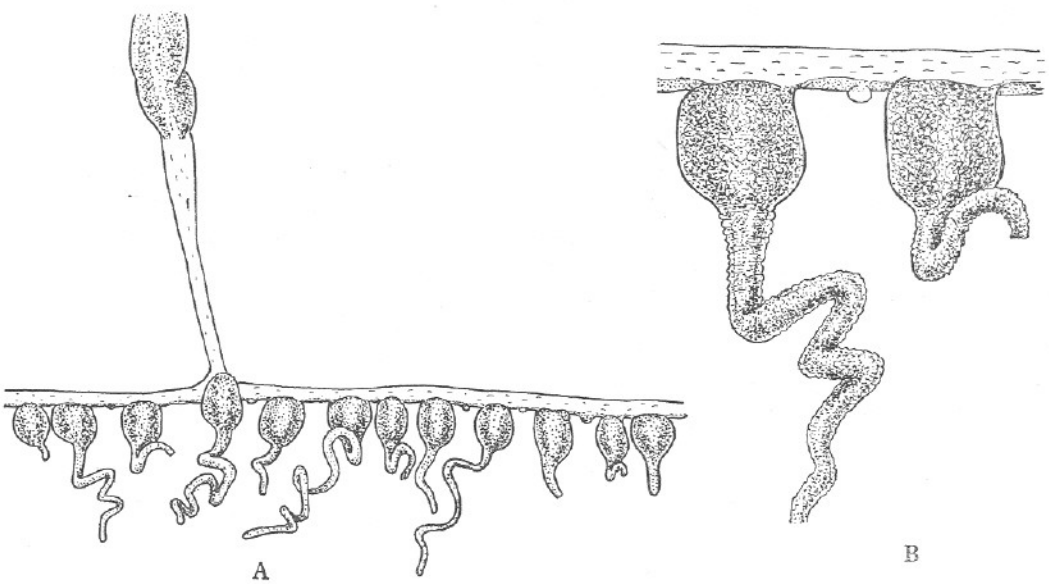
The species is quite distinct from *Phialidium hemisphaericum*, not only by its size and the large number of tentacles, but also by the number of marginal vesicles never exceeding the number

* Dr W. J. Rees tells me that he has noted similar differences in primary polyps he has reared from British medusae.

of tentacles. Furthermore the mouth-lips are larger and more crenulated than in the case of *Phialidium hemisphaericum*, and the gonads are longer. The sagittal sections through the tentacular bulbs show that the ectoderm on the adaxial side of the bulb is more highly developed in *Phialidium hemisphaericum* than in *P. islandicum*.



Text-fig. 180. *Phialidium islandicum.* Preserved specimen *c.* 25 mm. in diameter, Valencia, 8. v. 99 (E. T. Browne collection); 127 marginal tentacles shown, the actual number being nearer 137.



Text-fig. 181. *Phialidium islandicum.* A, portion of umbrella margin; B, marginal tentacles and marginal vesicle. (Same specimen as in Text-fig. 180.)

Kramp mentions a slight trace of an abaxial process at the bases of the marginal tentacles, but says that this is not always distinct; in *P. hemisphaericum* it is entirely lacking.

Owing to the state of preservation Kramp was unable to see concretions in the marginal vesicles.

Dimensions given by Kramp are:

Diameter of umbrella (mm.)	No. of marginal tentacles	Length of gonads (mm.)	Sex
21	152	—	♂
28	*c.* 175	10	♀
32	*c.* 200	11	♂
35	*c.* 185	11–12	♀
37	*c.* 200	15	♂
38	200	15	♀

He also records two very large specimens, about 40 mm. in diameter, both of which had lost the gastro-genital organs, but these were regenerating. In one specimen three new stomachs were developing, and there was a nematode enclosed in the gelatinous substance near the three stomachs.

Seasonal occurrence

The specimens recorded by Kramp & Damas (1925) between the Shetland Islands and Norway were taken in May. The specimens from Iceland were caught in July and August. The specimen in Mr Browne's collection from Valencia was caught on 8 May 1899.

Habits

Nothing is known of the habits of the living medusa. It is probably an inhabitant of the upper water layers.

HYDROID. Not known.

Historical

Phialidium islandicum was first described and figured by Kramp (1919) from specimens caught off Iceland. Kramp says that it is possible that the species 'will prove in time to be only a northern giant variety of a species already known to science; but as long as it cannot be referred with certainty to any known species, I prefer to describe it as an independent species, for which I propose the name of *Phialidium islandicum*, because all the specimens in hand have been found in the neighbourhood of Iceland'. The occurrence of a specimen as far south as Valencia seems to be evidence against the suggestion that the medusa is a northern variety of some other species.

SUBFAMILY OBELINAE

MEDUSAE. Campanulariidae with reduced velum; with solid marginal tentacles; with eight marginal vesicles.

HYDROID. *Obelia*-like, zigzag or well-branched colonies, with thin-walled hydrotheca.

The Obelinae are represented in British waters by one genus in which medusae are produced, *Obelia* Péron & Lesueur. In general appearance the medusae of this genus are unmistakable.

Genus **Obelia** Péron & Lesueur, 1809

MEDUSAE. Campanulariidae with characters as subfamily.

HYDROID. *Obelia.*

Three British species of hydroids, *Obelia geniculata* (L.), *O. dichotoma* (L.), and *O. longissima* (Pallas), are recognized by hydroid specialists. On the other hand only two species of medusae have been described from the plankton, *O. lucifera* (Forbes) and *O. nigra* Browne.

It is thought that *O. lucifera* comprises two species of medusae, at present indistinguishable, which are liberated from the hydroids *O. geniculata* and *O. dichotoma* respectively. By a process of elimination it is suggested that *O. nigra* may be the medusa of *O. longissima*.

As the difference between the two medusa species is only that of size at maturity with its associated structural differences and degree of pigmentation, it is not even certain that they are really separable, since the difference in size may be determined by available food supply or other factors. In fact, Kramp (1927, p. 125) has said, 'I have myself on several occasions, even with fairly large specimens of *Obelia*, been unable to determine whether they were "*nigra*" or not'.

It is quite evident that we are not yet in a position to describe the *Obelia* medusae as species. Whether the hydroids themselves are indeed separate species or only growth forms may also remain open to conjecture, and the truth will probably only be reached by genetic research.

NOTE. The genus *Obelia* was erected by Péron & Lesueur (1809) for a medusa which they called *O. sphaerulina*, and which they identified with *Medusa marina* of Slabber (1781). It is quite impossible to say to which of the now generally recognized hydroids of the *Obelia* type Péron & Lesueur's medusa belongs. Haeckel (1879) kept *O. sphaerulina*, giving the hydroid known as *O. dichotoma* as its synonym. Mayer (1910) gave Haeckel's *O. sphaerulina* as a synonym of *O. dichotoma*. The most reasonable course at present is to follow these two authors and list *O. sphaerulina* as a synonym of *O. dichotoma*, whose hydroid was described by Linnaeus as *Sertularia dichotoma*.

The details of the many supposed species of *Obelia* medusae are summarized in tabular form by Mayer (1910).

Obelia spp.

Plate XVIII, figs. 1, 2; Plate XIX, fig. 2; Text-figs. 182–5

As I have already mentioned, it is not possible to make a satisfactory distinction between the so-called species of *Obelia* medusae. They are therefore described here under the one head with references to pertinent literature and other information available.

The following is a list of names under which the British medusae have been described:

Thaumantias lucifera Forbes, 1848, *Monogr. Brit. Medusae*, p. 52, pl. x, fig. 2.
Laomedea geniculata, Gosse, 1853, *Devonshire Coast*, p. 84, pl. iv.
Obelia (*Laomedea*) *geniculata*, Allman, 1867, *Rep. Brit. Assoc.* p. 77.
Obelia geniculata, Hincks, 1868, *Brit. Hydroid Zooph.* p. 149, pl. xxv, fig. 1 (hydroid and young medusa).
Obelia dichotoma, Hincks, 1868, ibid. p. 156, pl. xxviii, fig. 1 (hydroid and young medusa).
Browne, 1905*a*, *Proc. Roy. Soc. Edinb.* vol. xxv, pt. ix, p. 769.
Obelia nigra Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. v, p. 721.
Browne, 1903, *Bergens Mus. Aarb.* no. 4, p. 16.
Browne, 1905*a*, *Proc. Roy. Soc. Edinb.* vol. xxv, pt. ix, p. 770.
Obelia lucifera, Browne, 1905*a*, ibid. p. 770.
Obelia spp., Kramp, 1927, *K. danske vidensk. Selsk. Skr.* natur. og math. Afd., 8. Raekke, xii, p. 124.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, xii, p. 574, figs. 37, 38.

Description of Adult

Umbrella flat; jelly thin. Velum quite rudimentary. Stomach short, with quadrangular base, without peduncle. Mouth with four short simple perradial lips. Four straight radial canals and ring canal narrow. Four round or oval sac-like gonads, situated singly on the middle of the course of each radial canal, without median furrow. Numerous solid, short, marginal tentacles, somewhat stiff, with axial core of single row of endoderm cells; each marginal tentacle with small basal swelling and short prolongation of endoderm into mesogloea of umbrella margin. No marginal nor lateral cirri. No ocelli. Eight adradial closed marginal vesicles, each situated on

under side of basal bulb of marginal tentacle; each with single concretion. Diameter of umbrella 2·5–6·0 mm. Colour of bases of marginal tentacles pale straw, yellowish brown, dark brown or black, or colourless; gonads and stomach yellowish brown or brown.

The above diagnosis will fit any of the so-called species of *Obelia*, which are only differentiated by size, number of marginal tentacles, and colour.

The provisional allocation of species is at present as follows:

Medusa	Hydroid	Medusa diagnosis
O. lucifera	*O. geniculata* *O. dichotoma*	Less than 100 marginal tentacles; tentacle bases colourless or faintly pigmented; diameter up to 2·5 mm.
O. nigra	? *O. longissima*	150–200 marginal tentacles; many of tentacle bases with black pigmentation; diameter up to 6 mm.

Distribution

Obelia medusae are to be found in the plankton all round the coasts of the British Isles. They are of world-wide distribution, but their specific identity is in a state of chaos.

Developmental Stages and Structural Details

The medusae of *Obelia* when first liberated from their hydroids are about 1 mm. in diameter. They have from sixteen to twenty-four marginal tentacles, and the gonads may be absent or visible as traces.

I give below published and other observations on the so-called species.

Obelia geniculata. Gosse (1853) states that the newly liberated medusa has twenty-three to twenty-four marginal tentacles; Browne (MS.) finds twenty to twenty-four marginal tentacles; Hartlaub (1894) also gives twenty-four tentacles.

Obelia longissima. Hartlaub (1894) states that medusae are liberated with twenty-four tentacles.

Obelia dichotoma. Browne (1903*a*) reared the medusae from this hydroid to maturity. Hydroid colonies collected from piles off Keppel Pier, Millport, were placed in a bell-jar on 17 September 1902. Within three days the jar was crowded with medusae (Pl. XVIII, fig. 2). About 100 medusae were transferred to a plunger jar.

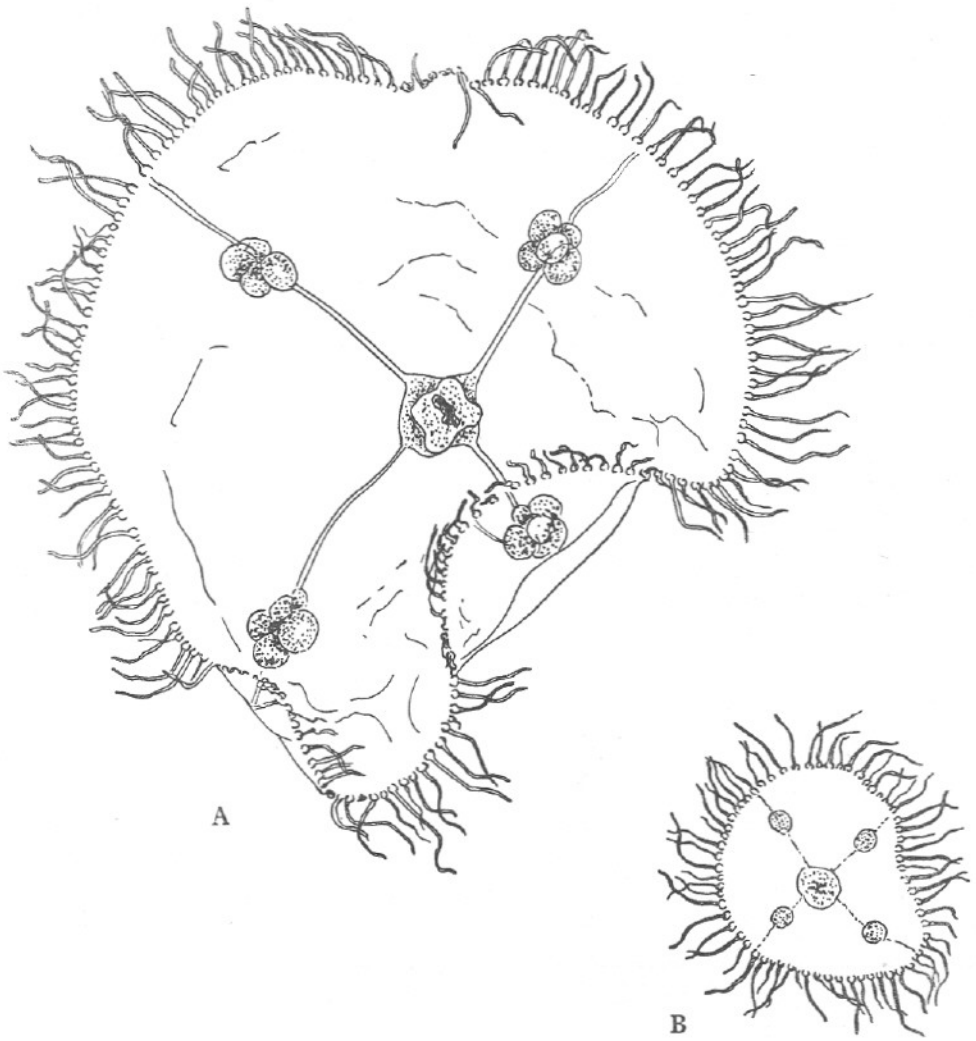
The young medusae on liberation had sixteen marginal tentacles and eight adradial marginal vesicles. They had no signs of gonads and were quite colourless. By 26 September the largest specimens were 2·0–2·5 mm. in diameter and had sixty-four marginal tentacles and ripe gonads. On 9 October the largest was 2·5 mm. in diameter and it had eighty-four marginal tentacles. The marginal tentacle bases were very small, and some contained a yellowish brown or brown pigment. The root of the marginal tentacle, within the margin of the umbrella, was semiglobular or oblong, and usually without a transverse septum, but occasionally with one. The gonads were nearer to the umbrella margin than to the stomach. The gonads and the stomach were yellowish brown or brown.

Obelia lucifera. Browne, in his manuscript notes, records the examination of forty-seven medusae collected at Plymouth in 1893. In these specimens the numbers of marginal tentacles ranged between forty-six and ninety.

Obelia nigra. Browne (1900) states:

The basal bulbs of the tentacles are of two kinds; the majority are colourless, but others, varying in number and position, contain a dark brown or black pigment. There are usually six coloured basal bulbs in each quadrant; they are about twice the size of the colourless bulbs, and

are situated on the inner side of the tentacles. The total number varies between 22 and 27. In some specimens, in addition to the completely coloured bulbs, there are bulbs only partly coloured, with just one or two small patches of colour. In one specimen 30 such bulbs were counted, but usually only two or three are present. They have the appearance of bulbs developing pigment.

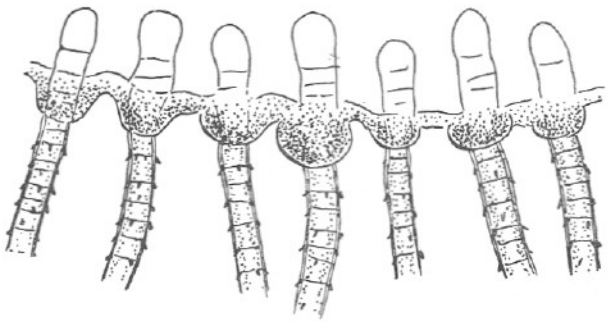


Text-fig. 182. *Obelia* sp. Preserved specimens from Balta Sound, Shetlands, 13. vii. 33. A, 5 mm. in diameter; B, 1·4 mm. in diameter.

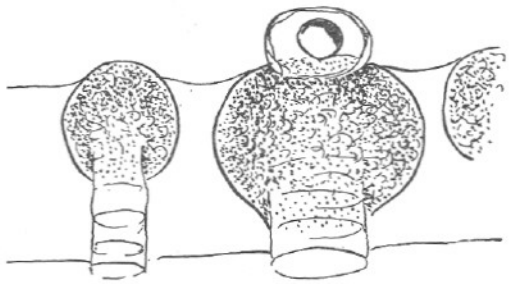
Browne (MS. notes) has observations on a number of medusae collected at Plymouth in May 1898. These varied in size from 4·0 to 5·5 mm. in diameter and had 134 to 196 marginal tentacles.

Kramp (1927) and Browne both devoted much time to the rearing of these medusae from their hydroids. The medusae of *O. geniculata* and of *O. dichotoma* have both been reared to maturity and no difference could be found between them. On the other hand the medusae of *O. longissima* have not yet been successfully reared. According to Kramp 'the characteristic peculiarities of *nigra* do not appear until the medusa has reached an advanced stage of development'.

The origin of the germ cells has been studied by Hartlaub (1884) among other authors. Studying his *O. helgolandica* and *O. adelungi*, he found that the germ cells were first seen in the interradial ectoderm of the stomach on the second day after the liberation of the medusa from the hydroid. Later they migrate to the position of the gonads on the radial canals, some of them having first moved into the endoderm of the stomach. The young eggs may be found in the endoderm of the radial canals, but they ripen in the ectoderm. The sperm cells originate in the interradial ectoderm of the stomach and are found in the ectoderm of the gonads. Apstein (1913), however, states that the egg cells of the youngest and oldest stages are always in the endoderm, while Faulkner (1929) found that the oocytes were situated between the ectoderm and the endoderm.



Text-fig. 183. *Obelia* sp. Portion of umbrella margin, showing bases of marginal tentacles and their endodermal roots.



Text-fig. 184. *Obelia* sp. Portion of umbrella margin seen from below, showing the position of the marginal vesicle on the inner side of the base of the marginal tentacle.

The eggs of *Obelia* are 0·2 mm. in diameter and have a colourless transparent yoke. They are remarkable in that their chromosomes can be seen in living material. The early prophases of the first oocyte division were thus examined by Faulkner (1929) in the living state. She gives the numbers of chromosomes as seventeen and thirty-four in the bivalent and univalent phases respectively. Other observations on the nuclei of *Obelia* were made by Mérejkowsky (1883), Metschnikoff (1886*a*) and Trinci (1906).

A very detailed study of variation and abnormality was made by Agassiz & Woodworth (1896) on *Obelia* from Newport, Rhode Island, U.S.A. Their results as summarized by Mayer (1910, p. 242) were as follows:

Among 3,917 specimens, 9 had 3 radial canals, 20 had 5, and 3 had 6 canals. In 14 specimens one of the radial canals forked. 3,871 had 4 radial canals. In other words, 98·8 per cent had 4 canals, 0·51 per cent had 5, 0·22 per cent had 3, 0·076 per cent had 6 canals, and 0·35 per cent had forked canals. It is remarkable that there were no variations in the lips, these being 4 in number in every specimen examined. On the other hand, the tentacles were very variable in number, and in 14 specimens they were forked or gave rise to basal spurs resembling those of *Laodicea*, etc. The egg or sperm seemed to develop to maturity with normal frequency even in abnormal specimens with 3, 5, or 6 canals. They also found that in *Obelia* the tendency to produce medusae with 5 radial canals is about twice as great as that to give rise to individuals with 3 or 6 canals. Yet medusae of *Obelia* with 5 canals have not succeeded in perpetuating a new 5-rayed species.

Browne (1900) recorded only seven abnormalities among 450 specimens taken at Valencia in August 1898. They were as follows:

One specimen with one radial canal.
Five specimens with three canals.
One specimen with five canals.

Seasonal occurrence

Obelia medusae may be found in the plankton round the British coasts almost at any time of the year. They are, however, most abundant from spring to late autumn.

Orton (1920) noted hydroids of *O. geniculata* with gonophores, or extruding medusae, from March to November, at Plymouth. Elmhirst (1925) gives evidence that the production of medusae by healthy colonies of the hydroid has a lunar periodicity, occurring during the ten-day periods beginning with the third week of the moon in July, August and September at Millport.

Habits

There have been numerous observations on the habits of *Obelia* medusae. This medusa swims in a manner quite unlike that of other hydromedusae, and this is probably related to the great reduction of the velum. The swimming movements take the form of a flapping of the water by the umbrella and the short marginal tentacles, the flat umbrella disk being everted above the horizontal before the downward stroke. In very small specimens the umbrella is often noticeably everted in this manner with the stomach hanging free in its centre, much like an umbrella blown inside out.

Lebour (1922, 1923) found miscellaneous types of food in the stomachs of *Obelia* in tow-nettings, including *Sagitta*, small crustacea, young fish, etc. She only once observed a specimen catch its food while in a plunger jar. This medusa, *c.* 4 mm. in diameter, caught a copepod with one of its marginal tentacles, which are not very contractile and hardly stretch out at all.

Obelia lucifera, as the name implies, may luminesce. Bles (1892) notes, 'On adding a saturated solution of corrosive sublimate to the sea water the stimulus caused the animals to become phosphorescent, and the position of each medusa was indicated by a small clear ring of blue light round the margin of the umbrella. The light did not fade until after about a minute'. M'Intosh (1926) records that shaking the vessel was in itself sufficient to stimulate phosphorescence.

Observations on the vertical distribution of *Obelia* in the sea (Russell, 1925, 1928, 1931) showed that this medusa had no marked tendency to move towards the surface at night. In the daylight, also, they appeared to show no consistency in their depth distribution (Russell, 1927).

Larvae of the pycnogon *Anaphia petiolata* may be found clinging to *Obelia* medusae (Lebour, 1916*a*), as well as the young stages of the actinian *Peachia*. Hovasse (1935) records the peridinian parasite *Protoodinium chattoni* from *Obelia dichotoma*.

Swithinbank & Bullen (1913) make the interesting observation that, while *O. nigra* was present in the plankton, no remains of the medusa could be found in the stomach contents of the pilchard. They note that at the same time *Obelia* caused 'considerable "briming" in the water along the fleet of nets, a fact which caused the fishermen to consider a large catch improbable'.

Obelia has been recorded as eaten by young *Cyanea* (M. & C. Delap, 1905).

Herbst (1904) investigated the effects of sodium, potassium, and calcium upon the pulsations of the medusa.

CAMPANULARIIDAE

HYDROIDS. (Text-fig. 185A–C.) *Obelia geniculata* (L.); *O. dichotoma* (L.); *O. longissima* (Pallas).

(For full descriptions see Hincks, 1868, *Brit. Hydroid Zooph.* pp. 149, 156, 154; pl. xxv, fig. 1, pl. xxviii, fig. 1, and pl. xxvii.)



Text-fig. 185. Hydroids of *Obelia* medusae. A, *Obelia geniculata*; B, *Obelia dichotoma*; C, *Obelia longissima*. (After Hincks, 1868, pl. xxv, fig. 1*a*; pl. xxviii, fig. 1*a*; and pl. xxvii, fig. *b*.)

Obelia geniculata. Stem zigzag, sometimes slightly branched, jointed at each of the flexures and thickened immediately below them, forming a series of projections from which pedicels arise. Hydrothecae somewhat obconical, slightly longer than wide, margin plain, borne on short, sub-erect, slightly tapering, annulated stalks with four to six rings.

Gonothecae axillary, urn-shaped, attached by short ringed stalk with three to four rings; each with several medusa buds.

Obelia dichotoma. Stem filiform, slender, nearly straight, irregularly branched, annulated above origin of branches; branches sub-erect, often very long and more or less ramified, ringed at intervals. Hydrothecae alternate, broadly campanulate and deep, polyhedral above, each side corresponding with a very slight sinuation of margin, borne on annulated pedicels, varying in length from four to sixteen rings.

Gonothecae axillary, slender, smooth, widening from base upwards, and terminating in raised somewhat conical aperture.

Obelia longissima. Stem filiform, flexuous, giving off much-ramified branches at short intervals, ringed above their origins; branches alternate, long and spreading, principal stem flexuous, with more or less branched pinnae springing from each bend, annulated above every division. Hydrothecae campanulate, rather large and deep, delicate, margin with blunt shallow teeth, borne on rather long, ringed, tapering pedicels.

Gonothecae axillary, ovate, smooth, with raised central aperture.

Historical

Sufficient has already been said to indicate the confusion that exists in the synonymy of *Obelia*. There is nothing to be gained by further mention.

Subfamily ORTHOPYXINAE

MEDUSAE. Reduced Campanulariidae without stomach or marginal tentacles; with eight marginal vesicles.

HYDROID. *Orthopyxis*-like, unbranched colonies, with thick-walled hydrotheca.

The Orthopyxinae are represented in British waters by one genus, *Agastra* Hartlaub.

Genus **Agastra** Hartlaub, 1897

MEDUSAE. Campanulariidae with characters as subfamily.

HYDROID. *Orthopyxis*.

There is only one British species of the genus, *Agastra mira* Hartlaub.

Agastra mira Hartlaub

Plate XIX, fig. 1; Text-figs. 186–8

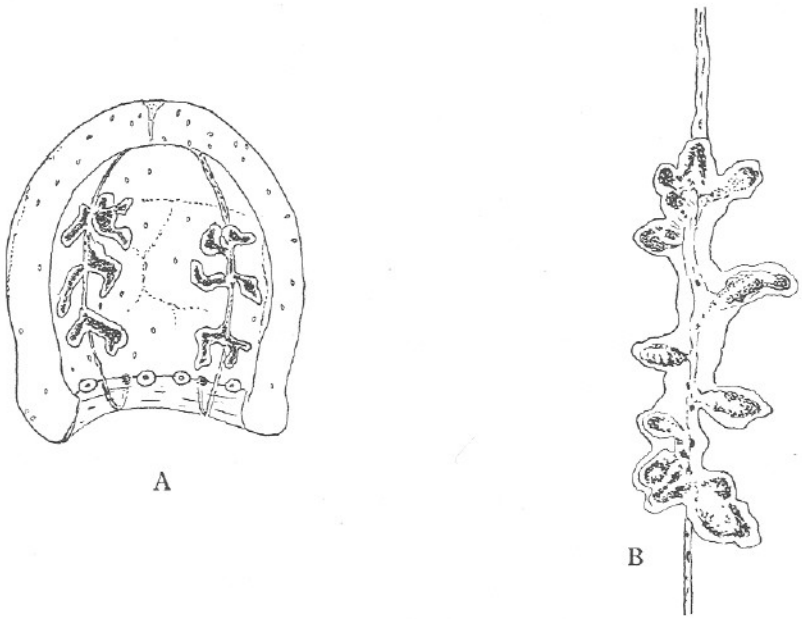
Leptomedusa (gen.? sp.?), Browne, 1897*a*, *Proc. Zool. Soc. London*, p. 832, pl. xlix, figs. 3, 3*a*.
Agastra mira Hartlaub, 1897, *Wiss. Meeresuntersuch.* N.F., Bd. II, Abt. Helgoland, Heft 1, x, p. 504, pl. xxii, figs. 8–10.
Mayer, 1910, *Medusae of the World*, vol. II, p. 234, fig. 121.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 575, fig. 39.
Campanularia caliculata Hincks, 1853, *Ann. Mag. Nat. Hist.* ser. 2, vol. XI, p. 178, pl. VB (hydroid).
Allman, 1858, *Proc. Roy. Soc. Edinb.* vol. IV, no. 48, p. 61 (hydroid and medusa bud).
Hincks, 1868, *Brit. Hydroid Zooph.* p. 164, pl. xxxi, fig. 2 (hydroid and medusa bud).
Giard, 1898, *C.R. Soc. Biol. Paris* (10), tome V, no. 1, p. 17 (hydroid and attached medusa).
Agastra caliculata, Browne, 1900, *Proc. Roy. Irish Acad.*, ser. 3, vol. V, no. 5, p. 714.

Specific Characters

Sac-like outgrowths on middle portions only of radial canals.

Description of Adult

Umbrella bell-shaped, higher than wide, with scattered nematocysts on exumbrella; jelly fairly thick. Velum broad. No stomach. Four narrow radial canals, either meeting at apex or closed before they meet; irregularly lobed sac-like outgrowths, one in middle of each radial canal. Ring canal narrow. Gonads situated on lobes of radial canal swellings. No marginal tentacles; four small perradial marginal bulbs. No marginal nor lateral cirri. Eight adradial closed marginal vesicles, each with single concretion. Height *c.* 1 mm. Colour of radial canal swellings and marginal bulbs dark brown; brown pigment granules present in radial canals and ring canal.



Text-fig. 186. *Agastra mira*. A, medusa; B, evacuated gonad. (After Hartlaub, 1897, pl. xxii, figs. 10, 8.)

Distribution

The medusa *Agastra mira* has been recorded from the plankton off British coasts only from near Dover, Plymouth, and Valencia, south-west Ireland. Its hydroid, *Orthopyxis caliculata*, has in addition been found near Ramsgate, off the Dorsetshire coast, at Ilfracombe, Newquay (Cornwall) and Co. Cork.

Elsewhere the medusa has been recorded from Helgoland, Jersey and Roscoff, and the hydroid with attached medusae from Wimereux.

The medusa is scarce and never seen in abundance. It is probably overlooked on account of its small size and probably only lives in the plankton a short while after liberation from its hydroid.

Structural Details

There is little to add to the details already given above on the structure of this remarkable little medusa. When liberated from its hydroid, it is already fully developed and shows no further structural change. There may sometimes be traces of an umbilical canal. The eggs are already developed on the lobed outgrowths from the centres of the radial canals and are somewhat

irregularly distributed. The male has not been seen. Hartlaub (1897) records a specimen with ten marginal vesicles, there being two additional interradial vesicles in addition to the normal eight adradial ones.

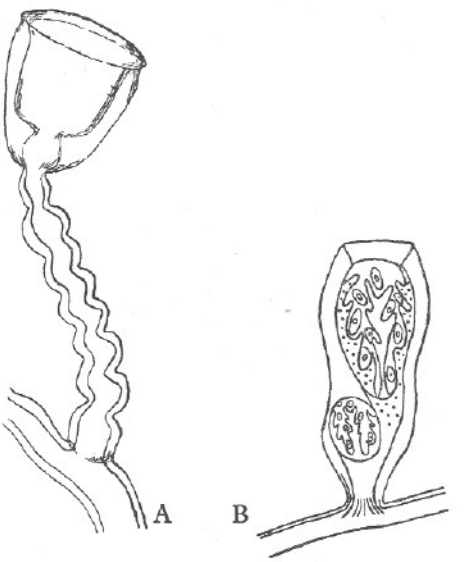
Seasonal occurrence

The medusa, *Agastra mira*, has been recorded from the plankton off British coasts in the following months: July, August and November (Plymouth), May, June, July, August, October and November (Valencia), August (near Dover). It is evidently liberated from its hydroid during summer and autumn.

Elsewhere it has been recorded from Roscoff in May and from Helgoland from the end of August to the beginning of October. At Wimereux the hydroids were carrying medusa buds at the end of the autumn.



Text-fig. 187. *Orthopyxis caliculata*, the hydroid of *Agastra mira*. (After Hincks, 1868, pl. xxxi, fig. 2*a*.)



Text-fig. 188. *Orthopyxis caliculata*, the hydroid of *Agastra mira*. A, hydrotheca; B, gonotheca. (After Hincks, 1868, pl. xxxi, figs. 2*b*, *d*.)

Habits

Giard (1898) states that at Wimereux the medusae are not liberated. When they are liberated they probably live only a short time in the plankton, although Hartlaub (1897) kept the medusa alive for many days. He states that it was full of vitality.

HYDROID. *Orthopyxis caliculata* (Hincks). (Text-figs. 187, 188A, B.)

(For full description see Hincks, 1868, *Brit. Hydroid Zooph.* p. 164, pl. xxxi, fig. 2, as *Campanularia caliculata*.)

Colonies of single hydranths rising from a creeping stolon. Hydrocaulus of variable length, perisarc crenulated or faintly annulated, with well-marked ring immediately below hydrotheca. Hydrotheca campanulate, with smooth rim; walls greatly thickened and projecting inwards at base to form a diaphragm with spherical cavity beneath it. Hydranth with single whorl of eighteen to twenty short filiform tentacles, generally held curving backwards; colourless. Gonothecae cylindrical, shortly stalked, irregularly oval in shape, with somewhat wavy outline; truncated at top, with wide aperture; one to three medusa buds in each gonotheca.

Historical

The first descriptions and figures of the medusa *Agastra mira* were published in the same year by Browne (1897*a*), as an unknown Leptomedusa, and by Hartlaub (1897), who gave the medusa its name. Its hydroid *Orthopyxis caliculata* was first described by Hincks (1853) without the gonotheca. Allman (1858) and Hincks (1868) described the gonothecae, and the medusa was first linked to its hydroid by Giard (1898).

A very similar medusa, *Agastra rubra*, has been described by Behner (1914), from the Mediterranean, whose hydroid is *Orthopyxis compressa*, regarded by Broch (1918) as synonymous with *O. caliculata*. The medusa described by Behner differs from *Agastra mira* in that the diverticula of the radial canals occupy nearly their whole length and the eggs are fewer and arranged in regular rows.

The hydroid *Orthopyxis integra* (Macgillivray, 1842) is regarded by some authors (see e.g. Broch, 1918, p. 160) as synonymous with *O. caliculata*. But the gonothecae of *O. integra* figured by Hincks (1868) appear to be sporosacs.

Family LOVENELLIDAE

Leptomedusae with small stomach; without peduncle; with four simple radial canals; without excretory pores; with gonads on radial canals separated from stomach; with hollow marginal tentacles; with lateral cirri; without marginal cirri; with closed marginal vesicles; without ocelli.

HYDROID. Where known, *Lovenella*-like, unbranched or slightly branched colonies; with single whorl of filiform tentacles, without webs between their bases; with hydrotheca with operculum.

As with the Campanulariidae there is no single distinctive character by which medusae of the family Lovenellidae can be separated from those of certain other families. They are at once separable from the Campanulariidae and the Phialellidae by the presence of lateral cirri, from the Eirenidae and Eutimidae by the absence of a peduncle, and from the Aequoreidae in having only four radial canals.

The Lovenellidae are represented in British waters by two genera, *Lovenella* Hincks and *Eucheilota* McCrady. Of these the hydroid of *Lovenella* is known but that of *Eucheilota* is uncertain. The two genera are kept distinct because it is possible that there is a generic distinction in the number of marginal vesicles. In *Lovenella* their number is indefinite, while in *Eucheilota* it is fixed, namely eight. The generic distinction thus becomes as follows:

Number of marginal vesicles indefinite	**Lovenella**
Number of marginal vesicles constantly eight	**Eucheilota**

Genus **Lovenella** Hincks, 1868

MEDUSA. Lovenellidae with sixteen or more marginal vesicles.

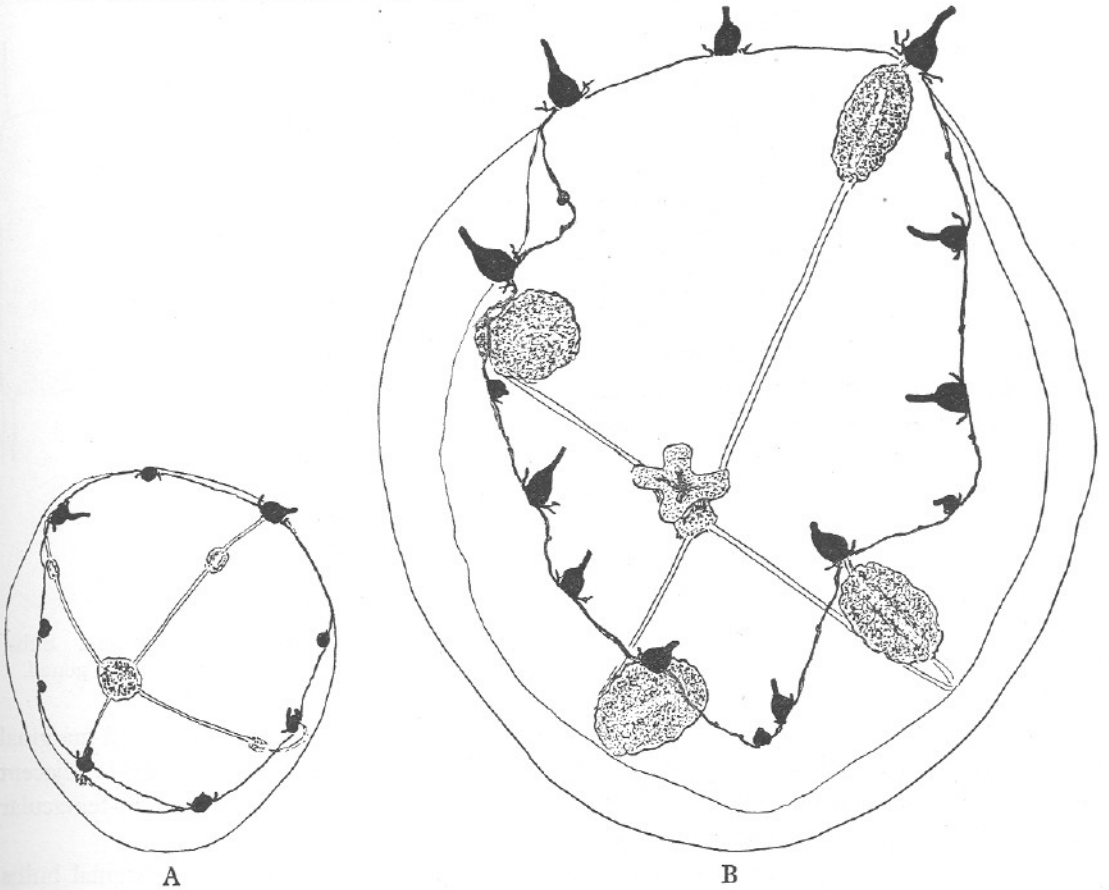
HYDROID. *Lovenella.*

There is one British representative of the genus, *Lovenella clausa* Hincks. This medusa is at first sight very similar in appearance to *Phialidium hemisphaericum* and has no doubt been confused with it in the past. It is, of course, distinguishable by the presence of the lateral cirri. The relative size of the bases of the marginal tentacles is also larger and the gonads have a distinct median furrow (Text-fig. 190).

Lovenella clausa Hincks

Plate XVI, fig. 2; Plate XVII, figs. 3, 4; Text-figs. 189–92

Campanularia clausa Lovén, 1836, *K. svenska VetenskAkad. Handl. för* 1835, p. 261, fn. 3 (hydroid).
Mitrocomium sp.(?) Browne, 1898*b*, *Journ. Mar. Biol. Assoc.* vol. v, no. 2, p. 190.
Lovenella clausa Hincks, 1871, *Ann. Mag. Nat. Hist.* ser. 4, vol. VIII, no. 44, IX, p. 79, pl. v, figs. 2, 2*a*, 2*b* (hydroid and young medusa).
'Medusa n.g., n.sp.' Hartlaub, 1917, *Nordisches Plankton*, Lief. 19, XII, p. 418, fig.
Eucheilota hartlaubi Russell, 1936*b*, *Journ. Mar. Biol. Assoc.* vol. XX, no. 2, p. 589, figs. 1–6.
Eucheilota clausa, Russell, 1936*c*, *Journ. Mar. Biol. Assoc.* vol. XXI, no. 1, p. 131, figs. 1–3.
Russell, 1938*a*, ibid. vol. XXII, no. 2, p. 432.



Text-fig. 189. *Lovenella clausa*. Preserved specimens, Plymouth. A, *c.* 3 mm. in diameter; B, *c.* 6 mm. in diameter.

Specific Characters

Marginal tentacles sixteen to twenty-four in number; sixteen to twenty-three marginal vesicles each with one concretion.

Description of Adult

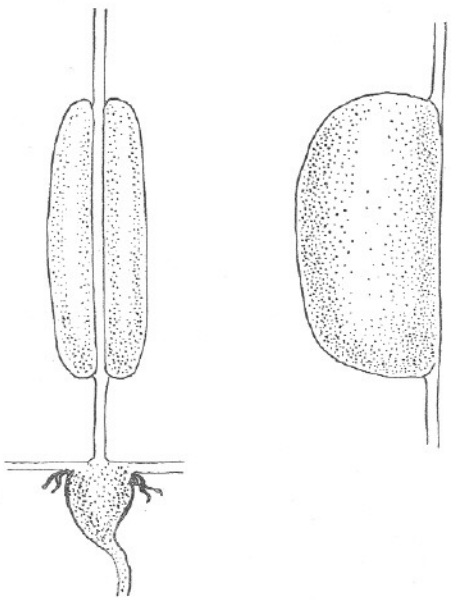
Umbrella hemispherical; jelly moderately thick. Velum narrow. Stomach short and small, without peduncle. Mouth with four small simple lips. Four straight radial canals and ring canal narrow. Gonads on four radial canals, oval, longitudinally divided; situated distally, very close

to ring canal. Marginal tentacles sixteen to twenty-four in number when fully developed, with large conical bases. Spiral lateral cirri, one to three on either side of each tentacle base. Sixteen to twenty-three closed marginal vesicles, approximately alternating with marginal tentacles, each with a single concretion. Diameter of umbrella 5–9 mm. Colour of manubrium pale greenish yellow; gonads with greenish tinge; marginal tentacle bases orange, with core of bright green, and reddish summit.

Distribution

Lovenella clausa has so far only been recorded from the following localities: Plymouth, Salcombe, Valencia, and Dalkey Sound and Sandycove, Co. Dublin.

It is common in the plankton at Helgoland. The species has probably in the past been often mistaken for *Phialidium hemisphaericum*. It is thus likely that it will be found to be more widely distributed round the British Isles than present records show.*



Text-fig. 190. *Lovenella clausa*. Subumbrellar and lateral views of gonad.

Developmental Stages and Structural Details

Descriptions of all developmental stages of *Lovenella clausa* have been given by Russell (1936*b*, *c*). When first liberated from its hydroid (Pl. XVII, fig. 3) the medusa is 0·75 mm. high and 0·75 mm. wide. The umbrella is conically bell-shaped and the jelly thin. There are a few scattered nematocysts on the exumbrella. The velum is well developed. The stomach is very short and the mouth is simple, without lips. The four radial canals and ring canal are narrow. There are no traces of gonads. There are two opposite perradial marginal tentacles, with one small or rudimentary lateral cirrus on either side of each marginal tentacle base. There are two opposite perradial marginal bulbs without tentacles and without lateral cirri. There are four marginal cirri situated interradially on the bell margin, one in each quadrant. There are four closed marginal vesicles, each with a single concretion and situated close to a marginal cirrus on that side adjacent to the nearest marginal tentacle. The colour of the marginal tentacle bases, the non-tentacular marginal bulbs and the stomach is pale straw.

The day after liberation the umbrella assumes a deeper bell-shape and the marginal bulbs and stomach become bright orange.

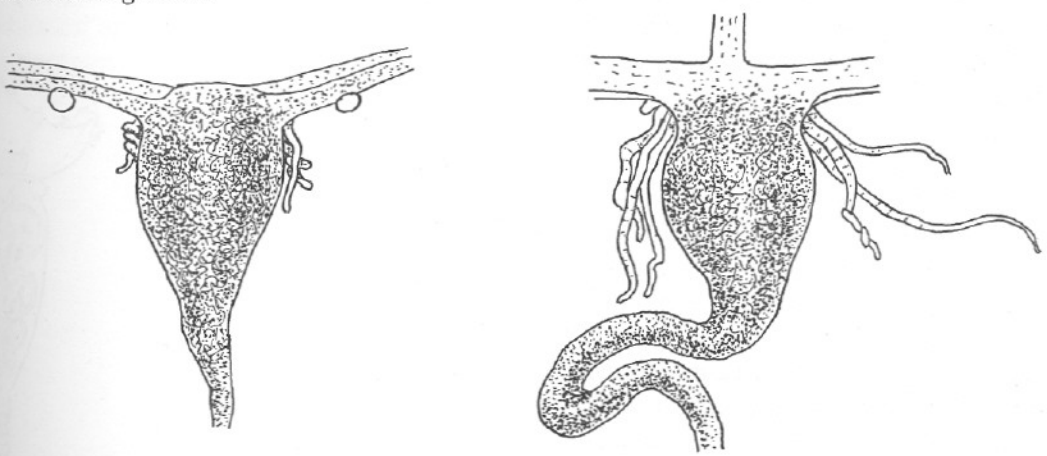
Two days after liberation one rudiment of a lateral cirrus appears on one side only of each of the two non-tentacular marginal bulbs. The medusa is now 0·9 mm. high (Pl. XVII, fig. 4). During the next two days the interradial marginal cirri disappear.

The two non-tentacular marginal bulbs now begin to develop tentacles, so that a second stage is reached with four fully developed marginal tentacles when the medusa is about 1·1 mm. high. At this stage there is usually one lateral cirrus on either side of each tentacle base, although sometimes a cirrus may be present only on one side. The small rudiments of four interradial marginal

* Dr W. J. Rees tells me that he has seen specimens taken in Fahy Bay and off High Island on the west coast of Ireland in collections of the Irish Fishery Board for April and May 1902.

tentacular bulbs, with their lateral cirri, are appearing close to the marginal vesicles. The mouth is still simple. The first signs of the gonads are appearing in the middle of the radial canals slightly nearer the proximal end. At a height of 1·25 mm. additional marginal vesicles may have developed on either side of one of the marginal tentacle bulbs.

The third stage is reached when the medusa is about 3·0–3·5 mm. in diameter. The umbrella is now more hemispherical and the mouth has four distinct lips. At this stage the four interradial marginal tentacles are developing and the rudiments of the eight adradial marginal tentacle bulbs are just beginning to appear in some segments. The gonads are now displaced to a position much nearer the ring canal.



Text-fig. 191. *Lovenella clausa*. Bases of marginal tentacles, lateral cirri and marginal vesicles (concretions not shown); preserved specimen.

The course of development up to this stage is shown in the following table:

Diameter of umbrella (mm.)	Perradial tentacles	Interradial tentacles (t.) or bulbs (b.)	Adradial bulbs	Marginal vesicles
1·0	4	4 b.	.	4
1·0	4	4 b.	.	6
1·5	4	4 b.	.	9
1·5	4	4 b.	3	10
2·0	4	4 b.	8	8
2·5	4	4 b.	.	11
3·0	4	4 t.	3	16
3·5	4	2 t.+2 b.	6	10

Development proceeds fairly regularly until in the adult stage there are eight fully developed perradial and interradial marginal tentacles and eight developing adradial marginal tentacles. Development of the marginal tentacles may go farther until there are twenty-four in all.

The structural details require no special comment, but it should be noted that *Lovenella clausa* may be rather easily confused with *Phialidium hemisphaericum* at first glance. The presence of lateral cirri (Text-fig. 191), however, is at once a decisive character, and when seen side by side the gonads and tentacle bases appear larger and more conspicuous in *Lovenella clausa* than in *Phialidium hemisphaericum*. When alive, the green coloration in the tentacle bases is a very obvious character for discrimination.

NEMATOCYSTS. ? Microbasic mastigophores and atrichous haplonemes (Russell, 1938*b*).

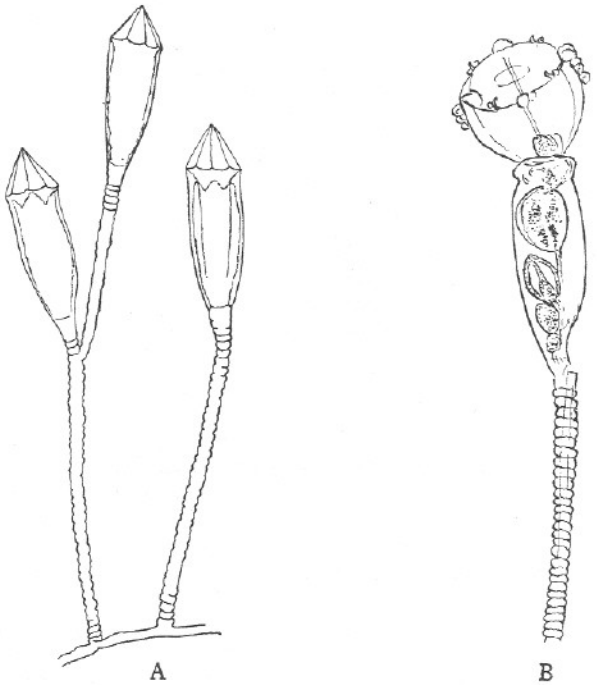
Seasonal occurrence

Lovenella clausa has been recorded in the plankton off Plymouth in the following months, January, April, and June to December, being probably most abundant in the autumn. It has also been recorded in September from Valencia and Co. Dublin; and in summer at Helgoland.

HYDROID. *Lovenella clausa* (Lovén). (Text-fig. 192.)

(For full description see Hincks, 1868, *Brit. Hydroid Zooph.* p. 177, pl. xxxii, fig. 2, and Hincks, 1871, *Ann. Mag. Nat. Hist.* ser. 4, vol. VIII, no. 44, IX, p. 79, pl. v, figs. 2, 2*a*, 2*b*.)

Colonies of single or very sparingly branched hydranths reaching a height of *c.* 10 mm. Hydrocaulus with a few annulations at top and base, with intervening portion slightly crenulated. Hydrothecae very long and slender, tapering off gradually below, with operculum of about eight converging segments. Hydranth colourless; *c.* fifteen tentacles, not webbed at base. Gonothecae borne on rather long annulated pedicels rising from hydrocaulus a short distance below hydrotheca; elongate, tapering from truncate apex to base, sides sometimes slightly sinuous, containing several medusa buds.



Text-fig. 192. *Lovenella clausa*. A, the hydroid (after Hincks, 1868, pl. xxxii, fig. 2); B, liberation of medusa from gonotheca, Plymouth, 10. iii. 36.

Historical

The adult stage of *Lovenella clausa* was first described in detail by Russell (1936*b*) as *Eucheilota hartlaubi*. A figure of this medusa, without a description, had previously been given by Hartlaub (1917), who reared the medusa from its hydroid. The first stage of the medusa immediately after liberation from its hydroid was described by Hincks (1871) under the name of the hydroid *Lovenella clausa*. The hydroid *L. clausa* was named by Hincks (1868) at a meeting of the British Association in 1864 and it was curious that he should have used the same specific name as that given by Lovén (1836) to a hydroid presumed to be this species.

Genus **Eucheilota** McCrady, 1859

MEDUSAE. Lovenellidae with eight marginal vesicles.

HYDROID. Not known.

There is only one British representative of the genus, *Eucheilota maculata* Hartlaub. This medusa is rather easily recognizable by the presence of a large black spot on each of the interradial walls of the stomach, which persists even in preserved material.

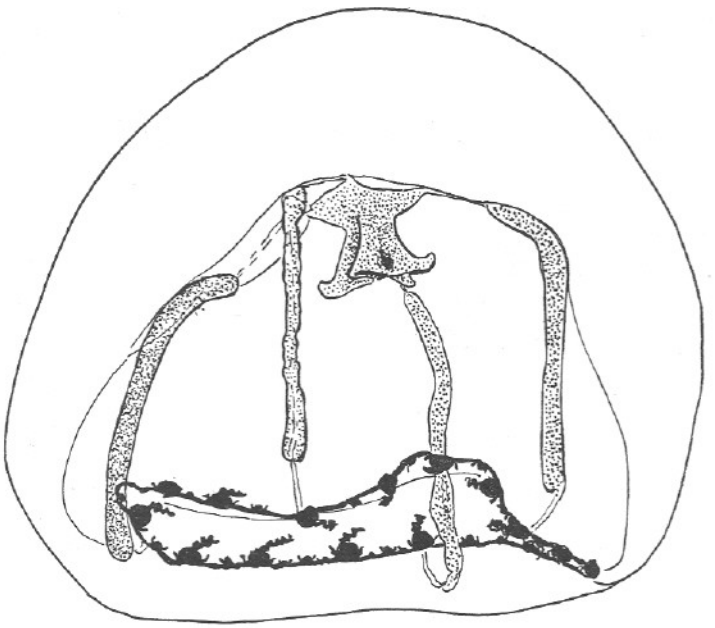
Eucheilota maculata Hartlaub

Text-figs. 193–5

Eucheilota maculata Hartlaub, 1894, *Wiss. Meeresuntersuch.* N.F., Bd. I, Abt. Helgoland, Heft 1, p. 193.
Hartlaub, 1897, ibid. Bd. II, Heft 1, p. 499, pl. xx, figs. 4–8 (fig. 21, young hydroid).
Kramp, 1926*b*, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. LXXXII, p. 244 (young stages).
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 583, fig. 51.
Ranson, 1934*a*, *Bull. Mus. Hist. Nat. Paris*, sér. 2, tome VI, no. 1, p. 68.

Specific Characters

Marginal tentacles sixteen to thirty in number; eight marginal vesicles, each with five to six, or more, concretions; large black spot on each interradius of stomach.



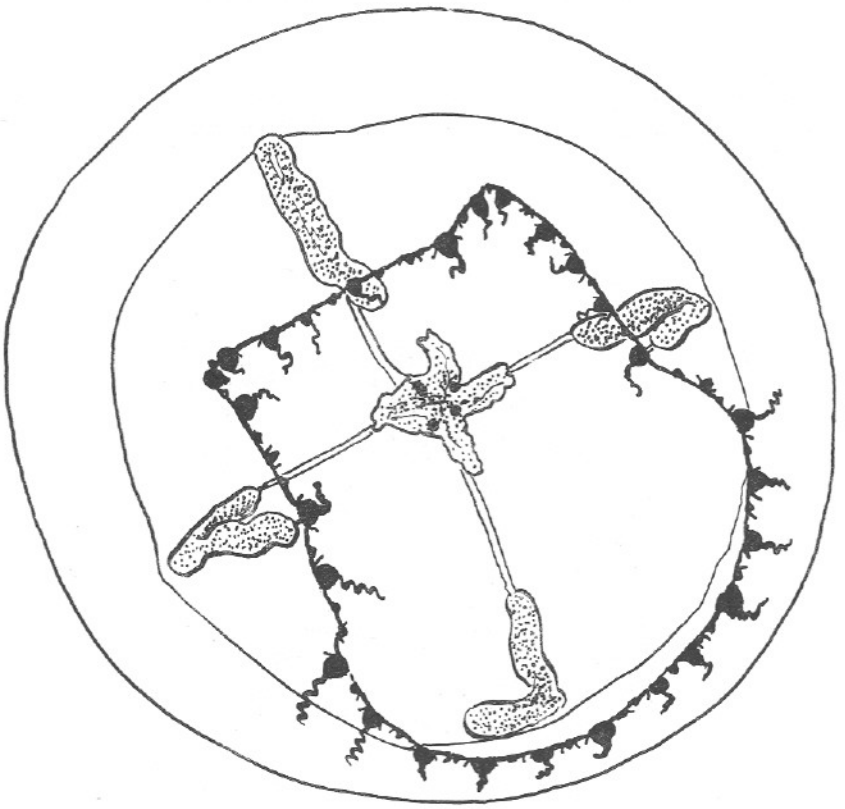
Text-fig. 193. *Eucheilota maculata.* Preserved specimen *c.* 6 mm. in diameter, Hirtshal's Harbour, Denmark. (Sent by P. L. Kramp.)

Description of Adult

Umbrella hemispherical; jelly in apical region thick, considerably thinner at sides. Velum broad. Stomach short, without peduncle; mouth with four wide unfolded lips with narrow rims. Four straight radial canals and ring canal narrow. Gonads on four radial canals, linear, leaving proximal third of radial canal free and not reaching quite to ring canal. Marginal tentacles sixteen to twenty in number, occasionally up to thirty, with large elongated conical bases. One to three rudimentary marginal bulbs between adjacent marginal tentacles. Spiral lateral cirri, one on each side of marginal tentacle bases and rudimentary marginal bulbs. Eight closed marginal vesicles, each with five to six, at most ten, concretions. Diameter of umbrella 13 mm.; height 10 mm. Colour of marginal tentacle bases and gonads bright reddish brown; one large black spot on each interradius of stomach.

Distribution

Eucheilota maculata has only been found off British coasts near Dover and at Southend. Its distribution is apparently somewhat limited to the southern half of the North Sea, for it has only been recorded from the Belgian coast, Helgoland, the Jutland coast, and the Kattegat. It is thus likely to occur off the south-eastern coasts of the British Isles in the North Sea and in the extreme eastern part of the English Channel.



Text-fig. 194. *Eucheilota maculata*. Preserved specimen *c.* 11 mm. in diameter, Helgoland, 1. iii. 01. (E. T. Browne collection.)

Developmental Stages and Structural Details

The hydroid of *Eucheilota maculata* is not yet known for certain and therefore the medusa has not been described when newly liberated from its hydroid. Kramp (1926*b*) has, however, described very early stages from the plankton, which must have been not long liberated from hydroids (see below, under 'Hydroid'). The smallest specimen had a diameter of *c.* 1 mm., and the umbrella was hemispherical. There were two large opposite perradial marginal tentacles, each flanked by one cirrus on either side; two opposite perradial marginal rudiments of tentacles, each with one lateral cirrus on one side only; and four tiny rudiments of interradial marginal tentacles, each with a rudiment of one lateral cirrus. There were no traces of gonads visible.

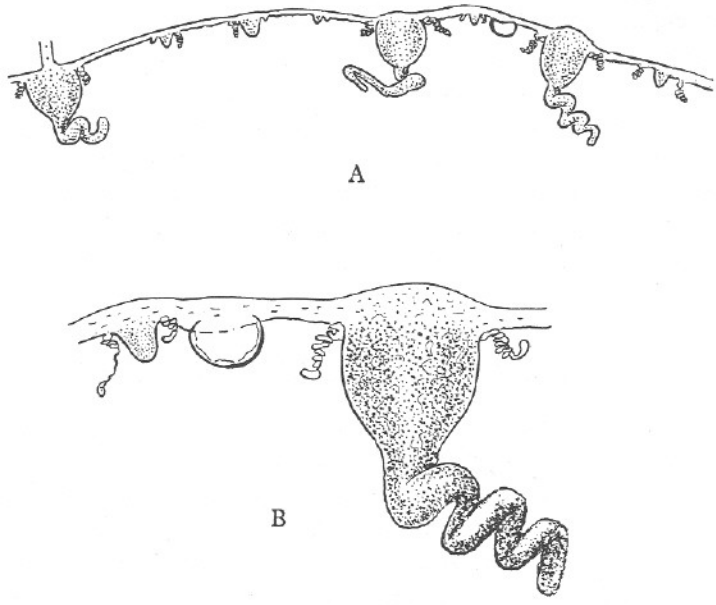
Kramp gives the following course of development for slightly later stages.

Diameter 1·0–1·2 mm.; two fully developed perradial marginal tentacles and two large perradial marginal bulbs, each with one lateral cirrus on either side; four very small rudiments of interradial marginal tentacles, each with one cirrus on one side only.

Diameter 1·5 mm.; four perradial marginal tentacles, each with one lateral cirrus on either side; four interradial marginal bulbs, each with one cirrus on one side only.

Diameter 2·5 mm.; eight marginal tentacles, each with one lateral cirrus on either side; eight very small adradial rudiments of marginal tentacles, each with one cirrus on one side and rudiments of one cirrus on the other side, except the two smallest which had no signs of cirri.

The gonads first appear in specimens 1·2–1·5 mm. in diameter, in the middle of the radial canals, as distinct, but small, spherical masses. When the medusa has a diameter of 2·5 mm. the



Text-fig. 195. *Eucheilota maculata*. Preserved. A, portion of umbrella margin; B, marginal tentacle, cirri, and marginal vesicle (without concretions).

gonads are oval and carried outwards so as to lie a distance of one-third of the length of the radial canal from the umbrella margin. Apstein (1913) states that the youngest egg cells are found in the endoderm; later they are surrounded by the mesogloea.

The four large black spots placed interradially on the walls of the stomach are a diagnostic character of this species, and they persist after preservation.

Seasonal occurrence

The only month that *Eucheilota maculata* has been recorded off British coasts is August, near Dover.

In the southern North Sea the species usually occurs in the plankton in late summer and autumn.

Hydroid. Not known.

Hartlaub (1897) reared small '*Campanulina*'-like hydroids from *Eucheilota maculata* medusae, which he identified with *Campanulina hincksii*, a hydroid he described for the first time in the

same publication. Kramp (1926*b*), however, has shown that the first stages of the medusa *Eucheilota maculata* have only two marginal tentacles, whereas Hartlaub obtained a medusa with four marginal tentacles from *Campanulina hincksii*. On these grounds it therefore seems that Hartlaub was mistaken in linking *Eucheilota maculata* with *Campanulina hincksii*, unless Kramp's specimens were really young *Lovenella clausa*.

Historical

Eucheilota maculata was first described by Hartlaub (1894, 1897) from specimens obtained at Helgoland. Unfortunately Hartlaub did not state the number of marginal vesicles, although, since he quotes McCrady's genus *Eucheilota* as having eight, his species presumably also had eight. The species is easily recognizable by the black spots on the stomach wall and it is now known that there are only eight marginal vesicles. Mayer (1910), evidently misconstruing Hartlaub's figure, says that the marginal vesicles alternate with the marginal tentacles, and this error was carried forward by Kramp (1933*b*). Ranson (1934*a*) has suggested that *E. maculata* is the same species as the American *E. ventricularis* McCrady. The gonad development is, however, quite different in the two species. In *E. maculata* they first appear when the medusa is only 1·2–1·5 mm. in diameter (Kramp, 1926*b*), while in *E. ventricularis* they do not appear until the medusa is quite large (Mayer, 1910). *E. ventricularis*, also, lacks the black spots on the stomach. The very restricted area of distribution of *E. maculata* is also in favour of its being a distinct species.

Family PHIALELLIDAE

Leptomedusae with small stomach; without peduncle; with four simple radial canals; without excretory pores; with gonads on radial canals separated from stomach; with hollow marginal tentacles; without marginal or lateral cirri; with closed marginal vesicles; without ocelli.

HYDROID. Where known, branched colonies; with single whorl of filiform tentacles, without webs between their bases; with hydrotheca with operculum (see Rees, 1939*b*).

In their characters the medusae of the Phialellidae resemble those of the subfamily Campanularinae of the Campanulariidae, but they differ in having a hydroid with a hydrotheca with an operculum. They are separable from the Lovenellidae by the absence of cirri, from the Eirenidae and Eutimidae by the absence of a peduncle, and from the Aequoreidae in having only four radial canals.

The Phialellidae are represented in British waters by one genus, *Phialella* Browne, the only genus of the family.

Genus **Phialella** Browne, 1902

MEDUSAE. Phialellidae with eight adradial marginal vesicles.

HYDROID. *Phialella*.

There is one British species of the genus, *Phialella quadrata* (Forbes). It is at first sight rather liable to be confused with *Phialidium hemisphaericum*. The fixed number of eight marginal vesicles each with two or more concretions is, however, a diagnostic character. The species differs also in having rather thicker jelly, and also in having gonads with median furrows.

The hydroid of this medusa is quite well known under the name *Campanulina repens*. It was shown by Rees (1939*b*) that this hydroid was no true '*Campanulina*', and the same author has shown that the old generic name *Eucope* can no longer stand for the medusa.

Phialella quadrata (Forbes)

Plate XVI, figs. 4–6; Plate XVII, fig. 5; Text-figs. 196–200

Thaumantias quadrata Forbes, 1848, *Monogr. Brit. Medusae*, p. 43, pl. ix, fig. 2.
Thaumantias aeronautica Forbes, 1848, ibid. p. 44, pl. ix, fig. 3.
Thaumantias octona Forbes, 1848, ibid. p. 44, pl. viii, fig. 4.
Thaumantias maculata Forbes, 1848, ibid. p. 45, pl. ix, fig. 4.
Thaumantias globosa Forbes, 1848, ibid. p. 46, pl. x, fig. 4.
?*Thaumantias neglecta* Green, 1857, *Nat. Hist. Rev.* vol. IV, p. 26, pl. iv, fig. 4.
Thaumantias achroa Cobbold, 1858, *Quart. Journ. Micr. Sci.* vol. VI, p. 1, pl. i.
Thaumantias cymbaloides Van Beneden, 1866, *Mém. Acad. R. Belg.* vol. XXXVI, p. 88.
Campanulina repens Hincks, 1868, *Brit. Hydroid Zooph.* p. 189, pl. xxxviii, figs. 1, 1*a* (hydroid and young medusa).
Tetranema aeronauticum, Haeckel, 1879, *System der Medusen*, p. 125.
Eucopium quadratum, Haeckel, 1879, ibid. p. 169.
Eucope octona, Haeckel, 1879, ibid. p. 171.
Epenthesis cymbaloidea, Haeckel, 1879, ibid. p. 183 (in part).
Epenthesis maculata, Haeckel, 1879, ibid. p. 183.
Phialidium cymbaloideum, Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 491, pl. xvii, figs. 1, 2.
Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. V, p. 724.
Browne, 1905*a*, *Proc. Roy. Soc. Edinb.* vol. XXV, pt. ix, p. 771.
Phialella cymbaloidea, Browne, 1902, *Ann. Mag. Nat. Hist.* ser. 7, vol. IX, p. 282.
Eucope globosa, Mayer, 1910, *Medusae of the World*, vol. II, p. 235.
Eucope quadrata, Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 576, figs. 40, 41.
Phialella quadrata, Rees, 1939*b*, *Ann. Mag. Nat. Hist.* ser. 11, vol. III, p. 441.

Specific Characters

Elongated oval gonads on distal third of radial canals; sixteen to thirty-two marginal tentacles.

Description of Adult

Umbrella nearly hemispherical; jelly fairly thick. Velum well developed. Stomach short, quadratic, with small base; no peduncle. Mouth with four short lips with slightly folded margins. Four straight radial canals and ring canal narrow. Gonads on four radial canals, elongated oval, with median groove, situated on distal third of radial canal, not reaching ring canal. Sixteen to thirty-two hollow marginal tentacles, smooth, with globular bases. No ocelli. No marginal nor lateral cirri. Eight adradial marginal vesicles, closed, each with two to eight concretions, usually three to four. Diameter of umbrella up to 13 mm. Colour of stomach and marginal tentacle bases reddish yellow or reddish brown (? sometimes black—Forbes, 1848, *maculata*); gonads yellowish; many specimens have four black spots at base of stomach, one in each interradius.

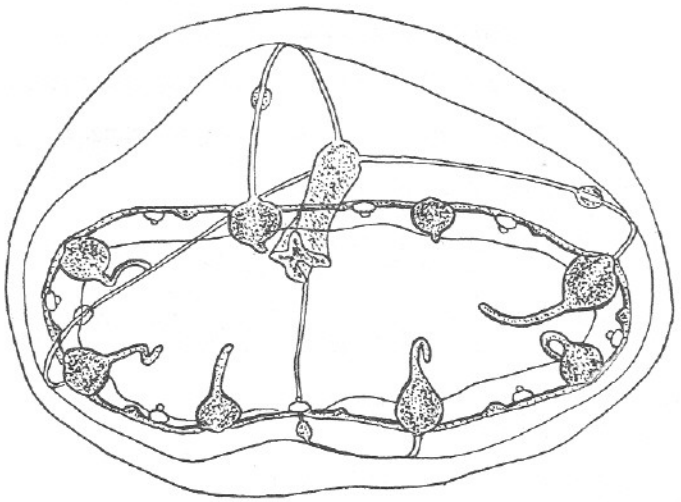
Distribution

Phialella quadrata occurs commonly round the British Isles, from the western half of the English Channel, along the western coasts, down to St Andrews on the east coast of Scotland, including the Hebrides, Orkneys and Shetlands. It does not appear to have been recorded on the east coast of England or in the eastern half of the English Channel.

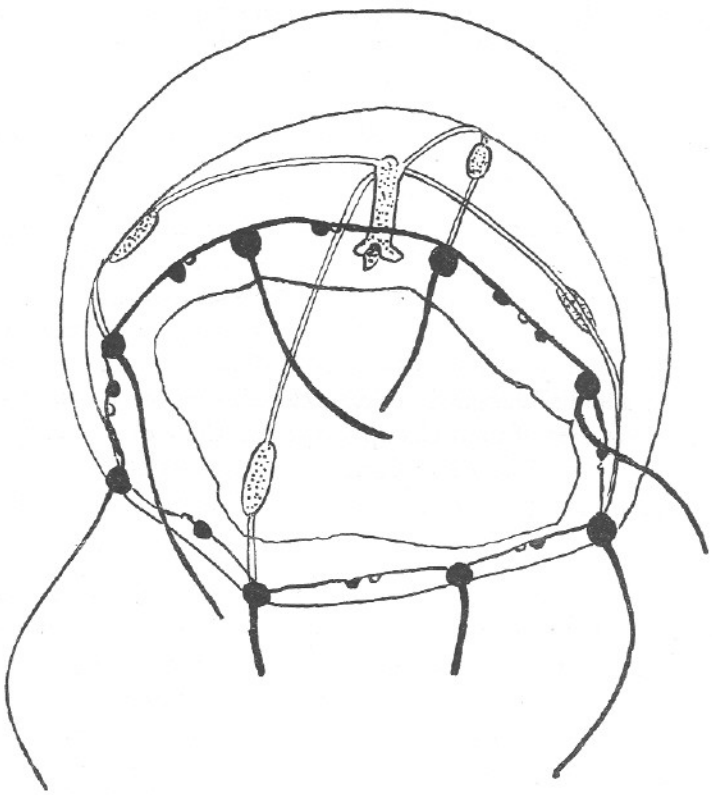
Elsewhere it has only been recorded from Ostende.* (But see footnote on p. 320.)

Its distribution as far as is yet known thus appears to be somewhat peculiar, since at times it is exceedingly abundant where it is found. The fact that it has been recorded from Ostend, however, suggests that it might occur on the remaining coasts of England.

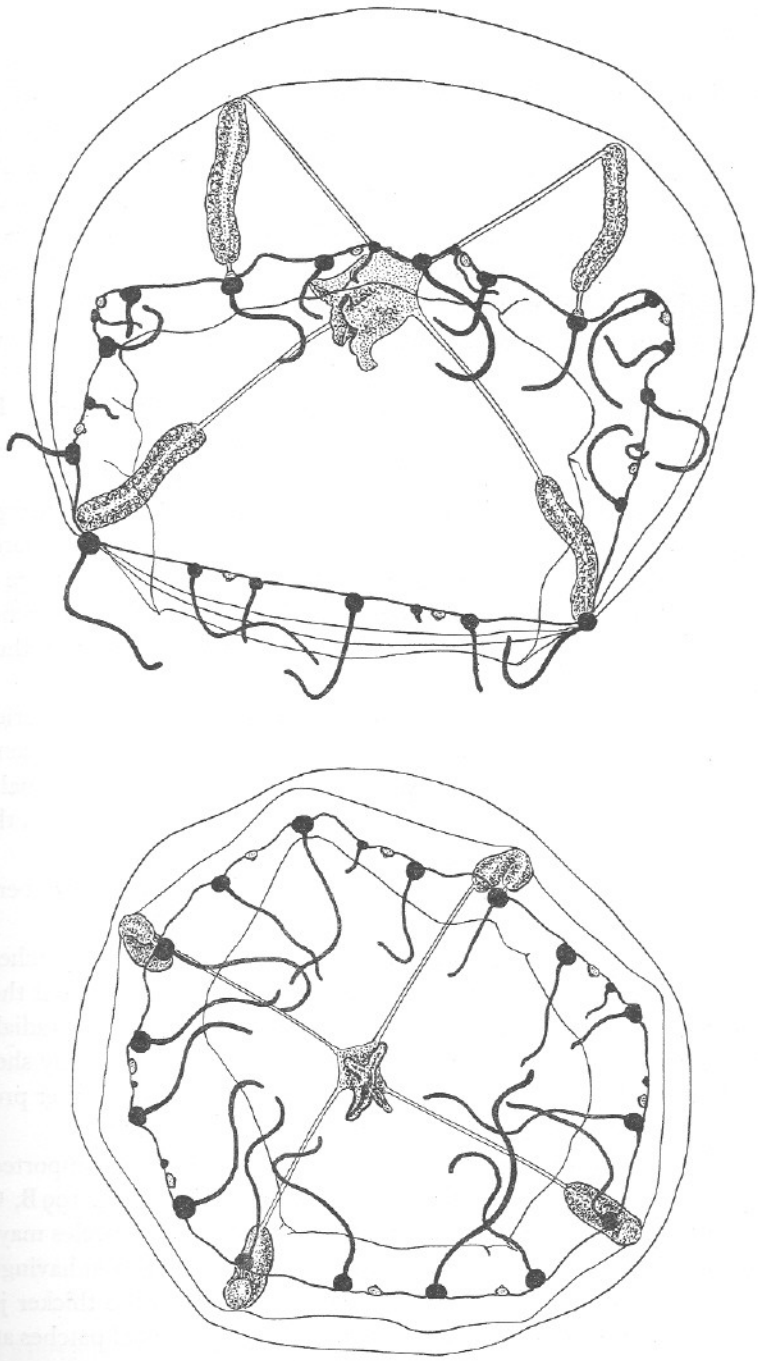
* Künne (1937*b*) records it erroneously from the Baltic (see Kramp, 1947, p. 52).



Text-fig. 196. *Phialella quadrata*. Preserved specimen 1·7 mm. in diameter, Plymouth, 18. iv. 35.



Text-fig. 197. *Phialella quadrata*. Preserved specimen 3·8 mm. in diameter.



Text-fig. 198. *Phialella quadrata*. Preserved specimens from the well of the fishing vessel, M.V. *Lutin*, Newlyn, Cornwall, 28. v. 37. (Collected by G. A. Steven.) Above, *c.* 9 mm. in diameter; below, *c.* 6 mm. in diameter.

Developmental Stages and Structural Details

The medusa, when first liberated from its hydroid, is about 1·5 mm. high and 1 mm. wide. It is thus about twice the size of the newly liberated medusa of *Phialidium hemisphaericum*. The umbrella is bell-shaped. The jelly is rather thick. There may be traces of an umbilical canal. There are scattered nematocysts on the exumbrella. The velum is broad. The stomach is short and the mouth has four small lips. The four radial canals and ring canal are narrow. The four gonads are apparent as small oval swellings situated at about the middle of each radial canal. There are four perradial marginal tentacles and the rudiments of four interradial marginal bulbs. There are eight adradial marginal vesicles, each with two to three concretions. The colour of the marginal tentacle bases and developing marginal bulbs is yellowish or reddish brown.

The development of the medusa has been described by Browne (1896*a*). Development is fairly regular and three stages may be distinguished before the final stage is reached (Pl. XVII, fig. 5; Pl. XVI, fig. 4).

The *first stage* is that described above, in which there are four perradial marginal tentacles.

The *second stage* has eight marginal tentacles. The umbrella has become more flattened, and is about 3 mm. in diameter. The four interradial marginal bulbs of the first stage have developed tentacles, bringing the total number up to eight. A few adradial marginal bulbs are beginning to appear. The marginal vesicles still contain usually two or three concretions, though sometimes four may be present.

The *third stage* has sixteen marginal tentacles. The umbrella is more hemispherical and 4–5 mm. in diameter. The adradial marginal tentacles, which bring the total up to sixteen, develop in no definite order, and when they have nearly reached their full size other marginal bulbs begin to grow. The gonads may now be fully developed and form elongated swellings on the radial canals. Each marginal vesicle contains two to four concretions.

With further development the marginal tentacles may increase in number up to thirty-two in all.

The gonads (Text-fig. 199A), which in the earliest stages form small oval patches about halfway along each radial canal, become removed outwards as the umbrella grows, but they do not reach the ring canal. A fully developed gonad is about one-third the length of a radial canal.

The numbers of concretions in the marginal vesicles (Text-fig. 199C) may show considerable variation in a single individual. Three or four appears to be the usual number present, but there may sometimes be more. Browne records a specimen with five to eight.

The appearance of the marginal vesicle is rather characteristic; it is supported at its base on a cushion-like swelling of cells from the wall of the ring canal (Text-fig. 199B, C).

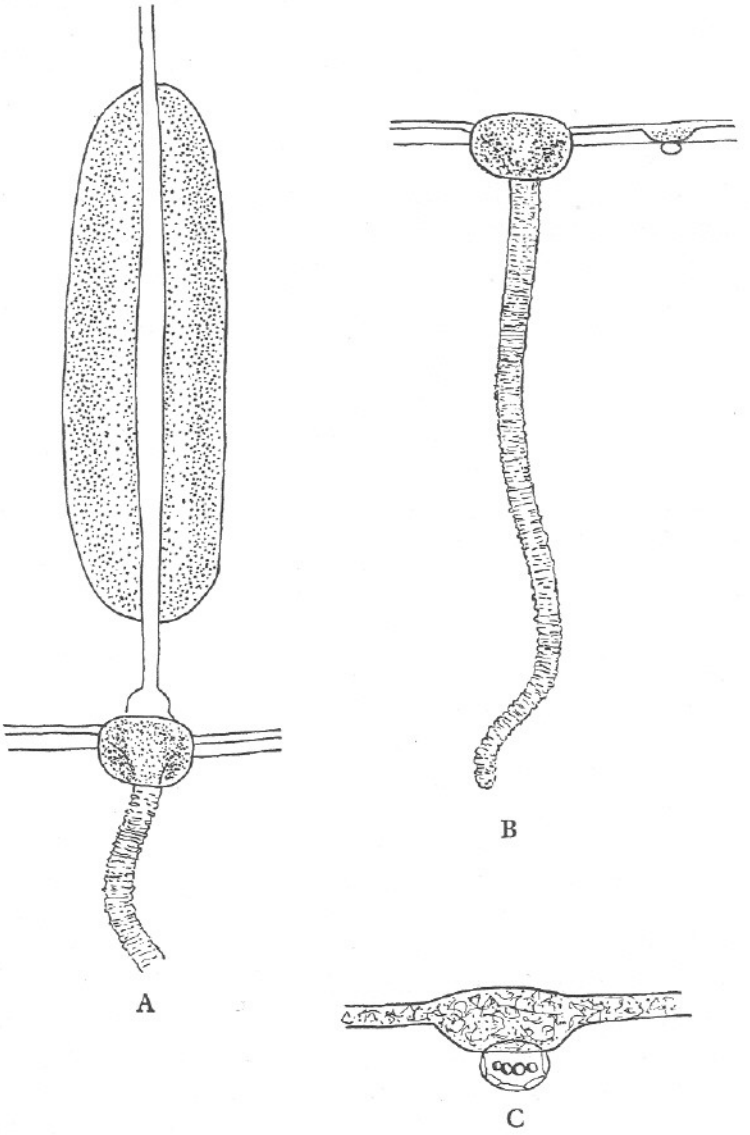
The remaining structures of the medusa require no comment. The species may at first be confused with *Phialidium hemisphaericum*. It differs from this latter species in having a fixed number of eight marginal vesicles, each with more than one concretion, in the thicker jelly of the umbrella, and in many specimens in the presence of the blackish interradial patches at the base of the stomach.

In July 1900 Mr Browne found an abnormal specimen from Salcombe which had two small manubria on an outgrowth from one of the radial canals between the gonad and the margin; apparently the mouths were open and with lips.

NEMATOCYSTS. ? Microbasic mastigophores and basitrichous haplonemes (Russell, 1938*b*).

Seasonal occurrence

The medusa *Phialella quadrata* is probably likely to be found in any month in the year. It has, for instance, been recorded from Valencia during the months January to November, and at



Text-fig. 199. *Phialella quadrata*. Preserved. A, male gonad; B, marginal tentacle and marginal vesicle; C, marginal vesicle (without concretions).

Plymouth from March to October. It is, however, most abundant between April and September, when it may occur in great numbers at times.

Habits

Considering its prolonged period of occurrence in the plankton it is likely that *Phialella quadrata* passes through at least two generations during the year.

I have noticed that when alive this species can be distinguished from *Phialidium hemisphaericum* not only by its thicker jelly, but also by its more rapid pulsations with their intermittent periods of rest.

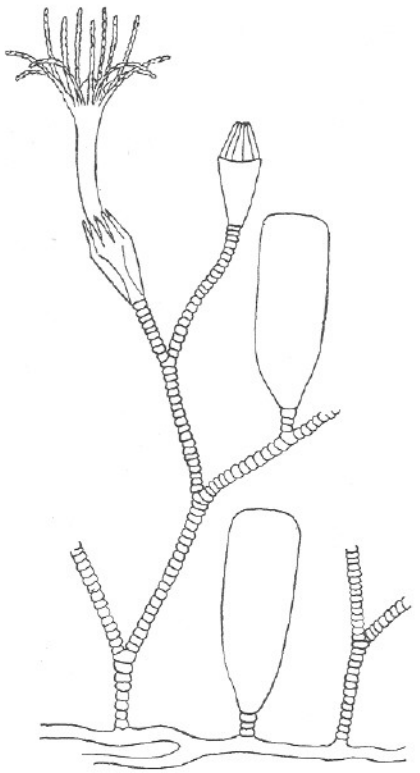
Specimens are sometimes found with the young stages of the anemone *Halcampa* attached to the manubrium (M. & C. Delap, 1905).

Large numbers of medusae found by Mr G. A. Steven in the well of a boat at Newlyn, Cornwall, proved to be this species.

HYDROID. *Phialella quadrata* (previously known as *Campanulina repens*, see Rees, 1939*b*). (Text-fig. 200.)

(For full description see Allman, 1864*b*, *Ann. Mag. Nat. Hist.* ser. 3, vol. XIV, p. 61, and Hincks, 1868, *Brit. Hydroid Zooph.* p. 189, pl. xxxviii, fig. 1.)

Colonies of simple or alternately branched hydranths rising from a creeping stolon. Hydrocaulus distinctly annulated. Hydrothecae conical, closed by a membranous operculum formed of deep and acute convergent segments. Hydranth very extensile, with *c.* sixteen filiform tentacles in one whorl.* Gonothecae large, obconic, rising from creeping stolon, or occasionally from hydrocaulus on short annulated stems.



Text-fig. 200. *Campanulina repens*, the hydroid of *Phialella quadrata*. (After Hincks, 1868, pl. xxxviii, fig. 1.)

Historical

Phialella quadrata was first described by Forbes (1848) as *Thaumantias quadrata*. This represented the first stage of this medusa, and Forbes described later stages as different species. Although Forbes did not mention the marginal vesicles, there can be little doubt as to the identity of his species. The characteristics of the thickened jelly and the black spots at the base of the stomach are confirmatory evidence. The first accurate and detailed description of the species was given by Cobbold (1858) under the name *Thaumantias achroa*. Browne (1896*a*) adopted Van Beneden's name of *cymbaloides* as being the first really identifiable description. Apparently he did not know of Cobbold's description at that time. Rather than introduce the new name *achroa* I have retained Forbes's *quadrata*, since Mayer and Kramp are both in agreement as to Forbes's species, and Browne (1905*a*) and Rees (1939*b*) were also of the same opinion.

A very nearly related species, if not the same, has been described by Uchida (1938*c*) as *Eucope fragilis*, from Japan.†

* Allman (1864*b*) states that the tentacles 'are united at their base by a very shallow web'. Later observations have not confirmed this.

† I have recently seen specimens of *Phialella quadrata* collected in February 1952 by Dr Elizabeth J. Batham from Otago harbour, New Zealand.

FAMILY EIRENIDAE

Leptomedusae with small stomach; with small or well-developed peduncle; with four or six radial canals; with or without excretory pores; with gonads on radial canals separated from stomach; with hollow marginal tentacles; with or without lateral or marginal cirri; with closed marginal vesicles; without ocelli.

HYDROID. Where known, with single whorl of filiform tentacles, with webs between their bases; with hydrotheca with operculum.

The Eirenidae are separable from the Campanulariidae, the Lovenellidae, and the Phialellidae by the presence of a peduncle, and from the Aequoreidae in having only four or six radial canals. In their family characters, however, the Eirenidae resemble the Eutimidae, but they differ in the form of the hydroid, since in those species of the Eutimidae in which the hydroid is known for certain there is no operculum and the polyp is not fully retractile into the hydrotheca.

The Eirenidae are represented in British waters by three genera, *Eirene* Eschscholtz, *Helgicirrha* Hartlaub, and *Phialopsis* Torrey. Of these genera the first two were revised by Kramp (1936). The true position of *Phialopsis* is uncertain, but it is convenient to place it in this family until its hydroid is known. In general appearance it resembles other medusae in the family but differs in the absence of excretory pores, and it is not certain what classificatory value such pores should be regarded as having.

The three genera are distinguishable on the following characters:

With excretory pores:
- Without lateral or marginal cirri . . . . . **Eirene**
- With lateral cirri . . . . . **Helgicirrha**

Without excretory pores; with marginal cirri . . . . **Phialopsis**

Genus **Eirene** Eschscholtz, 1829

MEDUSAE. Eirenidae with four or six radial canals; with excretory pores; without lateral or marginal cirri.

HYDROID. Where known, *Eirene*, with characters as family.

There is one British species of the genus, *Eirene viridula* (Péron & Lesueur). It is quite a characteristic medusa but is liable to be confused at first sight with either *Phialopsis diegensis* or *Helgicirrha schulzei*. Apart from the differentiating characters given above for the genera the very long pointed lips of *Eirene* are rather characteristic (Text-fig. 205).

The hydroid of *E. viridula* is not yet known. The hydroid of a foreign species, *E. ceylonensis* Browne, has, however, been described by Annandale & Lloyd (1916, see also Rees, 1939*b*, p. 443).

Eirene viridula (Péron & Lesueur)

Plate XX, figs. 3, 4; Text-figs. 201–5

Oceania viridula Péron & Lesueur, 1809, *Ann. Mus. Hist. Nat. Paris*, tome XIV, p. 346.
Dianaea viridula, Lamarck, 1817, *Animaux sans Vertèbres*, p. 506.
Eirene viridula, Eschscholtz, 1829, *System der Acalephen*, p. 94.
L. Agassiz, 1862, *Contrib. Nat. Hist. U.S.* p. 362.
Mayer, 1910, *Medusae of the World*, vol. II, p. 311 (in part: *non* fig. 172).
Künne, 1934, *Zool. Anz. Leipzig*, Bd. CVI, p. 30, fig. 2.
Kramp, 1936, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. XCIX, p. 244.

EIRENIDAE

Geryonia pellucida Will, 1844, *Horae tergestinae*, p. 70, pl. ii, figs. viii–xii.
Geryonopsis delicatula Forbes, 1848, *Monogr. Brit. Medusae*, p. 39, pl. ix, fig. 1 (as *Thaumantias cymbaloidea*).
Geryonopsis pellucida, Forbes, 1848, ibid. p. 40.
Tima pellucida, Gegenbaur, 1856, *Z. Wiss. Zool. Leipzig*, Bd. VIII, p. 253.
Irene pellucida, Haeckel, 1879, *System der Medusen*, p. 201 (in part); pl. xii, figs. 1, 2.
Neppi, 1910, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. XVIII, p. 165, figs. 1, 1*a*.
Irene viridula, Haeckel, 1879, *System der Medusen*, p. 202 (in part).
Hartlaub, 1909*a*, *Zool. Anz. Leipzig*, Bd. XXXIV, p. 86, fn.
Irene (*Tima*) *pellucida*, Claus, 1881*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. IV, Heft 1, p. 102, pl. iii, figs. 21–30.
Tima willi Neppi, 1909, *Arch. Entw. Mech. Org. Leipzig*, Bd. XXVIII, Heft 2/3, p. 368, figs. 3, 4, 7, 8, 12, 13, 15, 16, 18–25, 28–45, 47.
Phortis gibbosa, Ranson, 1926, *Bull. Mus. Hist. nat. Paris*, tome XXXII, p. 298.
Phortis pellucida, Ranson, 1934*b*, ibid. sér. 2, tome VI, p. 182.
Eirene pellucida, Kramp, 1936, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. XCIX, p. 244.

Specific Characters

Up to seventy or more marginal tentacles of rather unequal size; fifty or more marginal vesicles each with one to four concretions.

Description of Adult

Umbrella hemispherical; jelly in upper portion of umbrella moderately or very thick, thin at sides of umbrella. Velum narrow. Stomach short, situated on elongated conical peduncle, extending beyond umbrella margin, with four perradial basal projections at entrance of each radial canal. Mouth with four long pointed perradial lips with crenulated margins. Four straight radial canals and ring canal narrow. Excretory pores present, situated on large papillae projecting into subumbrellar cavity and leading from ring canal opposite base of each marginal tentacle. Gonads on radial canals limited to disk of subumbrella, not extending on to peduncle, reaching from near base of peduncle almost to ring canal, straight or very slightly sinuous, completely surrounding lower wall of radial canal without median furrow. Up to seventy or more marginal tentacles of rather unequal sizes, with conical bases. No lateral nor marginal cirri. Closed marginal vesicles up to fifty or more in number, each with one to four concretions. Diameter of umbrella up to 20–30 mm., or even larger. Colourless, except for greenish tinge in stomach.

Distribution

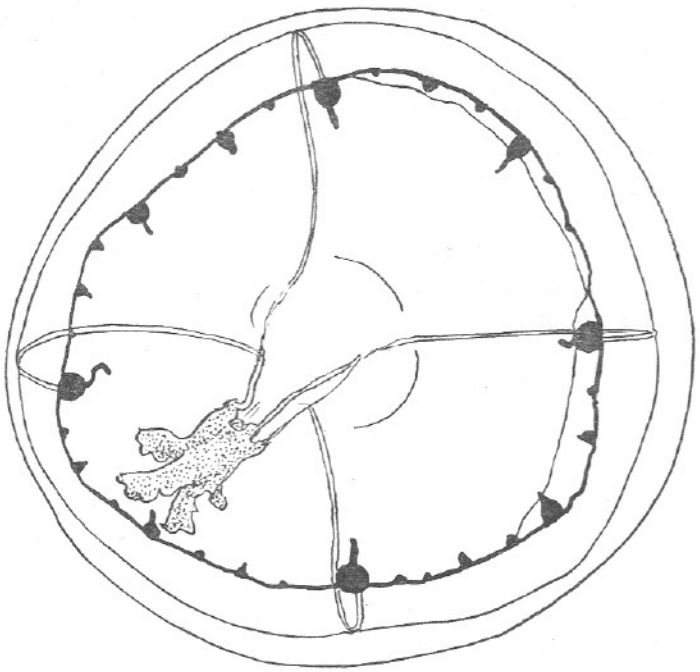
Round the British coasts *Eirene viridula* has been recorded from Plymouth, the coast of Dorset, the Dover Straits, the Firth of Clyde and the Dublin coast. It occurs abundantly in some years at the western end of the English Channel, and has been recorded in the southern North Sea, at Helgoland, and off the west coast of Jutland.

It is a common species in the Mediterranean and apparently occurs off east and west Africa.

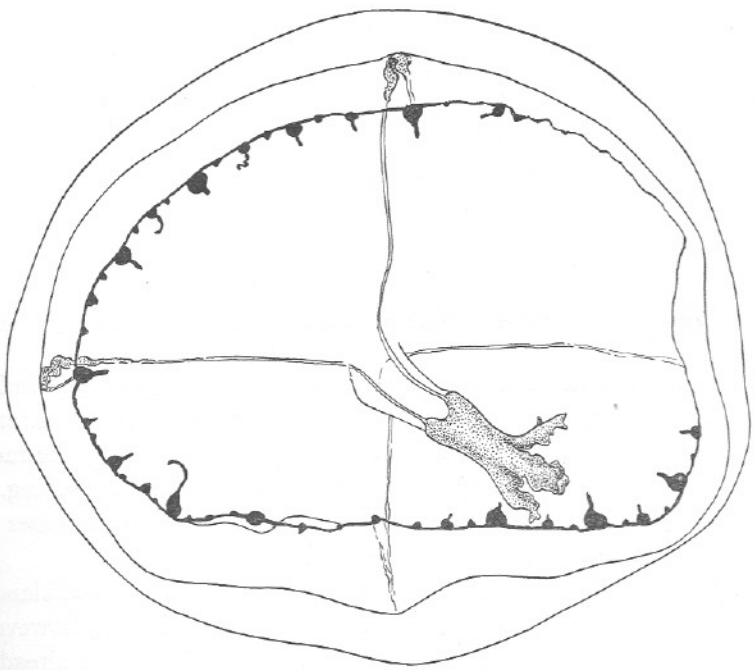
Developmental Stages and Structural Details

The first stage of *Eirene viridula*, immediately after liberation from the hydroid, has not been observed, neither is its hydroid known. The sequence of development from quite small stages upwards has, however, been described by Claus (1881*a*) from specimens in the plankton in the Adriatic.

The development of the medusa in our own waters has not yet been described, and there are certain minor differences between the Mediterranean form and that of northern waters, which have been regarded as specific. In spite of this it is worth recording Claus's observations here



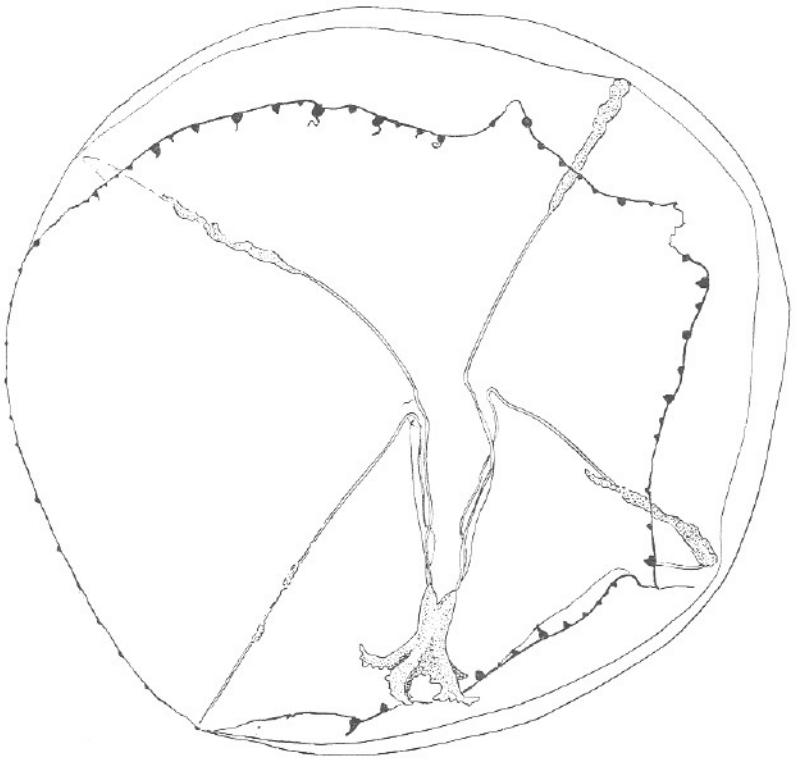
Text-fig. 201. *Eirene viridula*. Preserved specimen *c*. 4·5 mm. in diameter, Start Bay, 27. vii. 98. (E. T. Browne collection.)



Text-fig. 202. *Eirene viridula*. Preserved specimen *c*. 6·5 mm. in diameter, Start Bay, 27. vii. 98. (E. T. Browne collection.)

because they can obviously only differ in small details from those which may be found in the future in our own waters.

The youngest specimens were 1·5 mm. high and wide. The umbrella is bell-shaped and the jelly moderately thick. The stomach is short, but there is no peduncle. The mouth has four distinct short lips. The four radial canals and ring canal are narrow. The gonads are not yet visible. There are four perradial marginal tentacles with rounded bases; but there are no signs of developing interradial tentacular marginal bulbs. There are eight marginal vesicles, one on either side of each marginal tentacle, each with one concretion. There is brown pigment in the endoderm of the bases of the marginal tentacles, and also at the base of the stomach and extending interradially as far as the mouth.



Text-fig. 203. *Eirene viridula*. Preserved specimen *c.* 20 mm. in diameter, Plymouth, 27. ix. 38.

When the medusa has reached a diameter of 2·0–2·5 mm. the peduncle is indicated as a lens-shaped thickening at the base of the stomach. The gonads may sometimes already be apparent in medusae as small as this as four elongated thickenings on the walls of the radial canals. The first rudiments of the four interradial tentacular marginal bulbs are appearing. There are still eight marginal vesicles, but they are now situated a little farther from the bases of the perradial marginal tentacles, and some contain two concretions.

It is evident that in its earliest stages *E. viridula* bears a very close resemblance to *Phialidium hemisphaericum* immediately after liberation from its hydroid. It differs, however, in having no indications of gonads nor of interradial tentacular marginal bulbs. It is already differentiated at a size of 2·0–2·5 mm. by having a small peduncle. And if the gonads are already appearing they are more elongated and more proximally placed than in *Phialidium*.

At a diameter of 2·5–3·0 mm. the apical jelly of the umbrella is thick and the subumbrellar cavity is somewhat flatter. The peduncle is quite distinct. The interradial marginal bulbs are still without tentacles, but eight adradial marginal bulbs are just appearing. An additional marginal vesicle develops on one side of each interradial marginal bulb. The degree of development of the adradial marginal bulbs and the additional marginal vesicles is somewhat irregular in the different quadrants. In some marginal vesicles the number of concretions has increased to three.

The gonads usually appear as elongated thickenings on the radial canals when the medusa is 3·5–4·0 mm. in diameter. The four interradial marginal tentacles are now forming and are conspicuous when the medusa is 4·5–5·0 mm. in diameter. There are now four marginal vesicles in each quadrant, one on either side of each of the four perradial and four interradial marginal tentacles. By the time the medusa is 5 mm. in diameter the eight adradial tentacular marginal bulbs are well formed and an additional marginal vesicle has developed immediately adradially to each perradial marginal tentacle.

At a diameter of 5–6 mm. the apical jelly is thick and domed and the peduncle is well formed. The mouth-lips are much elongated, and extend just beyond the umbrella margin. There are four long perradial and four shorter interradial marginal tentacles and ten to twelve developing tentacular marginal bulbs. There are twenty-four to thirty-two marginal vesicles whose distribution is now becoming irregular.

At a diameter of 7–8 mm. there are eight long marginal tentacles and eight shorter marginal tentacles, and there are two developing marginal bulbs between every two marginal tentacles, one larger and one smaller. A new marginal vesicle develops at the side of each perradial marginal tentacle so that there are five vesicles in each octant, three of which are in one half and two in the other.

This sequence of development can be summarized as follows:

Diameter of umbrella (mm.)	No. of marginal tentacles			No. of developing marginal bulbs	Total marginal tentacles plus (bulbs)	No. of marginal vesicles
	Perradial	Interradial	Adradial			
1·5	4	·	·	·	4+ (0)	8
2·0–2·5	4	·	·	4	4+ (4)	8
2·5–3·0	4	·	·	12	4+(12)	12
3·5–4·0	4	4	·	8	8+ (8)	16
4·5–5·0	4	4	·	24	8+(24)	20
5·0–6·0	4	4	·	24	8+(24)	24–32
7·0–8·0	4	4	8	32	16+(32)	40

Small specimens I have seen at Plymouth, down to 3 mm. in diameter, appear to agree in essentials with these descriptions given by Claus. The only possible difference is that the marginal bulbs seem to develop their tentacles a little quicker than is indicated by Claus; but it is often rather an arbitrary decision at what degree of development a marginal bulb becomes a tentacle.

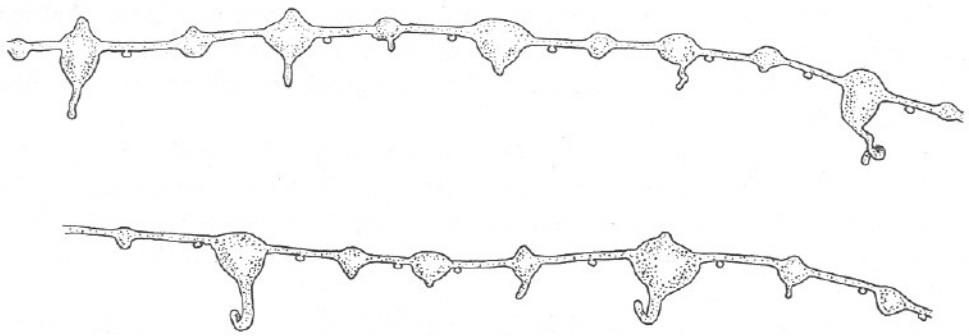
According to Claus the excretory pores appear very early in the course of development.

As in so many medusae, it is probable that there is an alternative sequence of development for the marginal tentacles for I have a drawing of a specimen (Pl. XX, fig. 4) in which quite obviously two interradial marginal tentacles developed simultaneously in each quadrant. This would lead to an increase in number of marginal tentacles according to the formula 4+8+12 instead of 4+4+8.

In the adult medusa the sides of the umbrella are thin and fairly sharply demarcated from the thick upper jelly. The thickness of this jelly is somewhat variable, as is the size of the peduncle.

The number of marginal tentacles of all sizes may reach sixty or more. Specimens caught at Plymouth in October 1931 gave the following results:

Diameter of umbrella (mm.)	No. of marginal tentacles	No. of marginal vesicles	Sex
13	65	45	♀
15	72	52	♀
16	72	52	♀
17	70	47	♀
20	66	—	♀
21	*c.* 72	—	♂



Text-fig. 204. *Eirene viridula*. Portions of umbrella margin showing excretory pores on the bases of some of the marginal tentacles, and marginal vesicles, from two preserved specimens *c.* 11 mm. in diameter. (E. T. Browne collection, 25. x. 13.)

Descriptions of specimens from the Mediterranean have tended to give the impression that the Mediterranean form has fewer marginal tentacles than that from northern waters. Neppi (1910), for instance, described the medusa as up to 25 mm. in diameter with twenty-eight very long marginal tentacles and ninety-seven marginal tubercles. Neppi's fig. 1*a* shows, however, forty-two marginal tentacles and twenty-eight marginal bulbs and is exactly similar in appearance to many specimens I have seen from Plymouth. I think that the discrepancy has arisen from insufficient discrimination between marginal tentacles and developing marginal bulbs. Actually very small marginal bulbs show minute developing tentacles, but often in preserved material these disappear by contraction. The differences in the sizes of the marginal tentacles or bulbs are considerable and usually only comparatively few are really large tentacles, although Künne (1934) says that the differences in size are not always obvious. The difficulty of deciding between marginal tentacles and bulbs is exemplified by Browne's (1905*a*) description of a specimen 10 mm. in diameter from the Firth of Clyde. He counted altogether sixty marginal tentacles and bulbs but said, 'the tentacles are very much contracted, and it is difficult to make sure whether some of the smaller bulbs have tentacles or not, but half the bulbs certainly have tentacles. The perradial, interradial, and adradial tentacles are much larger than the others, which vary very much in size.'

Specimens in northern waters do not usually much exceed 20 mm. and this agrees with Neppi's description of Adriatic specimens which were between 10 and 25 mm. in diameter and mostly under 20 mm. Claus's statement that they may reach 40, 50 or even 60 mm. in diameter seems to require confirmation.

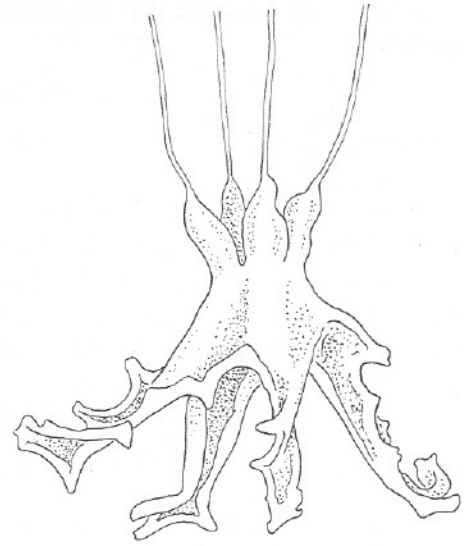
There appears to be a difference in the numbers of marginal vesicles in Mediterranean medusae as compared with those of our own waters. Hartlaub (1909*a*) stated that the northern medusae

had fewer vesicles. Neppi (1910) gave the number as up to eighty-one and mentions that while her observations agreed with Claus (1881*a*) as to the number of marginal tentacles, they did not agree as regards the size of the medusae and the number of vesicles which was given by Claus as far more than the number of tentacles. In northern waters the number of marginal vesicles does not appear to exceed much more than fifty.

Neppi (1909) has described a great number of abnormalities in *Eirene viridula* from Trieste. These abnormalities included reduction or increase in the numbers of radial canals, and their forking, and union, and displacement from the normal radial position; variation in the number of mouth-lips; polygastry; and variation in the number and shape of the gonads. The proportion of abnormal specimens was high, being 37% in 1907 and 19·3% in 1908. This species and *Helgicirrha schulzei* were the only medusae, amongst the other species present, which showed this unusually high proportion of abnormal individuals.

I have seen one or two similarly abnormal specimens at Plymouth.

NEMATOCYSTS. Atrichous haplonemes and microbasic mastigophores (Weill, 1934*b*).



Text-fig. 205. *Eirene viridula*. Stomach and mouth of preserved specimen.

Seasonal occurrence

Off Plymouth *Eirene viridula* has been recorded from the plankton in the months July to December inclusive, the months in which it was most abundant being September and October. In northern waters, where it has been recorded, it occurs in late summer and autumn.

Habits

When swimming the thin sides of the umbrella hang down like a curtain from the central mass of thick jelly. I have noticed that the velum does not expand and contract so much as in other medusae, such as for instance *Phialidium*; instead the sides of the umbrella themselves seem to function to a certain extent as a velum, the margin contracting when water is being expelled and reducing the subumbrellar aperture much as the velum does. I have also noticed that the contraction of the sides of the umbrella is not always simultaneous all round the margin.

Neppi (1910) records the presence of the larval anemone *Halcampa* on *Eirene viridula* from Trieste, but they seemed to prefer *Helgicirrha schulzei* and *Octorchis gegenbauri* to this species. I have seen specimens with Hemiurid larvae.

HYDROID. The adult hydroid is not known, but a primary polyp has been reared from what may have been either *Eirene viridula* or *Helgicirrha schulzei* by Metschnikoff (1886*a*, p. 80). This was described as being very similar to that of *Aequorea* in which the hydrotheca has an operculum. The bases of the tentacles of the hydranth were webbed.

A rather similar hydroid has been described by Annandale & Lloyd (1916) for *Eirene ceylonensis* Browne. It differed from that of *Aequorea* in having no annulated stalk at the base of the hydrotheca.

EIRENIDAE

Historical

Eirene viridula was first described by Péron & Lesueur (1809) from the English Channel as *Oceania viridula*. It was subsequently described and figured more fully by Will (1844) from the Mediterranean as *Geryonia pellucida*. I think there can be little doubt that the two are the same species. The synonymy of the species was, however, put into considerable confusion by Haeckel (1879) who included in his descriptions medusae with cirri. This was realized by Claus (1881*a*) and the confusion has only gradually been cleared by the work of Hartlaub (1909*a*), Neppi (1910) and finally Künne (1934). The genus was fully revised by Kramp (1936) who thought it very probable that *viridula* and *pellucida* would eventually be shown to be the same species.

Genus **Helgicirrha** Hartlaub, 1909

MEDUSAE. Eirenidae with four radial canals; with excretory pores; with lateral cirri.

HYDROID. Not known.

There is one British species of the genus, *Helgicirrha schulzei* Hartlaub. It can be separated from *Eirene viridula* in that it has lateral cirri and especially by its much shorter mouth-lips (Text-fig. 210). At first glance it is less easy to distinguish it from *Phialopsis diegensis*, but the presence of excretory pores is here the diagnostic character. Its hydroid is not known, nor is that of any other member of the genus.

Helgicirrha schulzei Hartlaub

Plate XX, figs. 1, 2; Text-figs. 206–12

Tima pellucida(?), F. E. Schulze, 1875*b*, *Jahresber. Comm. Wiss. Untersuch. deutsch. Meere Kiel* 1872–73, II. and III. Jahrg., p. 138, pl. ii, fig. 6.
Böhm, 1878, *Jena Z. Naturw.* Bd. XII (N.F., vol. v), pp. 76, 87, 100.
Helgicirrha schulzii Hartlaub, 1909*a*, *Zool. Anz. Leipzig*, Bd. XXXIV, p. 86 and fn.
Künne, 1934, *Zool. Anz. Leipzig*, Bd. CVI, p. 28, fig. 1.
Helgicirra schulzii, Hartlaub, 1909*b*, *Zool. Jahrb. Jena*, Abt. Syst. Bd. XXVII, p. 453.
Irene pellucida, Neppi, 1909, *Arch. Entw. Mech. Org. Leipzig*, Bd. XXVIII, p. 368, figs. 1, 2.
Tima plana Neppi, 1910, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. XVIII, p. 165, figs. 2, 2*a*, 2*b*.
Helgicirrha plana, Neppi, 1910, ibid. p. 166.
Eirene (*Irene*) *plana*, Neppi, 1912, *Sitz. Ber. Akad. Wiss. Wien*, math.-nat. Kl. Bd. CXXI, p. 729.
Eirene plana, Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. XX, p. 73.
Helgicirrha schulzei, Kramp, 1936, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. XCIX, p. 254.
Eirene viridula, Ranson, 1934*c*, *Bull. Mus. Hist. nat. Paris*, sér. 2, tome VI, p. 271 (in part).

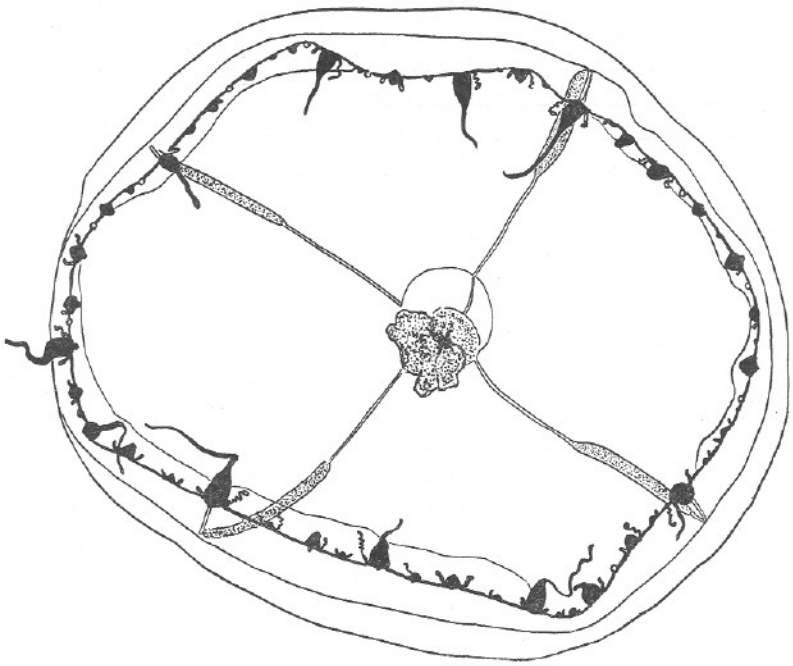
Specific Characters

Mouth-lips short. Fifty or more marginal vesicles.

Description of Adult

Umbrella somewhat flatter than a hemisphere. Jelly moderately thick. Velum narrow. Stomach short, situated on narrow elongated conical peduncle; extending beyond umbrella margin. Mouth with four short perradial slightly upward curved lips with folded margins; lips shorter than stomach. Four straight or slightly sinuous narrow radial canals. Ring canal narrow. One adaxial subumbrellar excretory papilla opposite each marginal tentacle base and rudimentary marginal bulb. Gonads on radial canals, usually limited to disk of subumbrella, extending from near base of peduncle almost to ring canal; straight, or sometimes sinuous, completely surrounding

lower wall of radial canal, without median furrow. Up to thirty to forty large marginal tentacles with elongated conical bases, with or without lateral spiral cirri. Up to 100 or more small marginal tentacles or rudimentary marginal bulbs each with one or a pair of lateral cirri. Closed marginal vesicles, up to fifty or more in number, each with one to four concretions. Diameter of umbrella 30–40 mm. Stomach, gonads and marginal tentacles colourless, or delicate green or reddish brown; fine deep indigo specks on umbrella margin and developing marginal bulbs.



Text-fig. 206. *Helgicirrha schulzei*. Preserved specimen *c.* 6·5 mm. in diameter, Valencia, 11. viii. 99. (E. T. Browne collection.)

Distribution

Round British coasts *Helgicirrha schulzei* has only been recorded off Plymouth but I have found some specimens in Mr Browne's collection from Valencia. It has, however, been recorded in the North Sea on the west coast of Jutland and at Helgoland.

This species has in the past been confused with *Eirene viridula* and it is probable that its known distribution in British waters will be considerably extended.

The species also occurs in the Mediterranean, where it has been found in the Straits of Gibraltar, off Tunis, and in the Adriatic.

Developmental Stages and Structural Details

The early stages of *Helgicirrha schulzei* have not been described, neither is its hydroid known. Neppi (1910) writes of specimens from the Adriatic less than 10 mm. in diameter, but gives no detailed description beyond remarking that at a size of 2 mm. there are no gonads and that the marginal tentacles are only regularly distributed up to the third rank, i.e. adradial. She also states that in quite young specimens the peduncle is very short or absent, but that the medusae correspond in form to full-grown specimens.

EIRENIDAE

In July 1938 two young specimens were taken in the plankton off Plymouth, 3 and 4·5 mm. in diameter respectively.

The smaller, 3 mm. in diameter, was hemispherical, with fairly thick jelly (Pl. XX, fig. 1). The peduncle was quite well developed. There were four fully developed perradial marginal tentacles, each flanked by a lateral cirrus, and four interradial marginal bulbs, with their lateral cirri, developing. There were eight adradial marginal vesicles, each with one large and two small concretions. The gonads were just beginning to develop on the subumbrellar portions of the radial canals where they turned downwards on to the peduncle. The medusa was colourless except for a faint greenish blue tinge on the stomach and marginal bulbs.

The larger specimen, 4·5 mm. in diameter, had four fully developed perradial marginal tentacles; four well-developed interradial marginal bulbs, still without tentacles, and the rudiments of eight adradial marginal bulbs. The gonads were much more elongated than in the smaller specimen, extending along the proximal half of the subumbrellar portion of the radial canals. The colour of the stomach was greenish, and the tentacle bases were pale brownish yellow.

The *stomach*, in adult preserved specimens, is somewhat square in section, the four perradial corners being produced into very short lips (Text-fig. 210).

The *gonads* occur usually only on that part of the radial canal confined to the disk of the subumbrella. Owing to contraction when preserved they are often extremely sinuous (Text-fig. 207). Neppi (1910) states that in specimens from the Adriatic the gonads sometimes extend along part of the peduncle. She also says that in large specimens the gonads on the disk may reach right to the ring canal, although there is usually a small portion of the radial canal left free in this distal region. The gonads are narrow and linear, and, having no median furrow, they completely cover the ventral wall of the radial canal. Apstein (1913) states that the egg cells differentiate in the ectoderm and soon pass into the endoderm.

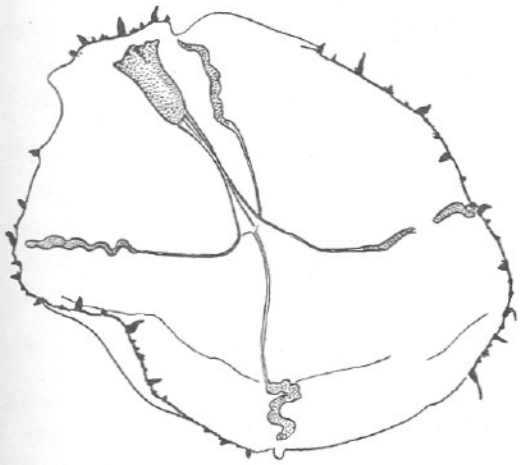
The *marginal tentacles* have elongated conical bases, which are not sharply demarcated from the remainder of the tentacle (Text-fig. 212). The excretory pores are on short papillae which carry nematocysts (Text-fig. 211). The length of the marginal tentacles approximately equals the diameter of the umbrella. The lateral cirri are typical spiral cirri with a terminal cluster of nematocysts (Text-fig. 211). According to Künne (1934) lateral cirri are absent from the bases of the largest marginal tentacles, but Neppi states that all the marginal tentacles have them. In fact these lateral cirri are often lost in old medusae. Neppi (1910) records that in the Mediterranean medusae may have as many as forty-eight marginal tentacles and 191 marginal tubercles.

The Valencia specimens appeared to be of slighter build than those from Plymouth, having smaller marginal tentacle bases and shorter stomachs.

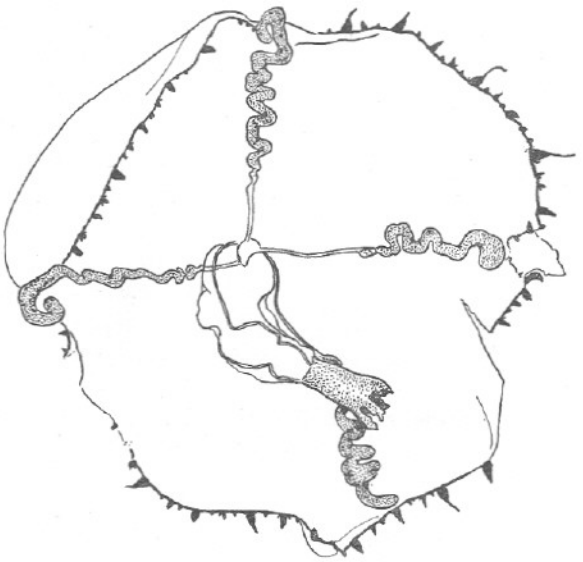
Abnormalities. Neppi (1909) has described a great number of abnormalities in *Helgicirrha schulzei* from Trieste. These abnormalities included reduction or increase in the numbers of radial canals, and their forking, and union, and displacement from the normal radial position; variation in the number of mouth-lips; polygastry; and variation in the number and the shape of the gonads. The proportion of abnormal specimens was high, being 27·1% in 1907 and 16·8% in 1908. This species and *Eirene viridula* were the only medusae, amongst the other species present, which showed this unusually high proportion of abnormal individuals.

Künne (1934) also recorded a specimen from Helgoland with two peduncles and stomachs.

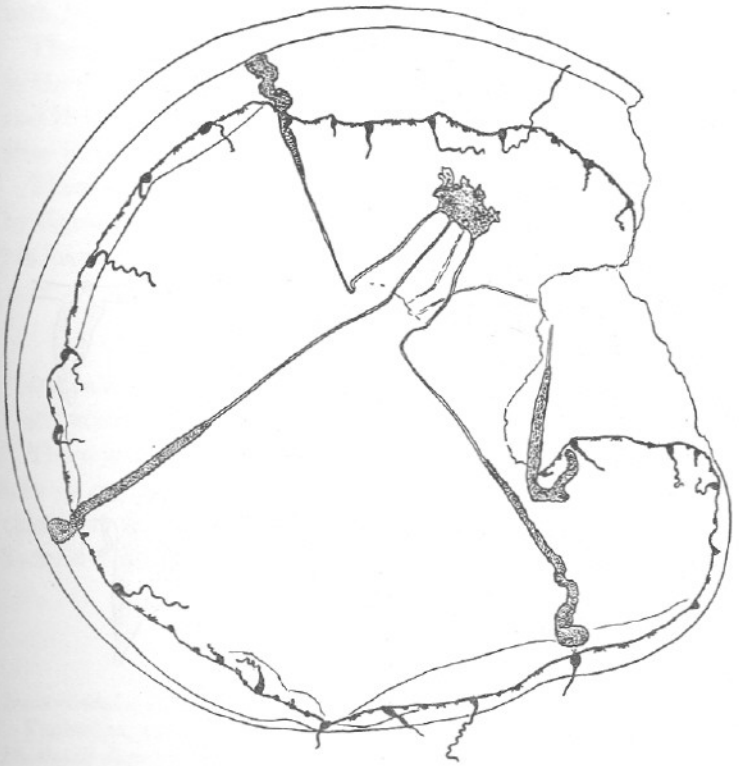
NEMATOCYSTS. Basitrichous haplonemes and atrichous haplonemes (Russell, 1938*b*).



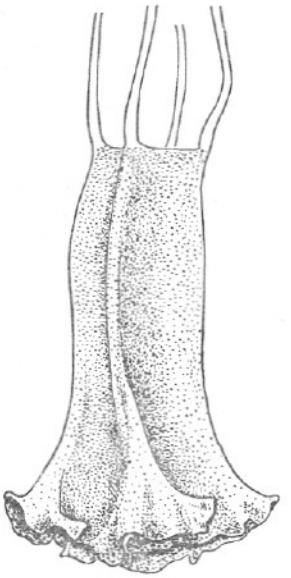
Text-fig. 207. *Helgicirrha schulzei*. Preserved specimen *c.* 12 mm. in diameter, Plymouth, 16. vi. 36.



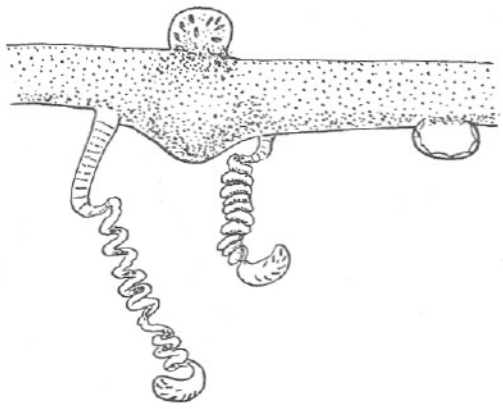
Text-fig. 208. *Helgicirrha schulzei*. Preserved specimen *c.* 15 mm. in diameter, Plymouth, 16. vi. 36.



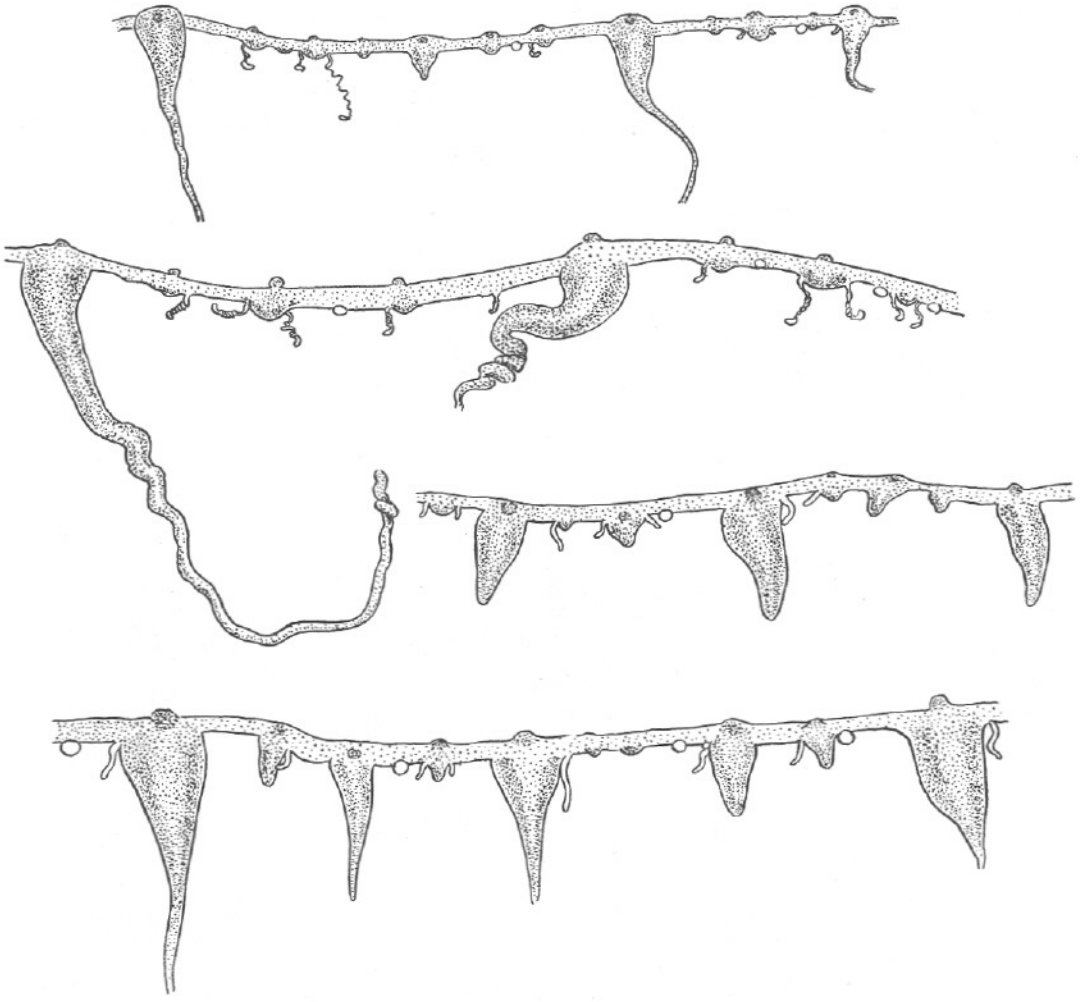
Text-fig. 209. *Helgicirrha schulzei*. Preserved specimen *c.* 20 mm. in diameter, Valencia, 11. viii. 99. (E. T. Browne collection.)



Text-fig. 210. *Helgicirrha schulzei*. Stomach and mouth of preserved specimen.



Text-fig. 211. *Helgicirrha schulzei.* Portion of umbrella margin showing excretory pore, lateral cirri, and marginal vesicle (without concretions), preserved.



Text-fig. 212. *Helgicirrha schulzei.* Portions of umbrella margins of preserved specimens: the two above from Valencia, 11. viii. 99; the two below from Plymouth, poorly preserved.

Seasonal occurrence

Off Plymouth *Helgicirrha schulzei* has been recorded from the plankton in the months June to October inclusive and in December. It would appear that its normal time of appearance is late summer and autumn.

At Trieste it has been recorded in all months of the year except July and August (Stiasny, 1910, 1912).

Habits

Neppi (1910) records the presence of the larval anemone *Halcampa* on *Helgicirrha schulzei* from Trieste and states that they seem to prefer this species and *Octorchis gegenbauri* to *Eirene viridula*. One specimen had as many as thirteen anemones attached. I have seen a specimen with a Hemiurid larva.

HYDROID. Not known. (See *Eirene viridula*, p. 327.)

Historical

The name *Helgicirrha schulzii* was first given by Hartlaub (1909*b*) to medusae figured by Schulze (1875*b*). In a footnote Hartlaub briefly noted that *Helgicirrha* differed from *Eirene* in lacking 'mouth arms' and possessing cirri. Simultaneously, Neppi (1909, 1910) pointed out that in the Adriatic two species of so-called *Eirene* existed, one with cirri and the other without. She described the two species and gave the name *Tima plana* to the species with cirri, which is synonymous with *Helgicirrha schulzei*.

The north European medusa was first described in detail by Künne (1934) who drew attention to Hartlaub's note and described and figured the species adequately. Kramp (1936) pointed out that Hartlaub's spelling of *schulzii* should strictly have been *schulzei* since the medusa was named after F. E. Schulze.

There appears to be little difference between this species and *Helgicirrha danduensis* described by Bigelow (1904) from the Maldive Islands in the Indian Ocean. Until more is known about the life histories of these medusae, however, it seems best to keep them distinct.

Genus **Phialopsis** Torrey, 1909

MEDUSAE. Eirenidae with four radial canals; without excretory pores; with marginal cirri.

HYDROID. Not known.

There is one British species of the genus, *Phialopsis diegensis* Torrey. It is at first sight rather easy to confuse with *Helgicirrha schulzei* but the absence of excretory pores is the diagnostic character. It can be distinguished from *Eirene viridula* by the presence of marginal cirri. Its hydroid is not known.

Phialopsis diegensis Torrey

Plate XX, fig. 5; Text-figs. 213–14

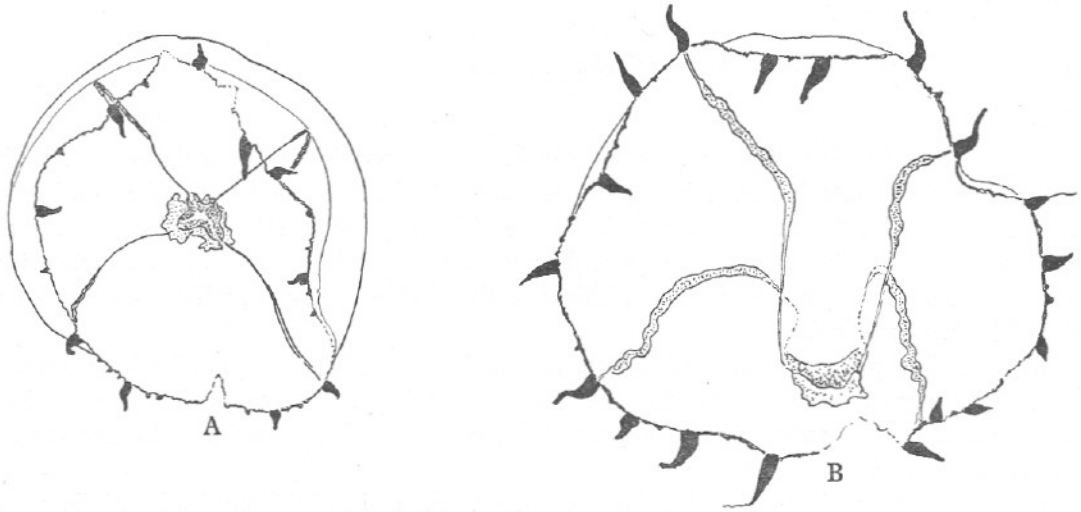
Irene viridula, ?Maas, 1893, *Ergeb. Plankton Expedit. Humboldt Stiftung*, Bd. II, K. c, p. 63, pl. vi, figs. 1, 2.
Vanhöffen, 1912*a*, *Deutsche Südpolar-Expedit.* 1901–3, Bd. XIII, Zool. V, p. 370.
Phialopsis diegensis Torrey, 1909, *Univ. Calif. Publ. Zool.* vol. VI, no. 2, p. 23, fig. 9.
Mayer, 1910, *Medusae of the World*, vol. II, Appendix, p. 495.
Vanhöffen, 1911, *Wiss. Ergeb. Deutsch. Tiefsee-Expedit. Valdivia* 1898–99, Bd. XIX (1925), Heft 5, p. 226, text-fig. 17.

Ranson, 1934*c*, *Bull. Mus. Hist. nat. Paris*, sér. 2, tome VI, no. 3, p. 275, fig. 2, I, II.
Kramp, 1936, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. XCIX, p. 243.
Russell, 1940*b*, *Journ. Mar. Biol. Assoc.* vol. XXIV, p. 528, figs. 2–3.
Kramp, 1948*a*, *Rep. Sci. Res. 'Michael Sars' N. Atlantic Deep Sea Expedit.* 1910, vol. V, no. 9, p. 21.
Eirene viridula, Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 163, pl. XXXVI, figs. 1–4.

Specific Characters. This is the only species of the genus.

Description of Adult

Umbrella flatter than a hemisphere, three to four times as wide as high; jelly thin, thicker in apical region. Velum narrow. Stomach very short, situated on short conical peduncle extending only about to umbrella margin. Mouth with four very short perradial lips with crenulated margins. Four straight radial canals and ring canal narrow. Gonads on radial canals, limited to



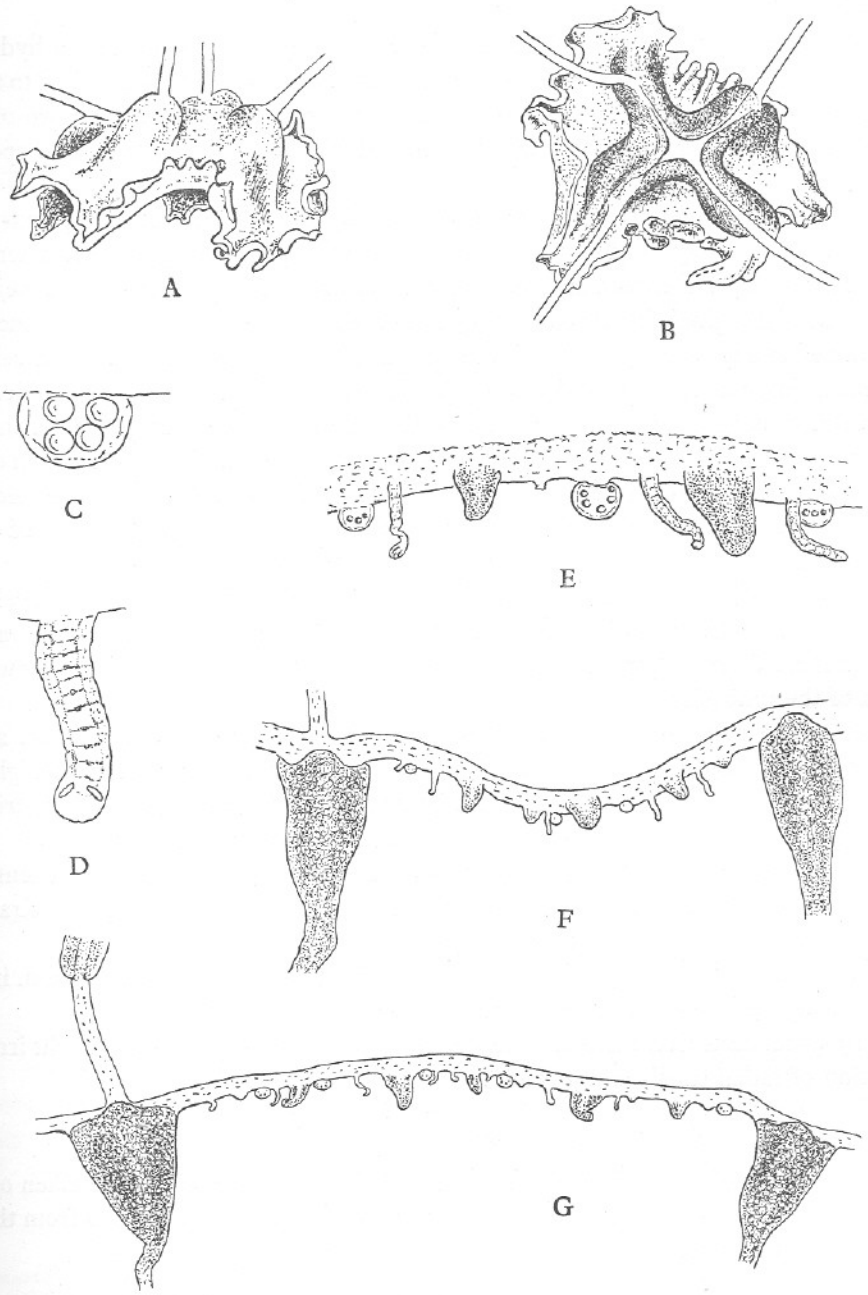
Text-fig. 213. *Phialopsis diegensis*. Preserved specimens from 49° 40′ N.; 11° 10′ W., 20. iv. 39 (collected by P. G. Corbin). A, 10 mm. in diameter; B, 14 mm. in diameter. (After Russell, 1940*b*, fig. 2.)

disk of subumbrella, linear, extending from base of peduncle nearly to ring canal, without median furrow. Sixteen to twenty-eight or more hollow marginal tentacles with elongated conical bases. Three to nine triangular rudimentary marginal bulbs, without tentacles, between adjacent marginal tentacles. Three to nine short marginal cirri between adjacent marginal tentacles. No lateral cirri. Two to five closed marginal vesicles between adjacent marginal tentacles, each with two to six concretions. Diameter of umbrella 20–30 mm. or over. Colourless; gonads and stomach opaque and milky.

Distribution

Phialopsis diegensis has not been recorded from British coastal waters. Four specimens were taken by Mr P. G. Corbin in a ring trawl collection 120 miles S.W. by S. from Fastnet in Ireland, in 49° 40′ N., 11° 10′ W. (Russell, 1940*b*). The species is thus likely to be found, in deep water at any rate, off the south-western and western coasts of the British Isles.

Elsewhere the species has been recorded from the south and equatorial Atlantic (Vanhöffen, 1911, 1912*a*), the North Atlantic (Kramp, 1948*a*; ? Maas, 1893), and in the Pacific off San Diego (Torrey, 1909) and south-west of the Galapagos Islands (Bigelow, 1909*a*). It thus appears to be a widespread oceanic species.



Text-fig. 214. *Phialopsis diegensis*. A and B, stomach of specimen 10 mm. in diameter viewed from side and from above; C, marginal vesicle; D, marginal cirrus; E, portion of umbrella margin of specimen 15 mm. in diameter; F and G, portions of umbrella margins between two adjacent marginal tentacles in specimens 13 and 15 mm. in diameter. (After Russell, 1940*b*, fig. 3.)

Developmental Stages and Structural Details

The full development of *Phialopsis diegensis* has not been described, and its hydroid is not known. Torrey (1909) described a young specimen which he provisionally ascribed to this species and Vanhöffen (1912*a*) also described one as small as 1 mm. Until more is known of the intermediate development it is, however, wiser to regard the identification of these specimens as doubtful.

Among the four specimens I have seen, one was only 10 mm. in diameter (Text-fig. 213A). The peduncle was scarcely indicated and the gonads were only just appearing. There were ten large marginal tentacles. Between adjacent marginal tentacles the numbers of rudimentary bulbs were two to six, of marginal cirri three to nine, and of marginal vesicles two to five; each marginal vesicle contained one to six concretions. It appears that the peduncle may still be scarcely apparent in specimens as large as 15 mm. in diameter. In larger specimens its size is variable.

The stomach is remarkably short and is attached to the subumbrella at the end of the peduncle along the arms of a perradial cross (Text-figs. 214A, B). There is a distinct dilatation on the base of the stomach at each of the four points where a radial canal enters. Four well-marked shoulders are thus formed, which run down to the mouth-lips and give the appearance of a raised cross when viewed from above.

The linear gonads run to within a short distance of the ring canal (Text-fig. 213B), and, as far as I could see by hand sections, were continuous over the lower wall of the radial canal, having no median furrow. At their distal ends they appear sinuous, probably owing to the contraction of the umbrella.

The bases of the marginal tentacles (Text-fig. 214F, G) are large and conical, and appear elongated or short and broad according to their degree of contraction; each has a slight rounded median spur clasping the umbrella margin. The rudimentary marginal bulbs are triangular in shape and usually the median one in any one sector is the largest.

The marginal cirri are very short and rather stiff (Text-fig. 214D). Each has a central core of single endodermal cells and terminates in a slight swelling with nematocysts. Kramp (1932, p. 331) regarded them as of a type similar to those of *Cosmetira pilosella*.

According to Vanhöffen (1912*a*) the medusa may grow to as large a size as 30 mm. in diameter and have as many as forty-eight marginal tentacles.

Torrey (1909) remarks that there is 'a tendency in the larger specimens to slight irregularities in the position of radial canals and gonads'.

Seasonal occurrence

The specimens referred to above, caught to the south-west of Ireland, were taken on 20 April 1939. Torrey gives for San Diego, May, June and July. Vanhöffen's specimens from the Atlantic were caught in September.

Habits

Although occurring over very deep water it seems probable that *Phialopsis diegensis* is an inhabitant of the upper layers; for instance it has been recorded from the surface by Torrey and Bigelow. Nothing else is known of its habits.

I have seen one specimen with two actinian larvae attached to its stomach.

HYDROID. Not known.

Historical

Phialopsis diegensis was first described by Torrey (1909) from San Diego under its present name. A description and good figures of the same species were given by Bigelow (1909*a*) at the same time under the name *Eirene viridula*. Torrey's species was also identified by Vanhöffen (1912*a*) with *Eirene*. These erroneous identifications were cleared up by Kramp (1936) in his synonymy of *E. viridula*. The identity of the *Irene viridula* described by Maas (1893) from the Irminger Sea must remain doubtful owing to the inadequate description, but it seems very probable that it is *Phialopsis diegensis*.

Family AEQUOREIDAE

Leptomedusae with small or very broad stomach; without peduncle; with eight or more simple or branched radial canals; with excretory pores; with gonads on radial canals separated from stomach; with hollow marginal tentacles; without marginal or lateral cirri; with closed marginal vesicles; with or without ocelli.

HYDROID. Where known, simple or slightly branched colonies; with single whorl of filiform tentacles, with webs between their bases; with hydrotheca with operculum (see Rees, 1939*b*).

Medusae of the Aequoreidae, which are essentially characterized by their large number of radial canals, often grow to a considerable size. The family Aequoreidae may be divided into two subfamilies, the Octocanninae and the Aequoreinae. Their distinctive characters are as follows:

With small stomach and eight radial canals	**Octocanninae**
With broad stomach and more than eight radial canals . .	**Aequoreinae**

Subfamily OCTOCANNINAE

MEDUSAE. Aequoreidae with small stomach; eight simple radial canals; with or without ocelli.

HYDROID. Not known.

The Octocanninae are represented in British waters by one genus, *Octocanna* Haeckel.

Genus **Octocanna** Haeckel, 1879

MEDUSAE. Octocanninae without ocelli.

HYDROID. Not known.

There is one British species of the genus, *Octocanna funeraria* (Quoy & Gaimard). It is a deep-water species.

Octocanna funeraria (Quoy & Gaimard)

Plate XXI, fig. 1; Text-figs. 215–19

Dianaea funeraria Quoy & Gaimard, 1827, *Ann. Sci. nat. Paris*, tome x, p. 184, pl. vi, figs. 10–15.
Oceania funeraria, Eschscholtz, 1829, *System der Acalephen*, p. 100.
Tholus funerarius, Lesson, 1843, *Hist. Nat. Zooph. Acalèphes*, p. 288.
L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 365 (in part).
Trachynema funerarium, Haeckel, 1879, *System der Medusen*, p. 261 (in part).
Octocanna funeraria, Maas, 1911, *Bull. Inst. Océanogr. Monaco*, no. 212, p. 3.
Kramp, 1924, *Rep. Danish Oceanogr. Expedit.* 1908–10, vol. II, Biology, H. 1, p. 19, fig. 15 and chart v.
Kramp & Damas, 1925, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. LXXX, p. 306, figs. 27–33.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 582, figs. 49, 50.
Ranson, 1936, *Rés. Camp. Sci. Monaco*, Fasc. XCII, p. 113.

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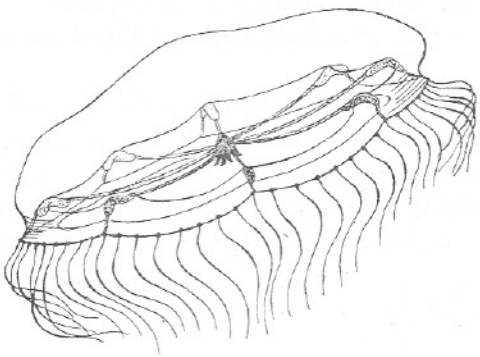
PLYMOUTH

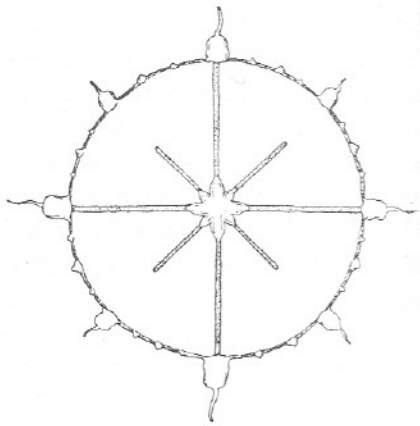
Specific Characters. Sixty-four to 128 marginal tentacles; excretory papillae small.

Description of Adult

Umbrella flatter than a hemisphere; jelly very thick except at umbrella margin; subumbrellar cavity extremely shallow. Velum fairly broad. Stomach small, with base in form of eight-rayed star; mouth with eight short pointed lips, with slightly wavy margins. Eight straight radial canals and ring canal narrow. Excretory pores present, situated on small papillae projecting into subumbrellar cavity and leading from ring canal at base of each marginal tentacle. Gonads short, about one-quarter length of radial canal; one at distal end of each radial canal, not quite reaching ring canal; each gonad continuous over lower wall of radial canal without median furrow in both sexes. About 64 to 128 hollow marginal tentacles with well developed bases; tentacular portion



Text-fig. 215. *Octocanna funeraria.* From life. (After Kramp and Damas, 1925, Fig. 28 from Kramp, 1933*b*, fig. 49.)



Text-fig. 216. *Octocanna funeraria.* Young specimen. (After Kramp and Damas, 1925, Fig. 33 from Kramp, 1933*b*, fig. 50.)

smooth. No ocelli. No marginal nor lateral cirri. One to three, usually two, closed marginal vesicles between adjacent marginal tentacles, each with one to three concretions. Diameter of umbrella 30–40 mm., sometimes reaching 50 mm. Colour of stomach and marginal tentacle bases dark brown or blackish violet, appearing almost black; gonads yellowish brown veined with violet.

Distribution

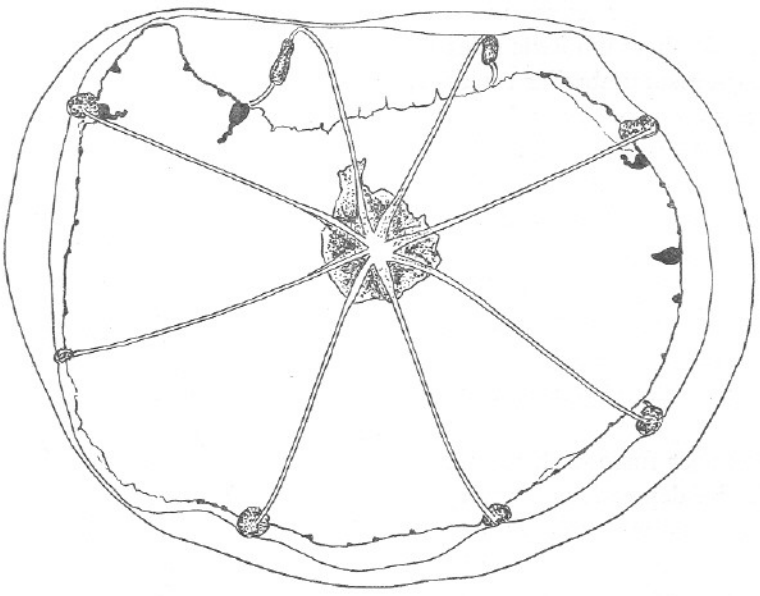
Octocanna funeraria is a deep-water medusa which has not yet been recorded in British waters. Its distribution is such, however, that it may be expected in deep water off the western coasts of the British Isles, since it has been recorded between Rockall and the west coast of Scotland (Kramp, 1947) and in the Norwegian fjords (Kramp & Damas, 1925) and in the Mediterranean. It has not so far been recorded elsewhere.

Developmental Stages and Structural Details

The earliest stages of *Octocanna funeraria* have not been described, neither is its hydroid known. Detailed descriptions of later stages have been given by Kramp & Damas (1925) and it is on the descriptions of these authors that the following account is chiefly based (Text-fig. 216).

The smallest specimen was 5 mm. in diameter. The jelly of the umbrella was relatively thin. There were eight radial canals, but of these only the four primary perradial canals reached the

ring canal; the other four secondary interradial canals only extended about half-way towards the ring canal and all four were not of the same length. The four interradial rays of the base of the stomach also were shorter than the perradial rays. Similarly the four interradial lips of the mouth were much smaller than the four perradial lips. There were traces of four gonads, one on each perradial canal; these were situated in the middle of each canal and not in the adult position at the distal end. There were eight fully developed marginal tentacles and fifteen rudiments of developing marginal tentacles. The marginal vesicles were not mentioned.



Text-fig. 217. *Octocanna funeraria*. Preserved specimen 18 mm. in diameter. (E. T. Browne collection, 'Thor' 1906.)

It is thus quite evident that when first liberated from its hydroid the medusa has only four radial canals. In a specimen 10 mm. in diameter all the eight radial canals reached the ring canal, and on each there was a gonad about 1 mm. long, whose distal end was about 1 mm. from the ring canal. There were about twenty-four marginal tentacles. Two other individuals, each 12 mm. in diameter, had twenty-five and twenty-nine marginal tentacles respectively. Maas (1911) recorded a specimen 13 mm. in diameter with twenty marginal tentacles. During the further development the number of marginal tentacles increases, and the gonads grow in length. As the size of the gonad increases, the distance between it and the ring canal also becomes longer.

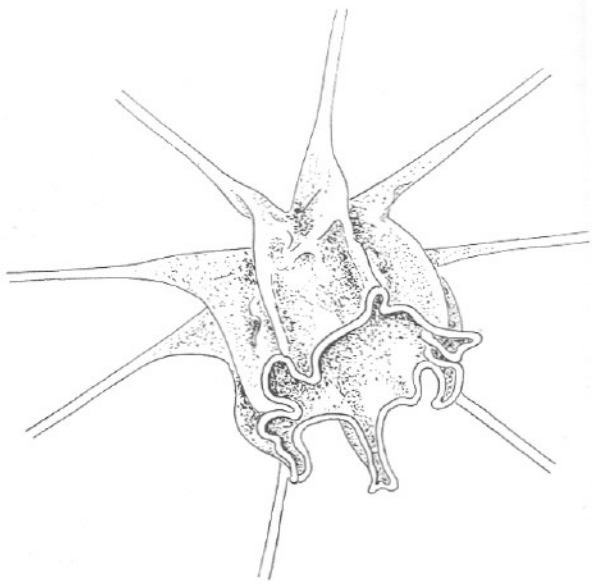
Approximate measurements in medusae of different sizes are given below.

Diameter of umbrella (mm.)	Length of gonad (mm.)	Distance between gonad and ring canal (mm.)
10	1	1
17	3	1·5
26	3–3·5	2–2·5
30–40	5–6	2–3

The majority of adults were 30–40 mm. in diameter; the largest, a male, was 52 mm. in diameter and its jelly was very thick. In all preserved young individuals the jelly is relatively thin and flexible.

The four interradial canals show their secondary nature even in advanced stages. They do r divide the angles between the four perradial canals perfectly in half, and there is not alwa a marginal tentacle exactly opposite their distal ends. This is because the four interradial margir tentacles have developed before the four interradial canals are completed and their subseque growth towards the ring canal may not be quite accurately directed.

The exumbrella has a slight circular depression surrounding its summit, and a second ev less marked depression running round its periphery. The central mass of jelly is lens-shap and at its margin it narrows suddenly to form the exceedingly short umbrella sides as a result of which a subumbrellar cavity is almost non-existent, and limited to a circular peripheral depression. The lens-shaped mass of jelly is biconvex, but the convexity of the subumbrellar surface is only slight. The line of demarcation between the central mass of jelly and the thin sides of the umbrella appears as a third circular furrow which is more or less marked according to the degree of contraction.



Text-fig. 218. *Octocanna funeraria*. Stomach of specime in Text-fig. 217, viewed from oral side.

Between the circular furrows there is a double series of radial depressions, forming sixteen crests alternating with sixteen troughs. These are hardly recognizable in preserved specimens. The margins of the umbrella are drawn in slightly opposite the ends of the radial canals. This also is not always obvious in preserved material.

The surface of the exumbrella is quite smooth and appears iridescent. The subumbrella muscles are only developed in the peripheral region of the umbrella.

The star-shaped form of the base of the stomach (Text-fig. 218) is produced by eight shor outgrowths from which the radial canals issue. As a result the body of the stomach shows eigh flutes. The diameter of the base of the stomach is about one-sixth of that of the umbrella anc its length is slightly less.

The eight radial canals are straight, but between the distal end of the gonad and the ring cana they bend rather sharply to the right (viewed from above) before entering the ring canal.

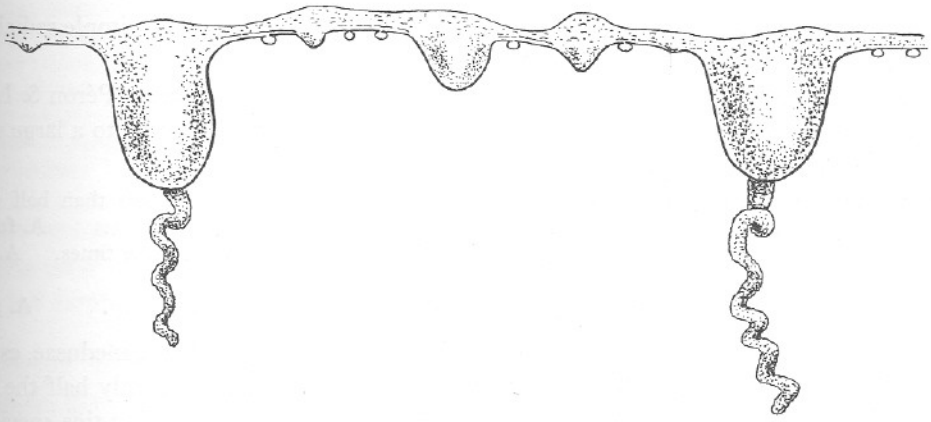
The number of marginal tentacles varies from eight to sixteen between two radial canals The marginal tentacle base is almost rectangular and clearly marked off from the rest of the tentacle, which issues from the adaxial side (Text-fig. 219). The length of the marginal tentacle is a little less than the diameter of the umbrella. The very dark brown and violet pigmentation is characteristic and this has been recorded by some observers (e.g. Maas, 1911) as black. Ranson (1936), however, raises the question whether the black appearance may not be due to the opacity of the very dense yellow-brown pigment. A similar black appearance is produced in this way in *Rathkea* (p. 138). In preserved specimens this dark pigment is very noticeable in the eight grooves of the stomach wall. According to Kramp & Damas the pigment is endodermal.

Apparently *Octocanna funeraria* is rather liable to abnormality; indeed the first description of the species, by Quoy & Gaimard (1827), gave only seven radial canals. Maas (1911) records a specimen with a seven-rayed stomach, but eight gonads and eight radial canals of which one was incomplete; he recorded another with an eight-rayed stomach but nine gonads.

Kramp (1924) recorded a specimen 18 mm. in diameter which had thirteen radial canals. Two neighbouring quadrants were normal, being equally divided by their respective secondary canals; but of the other two quadrants one had five and the other two secondary canals.

Kramp & Damas (1925) found specimens with seven or nine radial canals. A characteristic abnormality had a normal eight-rayed stomach, but one of the radial canals was short and ended blindly. In such an instance the neighbouring canal branches near its point of origin from the stomach and runs to join the ring canal at a point near which the blind canal should have normally entered.

Ranson (1936) also recorded an abnormal specimen with nine gonads and nine radial canals caused by the bifurcation of one of the canals about one-quarter of the way along its course.



Text-fig. 219. *Octocanna funeraria*. Portion of umbrella margin of specimen in Text-fig. 217.

Seasonal occurrence

In Norwegian waters *Octocanna funeraria* has been recorded by Kramp & Damas (1925) in April, May, June, July, September, October and November. The medusa probably breeds all the year round since young individuals and adults may be found together in quite different seasons.

Habits

Little is known of the habits of the living medusa. It appears normally to live in deep water and its coloration is rather typical of deep-water animals.

According to Kramp & Damas (1925) the thin marginal region of the umbrella alone is movable. A drawing of a swimming medusa is given by these authors (Text-fig. 215).

HYDROID. Not known.

Historical

Octocanna funeraria was first briefly described by Quoy & Gaimard (1827) from the Straits of Gibraltar, as *Dianaea funeraria*, from a specimen with seven radial canals. Drawings of the

medusa were given. The medusa was regarded by Haeckel (1879) as a species of *Trachynema* and its identity was so uncertain that Mayer (1910, p. 381) stated that 'it will never be possible to specifically determine Quoy and Gaimard's *D. funeraria*'. A year later, however, Maas (1911) reported that after seeing Quoy & Gaimard's plates there could be no doubt of the identity of their species with some medusae in the Monaco collections. Maas gave a concise description of the species, which was later described in fuller detail by Kramp & Damas (1925).

Subfamily AEQUOREINAE

MEDUSAE. Aequoreidae with broad stomach; with more than eight simple or branched radial canals; without ocelli.

HYDROID. *Aequorea*, characters as family.

The Aequoreinae are represented in British waters by one genus, *Aequorea* Péron & Lesueur.

Genus **Aequorea** Péron & Lesueur, 1809

MEDUSAE. Aequoreinae with subumbrellar surface without papillae; with simple radial canals.

HYDROID. *Aequorea*, with characters as family.

There are apparently three British species of the genus, *Aequorea forskalea* Péron & Lesueur, *A. vitrina* Gosse, and *A. pensilis* (Haeckel) (Modeer). All three species grow to a large size.

Number of radial canals 60 to 100:

Marginal tentacles usually approximating number of radial canals, rarely less than half or more than twice . . . . . **A. forskalea**

Marginal tentacles always exceeding number of radial canals by more than three times. **A. vitrina**

Number of radial canals *c.* 120 to 180:

Marginal tentacles usually much less than one-third number of radial canals . **A. pensilis**

There will always be some difficulty experienced at first in identifying these medusae, especially since there is a variety of *A. pensilis*, var. *macrodactyla*, which may have only half the normal number of radial canals. There are, however, other methods of distinguishing this species from *A. forskalea*. The form of the marginal tentacle base in *A. pensilis* (Text-fig. 220D) is conical and laterally expanded, and it often has a median exumbrellar spur. In *A. forskalea* the marginal tentacle base is much more elongated (Text-fig. 220A). A further check is supplied by an examination of the nematocysts. *A. pensilis* lacks the oval atrichous haplonemes present in *A. forskalea* (Russell, 1939*b*).

The very large number of marginal tentacles in *A. vitrina* makes this species easier to distinguish from the other two (Text-fig. 220B).

More observations are needed on the distribution of these three species.

Aequorea forskalea Péron & Lesueur

Plate XXI, fig. 3; Plate XXXII, figs. 1, 2; Text-figs. 220–1

Medusa aequorea Forskål, 1775, *Descriptiones animalium*, p. 110.
Forskål, 1776, *Icones rerum naturalium*, pl. xxxii.
Aequorea forskalea Péron & Lesueur, 1809, *Ann. Mus. Hist. nat. Paris*, tome XIV, p. 24.
Claus, 1881*b*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. III, Heft 3, p. 283.
Claus, 1883, *Organisation und Entwicklung der Medusen*, p. 61, pl. xvii–xx.
Mayer, 1910, *Medusae of the World*, vol. II, p. 325 (in part); figs. 186, 187; pl. xlii, figs. 1–4; ?pl. xliii, fig. 8.

Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. xx, p. 75.
Fraser, 1916, *Trans. Roy. Soc. Canada*, ser. III, vol. x, p. 97, figs. 1–8.
Russell, 1939*b*, *Journ. Mar. Biol. Assoc.* vol. XXIII, p. 348, figs. 1*a–c*, 2*a*.
Aequorea rissoana Risso, 1826, *Hist. nat. de Nice*, tome v, p. 294, pl. vii, figs. 37, 38.
Delle Chiaie, 1829, *Anim. senza Vert. Napoli*, pl. lxxiii, figs. 1, 2.
Aequorea forskalina Eschscholtz, 1829, *System der Acalephen*, p. 109.
Aequorea violacea H. Milne Edwards, 1841, *Ann. Sci. Nat.* tome XVI, Zool. p. 195, pl. i.
Haeckel, 1879, *System der Medusen*, p. 220.
Aequorea forbesiana Gosse, 1853, *Devonshire Coast*, p. 343, pl. xxiv.
Zygodactyla cyanea L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 361.
A. Agassiz, 1865, *N. Amer. Acalephae*, p. 107, fig. 159.
Mayer, 1900*b*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, no. 2, p. 60; pl. xi, figs. 23, 23*a*; pl. xv, figs. 33, 34.
Rhegmatodes forbesianus, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 361.
Mesonema eurystoma Haeckel, 1879, *System der Medusen*, p. 227.
Mesonema cyaneum, Haeckel, 1879, ibid. p. 227.
?*Polycanna fungina* Haeckel, 1879, ibid. p. 229, pl. xiv, figs. 4–7.
Polycanna germanica Haeckel, 1879, ibid. p. 230, pl. xiv, figs. 1–3.
Polycanna italica Haeckel, 1879, ibid. p. 230.
Rhacostoma dispar Mayer, 1900*b*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, no. 2, p. 61, pl. xiii, figs. 27–9.
Mesonema victoria Murbach & Shearer, 1903, *Proc. Zool. Soc. London*, vol. II (7), p. 180, pl. xix, figs. 1, 1*a*, 2; pl. xxii, fig. 2.
Aequorea aequorea Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, p. 38 (var. *aequorea*).
?*Campanulina paracuminata* Rees, 1938, *Journ. Mar. Biol. Assoc.* vol. XXIII, p. 33, fig. 10 (hydroid and young medusa).

Specific Characters

Usually sixty to eighty radial canals; marginal tentacles approximating to number of radial canals, but varying between one half and twice their number, rarely exceeding 120.

Description of Adult

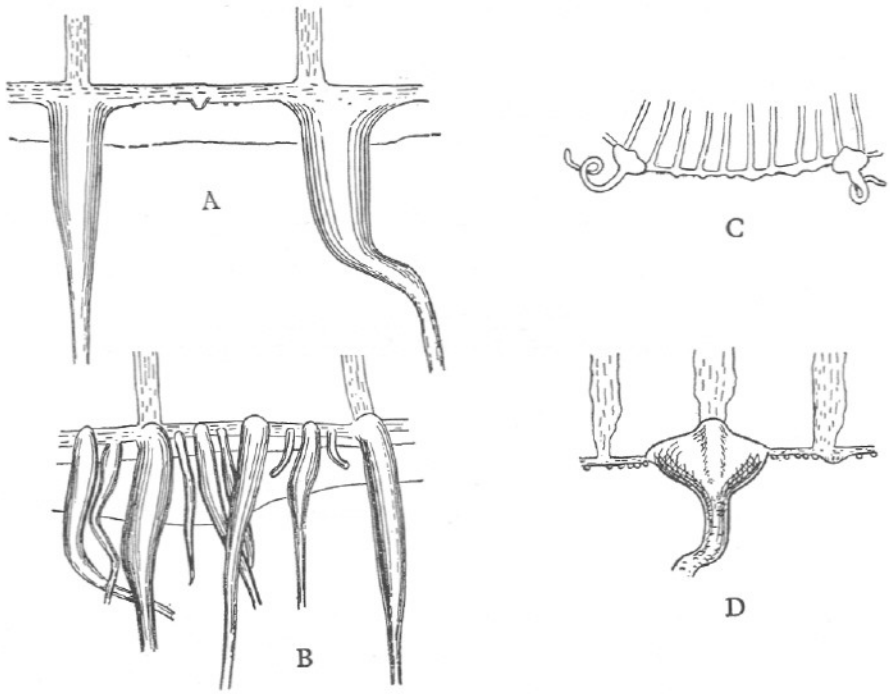
Umbrella flatter than a hemisphere, saucer-shaped, with solid jelly; jelly thickest in centre, thinning gradually and evenly towards umbrella margin. Velum narrow. Stomach large, with diameter of base somewhat variable, usually about one-half diameter of umbrella; lateral walls very extensile, with transparent lines radiating from ends of radial canals to mouth-lips; mouth-lips elongated, with crenulated margins, variable in number, usually approximately as numerous as radial canals. Radial canals straight and narrow, usually about sixty to eighty in number, sometimes fewer, sometimes slightly exceeding 100. Ring canal narrow. Excretory pores present, situated on short papillae projecting into subumbrellar cavity and leading from ring canal opposite bases of marginal tentacles and marginal bulbs. Gonads linear, bilamellar, on both sides of each radial canal, leaving short proximal and distal portions of radial canals free. Marginal tentacles ideally of approximately same number as radial canals, but varying from one-half to twice their number, their actual total rarely exceeding 120; irregularly distributed; hollow, with elongated conical bases narrowing suddenly distally; tentacular portion smooth. Partially developed tentacular bulbs often present. Marginal vesicles numerous, about five to ten between adjacent radial canals; closed, each with two to five concretions. Diameter of umbrella up to 175 mm. Umbrella of glass-like transparency; colour of gonads bluish, violet or pinkish; marginal tentacle bases sometimes likewise coloured and whole subumbrellar surface sometimes with suffused bluish tinge. According to Claus the male gonads are blue and the female rose.

AEQUOREIDAE

Distribution

Aequorea forskalea has only been recorded for certain in British waters off Plymouth, the mouth of the English Channel; at Valencia, south-west Ireland; and in the Moray Firth (Fraser & Saville, 1949). Owing to previous confusion as to the identity of species of *Aequorea* the distribution of this species in British waters is not really known.

Elsewhere *A. forskalea* is recorded from Norway; North Sea; Bay of Biscay; Mediterranean; Tortugas, Florida; eastern American coast in Gulf Stream water; and in the Pacific off Vancouver, Puget Sound and British Columbia.



Text-fig. 220. Bases of marginal tentacles and portions of umbrella margins of: A, *Aequorea forskalea*; B, *Aequorea vitrina*; C and D, *Aequorea pensilis* (A, B and D approximately to same scale; C, less enlarged). (After Russell, 1939*b*, fig. 2.)

Developmental Stages and Structural Characters

Although *Aequorea forskalea* has not been linked to its hydroid by rearing, nor have undeniable specimens of this species been reared from newly liberated medusae, yet it seems almost certain that its hydroid is a species of '*Campanulina*' (=*Aequorea*, see Rees, 1939*b*), quite possibly that described by Rees (1938) as *Campanulina paracuminata*, and that the newly liberated medusa begins its life with only two opposite perradial marginal tentacles (Text-fig. 221 C). If the medusa described by Rees should prove to be *Aequorea forskalea* the structure of the newly liberated medusa of this species is as follows. Umbrella bell-shaped, a little higher than wide, 1·4 mm. in height and 1·1 mm. in diameter. The jelly is fairly thick and there is a slight apical depression. There is a band of nematocysts surrounding the exumbrella and confined to its lower middle region (Pl. XXI, fig. 3). The velum is broad. The stomach is short, and the mouth has four simple lips. The four straight radial canals and ring canal are narrow. There are two

opposite perradial marginal tentacles with large elongated bases and two small opposite perradial marginal bulbs without tentacles. There are eight adradial marginal vesicles, each with a single concretion. There is no sign of excretory pores, nor are there any indications of developing gonads. The subumbrella is a vivid bluish green; the colour of the stomach is reddish yellow, and that of the marginal tentacle bases and non-tentacular marginal bulbs yellow with a single central strip of blue-black pigment.

The development of later stages of *A. forskalea* caught in the plankton in the Mediterranean has been described in considerable detail by Claus (1881*b*, 1883). The youngest stage described by Claus (1883, p. 68) was 1·5–2·0 mm. in diameter. At this stage the umbrella was high and conical, and the jelly was thick. The stomach was short with a broad base and the mouth had four well-developed simple lips. There were four radial canals. There were four perradial marginal tentacles, of which two opposite perradial ones were smaller than the other two. There were four interradial marginal bulbs without tentacles and one or two adradial marginal bulbs just appearing. Two interradial marginal vesicles were developing in addition to the eight adradial vesicles already present. The excretory pores were already distinctly visible.

At a diameter of 2–3 mm. the umbrella still has a high conical shape, but the beginnings of four interradial canals are appearing as short outgrowths from the stomach, these being canals of the second order. The numbers of marginal bulbs and marginal vesicles is also slightly increased.

The next stage is reached when the umbrella is about 6 mm. in diameter; the umbrella is about as wide as it is high. The jelly is thick. The four interradial canals of the second order, which do not all elongate at the same rate, have now all reached the ring canal. There are thus eight radial canals. The stomach base has increased in area and the rudiments of four interradial mouth-lips now appear, the original four perradial lips being more elongated and having crinkled edges. There are eight marginal tentacles, four perradial and four interradial. There are eight adradial marginal bulbs without tentacles and the rudiments of sixteen additional marginal bulbs, one between each interradial bulb and its adjacent tentacle. There are about thirty-five to forty marginal vesicles, i.e. four to five in each octant.

After this stage has been passed development becomes increasingly more irregular and it is not possible to describe typical stages. *A. forskalea* is probably a species whose idealized adult should have the same numbers of marginal tentacles and of mouth-lips as of radial canals. But owing to the unequal rates of development of these three structures they never agree exactly in number and often differ considerably. The marginal tentacles also do not always appear on the umbrella margin opposite the radial canals, probably because when the marginal tentacle develops first the corresponding radial canal does not grow along the exact line necessary to meet the marginal tentacle on the margin.

Thus ideally the stages in the development of *A. forskalea* would be as follows:

	Radial canals		
Stage	Order of development		Total
I	1st order	4	4
II	2nd order	4	8
III	3rd order	8	16
IV	4th order	16	32
V	5th order	32	64
VI	6th order	64	128

It is probable that normally the development of the radial canals of the sixth order is never fully completed.

AEQUOREIDAE

A summary of the data given by Claus (1883, pp. 70–6) in his descriptions of medusae of different sizes from the Mediterranean is shown in Table VII. In this table the numbers of developing marginal bulbs are omitted, only the number of marginal tentacles being given. The numbers of radial canals probably included both those that have reached the ring canal and those that have not, except where otherwise stated. When the number of canals of each kind is known, the fully completed canals are shown first and the number of developing canals follows in brackets. The numbers of mouth-lips include both large and small lips.

TABLE VII. *Aequorea forskalea* from the Mediterranean, after Claus (1883, pp. 70–6)

Diameter (mm.)	Sex	No. of radial canals	No. of marginal tentacles	No. of mouth-lips	No. of marginal vesicles	No. of gonads
1·5	—	4	4	4	8	—
2·5	—	4 (4)	4	4	12–16	—
4	—	6 (2)	4	4	16–32	—
6	—	10 (6)	8	4	24–40	—
8	—	8	8	4	24–40	—
12	—	16	16	8	40–56	—
15	—	32	16	8	—	—
20	—	35	32	16	—	—
35	—	30 (12)	29	16	—	16 just appearing
40	—	41 (7)	18	32	—	—
60	♂♀	60	60+	32	—	32
65	♂♀	64	<64	32	—	46
75	♂♀	70	72	53	—	64
75	♂♀	65	74	42	—	32
75	♂♀	65	76	42	—	32 well developed
80	♂♀	45	70	34	—	38 well developed
85	♂♀	59	72	45	—	47
95	♂♀	69	80	—	—	30 well developed
100	♂♀	59	101	52	—	55
100	♂♀	70	97	—	—	70
105	♂♀	60	91	—	—	26 well developed
110	♂♀	62	73	58	—	58 well developed
110	♂♀	51	92	45	—	51 (25 mm. long)
110	♂	66	76	56	—	30 well developed (20–22 mm. long)
125	♂	74	110	66	—	74 (28 mm. long)
125	♂	74	108	63	—	64 well developed
140	♂	61	111	66	—	? 61
150	♂	67	108	65	—	66 well developed

For comparison with Table VII some details are given in Table VIII of specimens of *A. forskalea* from British waters. It appears that in these medusae the numbers of radial canals develop at a slightly greater rate than they do in Mediterranean specimens. It seems too from observations made by Fraser (1916) that this species also develops more quickly in the Pacific, off Vancouver, than it does in the Mediterranean. Fraser's results may be summarized as follows:

Diameter (mm.)	No. of radial canals	No. of marginal tentacles
2	4 (4)	4
7	16 (16)	16
10	32 (+)	16
12	40 (8)	24
16	48 (16)	32
27	64	32

Fraser concludes that seventy-eight or eighty canals, however, appears to be about the upper limit in that locality. He also states that the number of mouth-lips is never more than half the number of radial canals.

The *umbrella* in full grown medusae varies somewhat in thickness. Claus gives the following measurements of the thickness of the disk for specimens of different sizes:

Diameter (mm.)	Thickness (mm.)
110	22
110	22
125	30
125	36

When the medusae are preserved there is a pronounced tendency for the umbrella margin to curl inwards.

TABLE VIII. *Aequorea forskalea* from British waters

Diameter of umbrella (mm.)	No. of radial canals	No. of marginal tentacles	No. of mouth-lips	Diameter of stomach (mm.)	Ratio of diameters of stomach and umbrella	Date	Locality
22	16 (33)	14	—	9	1 : 2·4	—	Valencia (E.T.B.)
23	33 (19)	17	16	9	1 : 2·5	—	,, ,,
25	47	22	—	9	1 : 2·8	—	,, ,,
36	71	25	25	14	1 : 2·6	—	,, ,,
45	64	—	48	24	1 : 1·9	July 1937	Mouth of Channel
45	67	58	—	—	—	June 1900	Valencia (M.D.)
55	99	36	—	23	1 : 2·4	July 1937	Mouth of Channel
55	60	30	—	—	—	Nov. 1901	Valencia (M.D.)
55	57	41	—	23	1 : 2·4	July 1937	Mouth of Channel
55	75	—	—	23	1 : 2·4	,,	,, ,,
60	71	54	—	30	1 : 2·0	,,	,, ,,
60	73	53	—	25	1 : 2·4	,,	,, ,,
60	72	—	—	27	1 : 2·2	,,	,, ,,
65	40	60	—	25	1 : 2·6	Sept. 1900	Valencia (M.D.)
65	70	56	49	27	1 : 2·4	July 1937	Mouth of Channel
70	72	41+	69	38	1 : 1·8	,,	,, ,,
70	85	<66	—	36	1 : 1·9	,,	,, ,,
70	71	—	—	33	1 : 2·1	,,	,, ,,
75	63	52	—	25	1 : 3·0	Nov. 1901	Valencia (M.D.)
80	79	55	74	40	1 : 2·0	July 1937	Mouth of Channel
80	92	51	—	40	1 : 2·0	,,	,, ,,
90	75	—	64	40	1 : 2·3	,,	,, ,,
90	83	—	—	37	1 : 2·4	,,	,, ,,
90	70	79	—	43	1 : 2·1	,,	,, ,,
95	63	67	*c.* 63	43	1 : 2·2	,,	,, ,,
100	99	65	—	55	1 : 1·8	,,	,, ,,
100	71	70	*c.* 71	43	1 : 2·3	,,	,, ,,
104	65	—	—	45	1 : 2·3	Sept. 1900	Valencia (M.D.)
105	63	76	—	35	1 : 3·0	,,	,, ,,
111	72	80	—	44	1 : 2·5	,,	,, ,,
120	65	64	—	45	1 : 2·7	Nov. 1901	,, ,,
130	70	74	—	45	1 : 2·9	Sept. 1900	,, ,,
175	63	84	—	70	1 : 2·5	,,	,, ,,

The *stomach* is circular and very wide, the ratio of its diameter to that of the umbrella in the larger specimens being from 1 : 3·0* to 1 : 1·8. The walls of the stomach are very contractile and have the appearance of frosted glass with transparent lines of large endodermal cells running downwards from approximately each radial canal and ending at the mouth in an elongated lip with crinkled edges. The number of these mouth-lips may vary considerably owing to unequal development and because of the general distorted appearance of the mouth is often difficult to estimate. The number of transparent lines is probably a surer guide. These seem usually, when the medusa is fairly fully developed, to approximate to the number of radial canals. In preserved specimens the mouth is usually wide open owing to the contraction of the stomach wall, and this mouth aperture may sometimes be nearly as wide as the diameter of the stomach.

* It is noticeable that this ratio is highest in the Valencia specimens. This difference may be due to observations on living specimens as against preserved specimens in which the umbrella will have been somewhat contracted.

The *radial canals* run out from slight projections from the stomach and are straight and narrow. They vary considerably in width in a single specimen according to their state of development, the thicker canals being those of the earlier order to develop. Specimens will often be found in which thick and thin canals alternate. The distal ends of the canals appear to be slightly broader than the proximal ends.

The *gonads* are developed on the side walls of the radial canals, which hang down as laterally compressed pouches in the gonadial region. The gonads are thus bilamellar, having a slight median streak without gonadial tissue; they are linear and straight, being about two-thirds the length of the radial canals and leaving the proximal and distal ends free. Of these gonad-free ends the distal is usually somewhat the longer. The gonads appear first on the canals of earlier order, when the medusa is between 20 and 30 mm. in diameter. Specimens will often be found with many well-developed gonads and a number of narrow intermediate radial canals of a later order without gonads. Owing to the contraction of the umbrella in preserved specimens the outlines of the gonads and radial canals may appear wavy, especially towards their distal ends, and the more fully developed gonads will then hang down in curtain-like folds.

The *marginal tentacles* in the older medusae have elongated conical bases. These bases are of considerable length, narrowing suddenly distally into the tentacle itself (Text-fig. 220 A). In young specimens the tentacle bases are more laterally expanded proximally in relation to their length. In fully grown specimens there are sometimes a few marginal bulbs which have not developed tentacles and these are very irregularly distributed.

The development of the egg and planula of *A. forskalea* has been described by Claus (1882, 1883). The membraneless eggs are laid at night or in the early morning. Segmentation is regular. Cleavage in the eggs has been studied by Häcker (1892); he states that the nucleus has twelve chromosomes. According to Metschnikoff (1886*a*) the eggs are 0·16 mm. in diameter.

Abnormalities are occasionally found in which there may be branching or anastomosis of a few radial canals (e.g. Neppi & Stiasny, 1913*a*, pl. iv, fig. 6).

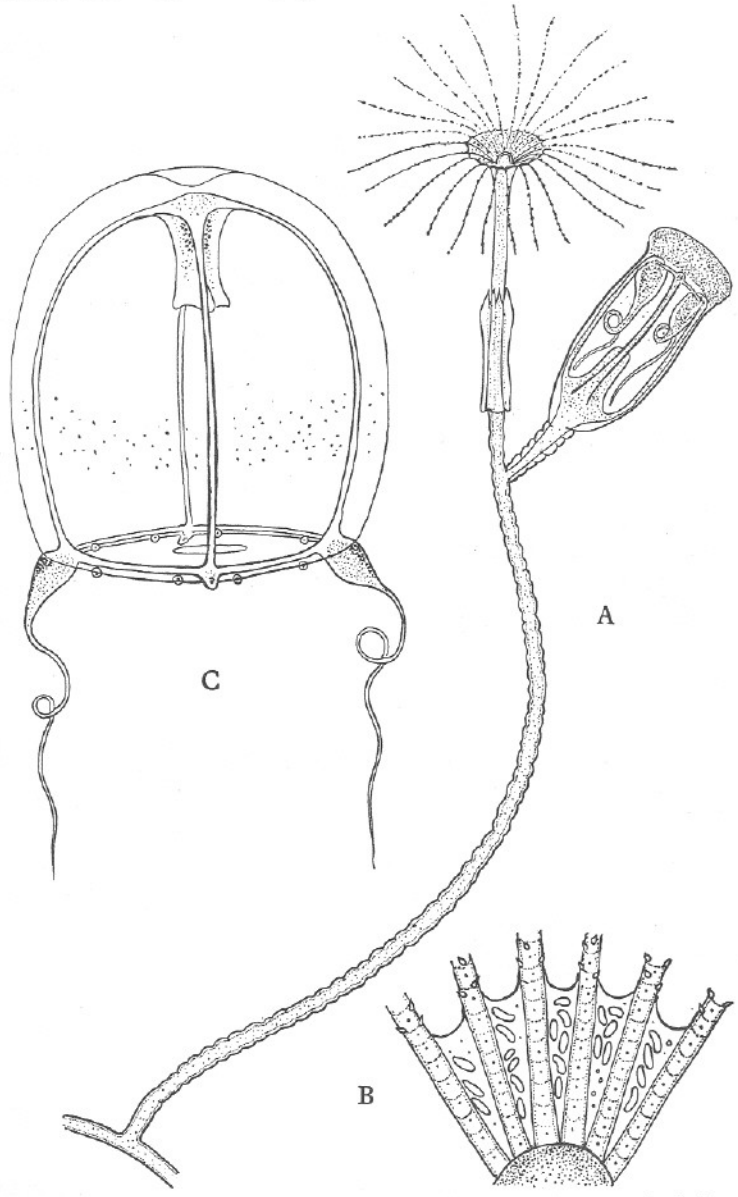
Note on identification

The identity of the species of *Aequorea* has been, and to some extent still is, a problem of considerable difficulty owing to their great variability. In identifying *A. forskalea* it is necessary first to examine the relationship of the number of marginal tentacles to that of the radial canals. If the number of marginal tentacles does not greatly exceed twice that of the radial canals, the specimen cannot be *A. vitrina*. If the number of marginal tentacles is not less than half that of the radial canals, the specimen cannot be a typical *A. pensilis*. There is, however, a variety of *A. pensilis*, the *macrodactyla* type, which has only about half the normal number of radial canals. The later stages of *A. forskalea* can easily be distinguished from those of this type of *A. pensilis* by the shape of the tentacle bases, which in *A. pensilis* are shorter and much more laterally expanded (Text-fig. 220 C, D). But in young specimens of *A. forskalea*, less than about 30 mm. in diameter, the tentacle bases are also laterally expanded. These may be distinguished from the *macrodactyla* type of *A. pensilis* of a similar size by an examination of the number of marginal vesicles. In *A. forskalea* there are only one or two between adjacent marginal tentacles or bulbs, whereas in *A. pensilis* they are very much more numerous.

NEMATOCYSTS. Atrichous haplonemes and ? basitrichous haplonemes or mastigophores (Russell, 1939*b*).

Seasonal occurrence

The only certain records of *Aequorea forskalea* in British waters are in April and July at the mouth of the English Channel, and in July at Valencia.



Text-fig. 221. '*Campanulina*' *paracuminata*, possibly the hydroid of *Aequorea forskalea*. A, single hydranth with fully developed gonophore, Plymouth, 4. ii. 37; B, a small portion of the web of a hydranth, Plymouth, 20. iii. 37; C, newly liberated medusa 1·1 mm. in diameter, Plymouth, 22. ii. 37. (After Rees, 1938, fig. 10.)

Habits

Owing to confusion in the past as to the identity of species of *Aequorea* little is known of the habits of *A. forskalea*. Ranson (1936) records observations on the movements of the mouth. This may open widely by contraction of the stomach walls, or the walls may elongate and the

mouth close. He found that when a medusa was placed in formalin and sea water the mouth opened considerably. A similar movement was observed by Murbach & Shearer (1903) in medusae from the Pacific coast of North America, who stated that when the mouth was closed the oval lobes were wrapped into a corkscrew-shaped mass.

If we are correct in supposing that *A. forbesiana* is a synonym of this species, it has been recorded by Gosse (1853) as being capable of phosphorescence, forming circles of light which reminded him of the 'rings of glory in the pictures of the Italian School, round the heads of the saints'. As regards its movements he observes that 'at the beginning of contraction after repose, the action of one side is frequently not simultaneous with that of the opposite, but presently they become so'.

HYDROID. ? '*Campanulina*' *paracuminata* Rees. (Text-fig. 221 A, B.)

(For full description see Rees, 1938, *Journ. Mar. Biol. Assoc.* vol. XXIII, p. 33, fig. 10.)

Colonies of single or slightly branched slender hydranths reaching a height of 2·5 mm. rising from a creeping stolon. Hydrocaulus imperfectly annulated throughout its length. Hydrothecae cylindrical, tapering to a fine toothed point, with base at right-angles to lateral wall; perisarc with fine longitudinal striations. Hydranth colourless, very extensile, with about twenty filiform tentacles, in one whorl, united at their bases by a membranous web. Gonothecae large and cylindrical, arising from hydrocaulus on short imperfectly annulated stem just below hydranth; containing one, or rarely two, medusa buds.

As explained on p. 344 it is not certain that this is the hydroid of *Aequorea forskalea*. It should also be mentioned that the hydroid was grown in the laboratory, so that the type of colony may not be natural.

Historical

Aequorea forskalea was first described and figured by Forskål (1775–6) as *Medusa aequorea*. Péron & Lesueur (1809) gave the name *Aequorea forskalea* to Forskål's medusa. In his description of the type Forskål says that there are 129 radial canals, but that these are paired, and Claus (1883) is probably right in assuming that he was referring to the lamellae of the gonads and that the radial canals were really half that number. There can, however, be no hesitation in identifying the medusa with Forskål's figure. The specific name *aequorea* is here discarded since it is a name given by Linnaeus and Loefling (1758) to unidentifiable species.

Aequorea vitrina Gosse

Plate XXI, figs. 2, 4, 5; Plate XXXII, fig. 3; Text-figs. 220 B, 222–4

Aequorea vitrina Gosse, 1853, *Devonshire Coast*, p. 340, pl. xxiii.
Wright, 1861, *Proc. R. Phys. Soc. Edinb.* vol. II, p. 316, pl. xv, figs. 1–6 (medusa and young hydroid).
Russell, 1939*b*, *Journ. Mar. Biol. Assoc.* vol. XXIII, p. 349, figs. 1*d*, *e*, 2*b*.
?*Laomedea acuminata* Wright, 1858*c*, *Edinb. New Philos. Journ.*, N.S. (Jan.), p. 108, pl. i, ii (hydroid and young medusa).
?*Wrightia acuminata*, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 354.
Zygodactyla vitrina, L. Agassiz, 1862, ibid. p. 361.
Hincks, 1868, *Brit. Hydroid Zooph.* p. 192, pl. xxxviii, fig. 2 (medusa and young hydroid).
?*Campanulina tenuis* Van Beneden, 1866, *Mém. Acad. R. Belg.* vol. XXXVI, p. 174, pl. xiii (hydroid and young medusa).
Non Van Beneden, 1847, *Reproduction des Animaux inférieurs*, p. 14, fig. 6 (hydroid).

?*Campanulina acuminata*, Hincks, 1868, *Brit. Hydroid Zooph.* p. 187, pl. xxxvii (hydroid and young medusa).
Polycanna vitrina, Haeckel, 1879, *System der Medusen*, p. 231.
Aequorea forskalea, Hartlaub, 1894, *Wiss. Meeresuntersuch.* N.F., Bd. I, Abt. Helgoland, Heft 1, IV, p. 196.
Mayer, 1910, *Medusae of the World*, vol. II, p. 325 (in part), figs. 185, 185*a*.
Aequorea norvegica Browne, 1903, *Bergens Mus. Aarb.* no. 4, p. 19, pl. v, figs. 1–5.
Evans & Ashworth, 1909, *Proc. Roy. Phys. Soc. Edinb.* vol. XVII, no. 6, p. 306.

Specific Characters

Usually sixty to ninety radial canals; marginal tentacles very numerous, always more than three times number of radial canals, probably reaching 600 or more.

Description of Adult

Umbrella flatter than a hemisphere, saucer-shaped, with solid jelly; jelly thickest in centre, thinning gradually and evenly to umbrella margin. Velum narrow. Stomach large, diameter of base somewhat variable, usually about half the diameter of umbrella; lateral walls very extensile, with transparent lines radiating from ends of approximately every alternate radial canal to mouth-lips; mouth-lips elongated, with crenulated margins, variable in number, usually approximately half the number of radial canals. Radial canals straight and narrow, usually about sixty to ninety in number. Ring canal narrow. Excretory pores present, situated on papillae projecting into subumbrellar cavity and leading from ring canal opposite bases of marginal tentacles and marginal bulbs. Gonads linear, bilamellar, on both sides of each radial canal, leaving short proximal and distal portions of radial canals free. Marginal tentacles very numerous, always more than three times the number of radial canals, probably reaching 600 or more; packed closely round umbrella margin; hollow, with elongated, slightly laterally compressed bases; tentacular portion smooth. Partially developed marginal tentacles present and few marginal bulbs. Marginal vesicles numerous; about one to two between adjacent radial canals; closed, each with two to five concretions. Diameter of umbrella up to 170 mm. Umbrella of glass-like transparency; gonads and marginal tentacle bases colourless.

Distribution

Aequorea vitrina has only been recorded* from British waters off Plymouth, Ilfracombe, mouth of English Channel, Valencia, Irish Sea, Menai Straits, and Firth of Forth. Elsewhere it has been recorded from Helgoland and the west coast of Jutland.

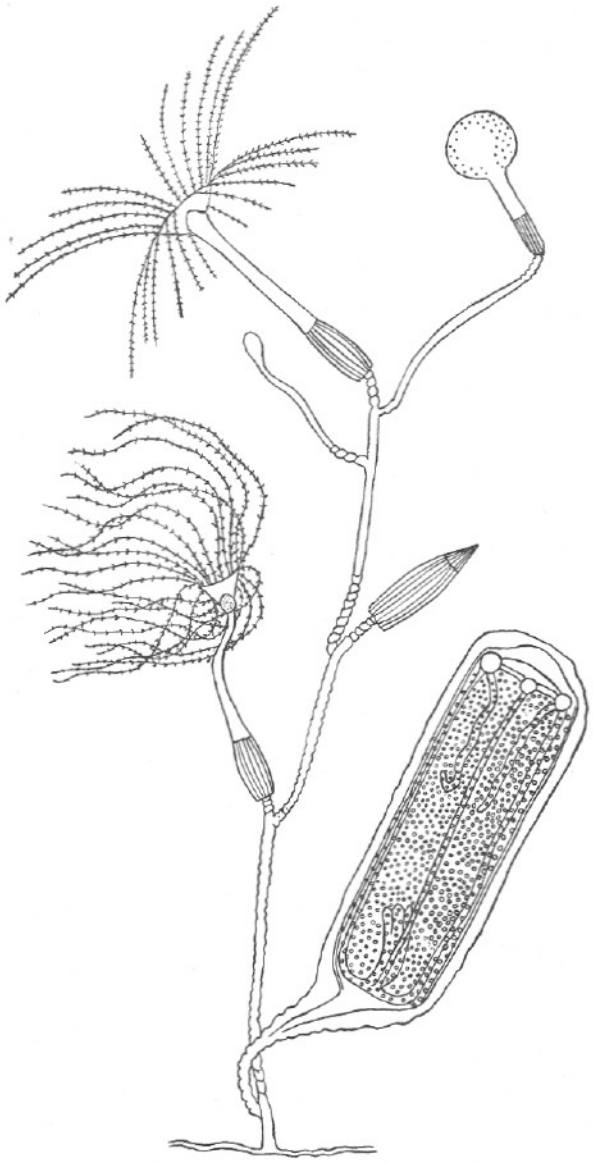
Developmental Stages and Structural Details

The specific identity of the hydroid of *Aequorea vitrina* is not known for certain; it is, however, very probable that it is *Campanulina acuminata* (Alder). Specimens liberated from a colony of this hydroid, sent to me at Plymouth by Dr H. O. Bull from Cullercoats, have been linked with slightly older medusae from the plankton at Plymouth (Pl. XXI, figs. 2, 4, 5; see also Pl. XXXIV, fig. 7, from material sent in 1951).

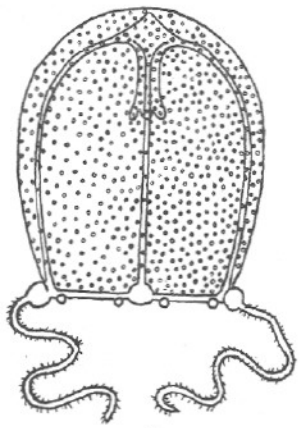
When first liberated from the hydroid (Pl. XXI, fig. 2) the medusa is bell-shaped, 1·6 mm. in height and 1·6 mm. in diameter. The jelly is fairly thick. There is no apical depression. There are numerous nematocysts scattered irregularly over the surface of the exumbrella. The velum is broad. The stomach is short and the mouth has four simple lips. The four straight radial canals and ring canal are narrow. There are two opposite perradial marginal tentacles with large bases

* Dr G. E. Newell tells me that it was numerous off Whitstable in early July in 1950.

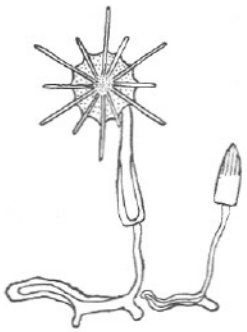
and two small opposite perradial marginal bulbs without tentacles. There are eight adradial marginal vesicles, each with a single concretion. There is no sign of excretory pores, nor are there any indications of developing gonads. The subumbrella is a vivid yellowish green, the stomach



Text-fig. 222. '*Campanulina*' *acuminata*, possibly the hydroid of *Aequorea vitrina*. (After Hincks, 1868, pl. xxxvii, fig. *b*, from Alder.)



A



B

Text-fig. 223. A, newly liberated medusa of the hydroid '*Campanulina*' *acuminata*, possibly *Aequorea vitrina*. (After Hincks, 1868, pl. xxxvii, fig. *c*, from Alder.) B, hydroid reared from *Aequorea vitrina*. (After Hincks, 1868, pl. xxxviii, fig. 2, from Wright.)

is colourless, and the marginal tentacle bases and non-tentacular marginal bulbs are yellowish with two lateral strips of bluish black pigment. The medusa agrees with the description and figure given by van Beneden (1866) for that liberated from his *C. tenuis* and Strethill Wright (1858*c*) for *Laomedea acuminata*.

A slightly later stage was taken in the plankton at Plymouth on 23 May 1934. The umbrella was already more flattened, being 1·8 mm. high and 2·5 mm. wide (Pl. XXI, fig. 4). The mouth had four simple lips. There were still only four radial canals, but there were now four fully developed perradial marginal tentacles, four partially developed interradial marginal tentacles and eight adradial marginal bulbs without tentacles.

TABLE IX. *Aequorea vitrina*

Diameter of umbrella (mm.)	No. of radial canals	No. of marginal tentacles	No. of mouth-lips	Diameter of stomach (mm.)	Ratio of diameters of stomach and umbrella	Date	Locality
2·5	4	4	4	—	—	May 1934	Plymouth
4·1	8 (8)	16 (16)	4	—	—	Nov. 1935	,,
c. 4	10 (6)	16 (24)	4	2	1 : 2	Aug. 1938	Valencia (W.J.R.)
6	17 (16)	33 (23)	8	3	1 : 2	,,	,, ,,
6	26	42	—	—	—	Aug. 1899	Valencia (M.D.)
6	20	25	—	2	1 : 3	Sept. 1900	,,
11	16 (14)	69	6	4	1 : 2·8	May 1899	,,
12	15 (19)	50	—	—	—	June 1900	,,
13	26 (9)	69	—	—	—	Aug. 1899	,,
15	24 (18)	84	—	5	1 : 3	,,	,,
25	40 (24)	> 123	16	14	1 : 1·8	Sept. 1930	Plymouth
25	22 (28)	94	—	—	—	June 1900	Valencia (M.D.)
28	60 (16)	146	—	13	1 : 2·2	Aug. 1899	,,
32	90	200	20	—	—	Aug.	Ilfracombe (Gosse, 1853)
38	76	120 (40)	—	18	1 : 2·1	Aug. 1899	Valencia (M.D.)
55	76	*c.* 304	—	25	1 : 2·2	Sept. 1938	Plymouth
75	68	*c.* 272	—	37	1 : 2·0	Apr. 1938	Mouth of Channel
80	68	> 300	39	40	1 : 2·0	Apr. 1937	,, ,,
90	90	*c.* 600	50	40	1 : 2·3	June 1937	Plymouth
90	98	*c.* 200	46	*c.* 45	1 : 2·0	March 1899	Lofoten Islands (Browne, 1903)
160	80	*c.* 400	40	—	—	—	Scotland (Wright, 1861)
170	73	450	46	—	—	Dec. 1908	Firth of Forth (Evans & Ashworth, 1909)

An older specimen was caught off Plymouth on 7 November 1935. It was 4·1 mm. in diameter (Pl. XXI, fig. 5). The umbrella was dome-shaped, with thick apical jelly becoming thin towards the margin. There were still only four mouth-lips. There were eight complete radial canals and an additional eight developing as short outgrowths from the stomach. There were sixteen fully developed marginal tentacles, four of which were perradial, four interradial, and eight adradial. There were also sixteen marginal bulbs without tentacles, one between adjacent tentacles. There were twenty-six marginal vesicles, each with one to four concretions. The subumbrella was still bright yellowish green. The marginal tentacle bases were yellowish with two lateral strips of bluish black pigment. A slightly more advanced stage of about the same size was collected at Valencia by Dr W. J. Rees on 6 August 1938. Of the sixteen radial canals ten had now joined the ring canal. There were sixteen marginal tentacles and twenty-four marginal bulbs. In addition to the four well-developed lips, four very small lips were just beginning to appear. From this stage onwards development becomes rather irregular. Data for medusae of different sizes are given in Table IX. In this table the total numbers of complete and developing radial canals are given, but, when known, the number of developing radial canals is given in brackets after the number of completed canals. Similarly, the total numbers of marginal tentacles and marginal bulbs are given, and, when known, the number of marginal bulbs is given in brackets after the number of marginal tentacles. Some of these data have been derived from information sent to Mr Browne by Miss Delap.

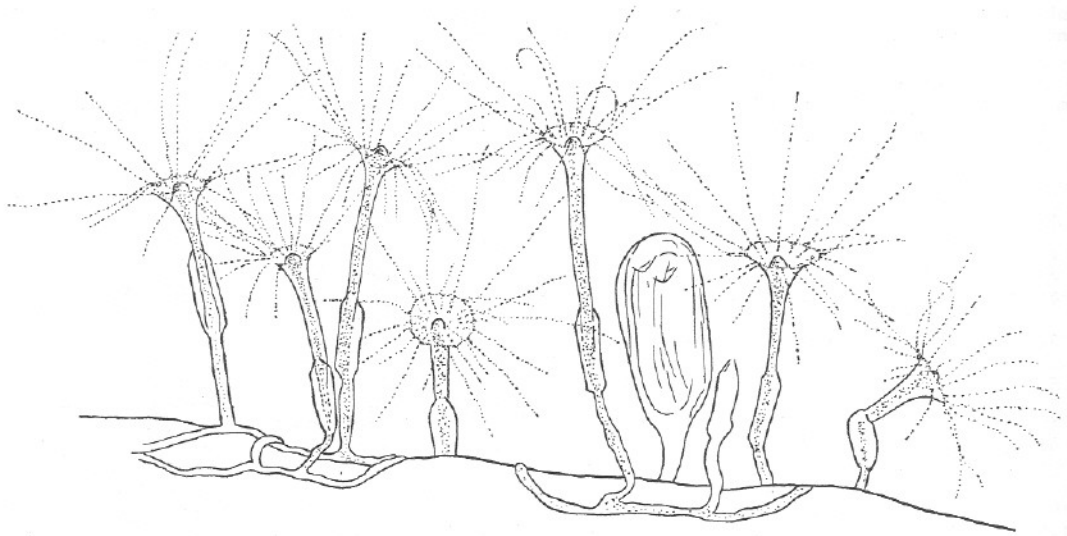
The young hydroid was reared from the medusa by Wright (1861, 1862).

AEQUOREIDAE

NEMATOCYSTS. Atrichous haplonemes and ? basitrichous haplonemes or mastigophores (Russell, 1939*b*).

Seasonal occurrence

Aequorea vitrina has been recorded from the plankton in British waters in the following months: January (North Berwick); December (Burntisland); August (Watermouth, N. Devon); May, June, September, and November (Plymouth); April (mouth of English Channel); May, June, August and September (Valencia).



Text-fig. 224. *Aequorea* hydroid sent from Cullercoats to the Plymouth laboratory by Dr H. O. Bull, December 1936. Drawn 10. iii. 37; medusa bud added 1. iv. 37. (Medusa bud had same green colour as in Pl. XXI, fig. 3.)

Habits

Gosse (1853) records having observed the mouth of the living animal dilate to its full extent so as to form a wide circular orifice. He remarks that 'in captivity it was moderately active, swimming gracefully, but keeping the tentacles generally contracted and inconspicuous. It was luminous when irritated in the dark.'

Gosse also states that 'at the point where the canals enter the circular frosted disk, they have thickened fleshy lips, capable of closing so as to make tubes, or of separating to form grooves'.

HYDROID. ? '*Campanulina*' *acuminata* (Alder). (Text-figs. 222, 224.)

(For full description see Hincks, 1868, *Brit. Hydroid Zooph.* p. 187, pl. xxxvii.)

Colonies of single, or more or less branched, slender hydranths reaching a height of *c.* 20 mm., rising from a creeping stolon. Hydrocaulus strongly annulated at base, annulations becoming less marked towards hydrotheca. Hydrothecae cylindrical, tapering to a fine toothed opercular point, with base at right-angles to lateral wall; perisarc with fine longitudinal striations. Hydranth colourless, very extensile, with about twenty filiform tentacles in one whorl, united at their bases by a membranous web. Gonothecae large and cylindrical, arising from stolon or from hydrocaulus on short, imperfectly annulated stems, containing one, rarely two, medusa buds.

Historical

Aequorea vitrina was first described by Gosse (1853) from specimens collected off the north Devon coast. Haeckel (1879) states that after seeing Lesueur's plates he had little doubt that *A. allantophora* of Péron & Lesueur was the same species. Péron & Lesueur's (1809) description is, however, quite inadequate, and their plates were never published. The specific name *vitrina* should therefore be kept.

In its chief characteristics the species appears to be indistinguishable from *A. coerulescens* (Brandt) as described by Bigelow (1909*a*). This latter species has blue-black marginal tentacle bases but it is perhaps doubtful whether this can be regarded as a specific difference. If it should eventually be concluded that the two species are the same, it would probably still be advisable to retain the name *vitrina*, since Brandt (1838), in his original description, stated that the medusa had two rows of marginal tentacles.

Aequorea pensilis (Haeckel) (Modeer)

Plate XXXIII, figs. 1–5; Text-figs. 220C, D, 225

Medusa sp. Forskål, 1776. *Icones rerum naturalium*, pl. xxviii, fig. B.
Medusa coelum pensile Modeer, 1791, *Nova Acta phys. med. L.C.* VIII, App., p. 32, no. 32.
Aequorea mesonema Péron & Lesueur, 1809, *Ann. Mus. Hist. nat. Paris*, tome XIV, p. 360.
Mesonema coelum pensile, Eschscholtz, 1829, *System der Acalephen*, p. 112.
L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 360.
Mesonema (*Mesonema*) *macrodactylum* Brandt, 1838, *Mém. Acad. Imp. Sci. St.-Pétersb.*, sér. 6, Sci. Nat., tome II, p. 359, pl. iv.
?*Mesonema coerulescens* Kölliker, 1853, *Zeit. Wiss. Zool. Leipzig*, Bd. IV, Heft 3/4, p. 325.
Mesonema pensile Haeckel, 1879, *System der Medusen*, p. 226.
Browne, 1904, *Fauna Geogr. Maldive and Laccadive Archipelago*, vol. II, p. 733, pl. lv, fig. 4; pl. lvii, figs. 2–9.
Browne, 1905*b*, *Rep. Pearl Oyster Fish. Ceylon, Roy. Soc. London, Suppl. Rep.* no. 27, p. 147, pl. ii, figs. 11–15.
Maas, 1905*b*, *Siboga Expedit.* Monogr. X, p. 42, pl. viii, fig. 52.
Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 173.
Browne, 1916, *Trans. Linn. Soc. London*, ser. 2 (Zool.), vol. XVII, pt. 2, p. 188.
Mesonema macrodactylum, Haeckel, 1879, *System der Medusen*, p. 226.
Maas, 1905*b*, *Siboga Expedit.* Monogr. X, p. 40, pl. viii, figs. 51, 54.
Polycanna purpurostoma Agassiz & Mayer, 1899, *Bull. Mus. Comp. Zoöl. Harvard*, vol. XXXII, p. 169, pl. viii, figs. 26–8.
Agassiz & Mayer, 1902, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXVI, p. 147.
Rhegmatodes lacteus Agassiz & Mayer, 1902, ibid. p. 147, pl. iii, figs. 15, 16.
Aequorea maldivensis Browne, 1904, *Fauna Geogr. Maldive and Laccadive Archipelago*, vol. II, p. 732, pl. lvi, figs. 4–12.
Aequorea macrodactylum, Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 174, pl. xxxvi, figs. 5–10.
Bigelow, 1919, *Bull. U.S. Nat. Mus.* 100, vol. I, pt. 3, p. 313, pl. xliii, fig. 7.
Aequorea macrodactyla, Mayer, 1910, *Medusae of the World*, vol. II, p. 333.
Browne, 1916, *Trans. Linn. Soc. London*, vol. XVII, pt. 2, p. 189.
Aequorea pensilis, Mayer, 1910, *Medusae of the World*, vol. II, p. 333.
Russell, 1939*b*, *Journ. Mar. Biol. Assoc.* vol. XXIII, p. 350, figs. 1*f*, 2*c*, *d*, 3.
Aequorea pensile, Bigelow, 1919, *Bull. U.S. Nat. Mus.* 100, vol. I, pt. 3, p. 311, pl. xlii, figs. 3, 4.

Specific Characters

Usually 120 to 180 radial canals (or half this number or less, var. *macrodactyla*); marginal tentacles usually much fewer than radial canals, about sixteen increasing to forty or more in old individuals.

AEQUOREIDAE

Description of Adult

Umbrella saucer-shaped, with thick central mass of jelly in form of plano-convex disk, jelly thin at margin. Velum narrow. Stomach large, diameter of base somewhat variable, usually about one-half to two-thirds of diameter of umbrella; lateral walls very extensile, with transparent lines radiating from ends of radial canals to mouth-lips; mouth-lips elongated, with crenulated margins, variable in number, usually approximately as numerous as radial canals. Radial canals straight and narrow, usually 120 to 180 in number, or half this number or less (var. *macrodactyla*). Ring canal narrow. Excretory pores present either as slits, or on poorly developed papillae projecting into subumbrellar cavity and leading from ring canal opposite bases of marginal tentacles or marginal bulbs. Gonads linear, bilamellar, on both sides of each radial canal, leaving short proximal and distal portions of radial canals free. Marginal tentacles usually much fewer than radial canals, about sixteen in number, increasing to forty or more in old individuals; hollow, with short laterally expanded, conical bases slightly clasping umbrella margin and with median abaxial spur and ridge; tentacular portion smooth. Marginal bulbs and swellings numerous, up to nine between adjacent marginal tentacles. Marginal vesicles exceedingly numerous, up to seven or eight between adjacent marginal bulbs, and often closely crowded on umbrella margin; closed, each with two to five concretions. Diameter of umbrella up to 100 mm. or more, usually about 60 mm. Umbrella of glass-like transparency; colour of gonads yellowish green masked by blue-grey pigment granules which alone persist after preservation; marginal tentacle bases and stomach colourless.

Distribution

In British waters *Aequorea pensilis* is only known for certain from Plymouth and Valencia, south-west Ireland. Its identity in these regions has only recently been established (Russell, 1939*b*) and it is possible that it may be found to occur farther north.

Elsewhere it occurs commonly in the warm waters of the Indian and Pacific Oceans; in the South Atlantic; Florida; and the Mediterranean.

Developmental Stages and Structural Details

Aequorea pensilis occurs in two varieties, the one being characterized by the full number of radial canals and the other by about half this number. This latter variety is known as *macrodactyla* and was regarded as a separate species. Russell (1939*b*) has, however, shown that the line of demarcation between the two varieties in this, the only character in which they differ, is so ill-defined that it is more convenient to regard it as a varietal distinction (but see Kramp, 1953).

The earliest stages of *A. pensilis* have not been described and its hydroid is not known. The smallest specimens known have been described by Claus (1883, as *A. discus*) from the Mediterranean. These were 7–8 mm. in diameter and had fifty-nine radial canals and eight marginal tentacles. The increase in the number of radial canals must be very rapid if, as might be expected, the medusa is liberated from its hydroid with only four. Bigelow (1919) also records a specimen from the east Pacific 8 mm. in diameter. This was the *macrodactyla* variety and had only twenty-nine radial canals, but (?) sixteen marginal tentacles.

The details of a representative collection of this species from Plymouth in September, 1938, are given in Table X.

This table shows that in these specimens, which were all the *pensilis* variety, the ratio of radial canals to marginal tentacles varied from 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 marginal tentacles increases owing to development of tentacles on some of the marginal bulbs. At the same time that this collection was made one specimen of the *macrodactyla* variety was caught. The occurrence of this single specimen amongst so many of the other variety raised the question whether *A. macrodactyla* was really a distinct species, as it had been regarded previously (Russell, 1939*b*). Accordingly the numbers of radial canals and marginal tentacles of most of the recorded specimens of the two types *A. pensilis* and *A. macrodactyla* were plotted on a single diagram, reproduced in Text-fig. 225. The figure shows that there is a tendency towards two distinct groupings, but the distinction between them is not sufficiently clear-cut to allow the borderline specimens to be allocated for certain either to one group or the other. It thus seems advisable and more convenient to regard them as one species *A. pensilis* with a variety *macrodactyla* with half the number of radial canals.

TABLE X. *Aequorea pensilis* caught off Plymouth, September 1938

Diameter of umbrella (mm.)	No. of radial canals	No. of marginal tentacles	Ratio of radial canals : marginal 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	*c.* 175†	—	—	55	1 : 1·5

* 18 large. † 85–90 in half—remainder damaged.

The *umbrella* is a characteristic feature of this species, for the central mass of jelly is very thick, and in the form of a plano-convex lens.

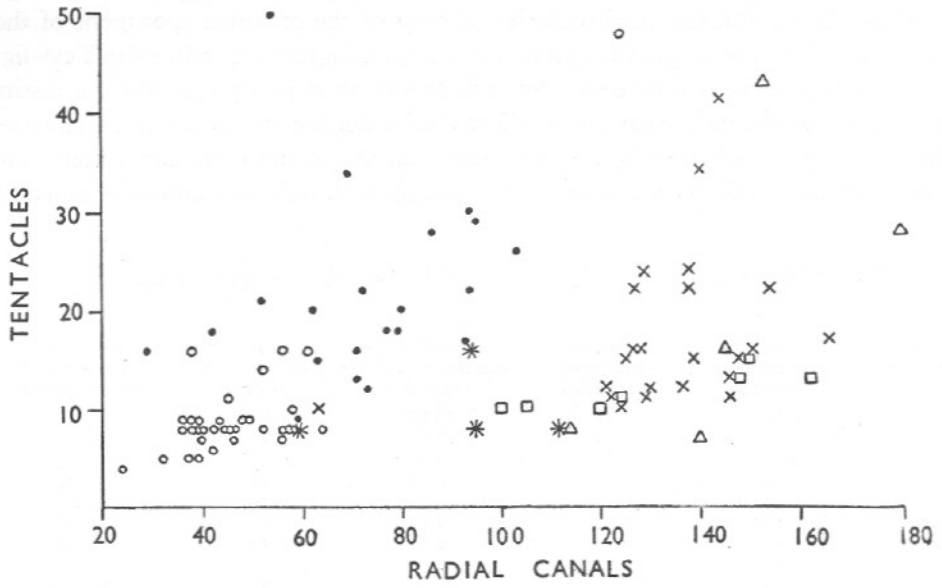
The *stomach* is essentially similar to that of *A. forskalea*, but on the whole its diameter is slightly greater in relation to that of the umbrella. Thus the radial canals appear to be short.

The *radial canals* are very slender and in *A. pensilis* there is a marked tendency towards branching and anastomosis. This is not so marked in the *macrodactyla* variety. The canals

vary considerably in width in a single specimen, and it is common to find about half the canals with gonads on them alternating with half which are only developed as very fine lines.

The *marginal tentacles* have very characteristic bases (Text-fig. 220D), but these are liable to be considerably distorted if the medusae are not in a perfect state of preservation.

NEMATOCYSTS. Basitrichous haplonemes (Russell, 1939*b*).



Text-fig. 225. 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 of Russell (1939*b*); *, *A. discus* of Claus (1883, p. 80); and △, *Polycanna forskalea* of Browne (1897*a*, p. 829). (After Russell, 1939*b*, fig. 3.)

Seasonal occurrence

Aequorea pensilis has only been recorded in the following months in British waters: September and November* (Plymouth); September (Valencia).

HYDROID. Not known.

Historical

Aequorea pensilis was first figured by Forskål (1776), but he gave no description and merely called it '*Medusa* species.' ('Medusa non descripta. Color coerulescens'). In 1791 Modeer gave Forskål's medusa the name *Medusa coelum pensile*. The question which specific name should be kept has been discussed by Bigelow (1919). He concludes that 'least confusion will result by following Browne and Mayer, and using *pensile*, but referring it to Haeckel on the ground that Modeer's name was a polynomial'.

The variety *macrodactyla* was first described by Brandt (1838) as *Mesonema* (*Mesonema*) *macrodactylum*. This medusa was shown by Russell (1939*a*) to be most probably a variety of *Aequorea pensilis*, but Kramp (1953) keeps it separate.

* Numerous in November 1948 (F.S.R.).

FAMILY EUTIMIDAE

Leptomedusae with small stomach; with peduncle; with four simple radial canals; without excretory pores; with gonads on radial canals separated from stomach; with hollow marginal tentacles; without marginal cirri; with or without lateral cirri; with closed marginal vesicles; without ocelli.

HYDROID. Where known, *Campanopsis*-like, with single whorl of filiform tentacles, with webs between their bases; polyp not completely retractile into reduced hydrotheca with or without operculum.

In their characters the medusae of the Eutimidae resemble those of the Eirenidae, with the difference that none of them has excretory pores. The chief difference, however, lies in the form of the hydroid which has a reduced hydrotheca with or without an operculum and into which the polyp is not completely retractile. The Eutimidae differ from the Campanulariidae, the Phialellidae, the Lovenellidae and the Aequoreidae in having a peduncle.

The Eutimidae are represented in British waters by four genera, *Eutima* McCrady, *Octorchis* Haeckel, *Eutonina* Hartlaub, and *Tima* Eschscholtz. The genera can be distinguished by the following characters:

With eight marginal vesicles, with lateral cirri:	
With marginal swellings without adaxial papillae	**Eutima**
With marginal swellings with adaxial papillae	**Octorchis**
With eight marginal vesicles, without lateral cirri	**Eutonina**
With more than eight marginal vesicles	**Tima**

Some authors have combined *Octorchis* with *Eutima*. But it seems to me that the presence of the adaxial papillae on the marginal swellings is sufficiently characteristic to form a generic character.

Genus **Eutima** McCrady, 1859

MEDUSAE. Eutimidae with lateral cirri; with marginal swellings without adaxial papillae; with eight marginal vesicles.

HYDROID. Where known, with characters as family.

There is one British species of the genus, *Eutima gracilis* (Forbes & Goodsir). The medusa is quite distinctive with its very long serpentine peduncle and in having only two or four marginal tentacles.

Eutima gracilis (Forbes & Goodsir)

Plate XXII, fig. 1; Text-figs. 226–32

Plancia gracilis Forbes & Goodsir, 1851, *Trans. Roy. Soc. Edinb.* vol. XX, p. 311, pl. x, fig. 1.
Goodsirea mirabilis Wright, 1859*a*, *Edinb. New Philos. Journ.* N.S. (July), p. 110, pl. ix, figs. 1–3 (and *Proc. Roy. Phys. Soc. Edinb.* vol. II, p. 80, pl. iv, figs. 1–3).
Peach, 1867, *Journ. Roy. Inst. Cornwall*, vol. II, p. 357, pl. i, fig. 5.
Saphenia dinema L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 363 (? in part). (*Non* Forbes, 1848.)
Siphonorhynchus insignis Keferstein, 1862, *Zeit. Wiss. Zool. Leipzig*, Bd. XII, p. 29, pl. ii, figs. 3–8.
Eutima insignis, Haeckel, 1879, *System der Medusen*, p. 192.
Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 492.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 588, fig. 56.

EUTIMIDAE

Saphenia mirabilis, Haeckel, 1879, *System der Medusen*, p. 192.
Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 493, pl. xvi, fig. 5; pl. xvii, fig. 3.
Browne, 1900, *Proc. R. Irish Acad.* ser. 3, vol. v, no. 5, p. 727.
Saphenia gracilis, Mayer, 1910, *Medusae of the World*, vol. II, p. 294, fig. 159.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 586, fig. 55.

Specific Characters

Two opposite perradial, or four perradial (var. *insignis*), marginal tentacles; gonads restricted to peduncle.

Description of Adult

Umbrella nearly hemispherical; jelly thick. Velum narrow. Stomach short, cross-shaped in section, situated on extremely long narrow peduncle with small conical base; extending far beyond umbrella margin. Mouth with four small simple lips. Four straight radial canals and ring canal narrow. Gonads, not on subumbrella, but restricted to canals on narrow portion of peduncle; extending almost from base of peduncle to stomach. Two long hollow opposite, or four (var. *insignis*) perradial marginal tentacles, smooth, very contractile; without distinct swelling at base. Fifty to eighty, or more, marginal swellings. Spiral lateral cirri present, one on each side of marginal tentacle bases and usually one on each side of most marginal swellings. Eight closed marginal vesicles, each with one to six, usually three, concretions. Diameter of umbrella up to 13 mm. Colour of stomach and gonads pale pink or greenish; marginal swellings colourless or with fine black pigment granules; remainder of medusa exceedingly transparent.

Distribution

Off the British coasts *Eutima gracilis* is common in the western end of the English Channel. It has been recorded in fair numbers from the Northumberland coast. Other records are from Valencia, Port Erin, Firth of Clyde, Sound of Mull, and Queensferry, Firth of Forth. It is thus likely to be found anywhere round the British coasts, except possibly the south-eastern area.

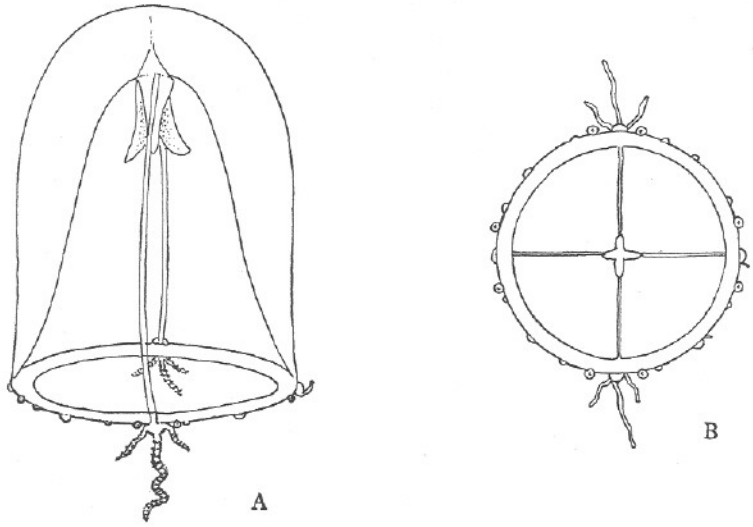
Elsewhere the medusa has been recorded from Danish North Sea waters, Skagerak, Kattegat, Helgoland, and in the Mediterranean in the Gulf of Trieste. It appears to be restricted to European waters.

Developmental Stages and Structural Details

The first stage of the medusa when just liberated from its hydroid has not been described, its hydroid being not fully known. The smallest stage most probably belonging to this species was described by Browne (1896*a*) from the plankton at Plymouth (Text-fig. 226A, B). It was only 0·5 mm. in height. The umbrella was bell-shaped, slightly higher than wide. The jelly was fairly thick and the velum narrow. The stomach was short and had no peduncle. There was a short conical knob at the base of the stomach, extending into the substance of the umbrella and terminating in a short apical stalk which did not reach to the exumbrella. The mouth had four small lips. The four radial canals and ring canal were narrow. There were no signs of gonads. There were two opposite perradial marginal tentacles, each flanked on either side of its base by a lateral cirrus; there were two opposite perradial marginal bulbs or swellings, one of which was flanked with a short lateral cirrus; there were also four interradial and eight adradial bulbs or swellings without lateral cirri. There were eight marginal vesicles situated adradially, each with a single concretion.

Browne (1895) also described a specimen 1 mm. in diameter from Port Erin. This had two long opposite perradial marginal tentacles; and two perradial, four interradial, and four adradial marginal bulbs or swellings, each flanked on either side by a lateral cirrus.

In its further development the medusa shows no great structural change except for increase in the number of marginal swellings and lengthening of the peduncle.



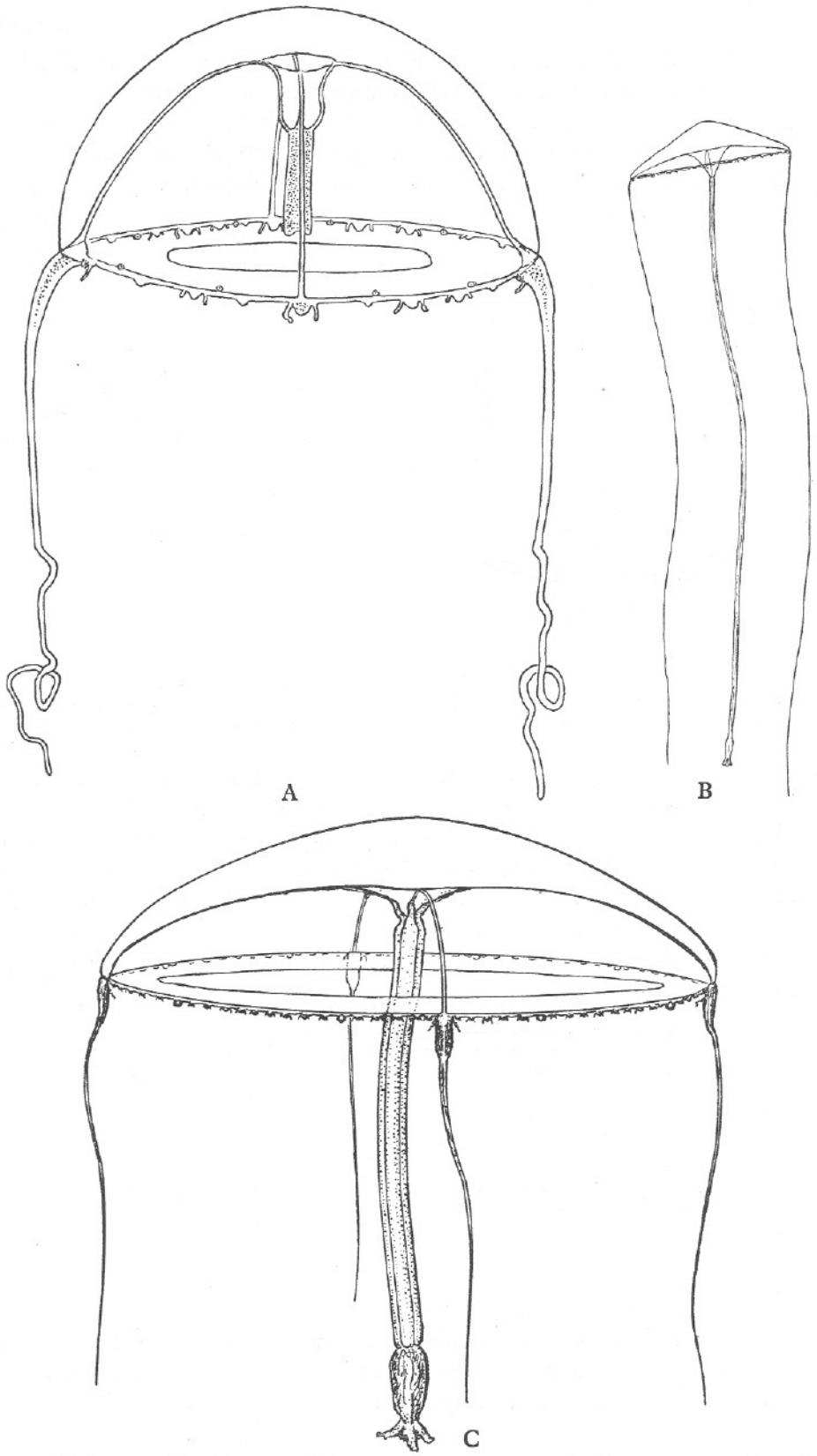
Text-fig. 226. *Eutima gracilis*. Probably a very young stage of this species, 0·5 mm. high. A, lateral view; B, diagram of umbrella margin. (After Browne, 1896*a*, pl. xvi, figs. 5, 5*a*.)

A specimen taken in May 1937 at Plymouth, 2·75 mm. in diameter, had ten marginal swellings each flanked by a lateral cirrus on either side, and eight rudimentary swellings without lateral cirri (Text-fig. 227 A). At this size the umbrella was hemispherical and there was a short peduncle at the base of the stomach, which did not project beyond the margin of the umbrella. The stomach was pale pink and there was a faint yellowish brown tinge at the bases of the two marginal tentacles and in the two perradial marginal swellings.

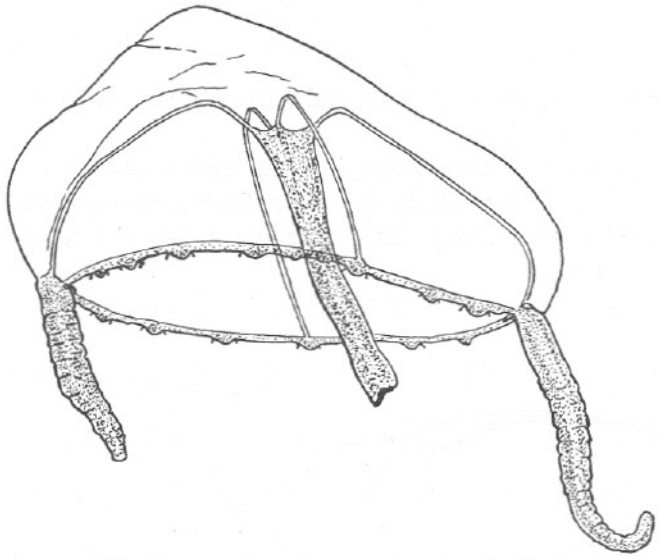
Observations on preserved specimens of different sizes at Plymouth, in April 1937, gave the following results:

Diameter of umbrella (mm.)	No. of marginal swellings			Total
	With two cirri	With one cirrus	Without cirri	
2·25	6	8	6	20
3·0	13	10	5	28
3·25	13	5	7	25
3·25	12	8	16	36
4·5	9	16	20	45
4·75	26	8	7	41
5·0	24	8	5	37
5·0	29	8	7	44
5·0	35	4	6	45
5·0	30	10	9	49
6·0	39	15	9	63
8·0	*c.* 32	12	22	66

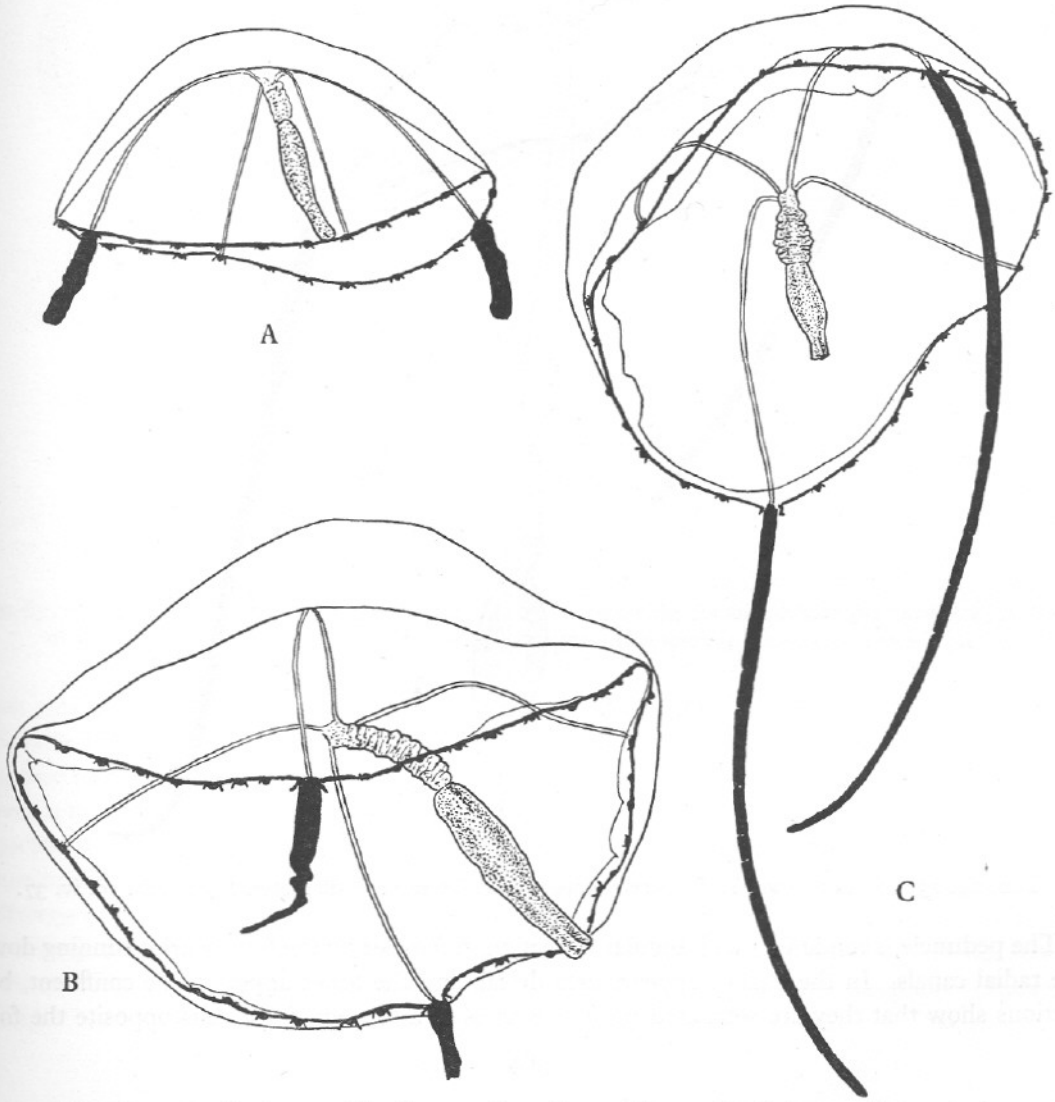
The increase in number of marginal swellings may thus be somewhat irregular. The swellings first appear as slight thickenings at the umbrella margin with dark pigment granules. The number of marginal swellings with flanking lateral cirri may reach about 100.



Text-fig. 227. *Eutima gracilis*. A, young living specimen 2·75 mm. in diameter; stomach and bases of marginal tentacles very pale pink or pinky yellow, Plymouth, 20. v. 37; B, adult drawn from life (from Kramp, 1933*b*, fig. 55); C, var. *insignis* (from Kramp, 1933*b*, fig. 56).



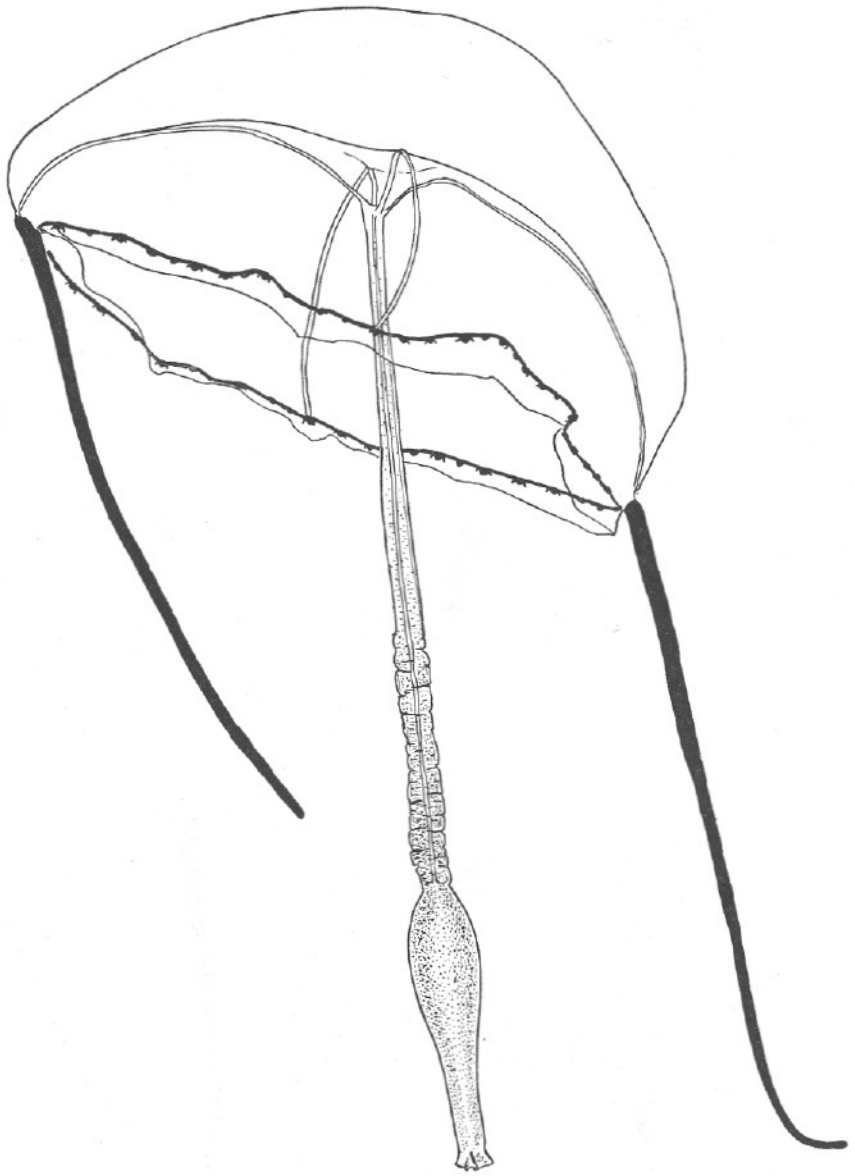
Text-fig. 228. *Eutima gracilis*. Preserved specimen *c.* 2·4 mm. in diameter, Plymouth, 28. iv. 37.



Text-fig. 229. *Eutima gracilis*. Preserved specimens, Plymouth, 28. iv. 37. A, *c.* 4 mm. in diameter; B, *c.* 5·5 mm. in diameter; C, *c.* 4·6 mm. in diameter.

The spiral lateral cirri are very contractile and terminate in a large oval swelling filled with nematocysts (Text-fig. 231 B, C).

The peduncle increases enormously in length as the medusa grows. Browne (1895) recorded a full-grown medusa in which the peduncle was about 30 mm. in length and the marginal tentacles when fully extended were 63 mm. long. In the medusa drawn by Kramp (Text-fig. 227 B) the peduncle was 45 mm. long.

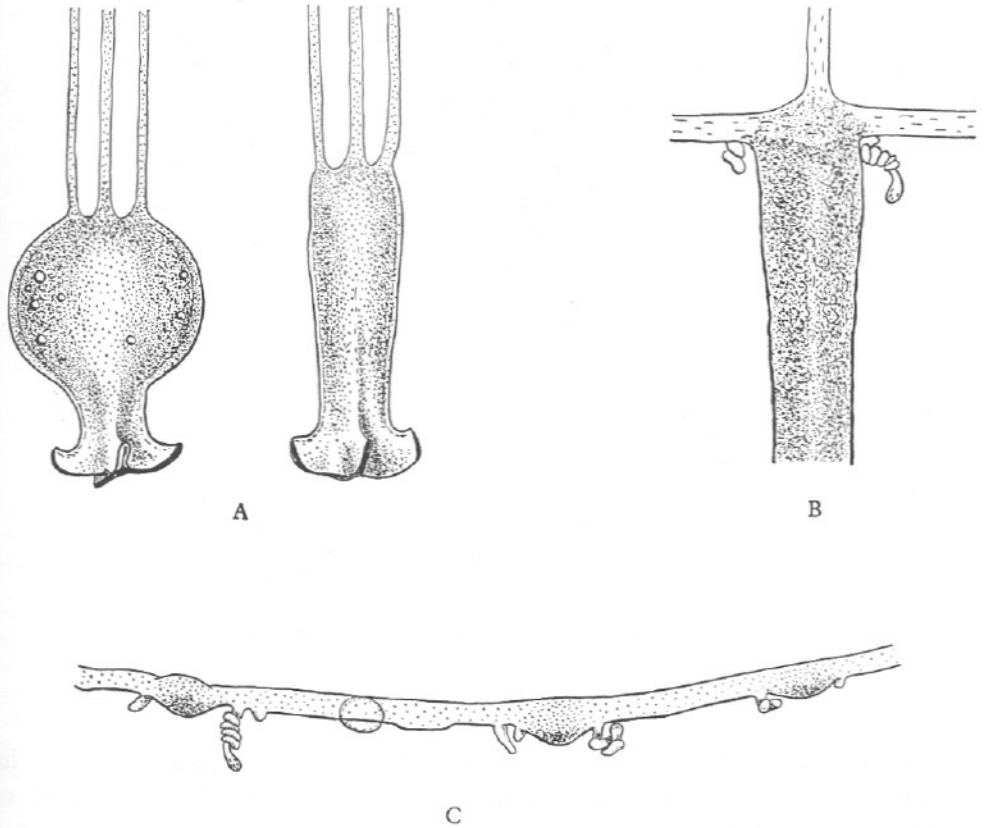


Text-fig. 230. *Eutima gracilis*. Preserved specimen *c.* 6·6 mm. in diameter, Plymouth, 29. iv. 37.

The peduncle is rendered quadrangular in section in females by the four ovaries running down the radial canals. In the male it appears cylindrical, and the testes appear to be confluent, but sections show that they are separated by four masses of a few ectoderm cells opposite the four

radial canals. They thus cover the surface of the peduncle between the radial canals. The sperm cells are in the ectoderm, which is separated from the endoderm by a well-marked lamella. The gonads begin to appear in specimens about 5 mm. in diameter.

Eutima gracilis may occur with four perradial marginal tentacles. This is the variety known as *insignis* (Text-fig. 227 C). Browne (1900, p. 727) records specimens from Valencia which indicate that the four-tentacled variety starts its free-swimming life with only two opposite marginal tentacles. Thus, his specimens had two long opposite marginal tentacles, and two marginal tentacles



Text-fig. 231. *Eutima gracilis*. A, stomach, that on left is probably distended by a pilchard egg; B, base of marginal tentacle; C, portion of umbrella margin. (Preserved, B and C to same scale.)

much smaller, varying in length in the different individuals. One of these specimens (Browne, MS. notes) was 12 mm. in diameter and had two opposite marginal tentacles each *c.* 10 mm. long, and two very small opposite marginal tentacles *c.* 2 mm. long. Since the two-tentacled form differs in no way from that with four marginal tentacles, except as regards the number of marginal tentacles, it is convenient at present to regard them as the same species because it is impossible to distinguish them in their young stages.

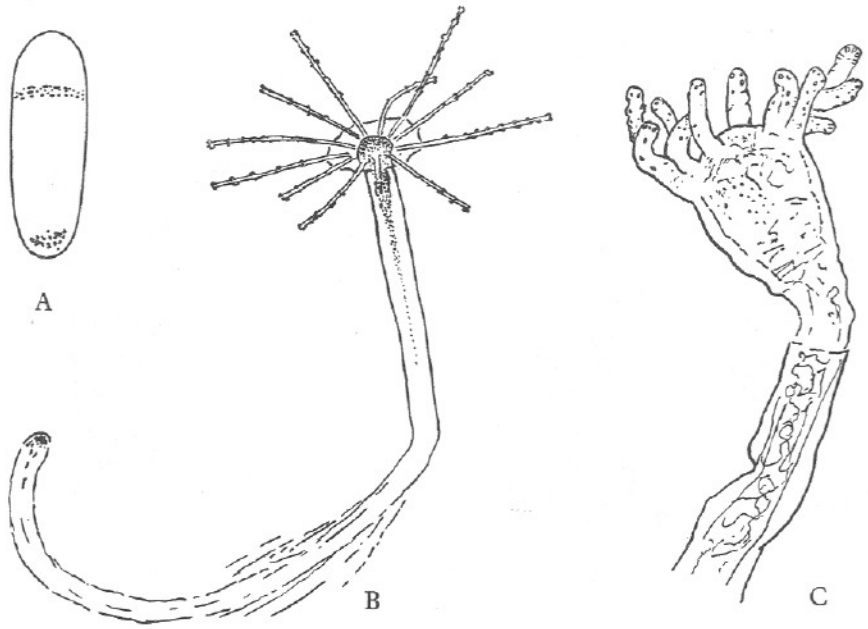
Browne (1900) records an abnormal specimen with ten marginal vesicles, and also (in his MS. notes) mentions two specimens with three marginal tentacles. (See also p. 20, Text-fig. 10 C.)

NEMATOCYSTS. Basitrichous haplonemes; atrichous haplonemes; and ? mastigophores (Russell, 1938*b*).

EUTIMIDAE

Seasonal occurrence

Eutima gracilis has been recorded in the plankton off Plymouth in every month of the year. It is most abundant from May to July, but may be quite common in August and September. At Valencia it has been recorded from April to September. Elsewhere on British coasts it has been found in the following months: September and October, Northumberland coast; September, Firth of Forth; July, Firth of Clyde; April, Port Erin.



Text-fig. 232. *Eutima gracilis*. Primary hydranth reared in the Plymouth laboratory from the medusa. (After Russell, 1949, fig. 1.)

Habits

Eutima gracilis is an extremely graceful medusa and is a beautiful object when living happily in an aquarium with its two marginal tentacles and long peduncle moving in waving curves. It has a glass-like transparency.

Lebour (1923) has observed the medusa eating *Sagitta*, copepods and *Obelia*. It may catch its prey with its long manubrium as well as with its marginal tentacles.

Off Plymouth the medusa generally lives in the daytime in the water layers below 20 m. (Russell, 1925, 1927, 1928, 1931). It migrates into the upper layers at night.

Hydroid (Text-fig. 232). The primary polyp has been reared in the laboratory at Plymouth (Russell, 1949). The hydranth had a single whorl of twelve filiform tentacles united at their bases by a membranous web. There was no hydrotheca. It resembled the hydroid of *Octorchis gegenbauri* (see p. 374).

Historical

Eutima gracilis was first described by Forbes & Goodsir (1851), as *Plancia gracilis*, from specimens caught in the Sound of Mull and off Staffa. Subsequently it was described in greater

detail by Strethill Wright (1859*a*) as *Goodsirea mirabilis*, from Queensferry in the Firth of Forth. There can be no doubt that the two are the same species. Haeckel (1879) placed the species in the genus *Saphenia* Eschscholtz.

The four-tentacled variety *insignis* was first described and figured by Keferstein (1862) as *Siphonorhynchus insignis*. Browne (1900) and Kramp (1933*b*) have both expressed the opinion that this medusa is possibly the same species as the two-tentacled *Eutima gracilis*, and I have here regarded it as such, as I have done for *Zanclea* (p. 104).

Genus **Octorchis** Haeckel, 1864

MEDUSAE. Eutimidae with lateral cirri; with marginal swellings with adaxial papillae; with eight marginal vesicles.

HYDROID. With characters as family.

There is one British species of the genus, *Octorchis gegenbauri* Haeckel. The medusa rather resembles *Eutima gracilis* in its long peduncle, but is easily identified by the gonads which are eight in number, four lying on the subumbrellar portions of the radial canals and four on the canals in the middle of the peduncle. It also has eight or more marginal tentacles. The hydroid is known under the generic name of *Campanopsis*.

Octorchis gegenbauri Haeckel

Plate XXII, fig. 4; Text-figs. 233–9

Octorchis gegenbauri Haeckel, 1864, *Jena Z. Naturw.* Bd. I, p. 331.
Haeckel, 1879, *System der Medusen*, p. 197, pl. xiii, figs. 10–16.
Claus, 1881*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. IV, Heft 1, p. 90, pls. i, ii (hydroid and medusa).
Browne, 1900, *Proc. Roy. Irish Acad.* ser. 3, vol. V, no. 5, p. 722.
Browne, 1905*a*, *Proc. Roy. Soc. Edinb.* vol. XXV, pt. IX, p. 771.
Apstein, 1913, *Zool. Jahrb. Jena, Abt. Anat. u. Ontog.* Bd. XXXVI, Heft 4, p. 582, pls. xlii, xliii.
Tima sp. Schulze, 1875*b*, *Jahresber. Comm. Wiss. Untersuch. deutsch. Meere Kiel*, Belter: II and III, Jahrg. Bd. V, *Zool. Ergeb.* p. 138, pl. ii, figs. 7*a*, *b*.
Liriopsis campanulatus Claus, 1876, *Verhandl. Zool. Bot. Ges. Wien*, Bd. XXVI, p. 11.
Octorchis campanulatus, Haeckel, 1879, *System der Medusen*, p. 197, pl. xiii, fig. 2.
Claus, 1881*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. IV, Heft 1, p. 90, pls. i, ii (hydroid and medusa).
Octorchandra germanica Haeckel, 1879, *System der Medusen*, p. 198, pl. xiii, figs. 3–8.
Hartlaub, 1894, *Wiss. Meeresuntersuch.* Bd. I, Abt. Helgoland, Heft 1, IV, p. 195.
?*Octorchandra canariensis* Haeckel, 1879, *System der Medusen*, p. 198, pl. xiii, fig. 1.
Octorchis orientalis Browne, 1905*b*, *Ceylon Pearl Oyster Fish.* pt. IV, *Suppl. Rep.* no. XXVII (Roy. Soc.), p. 139, pl. iii, fig. 4.
Eutima campanulata, Mayer, 1910, *Medusae of the World*, vol. II, p. 302, figs. 166, 167.
Eutima (*Octorchis*) *gegenbauri*, Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, Teil 3, p. 588, fig. 58.

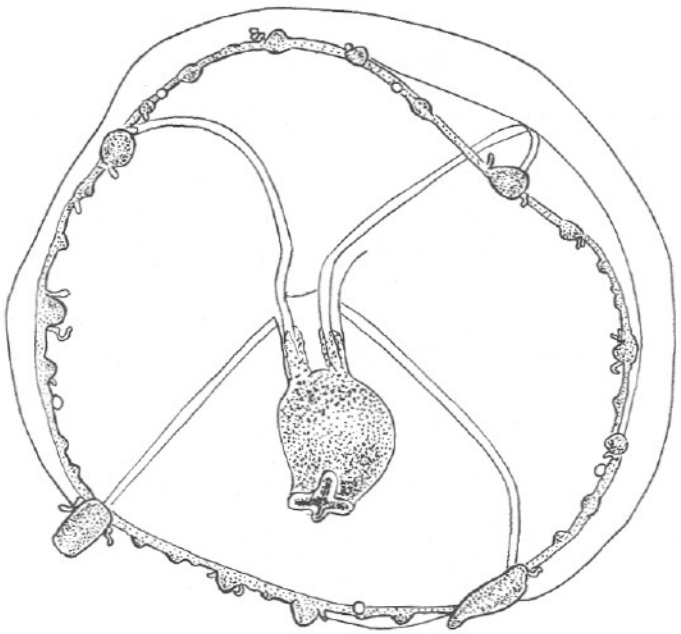
Specific Characters

Eight to sixteen, or more, marginal tentacles; eight gonads, situated on subumbrella and on peduncle.

Description of Adult

Umbrella nearly hemispherical; jelly thick, especially in apical region. Velum narrow. Stomach short, cross-shaped in section, situated on extremely long narrow prismatic peduncle with rather

broad base; extending far beyond umbrella margin. Mouth with four lips with crenulated margins. Four straight radial canals and ring canal narrow. Eight gonads; four on radial canals on subumbrella, each extending from base of peduncle nearly to ring canal, and four on radial canals on middle third of peduncle. Eight to sixteen, sometimes more, hollow marginal tentacles, thick and smooth, without distinct swelling at base. Sixty to eighty or more marginal swellings with adaxial papillae. Spiral lateral cirri present, one, rarely two, on each side of marginal



Text-fig. 233. *Octorchis gegenbauri*. Preserved specimen 2·75 mm. in diameter, Plymouth, 16. vii. 38.

tentacle bases and of marginal swellings. Eight closed marginal vesicles, each with six to twelve or more concretions. Diameter of umbrella up to 20 mm. or more. Colour of gonads, stomach and marginal tentacles greenish or bluish green, sometimes with yellowish tinge.

Distribution

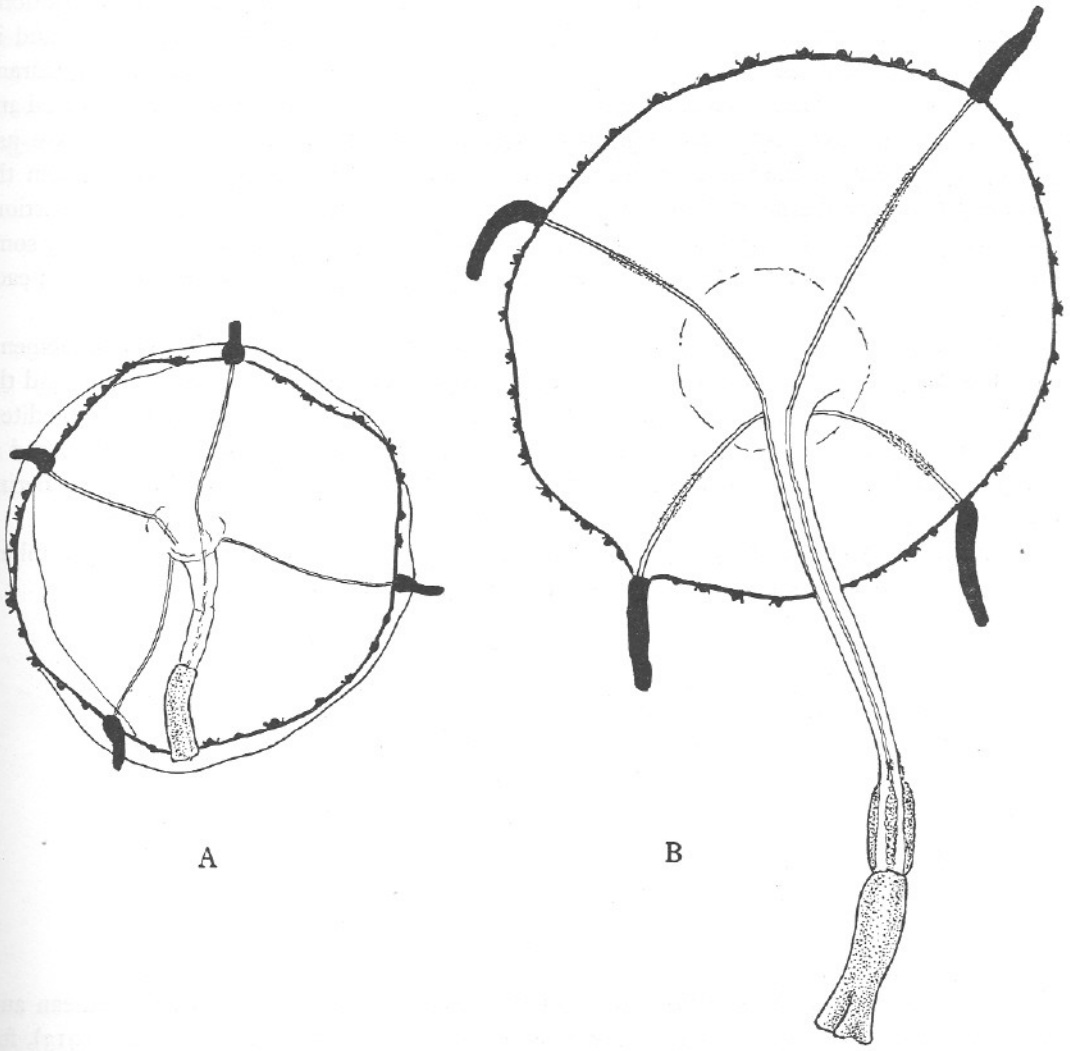
Octorchis gegenbauri has been recorded off British coasts in the following localities only: Plymouth, Valencia, Firth of Clyde, and Dover Straits. Elsewhere it has been recorded from the Skagerak, the Jutland coast, southern North Sea, Helgoland, Ostende, Oslo Fjord, the Canary Isles and the Mediterranean.

The species might thus be expected to be found anywhere round the western and northern shores of the British Isles at any rate, but it is never very abundant.

Developmental Stages and Structural Details

The first stage of the medusa has probably been described by Claus (1881 *a*) just after liberation from its hydroid, *Campanopsis*. The umbrella is bell-shaped, about 1·25 mm. high by 1 mm. wide.

The jelly is thin. The velum is broad. There are scattered nematocysts on the exumbrella, which according to Claus's drawing appear to be concentrated in an equatorial band (Text-fig. 239). The stomach is short and the mouth simple. The four straight radial canals and ring canal are narrow. There are no signs of gonads. There are two opposite perradial marginal tentacles and



Text-fig. 234. *Octorchis gegenbauri*. Preserved specimens, Plymouth, 16. vii. 38. A, 3 mm. in diameter; B, 4·5 mm. in diameter.

two opposite perradial marginal bulbs without tentacles. Spiral lateral cirri are present on both sides or one side only of each marginal bulb. The rudiments of four interradial marginal bulbs with their lateral cirri are appearing. There are eight adradial marginal vesicles, each with a single concretion.

Claus described the development of the later stages from specimens from the plankton. At a diameter of 1·5 mm. the umbrella was slightly flatter, and the four interradial marginal bulbs with their lateral cirri were formed. There were still no signs of a peduncle. When the medusa

is 2·0–2·5 mm. in diameter a short peduncle has developed. It still has only two marginal tentacles, but, besides the four interradial marginal bulbs, eight additional adradial marginal swellings with lateral cirri are developing; these develop in the interradial sides of each marginal vesicle. At a diameter of 3 mm. the medusa has four marginal tentacles, but of these the first two to form are still the larger. The peduncle is now more elongated and in each quadrant two additional marginal swellings with lateral cirri are developing, one between each marginal vesicle and its adjacent marginal tentacle. There are thus now five marginal swellings in each quadrant. At 3·5–4·0 mm. the four marginal tentacles are now of equal size. The peduncle is elongated and narrowing, and the mouth-lips are slightly folded. The first four gonads to develop are just beginning to appear on the radial canals on the peduncle just above the stomach. When the medusa is 5·5 mm. in diameter the beginnings of the four gonads on the subumbrellar portions of the radial canals are just appearing, while those on the lengthening peduncle have already some ripe sexual cells (Text-fig. 234B). There are now twelve to fourteen marginal swellings in each quadrant.

At a diameter of 7–8 mm. the gonads on the subumbrella show recognizable sexual elements for the first time. There are twenty to twenty-five marginal swellings in each quadrant, and the marginal vesicles have each six to eight concretions. These observations were made on Mediterranean medusae and Claus states that medusae with eight marginal tentacles are often found at this stage of development. Above this size they may have more marginal swellings, numbering about 120 in all.

Data on the dimensions and structure of a few British specimens are given below. The numbers of concretions in the marginal vesicles, when known, are given in brackets.

Umbrella		Length of manubrium (mm.)	No. of marginal tentacles	No. of marginal swellings	No. of marginal vesicles
Diameter (mm.)	Height (mm.)				
4	.	4	4	29	8
4	.	4	4	28	.
6	.	6	4	.	8 (10–12)
7	5	.	4	66	8 (6–9)
8	5	.	4	.	8 (3–5)
9	6	12	8	60	8 (6–10)
10	7	25	4	87	8
17	11	22	8	80	8

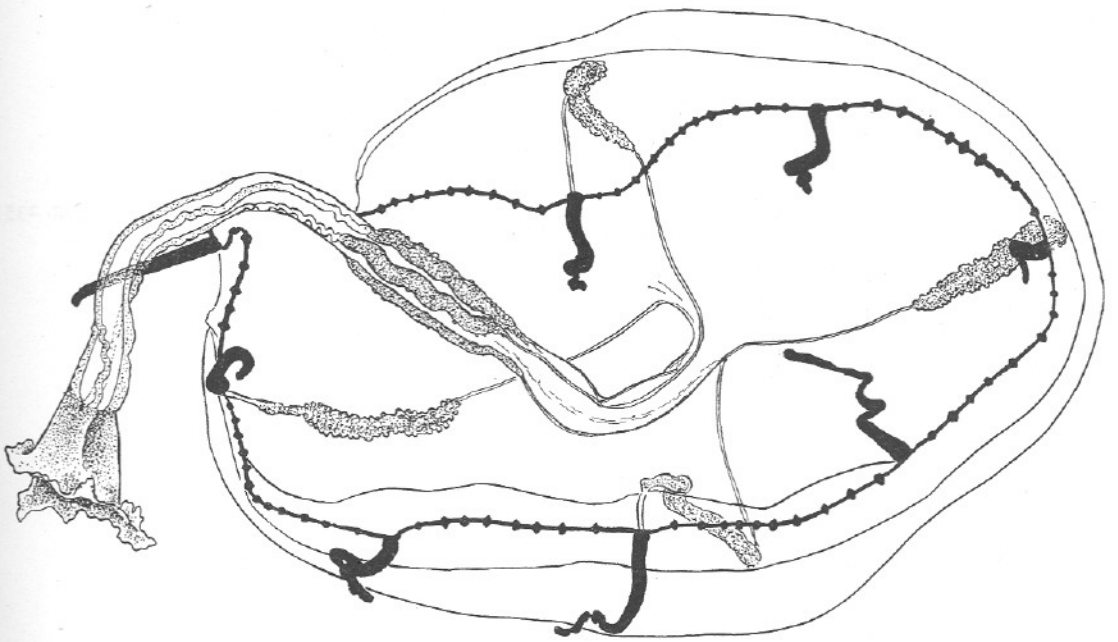
While eight appears to be the normal number of marginal tentacles in Mediterranean and perhaps southern British specimens, a greater number may be developed. Apstein (1913), for instance, gives the following figures for medusae from Helgoland:

Diameter of umbrella (mm.)	No. of marginal tentacles
3	4
5	11
10	8
10	12
10	21
11	10
12	13
13	20
14	16

These figures indicate that the number of marginal tentacles may not bear a strict relation to the size of the medusa.

The total number of marginal tentacles may reach thirty-two, if *Octorchandra canariensis* Haeckel (1879) is the same species.

In the adult medusa the peduncle has a short, but widely conical, base which narrows suddenly into the elongated portion. As already stated the gonads on the peduncle usually develop first and these may already have ripe sexual cells while the subumbrellar gonads are still rudimentary. This sequence of development, however, appears not always to be constant, for Apstein records a specimen in which it was reversed. He has also found specimens only 4 mm. in diameter which



Text-fig. 235. *Octorchis gegenbauri*. Preserved specimen *c.* 15 mm. in diameter, off Plymouth, 23. viii. 33.

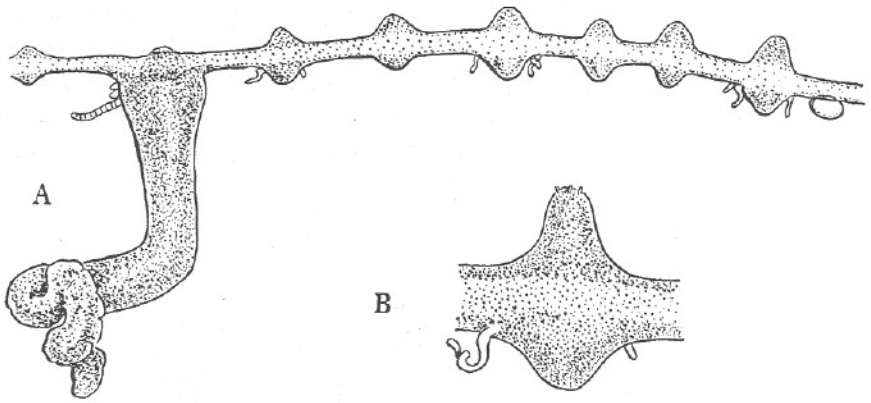
had all eight gonads already well developed and had eight marginal tentacles; it was thus further advanced than medusae of that size described by Claus.

When fully developed the gonads on the subumbrellar portions of the radial canals arch over the top of the subumbrella and extend for a short distance down the base of the peduncle. The subumbrellar gonads are usually about twice as long as those on the peduncle. The development of the gonads has been examined in detail by Apstein (1913). Each gonad is spindle-shaped, tapering away to a point at either end. The peduncular gonads, which first appear just above the stomach, become separated from it by the lengthening of the intermediate portion of the peduncle, until they reach their final position in the middle of its length.

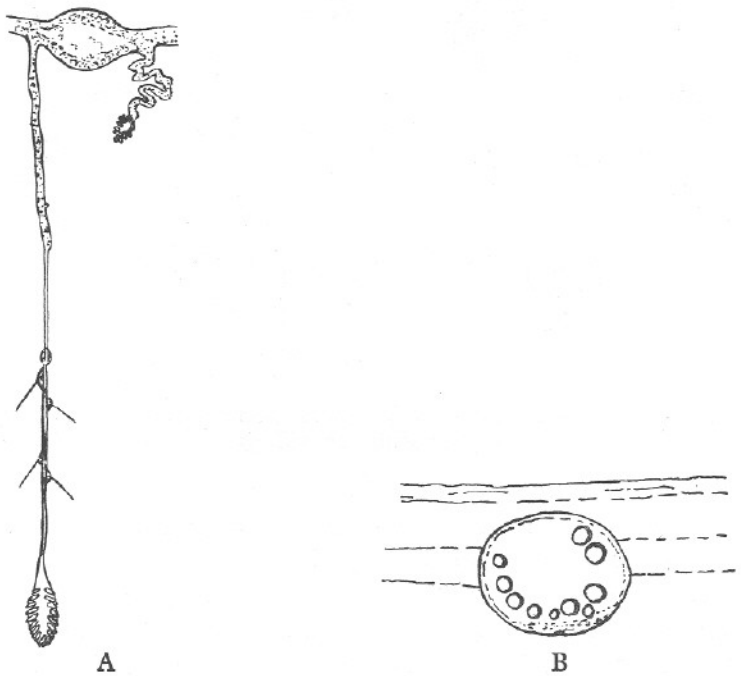
According to Apstein the egg cells first develop in the ectoderm and later become surrounded by the mesogloea or supporting lamella and project into the endoderm. Those which become separated from the mesogloea in the endoderm come to nothing. A few eggs also may be found

in the stomach walls, probably remnants from the gonads when they first began to develop on the radial canals immediately adjacent to the stomach. These also disappear.

In preserved specimens contraction of the umbrella or the peduncle may give the gonads a wavy appearance.



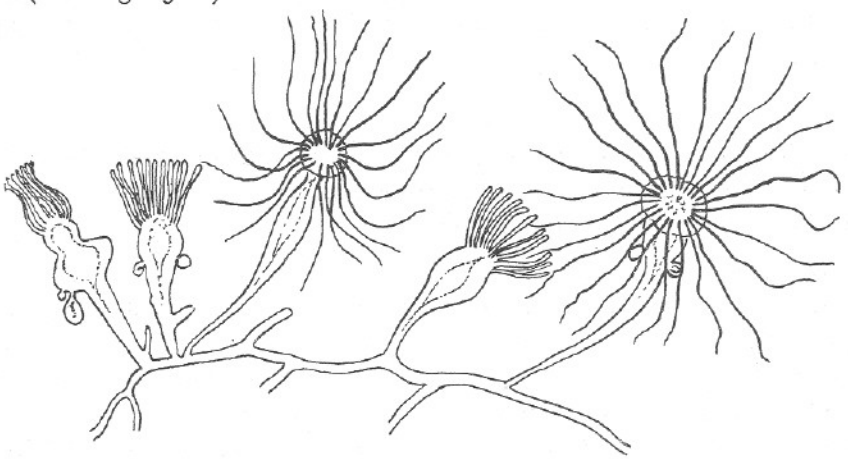
Text-fig. 236. *Octorchis gegenbauri.* A, portion of umbrella margin of preserved specimen in Text-fig. 235; B, non-tentacular marginal swelling with adaxial papilla with nematocysts, enlarged from A.



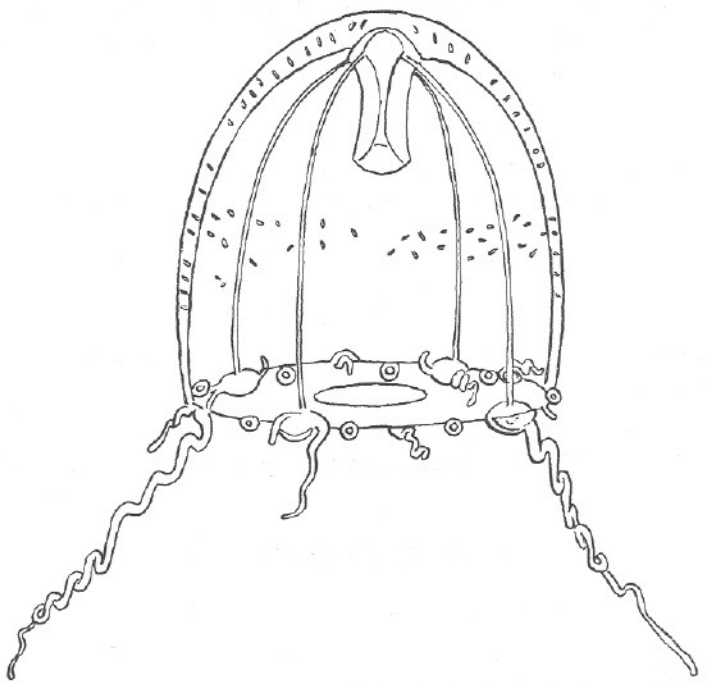
Text-fig. 237. *Octorchis gegenbauri.* A, marginal cirri; B, marginal vesicle. (From pencil drawings by E. T. Browne, 4. viii. 99.)

The marginal swellings have characteristic papillae on their adaxial or subumbrellar sides (Text-fig. 236A, B). These papillae are armed with nematocysts, and there are thus in fact two rows of marginal swellings, one pointing inwards and the other outwards. According to Claus (1881*a*) they open to the exterior, in which event they must be regarded as excretory pores.

The spiral lateral cirri are very contractile and terminate in a large oval swelling filled with nematocysts (Text-fig. 237A). These lateral cirri may sometimes be missing from the marginal tentacle bases (Text-fig. 236A).



Text-fig. 238. *Campanopsis*, probably the hydroid of *Octorchis gegenbauri*. (After Claus, 1881*a*, pl. i, fig. 1.)



Text-fig. 239. Newly liberated medusa from the hydroid *Campanopsis*, probably *Octorchis gegenbauri*. (After Claus, 1881*a*, pl. ii, fig. 10.)

The young polyp has been reared from the egg by Metschnikoff (1886*a*). The ripe eggs are 0·14 mm. in diameter.

NEMATOCYSTS. Atrichous haplonemes and ? basitrichous haplonemes or mastigophores (Russell, 1938*b*).

EUTIMIDAE

Seasonal occurrence

Octorchis gegenbauri occurs in the plankton usually in late summer and autumn. It has been recorded in the following months, January, July, August, September and October (Plymouth, most abundant in August); July, August and September (Valencia); September and November (Firth of Clyde).

Habits

According to Metschnikoff (1886*a*) the eggs of Mediterranean specimens are laid at 8 o'clock in the evening in February. Neppi (1910) records the presence of the larval anemone *Halcampa* on specimens of *Octorchis gegenbauri* at Trieste.

HYDROID. *Campanopsis*. (Text-fig. 238.)

(For full description see Claus, 1881*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. IV, Heft 1, p. 90, pl. i.)

Colonies of single hydranths rising from a creeping stolon. Hydrocaulus with thin smooth perisarc reaching nearly to base of hydranth where it thins away. No hydrotheca. Hydranth club-shaped with a single whorl of eighteen to twenty filiform tentacles connected at their bases by a membranous web. Medusa buds produced singly on stalks in two, rarely three, whorls on basal portion of hydranth.

This hydranth appeared in an aquarium tank in which Claus was keeping medusae. It has been found in the Adriatic on shells and stones (Graeffe, 1884), but has not been recorded yet from British coasts (see also Stechow, 1913).

Historical

Octorchis gegenbauri was first described by Haeckel (1864) from Nice in the Mediterranean. The history of the species has been discussed in detail by Apstein (1913).

Genus **Eutonina** Hartlaub, 1897

MEDUSAE. Eutimidae without lateral cirri; with eight marginal vesicles.

HYDROID. Not known.

There is one British species of the genus, *Eutonina indicans* (Romanes). The medusa is easily recognizable by its well-developed peduncle and very numerous marginal tentacles.

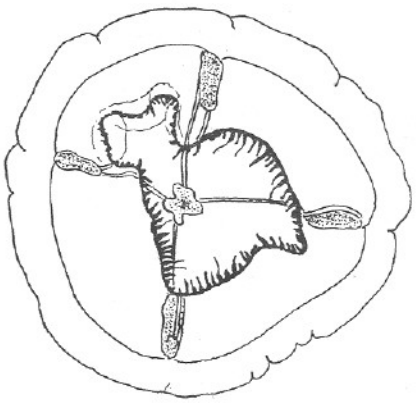
Eutonina indicans (Romanes)

Plate XXII, fig. 2; Text-figs. 240–5

Tiaropsis indicans* Romanes, 1876*a*, *Journ. Linn. Soc. London, Zool.* vol. XII, no. 64, p. 525.
Romanes, 1877*a*, ibid. vol. XIII, no. 68, pl. XV, fig. 1.
Romanes, 1877*b*, *Philos. Trans. Roy. Soc. London*, vol. CLXVII, pt. II, p. 699, pl. XXX.
Eutimalphes indicans, Haeckel, 1879, *System der Medusen*, p. 195.
Hartlaub, 1894, *Wiss. Meeresuntersuch.* N.F., Bd. I, Abt. Helgoland, Heft 1, IV, p. 194.
Thaumantias sp. M'Intosh, 1889, *VIIth Rep. Fish. Bd. Scot.* pt. III, *Sci. Invest.* sect. B, IV, pp. 282, 288, 293, pl. V, figs. 6–9.
M'Intosh, 1890*b*, *Ann Mag. Nat. Hist.* ser. 6, vol. V, p. 40, pl. viii, fig. 1.

* In his first description Romanes used the name *Tiarops*.

Eutonina socialis Hartlaub, 1897, *Wiss. Meeresuntersuch.* N.F., Bd. II, Abt. Helgoland, Heft 1, x, p. 506, pl. xxii, figs. 1, 3, 4, 6, 7; pl. xx, figs. 19, 20 (young hydroid and medusa).
Hartlaub, 1904, ibid. Bd. v, Heft 2, p. 103.
Eutimium socialis, Mayer, 1910, *Medusae of the World*, vol. II, p. 306, fig. 169*a*.
Eutonina indicans, Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, p. 34.
Kramp, 1919, *Danish Ingolf-Expedit.* vol. v, pt. VIII, p. 98, chart XIII.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 585, fig. 54.
Eutonia indicans, Uchida, 1933, *Journ. Fac. Sci. Hokkaido Univ.* ser. VI, *Zool.* vol. II, no. 3, p. 131, fig. 7 (photograph).



Text-fig. 240. *Eutonina indicans*. Preserved specimen *c.* 10 mm. in diameter, Firth of Forth, 5. vi. 09. (E. T. Browne collection.)

Specific Characters

Marginal tentacles *c.* 150 to 230 in number. Marginal vesicles with twelve concretions.

Description of Adult

Umbrella slightly flatter than a hemisphere; jelly rather thick. Velum narrow. Stomach short, situated on an elongated conical peduncle, reaching a little beyond umbrella margin; mouth with four folded lips. Four straight radial canals and ring canal narrow. Gonads linear and sinuous, situated only on subumbrellar portions of radial canals, extending from short distance from base of peduncle almost to ring canal. Marginal tentacles *c.* 150 to 230 in number, with conical bases. No lateral cirri. Eight adradial closed marginal vesicles, each with *c.* twelve concretions. Diameter of umbrella 25–35 mm. Colour of stomach, gonads and marginal tentacle bases bright sepia (Hartlaub, 1897); dark pigment on marginal tentacle bases, along dorsal surface of gonads, and along dorsal surface of grooves in roof of stomach (Sanderson, 1930).

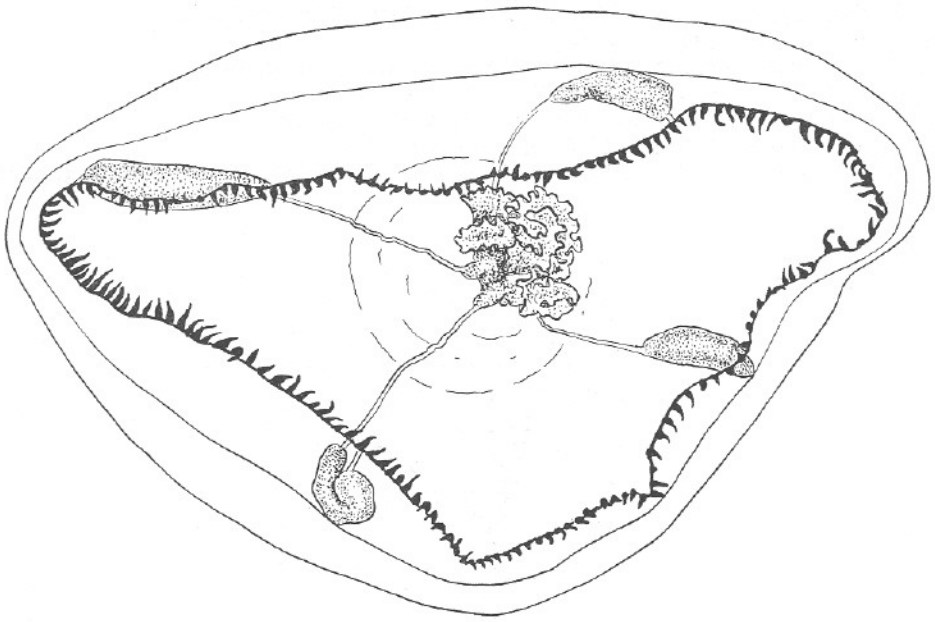
Distribution

In British waters *Eutonina indicans* has only been recorded from Dunbar harbour, Burntisland, Granton harbour, North Berwick, Isle of May, St Andrews and Cromarty Firth, on the east coast of Scotland, and from the Northumberland coast.

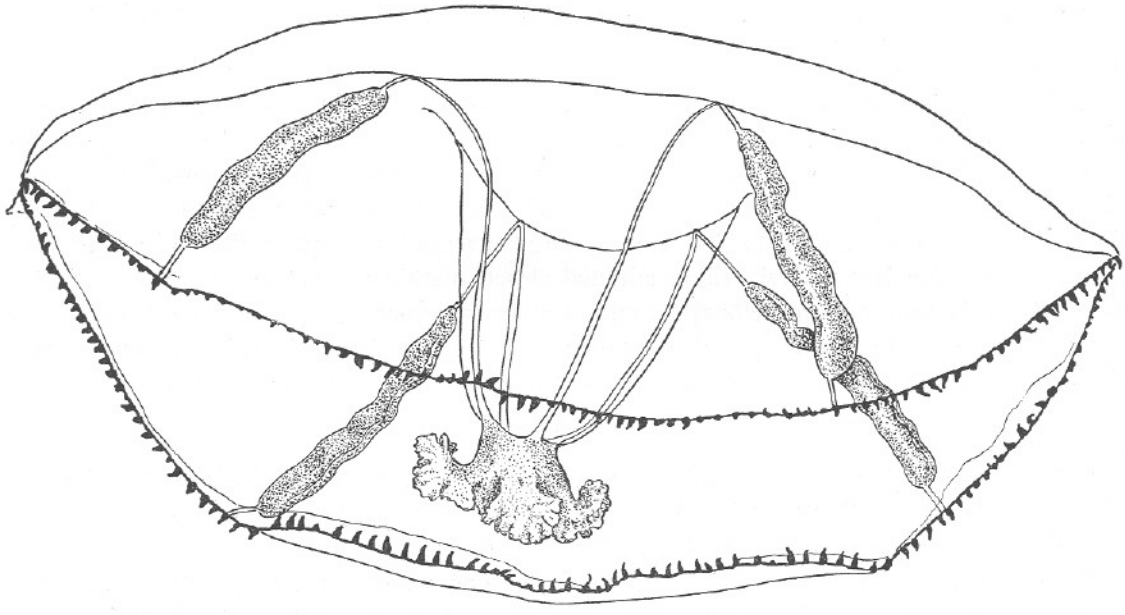
Elsewhere it has been recorded from Blankenberghe on the Belgian coast;* Helgoland; Skagerak, Kattegat, and Belt Sea; western Baltic; Norwegian coast; Iceland; Bering Sea, North Pacific; Kamchatka; Japan.

The medusa is regarded as an indicator species by Künne (1937*b*) in the western Baltic.

* I have found some specimens in Mr E. T. Browne's collection from the river Scheldt.



Text-fig. 241. *Eutonina indicans*. Preserved specimen *c*. 20 mm. in diameter, St Andrews, 1905. (E. T. Browne collection.)

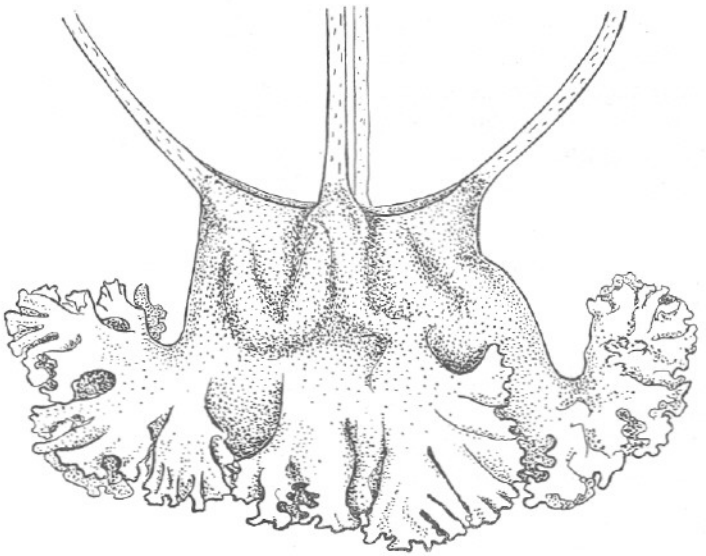


Text-fig. 242. *Eutonina indicans*. Preserved specimen *c*. 35 mm. in diameter, R. Scheldte, Belgium, 12. v. 08. (E. T. Browne collection.)

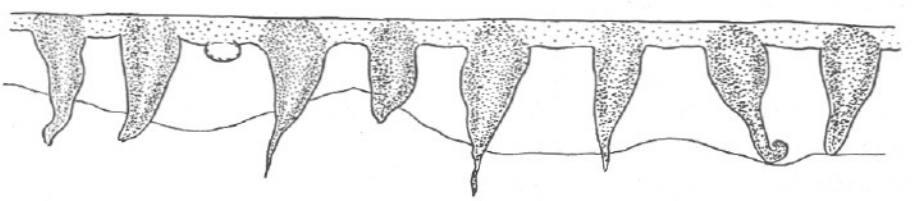
Developmental Stages and Structural Details

Although *Eutonina indicans* is quite common in the North Sea the young stages of the medusa have not been described in detail. Its hydroid is not known and the earliest stages have not been seen.

The smallest specimen mentioned in the literature was recorded by Hartlaub (1897). He had specimens 2 mm. in size and reared them in aquaria to as large as 12 mm. At their smallest stage they had eight marginal tentacles and were very similar to young *Phialidium* except that the bell was somewhat higher and rudiments of gonads were absent.



Text-fig. 243. *Eutonina indicans*. Stomach and mouth of preserved specimen in Text-fig. 242.



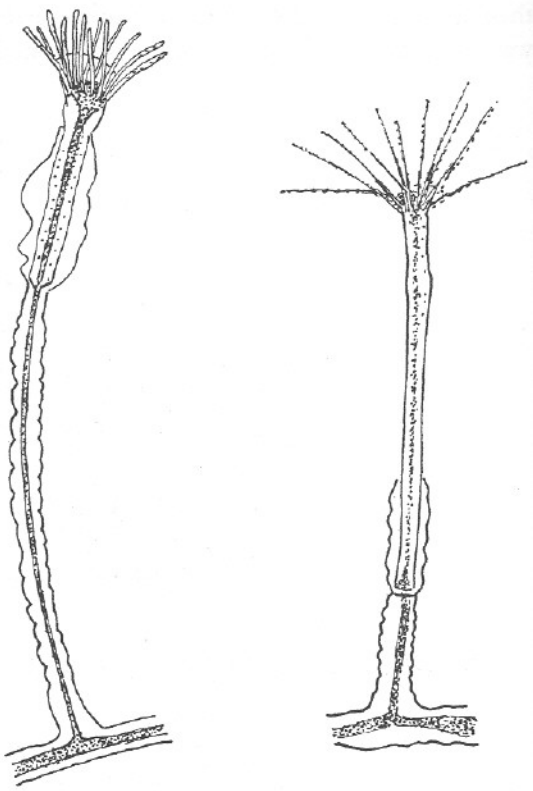
Text-fig. 244. *Eutonina indicans*. Portion of umbrella margin of preserved specimen in Text-fig. 242.

Kramp (1919, p. 100) gives the following figures for numbers of marginal tentacles and length of gonads in specimens of different sizes:

Diameter (mm.)	No. of marginal tentacles	Length of gonads (mm.)
12	171	4·5
14	*c.* 185	—
17	169	—
19	175	4
22	—	7–8
25	206	6·5
26	*c.* 196	7
26	188	6
27	204	8
27	213	6·5

Evans & Ashworth (1909) record specimens from Dunbar harbour which were 15–25 mm. in diameter when preserved and had *c.* 160 marginal tentacles. They also recorded mature specimens from Burntisland reaching a diameter of 35 mm. (see also Evans, 1916). Bigelow (1913) records a specimen from the Atlantic 28 mm. in diameter with 176 marginal tentacles, there being respectively forty-eight, forty-one, forty-five and forty-two in the four quadrants.

In all the Atlantic specimens so far examined the gonads start 1·25–3·5 mm. from the base of the peduncle. Bigelow (1913), however, obtained medusae from the Bering Sea in which the gonads started close up to the peduncle base. Neither he nor Kramp (1919) regard this as a specific difference. According to Kramp the distal end of the gonad reaches to within 1·0–1·5 mm. from the margin. Apstein (1913) states that the youngest egg cells are found in the ectoderm; they later pass into the mesogloea.



Text-fig. 245. *Eutonina indicans*. Primary hydranths reared from medusae. (After Hartlaub, 1897, pl. xx, figs. 19, 20.)

Seasonal occurrence

In British waters *Eutonina indicans* has been recorded from the plankton during the following months: May to August, Cromarty Firth; July, August and September, St Andrews; June and July, Dunbar harbour; June, Burntisland, Granton harbour, North Berwick, and Isle of May; April, June, July and August, Northumberland coast.

Habits

Romanes (1877*b*) used *Eutonina indicans* as a subject for some of his researches on the nervous responses of medusae. He found that if the umbrella were stimulated with a needle, or other object, the peduncle immediately moved so that the mouth was applied to the point of stimulation. Furthermore, if successive stimuli were given at different points the mouth moved in succession from one to the next; and, after the cessation of the stimulus, it continued to pass from one point to the next, lingering longest at those points which had been most severely irritated. It was because of this habit that he named the species *indicans*, i.e. 'pointing' to a seat of irritation located in the bell. He also stated (1876*a*) that the medusa becomes luminous when irritated, the light being restricted to a narrow but continuous line round the margin of the umbrella.

Künne (1948) records the occurrence of the larval stages of *Peachia* on this medusa in the North Sea.

Hydroid (Text-fig. 245).

The adult stage of the hydroid of *Eutonina indicans* is not yet known. Hartlaub (1897) reared primary polyps from the medusa and stated that the hydroid was a '*Campanulina*' (see Rees, 1939*b*). His figures show that there is a typical '*Campanulina*'-like hydrotheca, and that the polyp has eleven to thirteen tentacles whose bases are apparently joined by a web.

Historical

Eutonina indicans was first described briefly by Romanes (1876*a*) from the Cromarty Firth as *Tiarops indicans*, and was figured by him a year later as *Tiaropsis indicans* (1877*a*). The medusa was also recorded and figured by M'Intosh (1889, 1890*b*) from St Andrews as an unknown *Thaumantias*. In 1897 Hartlaub described the same species from Helgoland as *Eutonina socialis*. Although Romanes's description is insufficiently detailed, there can be little doubt from his figure that his and Hartlaub's species are the same. Hartlaub (1904) himself examined M'Intosh's specimens of *Thaumantias* sp. and found that they were identical with his Helgoland medusae. Other historical observations are given by Kramp (1919, 1927). Attention should, however, be drawn to two doubtful species, *Tima forbesii* Peach (1867) and *Geryonopsis forbesii* van Beneden (1866). I have discussed the identity of these two species with Dr Kramp. He points out that in Peach's species the gonads are too short for a medusa with so many marginal tentacles if it were *Eutonina indicans*. Again in van Beneden's species the gonads are more like those of *Tima bairdi*. It is evident that either these species have been inaccurately drawn or that they are something different, and on these grounds it is best to leave them out of the synonymy of *Eutonina indicans*. Their inclusion would involve changing the name of this medusa for one about which there would for ever be difference of opinion.

Genus **Tima** Eschscholtz, 1829

MEDUSAE. Eutimidae without lateral cirri; with more than eight marginal vesicles.

HYDROID. Not known.

There is one British species of the genus, *Tima bairdi* (Johnston). It is a very striking medusa on account of its large size and cannot very well be confused with any other species.

Tima bairdi (Johnston)

Plate XXII, fig. 3; Text-figs. 246–9

Dianaea bairdii Johnston, 1833, *Loudon's Mag. Nat. Hist.* vol. VI, p. 320, pl. xli.
Thompson, 1844, *Rep. XIIIth Meeting Brit. Assoc.* p. 282.
Medusa (*tima*, Eschscholtz) Dalyell, 1848, *Rare and Remarkable Animals of Scotland*, vol. II, p. 250, pl. lii, fig. 5.
Tima bairdii, Forbes, 1848, *Monogr. Brit. Medusae*, p. 37, pl. v, figs. 1, 1*a*, 1*b*.
Allman, 1871, *Monogr. Gymnobl. Hydroids*, p. 36, figs. 11, 12; p. 140.
Böhm, 1878, *Jena Z. Naturw.*, Bd. XII (N.F., Bd. V), pp. 143, 145.
Haeckel, 1879, *System der Medusen*, p. 205.
Evans & Ashworth, 1909, *Proc. Roy. Phys. Soc. Edinb.* vol. XVII, no. 6, p. 304.
Kramp, 1919, *Danish Ingolf-Expedit.* vol. V, pt. VIII, p. 102, pl. V, figs. 4–10, chart XIV.
Kramp, 1933*b*, *Nordisches Plankton*, Lief. 22, XII, p. 592, fig. 62.

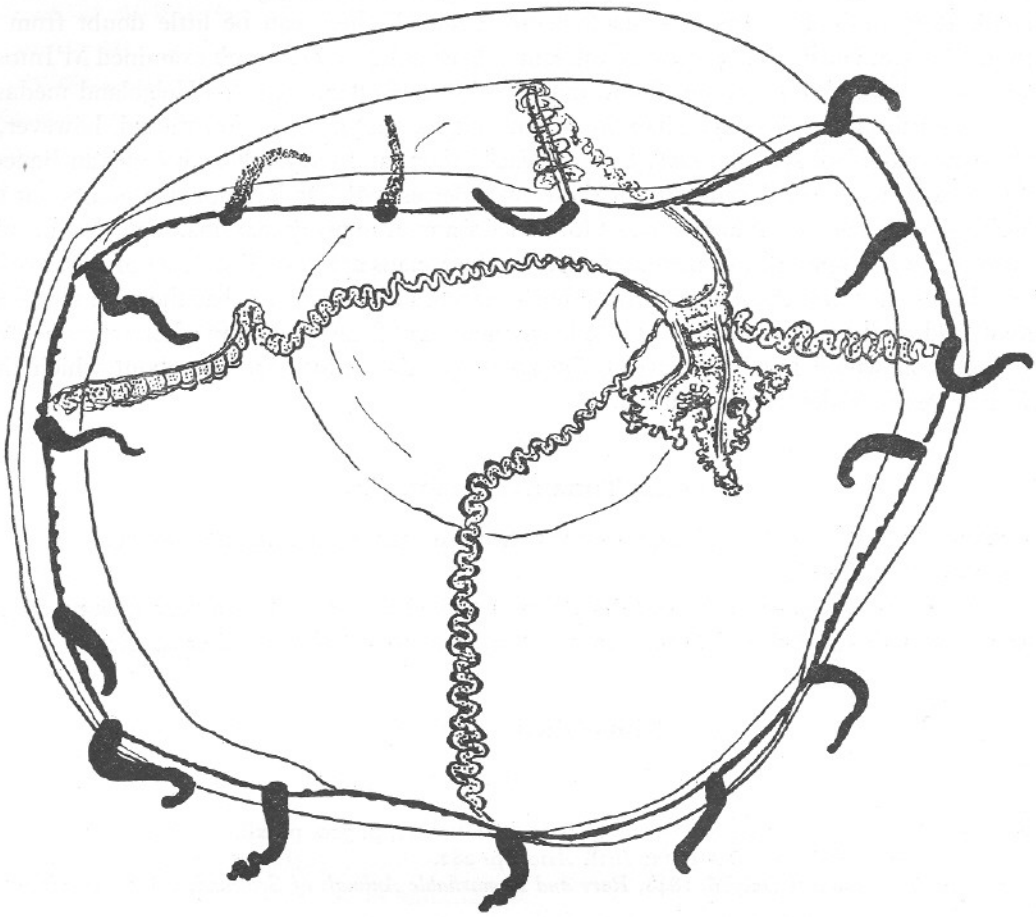
Specific Characters

Marginal tentacles normally sixteen in number; *c.* 200 to 250 marginal swellings.

Description of Adult

Umbrella hemispherical or slightly higher than a hemisphere; jelly very thick. Velum fairly narrow. Stomach small, four-sided, attached to conical peduncle by cross-shaped base, forming four triangular pouches between its dorsal wall and end of peduncle; extending slightly beyond

margin of umbrella. Mouth with four large pointed lips with much folded margins. Four straight radial canals and ring canal narrow. Gonads linear, folded, on both sides of four radial canals on subumbrella and peduncle, extending nearly from ring canal to within short distance of stomach. Marginal tentacles normally sixteen in number, with oblong carrot-shaped bases. Numerous marginal swellings between adjacent marginal tentacles, *c.* 200 to 250 in all. No lateral



Text-fig. 246. *Tima bairdi.* Preserved specimen *c.* 45 mm. in diameter, Dunbar, December, 1908. (E. T. Browne collection.)

cirri. Closed marginal vesicles about half as numerous as marginal swellings, each with four to twenty concretions. Diameter of umbrella reaching *c.* 60 mm. Colour of marginal tentacles pale pink, or faint brownish at base; gonads milky white.

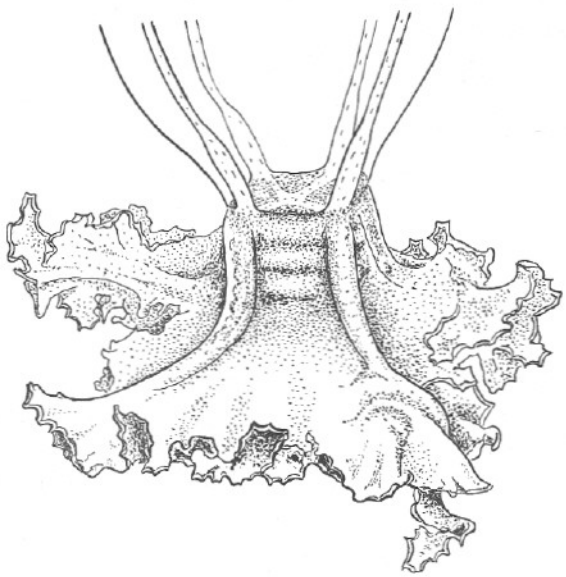
Distribution

Tima bairdi has only been recorded from the eastern coasts of the British Isles, at St Andrews, Berwick, Dunbar, Burntisland, near May Island, and on the Northumberland coast. Elsewhere it occurs off the Norwegian coast, in the Skagerak, Kattegat, Little Belt, West Baltic, North Sea, and Helgoland. Künne (1937*b*) states that it is a visitor in the Western Baltic.

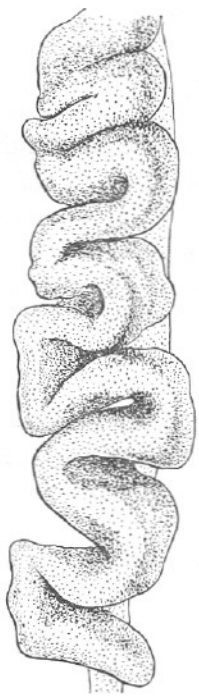
As regards its distribution in British waters Kramp (1927) says: 'It is almost certainly not indigenous off the east coast of Scotland, but appears there only as an occasional visitor in winter,

mostly November–January, when it may be very numerous....It rarely moves down along the east coast of England, but may occasionally, at intervals of several years, appear quite suddenly in great hosts.'

M'Intosh (1890*b*) states that it occurs along the east coast as far as the Thames; Hardy (1923) records its occurrence as far south as the Wash in the abnormal year 1921, and Savage (1931) as far south as Lowestoft in 1926.



Text-fig. 247. *Tima bairdi*. Stomach and mouth of preserved specimen in Text-fig. 246.



Text-fig. 248. *Tima bairdi*. Portion of male gonad of preserved specimen in Text-fig. 246.

Developmental Stages and Structural Details

The very early stages of *Tima bairdi* have not been described. Kramp (1919) has given descriptions of young specimens, the smallest of which was 6 mm. in diameter. This medusa was 4 mm. in height, the apical jelly being 2 mm. thick and the depth of the subumbrellar cavity being also 2 mm. The peduncle was short.

Three specimens, 6, 7 and 10 mm. in diameter respectively, had each four perradial and four interradial marginal tentacles equally developed; there were also eight adradial marginal swellings just visible, being the rudiments of the remaining marginal tentacles.

In two specimens, 11 and 13 mm. in diameter respectively, one adradial marginal tentacle was developed, but it was smaller than the other eight. The number of marginal vesicles in specimens 8–13 mm. in diameter was twenty-nine to thirty-four.

In a specimen 13 mm. in diameter the peduncle was 4 mm. long and 3 mm. wide at its base.

In medusae of a diameter less than 13 mm. only slight traces of the gonads are visible, and these are confined to the subumbrellar portions of the radial canals and extend from the base of the peduncle nearly to the ring canal.

A specimen 23 mm. in diameter had eighty-four marginal vesicles.

The structural details of the adult have been well described by Kramp (1919).

Stomach. The stomach (Text-fig. 247) is attached to the end of the peduncle along the arms of a perradial cross. When seen from above, the lines of attachment show as four narrow grooves from the ends of which the radial canals issue. The entrance to the radial canal can apparently be closed at its point of issue by contraction of the stomach wall. The method of attachment of the stomach leaves four triangular pouches between its upper wall and the end of the peduncle.

The conical *peduncle* has a broad base which is about half to two-fifths of the diameter of the umbrella; when fully extended its length is about equal to the diameter of the umbrella, and reaches a short distance beyond the margin of the umbrella.

The *radial canals* are slightly widened at their point of issue from the stomach and have a number of fine transverse folds in that region. The line of attachment of the radial canal to the subumbrella and peduncle is somewhat broadened by the fusion of endoderm cells from the lateral walls of the canal to the surface of the subumbrella and peduncle, in addition to the usual median streak of endoderm cells.

The *gonads* are developed on the lateral walls of the radial canals, leaving a free median streak ventrally. They are much folded into a series of regular waves (Text-fig. 248). They are most developed and folded on the subumbrellar portions of the canals and become more attenuated as they proceed down the peduncle.

The *marginal tentacles* have elongated conical bases (Text-fig. 249 A), somewhat carrot-shaped, with abaxial median longitudinal grooves. The marginal tentacles are typically sixteen in number, but Evans & Ashworth (1909) record that frequently they are not all developed, some of them being represented by minute bulbs. An examination of thirty-three specimens gave the following results:

No. of specimens	No. of marginal tentacles
9	16
9	15
5	14
6	13
2	11
1 (small)	10
1	9

In one specimen there was an extra marginal bulb besides the sixteen marginal tentacles.

Kramp (1919) states that on the abaxial sides of some of the marginal swellings there may be 'a small tenon, a rudimentary tentacle'.

The *marginal vesicles* (Text-fig. 249) have broad bases and are situated in the middle of the adaxial sides of the marginal swellings, close to the velum; those marginal bulbs with tentacular rudiments never have marginal vesicles on them.

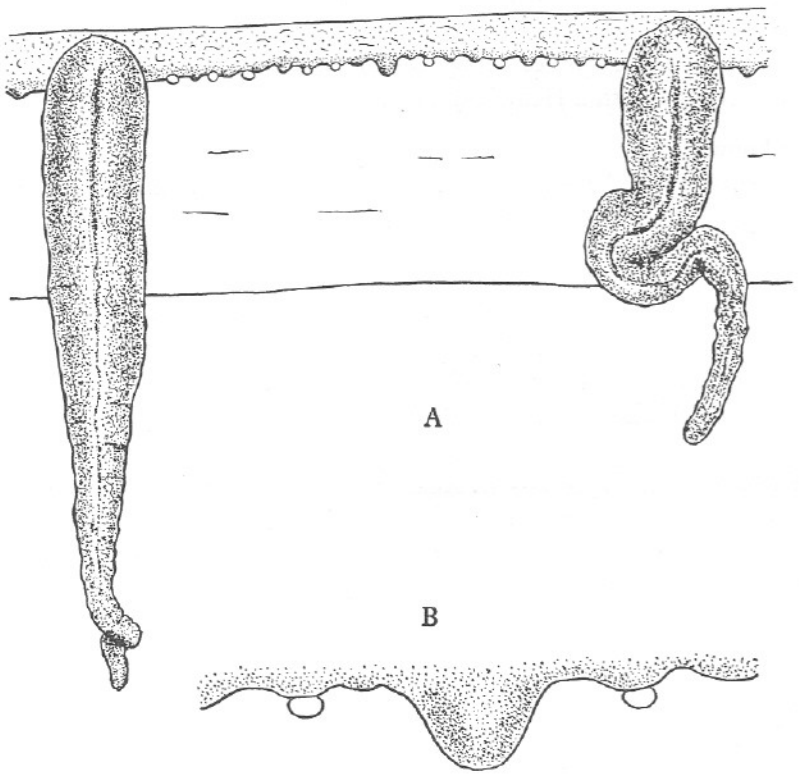
Kramp records abnormal specimens in which one of the four quadrants was narrower than the others and had no marginal tentacles between adjacent radial canals.

Seasonal occurrence

Along the east coast of the British Isles *Tima bairdi* has been recorded in the following months: January, February, May, and July to December. The greatest numbers are usually recorded in the winter.

Habits

Observations on the habits of this striking medusa have been made by Evans & Ashworth (1909), who kept some specimens alive for a week at Dunbar. When swimming, the umbrella pulsated at the rate of about forty pulsations a minute. At night, when left in the dark, they appeared to remain motionless at the bottom of the jar, but when brought into a lighted room they soon began to swim about.



Text-fig. 249. *Tima bairdi*. A, portion of umbrella margin; B, rudimentary marginal bulb, non-tentacular marginal swellings and marginal vesicles (concretions not shown), enlarged from A. (Preserved specimen in Text-fig. 246.)

If the jar was sharply struck or shaken, when in the dark, the medusae emitted flashes of pale greenish white light. A similar observation is also quoted by Forbes (1848) as having been made by Johnston in 1832.

The medusa is rather long-lived, probably taking about seven months to mature, and spawning takes place probably from November to January. M'Intosh (1889), for instance, records that at St Andrews in September they were about 1·5 inches (38 mm.) in diameter and all immature, and that in October they were at or below 1·25 inches (32 mm.) in diameter. He records further (1890*a*) that there were no ripe or nearly ripe specimens until December.

Tima bairdi is sometimes stranded on the beach in great numbers. Such records are: St Andrews, winter 1839 (Forbes, 1848); east of North Berwick, 16 March 1909 (Evans & Ashworth, 1909) and the following winter (Evans, 1916); Cullercoats and Whitley Bay, 21 November to 3 December 1921 (Storrow, 1922).

Evans & Ashworth also found it in great abundance in Dunbar harbour in December 1908, swimming at or near the surface in every sheltered corner. The majority were mature, or nearly so, and averaged *c.* 35 mm. in diameter (the largest *c.* 50 mm.), but there were also a few immature specimens 15–25 mm. in diameter. Similarly they found mature specimens, 50–60 mm. in diameter, very abundant in Burntisland harbour on 21 December 1908.

Storrow also recorded these medusae as present in great numbers off the Northumberland coast in October and November 1908.

The crustacea *Hyperia galba* and *Metopa alderi* (Bate) were found clinging to the medusae by Evans & Ashworth, the latter species being the more common.

I have seen a specimen with a Hemiurid larva.

HYDROID. Not known.

A polyp was reared by A. Agassiz (1865) from the closely related medusa *Tima formosa*. This was a small Campanularian with webbed tentacles and a short hydrotheca.

Historical

Tima bairdi was first recorded from Berwick Bay on 27 September 1832 by Johnston (1833) who described it as *Dianaea bairdii*. He named it after Dr Baird, 'one of the unselfish band of worthy assistants in the National Museum' (Forbes, 1848). It was re-described as *Tima bairdii* by Forbes (1848), since when no really adequate description was given until that of Kramp (1919).

A closely related species, *T. formosa* L. Agassiz, occurs on the American side of the Atlantic. This medusa grows to about twice the size of *T. bairdi* and has twice as many marginal tentacles. It has, however, only about half the number of marginal swellings. It is possible, as suggested by Kramp (1933*b*), that *T. formosa* is a variety of *T. bairdi*.

ORDER

LIMNOMEDUSAE

Hydromedusae with gonads either on stomach wall with continuation along radial canals, or only on radial canals; with hollow marginal tentacles; with or without internal marginal vesicles with endodermal axes.

Hydroid sessile; with or without tentacles; endoderm of tentacle in direct continuation with that of gastric cavity.

The Order Limnomedusae was erected by Kramp (1938*a*) to include the medusae of a number of genera which had been variously placed among the Anthomedusae, Leptomedusae and Trachymedusae, whose true systematic position had always been a matter for discussion. In a number of characters they show parallels between those three Orders. Thus the genera with gonads on the stomach resemble the Anthomedusae in having no marginal vesicles; while those with gonads only on the radial canals resemble the Leptomedusae in having marginal vesicles, but these have endodermal axes as in the Trachymedusae. They differ from the Trachymedusae in the structure of the marginal tentacles, which while appearing solid are really hollow, having endodermal cores consisting of a number of peripheral rows of cells and not of a column of single cells. They also differ from the Trachymedusae in having a hydroid stage in their life histories, all Trachymedusae having as far as is known direct development.

Another characteristic feature of the Limnomedusae is the absence of bulbous swellings at the bases of the marginal tentacles, which have a distinct endodermal root. This is not peculiar to the Order since a similar structure is shown among some Anthomedusae, e.g. *Bythotiara*. The nematocysts of the marginal tentacles are arranged in annular or clasp-shaped clusters. A thickening of nematocyst tissue round the umbrella margin is present as in the Trachymedusae.

The marginal vesicles, when present, are always embedded in the mesogloea between the ring canal and the umbrella margin, and they have an axis of endodermal origin. The only exception is *Craspedacusta* in which they have prolongations into the velum.

The hydroids are often considerably reduced, but when they have tentacles the direct continuation of the tentacle endoderm with that of the gastric cavity is a characteristic feature.

Kramp introduced the name Limnomedusae because most of the species lived in fresh or brackish water, the Proboscidactylidae, which are marine, being added later.

The Order contains three families, the Proboscidactylidae, the Moerisiidae, and the Olindiidae. They are distinguished as follows:

Without marginal vesicles:	
Radial canals branched	**Proboscidactylidae**
Radial canals unbranched	**Moerisiidae**
With marginal vesicles	**Olindiidae**

The Moerisiidae are not represented in British waters.

Family PROBOSCIDACTYLIDAE

Limnomedusae with or without exumbrellar nematocyst clusters; with stomach with four to six radial lobes; with four to six branching (sometimes simple, e.g. *Pochella*) radial canals; without centripetal canals; with gonads surrounding stomach and extending on to basal lobes (or only interradial on stomach wall, as in *Pochella*); with marginal tentacles without organs of adhesion; without marginal vesicles; without ocelli.

HYDROID. Where known, *Lar*-like, usually with two tentacles.

The Proboscidactylidae are represented in British waters by two genera, *Proboscidactyla* Brandt and *Pochella* Hartlaub. Of these the true systematic position of *Pochella* is uncertain, but it seems most convenient to place it in this family until more is known about its development and life history. The characteristic feature of the family is the branching of the radial canals; specimens of *Pochella* have, however, been seen in which no branches could be found issuing from the radial canals.

Genus **Proboscidactyla** Brandt, 1838

MEDUSAE. Proboscidactylidae with exumbrellar nematocyst clusters; with four to six branching radial canals.

HYDROID. Where known, *Lar*.

The genus *Proboscidactyla* has always been kept distinct from *Willia* on the grounds that the former had four radial canals while the latter had six. But since abnormal specimens of *Willia* occur with only four radial canals,* and the number of radial canals in *Proboscidactyla* itself varies from four to five, the two genera can no longer be kept distinct.

There is one British species of the genus, *Proboscidactyla stellata* (Forbes). The yellowish star-shaped base of the stomach gives this medusa a characteristic appearance. Its hydroid is well known under the name *Lar sabellarum*.

Proboscidactyla stellata (Forbes)

Plate XXIII, figs. 3, 4; Text-figs. 250–6

Willsia stellata Forbes, 1846, *Ann. Mag. Nat. Hist.* ser. 1, vol. XVIII, p. 286.
Forbes, 1848, *Monogr. Brit. Medusae*, p. 19, pl. i, fig. 1.
Gosse, 1853, *Devonshire Coast*, p. 359, pl. xx.
Mayer, 1910, *Medusae of the World*, vol. I, p. 193.
Willia stellata, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 346.
Haeckel, 1879, *System der Medusen*, p. 158.
Browne, 1904, *Fauna of Maldive and Laccadive Archipelagoes*, pp. 725, 729.
Hartlaub, 1917, *Nordisches Plankton*, Lief. 19, XII, p. 374, figs. 324–8.
Uchida, 1927*a*, *J. Fac. Sci. Univ. Tokyo, Zool.* vol. I, pt. III, p. 235.
Kramp, 1939*a*, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. CIII, p. 506, figs. 1–5 (hydroid and medusa).
Willsia cornubica Peach, 1867, *Journ. Roy. Inst. Cornwall*, vol. II, p. 355, pl. i, figs. 1, 2.
Lar sabellarum, Hincks, 1872*a*, *Ann. Mag. Nat. Hist.* ser. 4, vol. X, p. 313, pl. xix (hydroid and young medusa).
Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 468, pl. xvi, figs. 3, 4.
Browne, 1897*a*, *ibid.* p. 818, figs. 1–9.

Specific Characters

Stomach with six lobes. Twenty-four marginal tentacles.

* I have seen two such specimens collected by Dr W. J. Rees at Millport in October 1940.

Description of Adult

Umbrella dome-shaped, slightly wider than high; jelly thick. Twenty-four or more nematocyst clusters on exumbrella between marginal tentacles. Velum narrow. Stomach short, six-sided, with six lobes prolonged for a short distance over the subumbrellar surface. Mouth with six folded lips. Very short peduncle. Six primary radial canals, each giving rise to three additional branches making twenty-four in all; branching subject to considerable variation. Radial canals



Text-fig. 250. *Proboscidactyla stellata*. Preserved specimen 2·75 mm. in diameter.

narrow. No ring canal, but solid core of endodermal cells round umbrella margin. Gonads situated at base of stomach wall and continued along the six lobes of the stomach. Twenty-four marginal tentacles, each situated at end of a radial canal branch, hollow, with adaxial basal nematocyst cushions. Colour of tentacle bases yellowish brown, dark purple-brown or black; colour of stomach and gonads yellow or reddish yellow. Dimensions when full grown *c.* 8 mm. high and 9 mm. wide.

Distribution

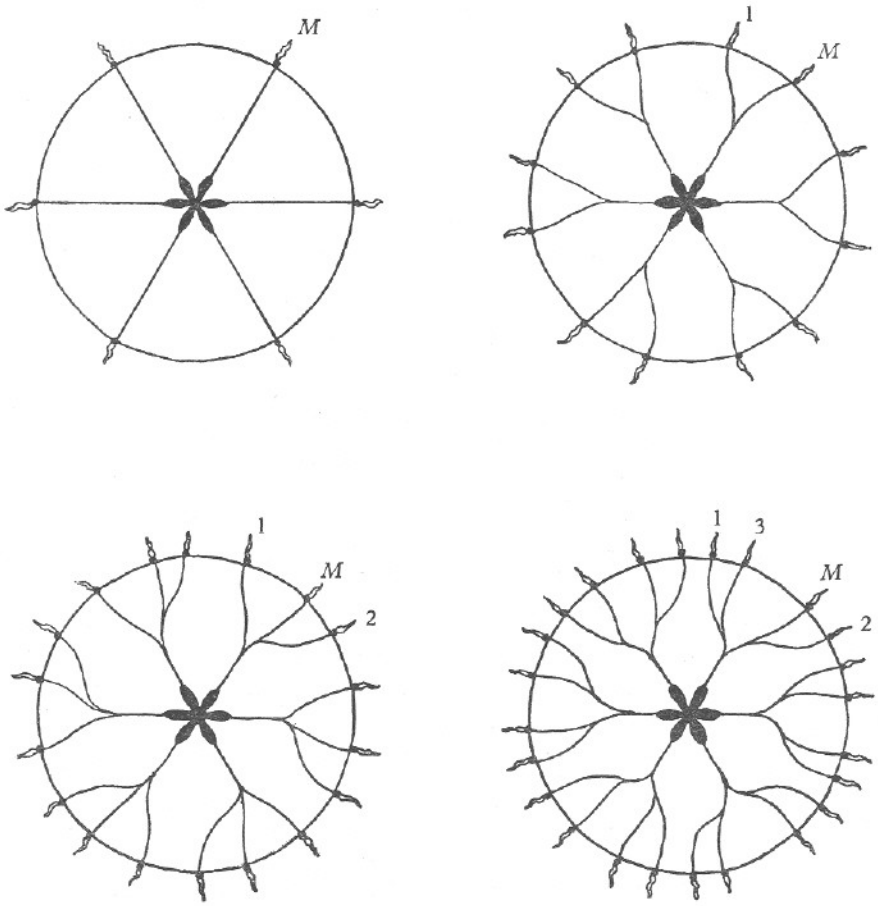
Proboscidactyla stellata has been recorded from the following localities and it is thus likely to be found all round the British coasts: Valencia and Tralee Bay, Ireland; Berry Head, Devon; Plymouth, Fowey, Falmouth, Penzance, Scilly Isles, Newquay (Cornwall); Ilfracombe, Thames Estuary, Newhaven; Lamlash, Arran; Firth of Clyde, Loch Fyne, Oban, Isle of Muck, Kirkwall, St Andrews. The species has also been recorded from Norway; Concarneau, France; and Japan.

Developmental Stages and Structural Details

The following account of the development of the medusa is based mainly on Browne (1896*a*, 1897*a*):

First stage—six uniform marginal tentacles. When first liberated from its hydroid the medusa is bell-shaped and about 1 mm. in height (Pl. XXIII, fig. 4). An umbilical canal may be present. The velum is broad. The stomach is cylindrical and about half the length of the subumbrellar cavity. It is situated on a very short peduncle and has six short prolongations or lobes from

which the six primary radial canals start. The mouth is variable in shape, being either round or with four to six lips. The six radial canals run from the lobes of the stomach direct to the umbrella margin without giving off any branches. There are six marginal tentacles, equal in size, on the margin of the umbrella, one opposite the termination of each radial canal. The base of each marginal tentacle is large and conspicuous, containing dark brown or blackish pigments. Alternating with the marginal tentacles are small clusters of nematocysts, evenly spaced on the exumbrella just above the margin.



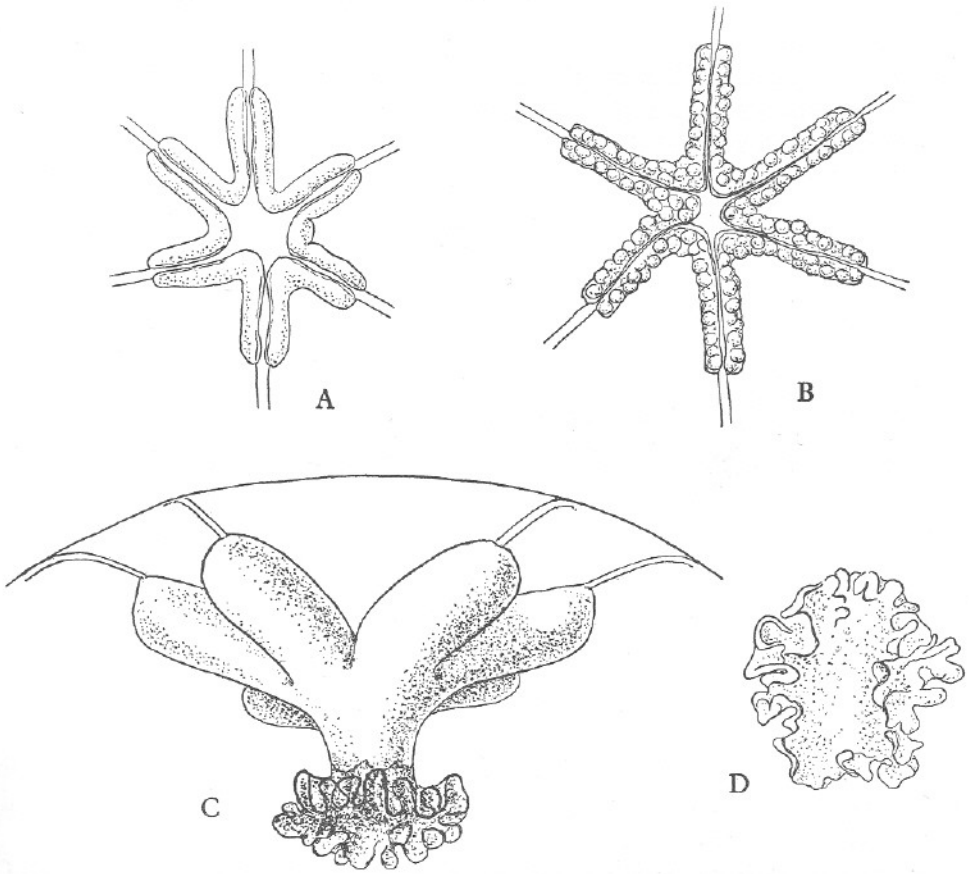
Text-fig. 251. *Proboscidactyla stellata*. Diagrams showing normal development of radial canals. *M*, primary tentacles opposite main radial canal. (After Browne, 1897*a*, figs. 1–4.)

During the growth of the medusa the radial canals branch three times so that the life history may be separated into four successive stages, including the first just described (Text-fig. 251).

Second stage—twelve uniform marginal tentacles. The commencement of the second stage is indicated by the growth of six small bulbs on the margin of the umbrella, midway between the primary marginal tentacles. From each of these marginal bulbs a tentacle grows until it resembles in size the marginal tentacles belonging to the first stage. A marginal bulb on its first appearance is of a yellowish brown colour, but when fully grown it becomes dark brown or black. As soon as a bulb makes its appearance on the margin of the umbrella, a branch is given off from the radial canal and runs to the umbrella margin opposite the bulb. The branch is always given off

from the same side of each radial canal, and leaves the canal about the middle of its course on the side of the umbrella. The six lobes of the stomach have now become more conspicuous and extend over the upper part of the subumbrella. The clusters of nematocysts belonging to the first stage still remain, and twelve new clusters appear close to the margin, one midway between adjacent marginal tentacles. Medusae belonging to the second stage are about 2 mm. in diameter.

Third stage—eighteen uniform marginal tentacles. This stage commences with the growth of another set of six marginal bulbs, which develop tentacles in the same manner as in the previous



Text-fig. 252. *Proboscidactyla stellata.* Details of preserved specimens from West Cove, Kenmare Bay, County Kerry, Ireland, August 1939. (Collected by S. W. Kemp.) A and B, male and female gonads; C, stomach; D, mouth-lips from below.

stage. The new marginal bulbs are not on the same side of the main radial canals as those belonging to the second stage, but on the opposite side. A new branch leaves each radial canal nearly opposite the junction of the first branch and runs down to the bulb on the umbrella margin. Thus in this stage each radial canal has two branch canals, one on each side of it. At this stage the reproductive cells are clearly visible, and are situated along the six lobes of the stomach and arch over the top of the subumbrella, forming a star-like pattern of a yellowish brown colour, hence Forbes's specific name of the medusa (Text-fig. 252A–C).

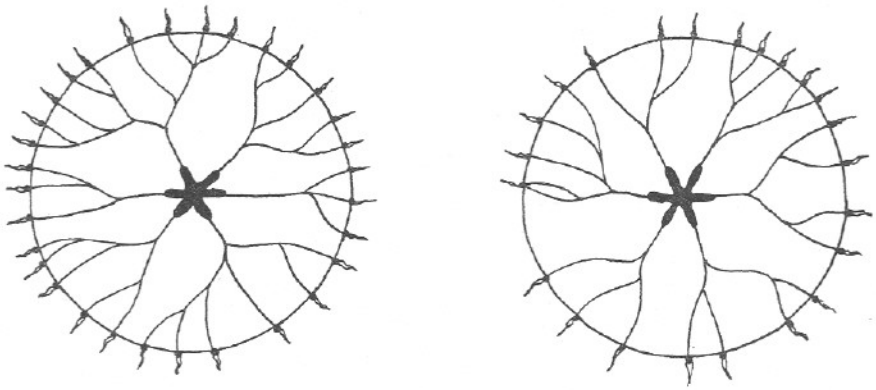
The clusters of nematocysts belonging to the first stage, and probably some belonging to the second stage, have now disappeared, and a new cluster is developed midway between every pair

of marginal tentacles. The clusters of nematocysts form an excellent mark for measuring in length the growth of the umbrella. Each series arises either on or very close to the margin, and as the umbrella grows in length so does the distance increase between the margin and each series (Text-fig. 254B).

If all the clusters were present, they would form, at the adult stage, four rows, one above the other—the uppermost set, with six clusters, representing the first stage, and the lowest, with twenty-four, belonging to the adult stage. Signs of the original clusters are often present and owing to their original interradial position they now lie immediately opposite marginal tentacles that have developed later.

Adult stage—twenty-four uniform marginal tentacles. The addition of a fourth set of six marginal tentacles brings the medusa to its adult stage. The fourth and final branch of the radial canal comes off from the first branch a little below its point of origin with the primary canal.

Considerable variation is found in the branching of the radial canals (Browne, 1897*a*) and two examples are given in Text-fig. 253. Browne also records specimens with five and seven primary canals respectively; another showed union of two lobes of the stomach to form one



Text-fig. 253. *Proboscidactyla stellata.* Examples of abnormal development of radial canals. (After Browne, 1897*a*, figs. 5, 6.)

canal which was itself abnormally branched. Hartlaub (1917*a*) records a specimen with eight rays and Uchida (1927*a*) states that in specimens from Japan the number of lips and radial canals is very variable (five to nine).

In preserved specimens the mouth-lips appear considerably crenulated (Text-fig. 252C, D).

The number of marginal tentacles in full-grown specimens is usually twenty-four; four specimens taken at Valencia in November 1896 and September 1897 had twenty-six, twenty-seven, twenty-eight and thirty-one marginal tentacles; that with twenty-eight marginal tentacles had six primary radial canals but the mouth had twelve folds.

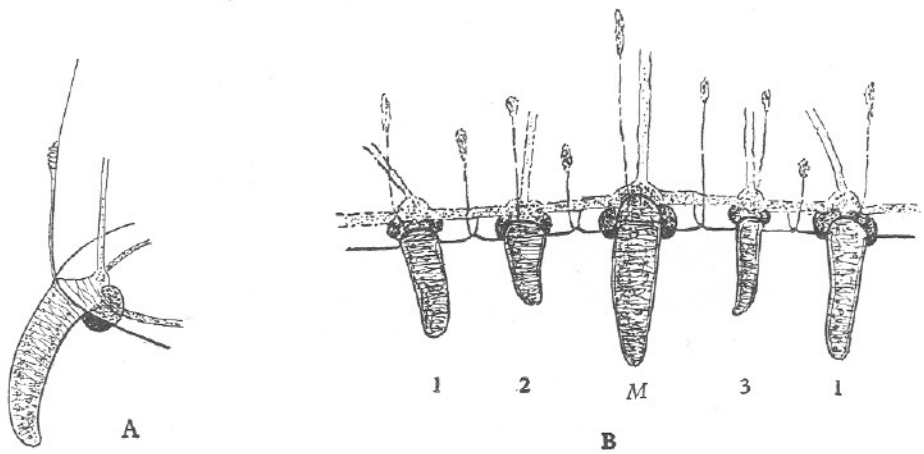
Browne (1904) examined sections of *Proboscidactyla stellata* and found that there was no true ring canal. In place of a canal there is a solid core of endodermal cells. This unusual lack of a ring canal was confirmed by Browne on examination of living material; while there was an active circulation going on in the radial canals and inside the bases of the marginal tentacles, none could be seen round the margin of the umbrella. Externally this solid core closely resembles a canal (Text-fig. 254B) and could be easily mistaken for one.

The marginal clusters of nematocysts are connected to it by a similar solid canal just beneath the surface of the exumbrella (Ranson, 1937). The number of nematocysts in a cluster, and the

shape and number of clusters, is very variable in adults; the nematocysts may be arranged in longitudinal rows or in clusters.

The gonads are situated on the six lobes of the stomach and also on the base of the stomach itself before it branches (Text-fig. 252A–C). Browne (1896*a*) showed that the stomach lobes may be regarded as part of the stomach itself. The gonads are continued along the whole of each lobe and where they end distally the lumen of the lobe suddenly decreases in diameter. Examination of sections showed that the endoderm cells of the stomach were continued without any change in size or shape along the whole portion on which the gonads are situated. Where the gonads end distally the endoderm cells become very small and flat.

The gonads may mature before the adult stage is reached, specimens between the second and third stages having ripe sexual cells. Kramp & Damas (1925) record a few specimens late in the year, August, October and November, from Norway, which had only developed as far as Stage 2.



Text-fig. 254. *Proboscidactyla stellata*. A, diagram to show the insertion of the marginal tentacle and the position of the adaxial nematocyst pad; B, the appearance of the umbrella margin in a preserved specimen with the marginal tentacles numbered in their order of development. *M*, primary tentacle opposite main radial canal.

Kramp (1939*a*, p. 507) pointed out that 'the proximal part of the marginal tentacle is partly imbedded in the gelatinous substance of the bell-margin like a hollow, endodermal root with a thickened ectodermal pad below, the point of issue of the free part of the tentacle being somewhat displaced towards the exumbrella, and more in old tentacles than in young ones'. (Text-fig. 254A.)

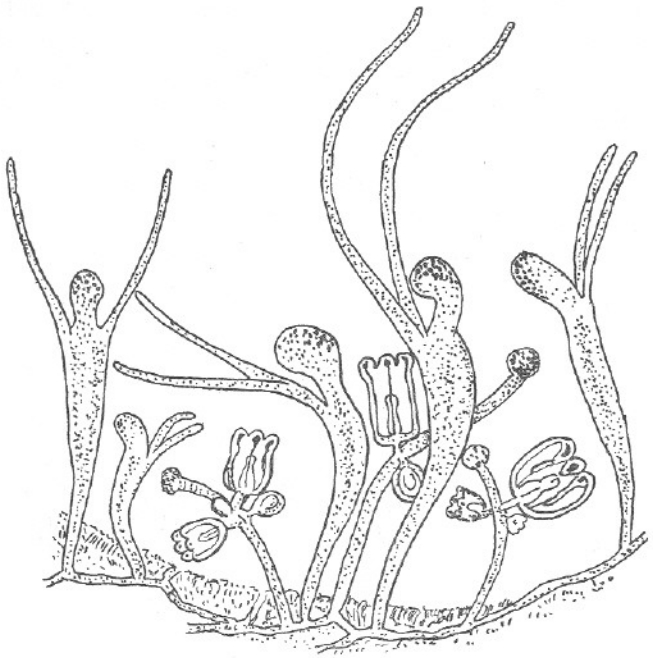
The marginal tentacles are hollow with irregularly arranged endoderm cells. In preserved specimens the marginal tentacles are often curled inwards into the subumbrellar cavity. (Text-fig. 250.)

NEMATOCYSTS. Macrobasic mastigophores, microbasic euryteles and desmonemes in hydroid; not described for medusa (Russell, 1938*b*).

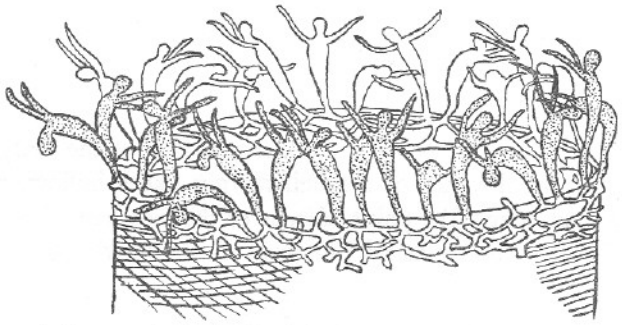
Seasonal occurrence

In the regions from which *Proboscidactyla stellata* has been most commonly recorded, namely the south-west of the British Isles, the medusa may be found in any month of the year. It has, for instance, been recorded from Valencia in every month and from Plymouth in every month except March, at the end of which month, however, the hydroid has been found liberating medusae.

It is noticeable, however, that while the youngest stages may be found in any month of the year, the older stages do not usually appear in numbers until later. For instance, at Valencia (Browne, 1900) the stage with twelve tentacles first appeared in April, that with eighteen tentacles in May, the fully grown stages with twenty-four tentacles from July to November. It appears from its



Text-fig. 255. *Lar sabellarum*, the hydroid of *Proboscidactyla stellata*; colony with medusa buds. (After Hincks, 1872*a*, from Hartlaub, 1917, fig. 325.)



Text-fig. 256. *Lar sabellarum*, the hydroid of *Proboscidactyla stellata*; a colony on the edge of a tube of the polychaete *Sabellaria*. (After Gosse, 1859, p. 345.)

seasonal abundance in those waters that the main period of liberation from the hydroid is in spring and summer. In the Firth of Clyde the medusa has been found in the plankton in the months May to December inclusive.

Habits

A specimen of *Proboscidactyla*, *c.* 4 mm. in diameter, was kept in a plunger jar by Dr M. V. Lebour (1923) and ate a *Sagitta*.

Specimens may often be found parasitized by the trematode *Hemiurus*.

HYDROID. *Lar sabellarum* Gosse. (Text-figs. 255, 256.)

(For full description see Gosse, 1857, *Trans. Linn. Soc. London*, vol. XXII, p. 113, Tab. 20; Hincks, 1872*a*, *Ann. Mag. Nat. Hist.* ser. 4, vol. X, p. 313, pl. XIX; Allman, 1872, *Monogr. Gymnobl. Hydroids*, p. 425; and Kramp, 1939*a*, *Vidensk. Medd. naturh. Foren. Kbh.* Bd. CIII, p. 508, figs. 3–5.)

Colonies of single naked hydranths less than 1 mm. in height arising from a creeping stolon. Hydranths very slender towards base and enlarging above to form a proboscis separated from rest of body by a constriction. There is a patch of nematocysts near the summit of the proboscis. Two smooth tentacles arise close together from base of proboscis. Medusae borne in clusters on slender filiform blastostyles, with terminal nematocyst clusters arising from stolon. Medusae without ectothecal covering.

The hydroid occurs commonly on the upper edges of tubes of the polychaetes *Sabellaria* and *Potamilla torelli*. Its actions have been vividly described by Gosse as bearing a close resemblance to those of human beings 'as if to mimic the actions of the most tumultuous human passion'.

Historical

The medusa *Proboscidactyla stellata* was first found by Forbes and Mr M'Andrew in September 1845 in the Bay of Oban. Forbes (1846) raised the genus *Willsia* for this species in honour of Dr Friedrich Will, the German author of the *Medusae of the Adriatic*. L. Agassiz (1862) pointed out that Forbes's spelling *Willsia* should have been more strictly *Willia*. The hydroid was first described by Gosse (1857) from specimens found on the tubes of a Sabellid worm growing in an aquarium in 1855. He gave it the generic name *Lar* (a household god) in allusion to its association with the worm. In 1872 Hincks discovered a colony with medusa buds at Ilfracombe. The newly liberated medusa had six radial canals and Hincks pointed out that this was only known in *Clavatella* and *Willia*. Subsequently Browne (1896*a*) described all the stages of development of *Proboscidactyla stellata* in full and showed without doubt that the medusa liberated from Hincks's hydroid was the same species.

A species *P. furcata* was described by Haeckel (1879) from the Atlantic coast of France in which the folded mouth was not clearly lipped and the tentacle bases were very large. It seems very probable that this species was really *P. stellata*. Mayer (1910) also described a new species *P. brooksii* in which the stomach is three-rayed before branching into the six lobes. It was found by Professor W. K. Brooks at Beaufort, N. Carolina, and Mayer says that 'it is closely allied and possibly identical with the European *Willsia stellata*'.

In view of the abnormal branching of the radial canals and the variation in the number of primary canals, the possibility that *Misakia* (Uchida) is really a *Proboscidactyla* should be borne in mind.

Genus **Pochella** Hartlaub, 1917

MEDUSAE. Proboscidactylidae without exumbrellar nematocyst clusters; with gonads on interradial walls of stomach; with four simple or branching radial canals.

HYDROID. Not known.

There is only one species in the genus, *Pochella polynema* Hartlaub. It is a rare species, but it has been found in British waters.

Pochella polynema Hartlaub

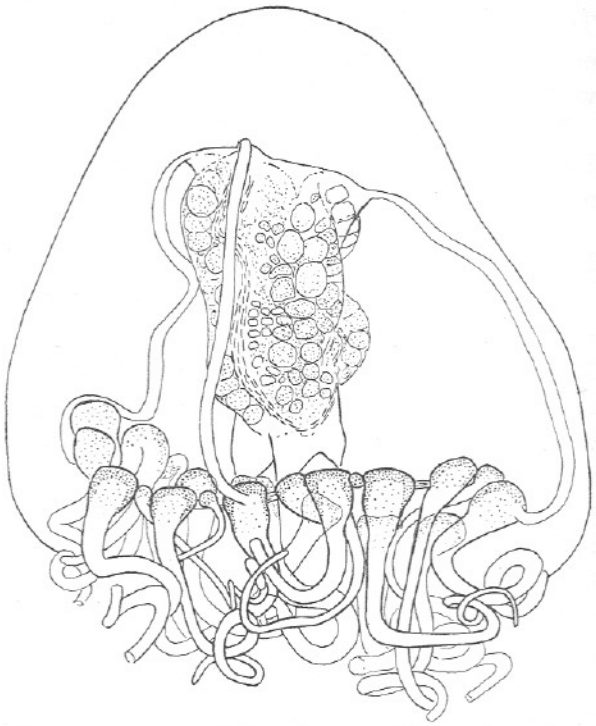
Text-figs. 257–62

Pochella polynema Hartlaub, 1917, *Nordisches Plankton*, Lief. 19, XII, p. 414, figs. 344–6.
Russell, 1938*a*, *Journ. Mar. Biol. Assoc.* vol. XXII, p. 425, figs. 2, 3.
Proboscidactyla polynema, Foerster, 1923, *Contr. Canad. Biol.* N.S., vol. I, no. 12, p. 30, pl. iii, figs. 5–7; pl. iv, fig. 1.

Specific Characters. This is the only species of the genus.

Description of Adult

Umbrella somewhat bell-shaped or hemispherical; jelly fairly thick. No exumbrellar nematocyst tracks. Velum fairly broad. Stomach large, four-sided, about two-thirds the height of sub-umbrellar cavity in length. Mouth with four slightly wavy lips. Four straight smooth radial canals fairly broad, often with exceedingly fine lateral branches. Ring canal ? solid. Four interradial gonads on stomach wall, cushion-like, each gonad covering almost entire interradial wall of stomach. Thirty to forty, or more, solid marginal tentacles with large rounded basal swellings. No ocelli. Diameter of umbrella 2–3 mm. Colour of stomach and marginal tentacle bases brown.



Text-fig. 257. *Pochella polynema*. Mounted specimen collected by Mr P. Gray from Loch Fyne, Scotland, April 1934. (After Russell, 1938*a*, fig. 2*b*.)

Distribution

Pochella polynema appears to be an extremely rare medusa. It has only been recorded in British waters from Plymouth and Loch Fyne in the Firth of Clyde, and only three and two specimens respectively have been found at these localities (Russell, 1938*a*).

Elsewhere it has been recorded by Hartlaub (1917) from the northern North Sea, at 59° 33′ N., 1° 7′ W., where seventeen specimens were caught, and in Departure Bay on the Pacific coast of North America (Foerster, 1923) where twenty-five specimens were obtained.

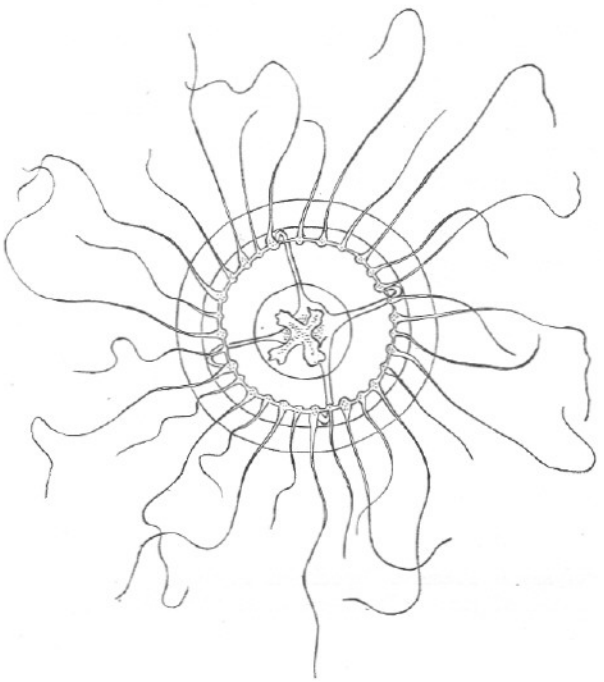
Structural Details

The earliest stages of *Pochella polynema* have not been described, and its hydroid is not known.

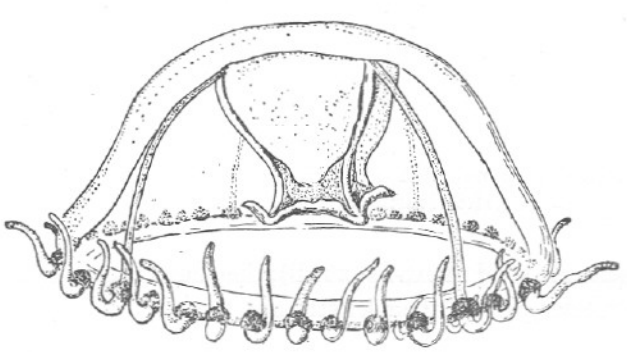
The only descriptions of the medusa are those of Hartlaub (1917), Foerster (1923), and Russell (1938*a*).

The radial canals may apparently have extremely fine lateral branches running towards the umbrella margin, and these branches may themselves divide (Text-fig. 262). According to Hartlaub these branches start about the middle of the radial canal, some being short and blind,

and others longer. Foerster also describes fine thread-like branches 'invisible except under the high power of the microscope'. He states that there were about six of these branches on each side of a radial canal. As his figures show, three branches leave each side of a canal which them-



Text-fig. 258. *Pochella polynema*. Living medusa, 2·7 mm. in diameter, Plymouth, 25. v. 34. (After Russell, 1938*a*, fig. 2*a*.)



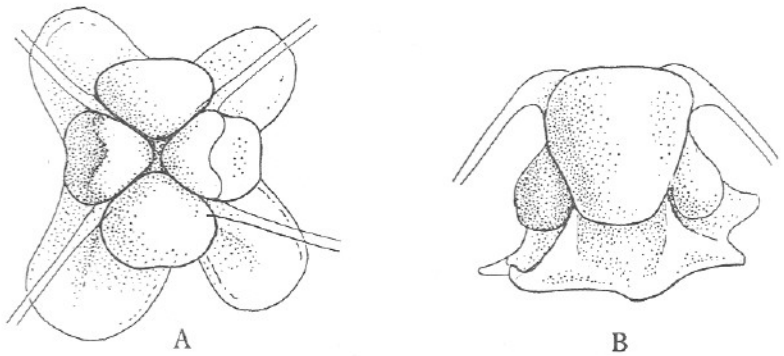
Text-fig. 259. *Pochella polynema*. Specimen from North Sea. (After Hartlaub, 1917, fig. 344.)

selves branch again, thus giving rise to six branches running to the margin. Sometimes these branches anastomose.

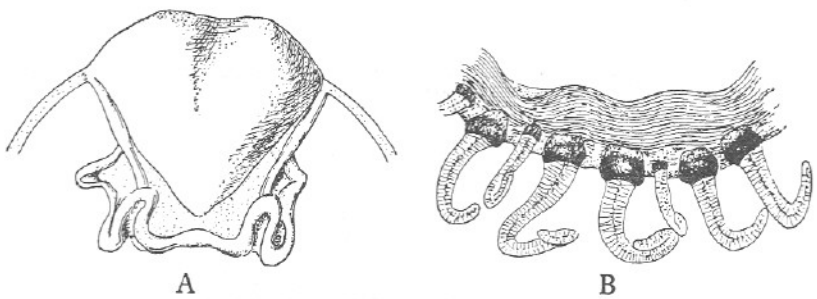
Similar very delicate branches could also be seen in two of the Plymouth specimens, but there were definitely no branches in one of the Loch Fyne specimens, and Hartlaub states that some of his specimens had unbranched canals. There is, of course, the possibility that the medusae with unbranched radial canals may be a different species from those in which the radial canals are

branched. The fact that Hartlaub caught his seventeen specimens all together, some of which were with branched canals and others without, rather suggests, however, that they were all one species.

According to Hartlaub the gonad, which covers the whole interradial wall of the stomach, is more or less pointed at its lower end near the mouth (Text-fig. 261). In a specimen caught at Plymouth by Mr Browne (Russell, 1938*a*) two opposite gonads have the form of large cushions with their thickest parts at the upper ends. The other two gonads are thickest at their lower ends, so that when viewed laterally they may be seen projecting as lobes on either side of the lower halves of the other two gonads (Text-fig. 260A, B).



Text-fig. 260. *Pochella polynema*. Preserved specimen, Plymouth, 30. vi. 98 (E. T. Browne collection). A, aboral view of gonads; B, lateral view. (After Russell, 1938*a*, fig. 3.)



Text-fig. 261. *Pochella polynema*. A, stomach and gonad; B, portion of umbrella margin. (After Hartlaub, 1917, figs. 345, 346.)

The marginal tentacles are solid (Text-fig. 261 B); they have a central core of single endodermal cells throughout the greater part of their length, but this core becomes multicellular near the tentacle base.

The numbers of marginal tentacles in specimens so far seen were as follows:

Locality	Date	Size	No. of marginal tentacles
Plymouth	26 May 1898	1·4 mm. high (in alcohol)	33
Plymouth	30 June 1898	2·0 mm. diameter (in formalin)	32
Plymouth	25 May 1934	2·7 mm. diameter (alive)	30
Loch Fyne	April 1934	2·4 mm. high (mounted in Canada balsam)	27
North Sea	27 June 1905	2–3 mm. diameter (preserved)	30–40
Pacific	April–June	2–4 mm. diameter (preserved)	48

In the specimens I have seen, the marginal tentacles were of two sizes, larger and smaller approximately alternating.

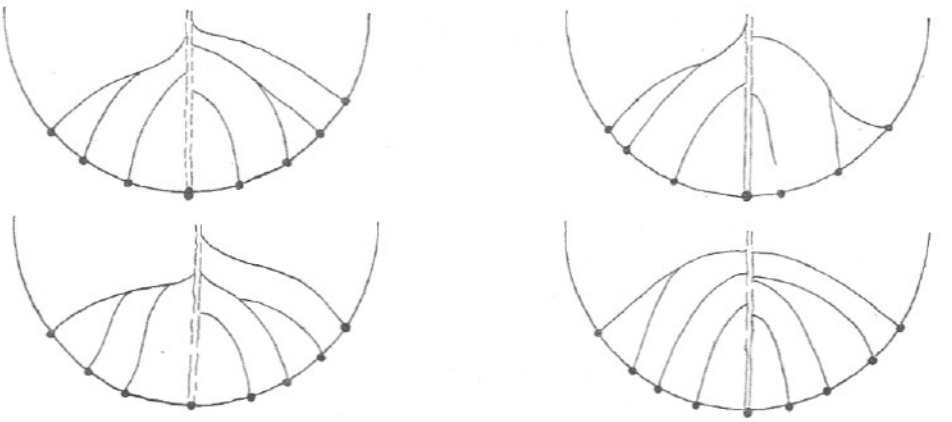
Seasonal occurrence

The records for *Pochella polynema* were: Firth of Clyde, April; Plymouth, May and June; northern North Sea, June.

Habits

I have myself seen a living specimen but did not note anything as to its habits. Text-fig. 258 was drawn from this living medusa.

HYDROID. Not known.



Text-fig. 262. *Pochella polynema*. Radial canal system. (After a pencil drawing by E. T. Browne, Plymouth, 26. v. 98.)

Historical

Pochella polynema was first described by Hartlaub (1917) from the northern North Sea and further descriptions of the medusa have been given by Foerster (1923) and Russell (1938*a*).

The systematic position of the medusa remains uncertain. Foerster placed the species in the genus *Proboscidactyla*, but the gonads are not radial outgrowths from the stomach, neither are there exumbrellar nematocyst channels.

Two of the Plymouth specimens were taken by Mr E. T. Browne in 1898 and the two specimens recorded from Loch Fyne were collected by Mr P. Gray.

FAMILY OLINDIIDAE

Limnomedusae with or without peduncle; with four or six simple or branched radial canals; with or without centripetal canals; with gonads only on radial canals, or on radial canals and stomach; with marginal tentacles of one or of two kinds, with or without organs of adhesion; with enclosed marginal sensory clubs.

HYDROID. Where known, very small, with or without tentacles.

OLINDIIDAE

The family Olindiidae is represented in British waters by three genera, *Gonionemus* L. Agassiz, *Gossea* L. Agassiz, and *Craspedacusta* Lankester. Of these it is possible that *Gonionemus* is not truly indigenous. The three genera may be distinguished by the following characters:

Marginal tentacles with organs of adhesion . . . . . **Gonionemus**
Marginal tentacles without organs of adhesion:
Thirty-two to forty marginal tentacles some of which are arranged in groups . . **Gossea**
Two hundred or more marginal tentacles not in groups . . . . . **Craspedacusta**

There should be no difficulty in distinguishing these genera in British waters on these characters alone, and while the first two are marine, *Craspedacusta* is only found in fresh waters.

Genus **Gonionemus** L. Agassiz, 1862

MEDUSAE. Olindiidae without or with slight peduncle; with four simple radial canals; without centripetal canals; with folded ribbon-like gonads on radial canals only; with evenly distributed marginal tentacles all of one kind, with organs of adhesion; with sensory clubs enclosed in mesogloea.

HYDROID. Where known, with tentacles.

There is one British species of the genus, *Gonionemus vertens* L. Agassiz.* This species was found in the tanks at Port Erin, Isle of Man, and it is possible that it was imported.

Gonionemus vertens L. Agassiz

Plate XXIII, fig. 2; Text-fig. 263

Gonionemus vertens L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 350.
A. Agassiz, 1865, *N. Amer. Acalephae*, p. 128, figs. 197–201.
Murbach & Shearer, 1903, *Proc. Zool. Soc. London*, vol. II (7), p. 183.
Mayer, 1910, *Medusae of the World*, vol. II, p. 343.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 485, fig. 1.
Gonynema vertens, Haeckel, 1879, *System der Medusen*, p. 147.

Specific Characters

Umbrella bell-shaped, higher than a hemisphere; gonads extending over greater part of radial canal and ending short distance from ring canal; marginal vesicles approximately alternating with marginal tentacles.

Description of Adult

Umbrella bell-shaped, as high as or slightly higher than wide; jelly moderately thick. Velum very broad. Stomach fusiform, of moderate length, not extending beyond umbrella margin, with slight peduncle. Mouth with four perradial lips with slightly crenulated margins. Four radial canals and ring canal moderately broad. Four gonads, each extending over greater part of radial canal and ending short distance from ring canal; each in form of pendant sac folded sinuously on alternate sides of radial canal. About sixty hollow marginal tentacles, each with many spiral or annular nematocyst clusters, with adhesive organ short distance from distal end; marginal tentacles without basal swellings; oval sac-like swellings present on umbrella margin, usually one immediately beneath base of each marginal tentacle. Closed marginal vesicles approximately

* *Gonionemus murbachi* should now be added: see note on p. 402.

alternating with marginal tentacles, each vesicle embedded in jelly near ring canal and with single endodermal club. Height of umbrella up to 17·5 mm., width 15 mm. Colour of umbrella yellowish green, gonads deep red, radial canals dark brown.

Distribution

Strictly speaking *Gonionemus vertens* is probably not a British species. It has only been recorded twice previously, and both records are from the Pacific coast of North America (L. Agassiz, 1862; Murbach & Shearer, 1903).

I found two specimens in Mr Browne's collection and a covering letter from the late Mr H. C. Chadwick, Curator of the Port Erin Biological Station. The letter was dated 3 December 1924 and said: 'A dozen specimens of the enclosed medusa were found yesterday in one of the storage tanks while it was undergoing its biannual cleaning.' It can only be conjectured that the medusa or the hydroid was imported on the bottom of a ship coming from the Pacific. The closely allied species, *G. murbachi* (see note on p. 402), has been recorded from Oslo Harbour (Kramp, 1937) and it was suggested that it was carried there by a ship; Gullmarfjord (Lönnberg, 1930); Roscoff (Teissier, 1930); and Ostende (Leloup, 1948), probably imported with *Ostrea virginica*; Sylt (Werner, 1950*a*, *b*).

Developmental Stages and Structural Characters

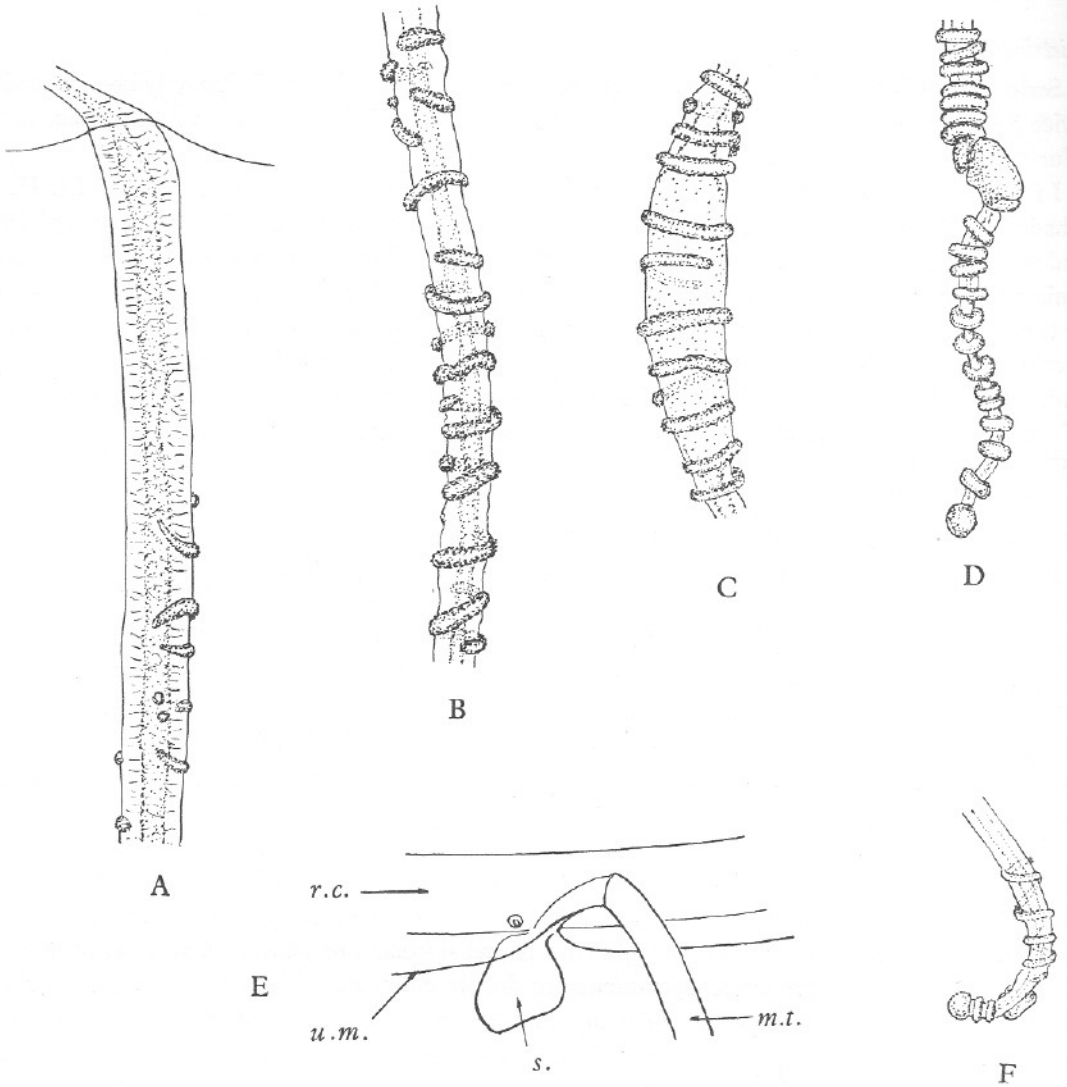
Neither the young stages of *Gonionemus vertens* nor its hydroid are known, only adult specimens of the medusa having been recorded. The development of the medusa and of the hydroid in other species of *Gonionemus* has, however, been described (see, e.g., Mayer, 1910; Joseph, 1925; and Uchida, 1929), and it seems probable that that of *G. vertens* will be found to be very similar.

The two specimens in Mr Browne's collection were 11 mm. high by 12 mm. wide and 11 by 11 mm. respectively. In all respects they resemble exactly the descriptions given by A. Agassiz (1865) and Murbach & Shearer (1903), except that they are a little smaller and the umbrella is not quite so high in relation to its width.

The velum was very broad and nearly closed the subumbrellar opening. In the larger specimen (Pl. XXIII, fig. 2) the stomach was fairly long but in the smaller specimen it was more contracted and its length was only about half the height of the subumbrellar cavity. As Murbach & Shearer state, there is a slight depression over the base of the stomach, or peduncle, and the four radial canals, which in these preserved specimens are deeply coloured with brown pigment, 'pass to the highest point in the bell and then dip under the conical depression above mentioned'. The radial canals widen just before their junction with the ring canal. The gonads, which appear as sinuous folds alternately on one side of the radial canal and the other, end a short distance from the ring canal and do not extend so near to this canal as they do in *G. agassizi*.

The marginal tentacles (Text-fig. 263) are of different ages and the oldest tentacles are inserted rather markedly higher on the exumbrella than the younger. Each marginal tentacle has an endodermal root running to the ring canal. Each large marginal tentacle has about sixty or seventy spiral or annular nematocyst clusters evenly spaced along its length. It kinks near its end where there is an organ of adhesion which is followed by a short thinner portion of tentacle with about thirteen to fifteen nematocyst rings and a round terminal cluster (Text-fig. 263 D). In the larger specimen there were forty-eight large and moderate sized marginal tentacles, nine quite small, and six just developing, or sixty-three in all. In the smaller specimen there were thirty-eight larger marginal tentacles, eight small, and eight just developing, or fifty-four in all. On the

umbrella margin, beneath the bases of the marginal tentacles, there were the typical sac-like oval swellings, most of which were actually beneath a tentacle but a few of which were isolated between adjacent tentacles.



Text-fig. 263. *Gonionemus vertens*. Details of marginal tentacles of a preserved specimen from the storage tanks at Port Erin, Isle of Man, 1924 (E. T. Browne collection). A, base; B, middle portion; C, swollen middle portion; D, terminal portion with adhesive organ; E, diagram to show base of marginal tentacle (*m.t.*), sac-like swelling (*s.*) on umbrella margin (*u.m.*), and marginal vesicle (*r.c.* ring canal); F, young marginal tentacle.

The marginal vesicles were difficult to see when the bases of the marginal tentacles were contracted together. Murbach & Shearer (1903) said: 'There appears to be an otocyst between each pair of tentacles.' In the Port Erin specimens, wherever the marginal tentacle bases were sufficiently far apart to enable me to see clearly, I always found one vesicle. In one quadrant I was able to count ten for certain, and in view of the fact that some of the marginal tentacles were

not fully developed the conclusion that the vesicles alternate with the marginal tentacles appears to be correct. There was no indication that they were more numerous than the marginal tentacles.

Mr Chadwick gave no information as to the colour of the living medusa, but when I examined the preserved specimens, fifteen years after they were caught, the whole subumbrella, stomach, canals and gonads had a brownish yellow tinge; the marginal sac-like swellings were quite a dark yellow brown, and the dark brown pigment in the upper portions of the radial canals was still very conspicuous.

Seasonal occurrence

The medusae were found in the Port Erin tank at the beginning of December 1924. The records from the North Pacific are for July.

Habits

A description of the habits of the living medusa was given by A. Agassiz (1865):

> This Medusa was quite commonly found during the month of July, swimming in patches of kelp. It at once attracted my attention by its peculiar mode of moving. I could see these Jelly-fishes, with the tentacles spread out to their fullest extent, sinking slowly to the bottom, the disk turned downward; the moment a blade of kelp touches the disk, they stop, bend their tentacles like knees, and remain attached to the sea-weed. . . ; after remaining attached in this way a moment, with their tentacles extended and mouth turned upwards, they suddenly let go their hold, turn upside down, contract their tentacles to a third of their former length, and begin their upward movements by means of short, rapid jerks, given by the sudden expanding and contracting of the tentacles as they are violently thrown out from the cavity covered by the veil. They keep up this rapid motion until they reach the surface of the water; at the instant the upper part of the disk touches the top of the water, the Medusa inverts itself, and sinks, with its tentacles fully expanded, until it reaches the bottom, or another piece of sea-weed, where it attaches itself, and after remaining suspended a little while, repeats the same operation; when attached, it requires strength enough to break the tentacles to make them loose their hold. I have never found single individuals, but have always seen them in large numbers swimming among the sea-weed in the manner described.

Murbach & Shearer also record that they were found swimming vigorously in groups of threes and fours.

The medusa attaches itself by means of the organ of adhesion, and Murbach & Shearer suggested that this may enable them to capture animals as large as themselves without being carried away by the prey. They found that they would readily try to eat pieces of meat almost twice their size if given to them; and that they seemed very hardy and could remain alive in a jar for several days without change of water.

A great many observations of an experimental nature have been made on the closely allied species *Gonionemus murbachi*. These have been summarized by Mayer (1910, p. 344).

HYDROID. Not known.

Descriptions of hydroids of this genus are to be found in Mayer (1910) and Joseph (1925).

Historical

Gonionemus vertens was first described very briefly by L. Agassiz (1862). It was later described in more detail and figured by A. Agassiz (1865). The medusa was not found again until it was recorded by Murbach & Shearer (1903), and it has not been recorded since until now.

The species is evidently closely allied to medusae of the *G. murbachi* type, and in time it may be regarded as merely a geographic variety of that species, in which event the name *vertens* will have priority. The chief difference, which appears to be constant, is in the shape of the umbrella; in *G. murbachi* it is much flatter than in *G. vertens*.

Agassiz gave the medusa the name *vertens* on account of its habit of turning over on its back and sinking downwards in this position, a habit also shown by the freshwater medusa *Craspedacusta*.

NOTE. (*Added in Proof.*)

GONIONEMUS MURBACHI Mayer

Plate XXXV

A small medusa from the Dove Marine Laboratory tanks at Cullercoats was described and figured by Robson (1913, p. 27; 1914*b*, p. 90) as *Cladonema* sp. Subsequently, Joseph (1925) pointed out that this was really a species of *Gonionemus*. The medusa and its hydroid were re-discovered in the laboratory tanks at Cullercoats by Dr H. O. Bull in May, 1951. Dr Bull kindly sent a number of young living medusae to me at Plymouth where I succeeded in rearing them to the adult stage.

The smallest specimens were about 1·5 mm. in diameter, and had 4 perradial, 4 interradial and 4 to 8 adradial marginal tentacles of varying sizes. There were four marginal vesicles, and the colour of the stomach, bases of marginal tentacles and umbrella margin was brownish orange.

The most fully developed specimen after nearly two months in the laboratory was about 10 mm. in diameter across the umbrella. It had 67 marginal tentacles and 31 marginal vesicles. The gonads occupied the distal portions of the radial canals, each being slightly longer than half the length of a radial canal and leaving a short length of canal near the umbrella margin free of gonad. Each gonad was folded to form two complete sinusoidal waves decreasing in amplitude from the margin inwards. The stomach when fully extended reached slightly beyond the umbrella margin when the medusa was at rest, the whole umbrella being somewhat flatter than a hemisphere.

Details of developmental stages were as follows:

Diameter (mm.)	Number of marginal tentacles (in brackets = developing)	Number of marginal vesicles	Date (1951)
1·5	8+ (7) = 15	4	16 May
2·0	16+ (5) = 21	4	16 May
2·2	16+ (5) = 21	6	24 May
2·2	16+ (6) = 22	8	24 May
	16+(13) = 29	10	31 May
	16+ (7) = 23	11	31 May
	16+(16) = 32	12	5 June
3·5	32+ (4) = 36	16 (gonads appearing)	8 June
3·25	32+ (1) = 33	16	9 June
	32+ (9) = 41	13	11 June
	32+ (8) = 40	17	13 June
4·0	32+ (9) = 41	19	13 June
	32+(15) = 47	20	18 June
10·0	32+(31) = 63	27	26 June
	64	30	28 June
	67	31	3 July

After the medusae were about 3·5 mm. in diameter they started to swim more actively and began regularly inverting. They often lay upside down with their marginal tentacles attached to the bottom, whereas previously they had been attached the right way up. The smaller specimens fed on harpacticid copepods but, when about 3–4 mm. in diameter, I started feeding them individually on *Calanus* and later on mussel, squid or prawn flesh. They were kept in the same bowls without change of water or addition of fresh water for the whole period of their development. My thanks are due to Dr J. S. Alexandrowicz for kindly caring for these medusae at times when I had to be away from the laboratory.

Excellent photographs of different stages of the medusa taken by Dr Douglas P. Wilson are reproduced in Plate XXXV, and there can be little doubt that the medusa is *Gonionemus murbachi*, although the gonads are not as fully developed as in typical specimens. For literature and further details on this species see Werner (1950*a*). For description of the hydroid (*Haleremita*) see Werner (1950*b*).

Genus **Gossea** L. Agassiz, 1862

MEDUSAE. Olindiidae with or without peduncle; with four simple radial canals; without centripetal canals; with folded ribbon-like gonads only on radial canals; with marginal tentacles all of one kind some of which are grouped; without true organs of adhesion; with sensory clubs enclosed in mesogloea.

HYDROID. Not known.

There is one species of the genus in British waters, *Gossea corynetes* (Gosse). There should be no difficulty in identifying this medusa.

Gossea corynetes (Gosse)

Plate XXIII, fig. 1; Text-figs. 264–7

Thaumantias? corynetes Gosse, 1853, *Devonshire Coast*, p. 407, pl. xxi.
'Medusoid of *Coryne*?' Gosse, 1853, ibid. p. 331, pl. xxii, figs. 1–4 (young medusa).
Gossea corynetes, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 366.
Haeckel, 1879, *System der Medusen*, p. 251.
Mayer, 1910, *Medusae of the World*, vol. II, p. 367, fig. 210.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 490, fig. 5.
Kramp, 1930, *Mém. Mus. Roy. Hist. Nat. Belgique*, Mém. no. 45, p. 32, fig. 14.
Russell, 1939*a*, *Proc. Zool. Soc. London*, ser. B, vol. CVIII, pt. IV, p. 709, text-fig. 2.
Gossea circinata Haeckel, 1879, *System der Medusen*, p. 252, pl. xviii, fig. 4.
Browne, 1900, *Proc. Roy. Irish Acad.* ser. 3, vol. V, p 729.

Specific Characters

Stomach without peduncle; twenty-four large marginal tentacles in four perradial and four interradial groups of three each; eight to sixteen small or rudimentary marginal tentacles, one to two between adjacent groups. Twenty-four, or more, marginal vesicles, three between adjacent groups of marginal tentacles.

Description of Adult

Umbrella somewhat bell-shaped or hemispherical, generally wider than high; jelly thick, especially in apical region. Velum broad. Stomach small, quadratic, one-third to one-half the height of subumbrellar cavity; with square base; no peduncle. Mouth with four simple or slightly folded lips. Four straight radial canals and ring canal narrow. Four gonads linear, forming deep hanging pouches along two-thirds of each radial canal, leaving distal ends of canals free; somewhat wavy, with distal ends unattached. Eight groups of three large marginal tentacles, four perradial and four interradial; marginal tentacles solid, with endoderm core extending into substance of marginal jelly and with hemispherical adaxial nematocyst pad. Eight to sixteen small or rudimentary marginal tentacles, situated singly, one or two between adjacent groups. All marginal tentacles with nematocyst rings, but with no distinct suckers. Usually twenty-four, sometimes more, marginal vesicles, imbedded in jelly on exumbrellar side of ring canal; three between adjacent groups of marginal tentacles, each with a single concretion. Diameter of umbrella

12–16 mm.; height 8–10 mm. Colour of stomach greenish; mouth and gonads pinkish; marginal tentacles pinkish or yellowish brown; whole effect appears fluorescent, changing from pink to green and yellowish brown.

Distribution

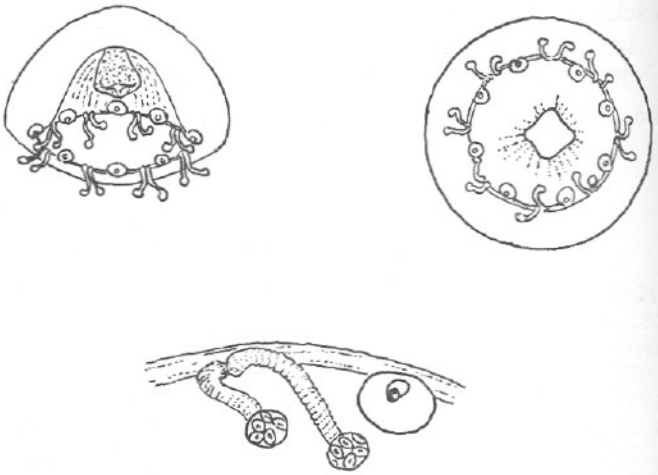
The medusa *Gossea corynetes* is rather restricted in its distribution in British waters. It occurs in the southern North Sea, English Channel, Bristol Channel, and waters south of Ireland.

Elsewhere it has only been recorded in the Mediterranean.

According to Kramp (1930) the medusae immigrate into the North Sea from the English Channel.

Developmental Stages and Structural Details

The first stage of *Gossea corynetes* after liberation from its hydroid has not been described for certain and its hydroid is not known.



Text-fig. 264. Probable early stage of *Gossea corynetes*. (After Gosse, 1853, pl. xxii, figs. 1–4.)

The earliest known stage, which probably belongs to this species, is that described by Gosse (1853) as 'Medusoid of *Coryne*?' Gosse found this in August in one of his glass aquaria at Ilfracombe. He did not mention the size of the medusa. In his drawing (Text-fig. 264) the umbrella is shown as slightly wider than high, with thick jelly. He mentions that 'the umbrella contained many oval clear granules', presumably exumbrellar nematocysts. The stomach is short and simple. There are sixteen marginal tentacles, arranged in four perradial and four interradial groups of two; each marginal tentacle terminates in a nematocyst cluster. There are eight marginal vesicles, one between adjacent pairs of marginal tentacles, each with a single concretion.

An almost identical specimen was found by Miss M. Delap in August 1902 in one of her aquaria at Valencia. This specimen agreed almost exactly with Gosse's description, and Miss Delap noted that there were large nematocysts in the exumbrella. The umbrella was bell-shaped, somewhat higher than wide, and about 1 mm. in diameter.

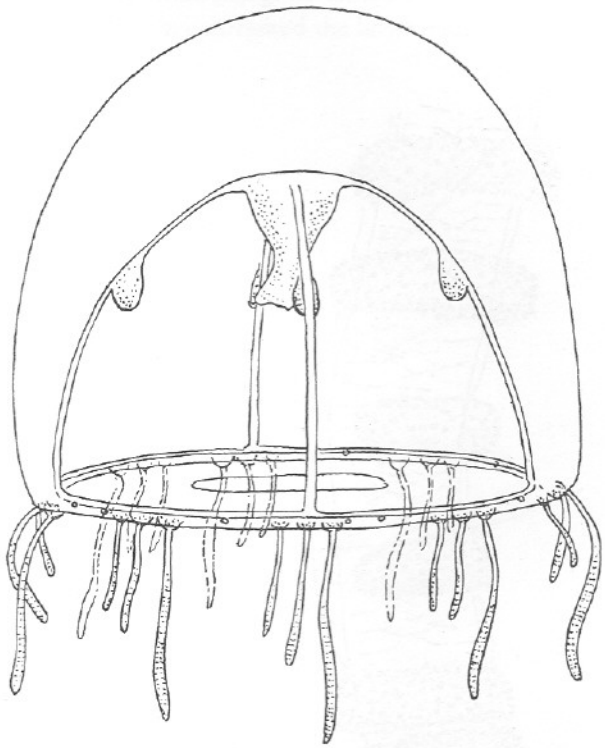
That these medusae were young *Gossea* appears almost certain from the sequence of development of the marginal tentacles in the following slightly later stages caught at Salcombe, South Devon, on 17 August 1900.

A specimen 2 mm. in height and 1·5 mm. wide had a *Sarsia*-like umbrella, with very thick jelly. The stomach was about one-third the length of the subumbrellar cavity. The mouth had no lips. There were two opposite perradial groups each of three marginal tentacles, and the remaining two opposite perradial groups and the four interradial groups each had two marginal tentacles. All the marginal tentacles had a terminal battery of nematocysts and one transverse row above it, while a few showed the beginning of a third row. There were no small marginal tentacles between the groups. There were seven marginal vesicles, each with a single concretion.

A slightly later stage at the same size had three marginal tentacles in each of the eight groups. Most of these tentacles had two bands of nematocysts. The central marginal tentacle of each group was situated behind the other two, more towards the exumbrella. There were still no small marginal tentacles between the groups. There were eight marginal vesicles.

At a slightly larger size, 2·5 mm. high and 1·75 mm. wide, the mouth has four small lips.

In a specimen 2·75 mm. high and 2 mm. wide the first small marginal tentacle had developed adradially between two of the groups of three. There was also an additional marginal vesicle. At this stage it is already noticeable that the outer right-hand marginal tentacle in each of the eight groups of three is considerably larger than the others; it has up to eight bands of nematocysts. There are as yet no traces of gonads.



Text-fig. 265. *Gossea corynetes*. Preserved specimen *c.* 3 mm. high, Plymouth, 23. viii. 33.

A slightly larger specimen, 3·0 mm. high and 2·5 mm. wide, caught at Plymouth on 23 August 1933, still had no small marginal tentacles, but the gonads were just appearing (Text-fig. 265). The gonads were situated on the four radial canals about one-third of their length from the stomach.

On 23 October 1933 a specimen was caught at Plymouth, 3 mm. high and 3 mm. wide, which had the rudiments of five of the small marginal tentacles, there being only one between any two groups of large marginal tentacles.

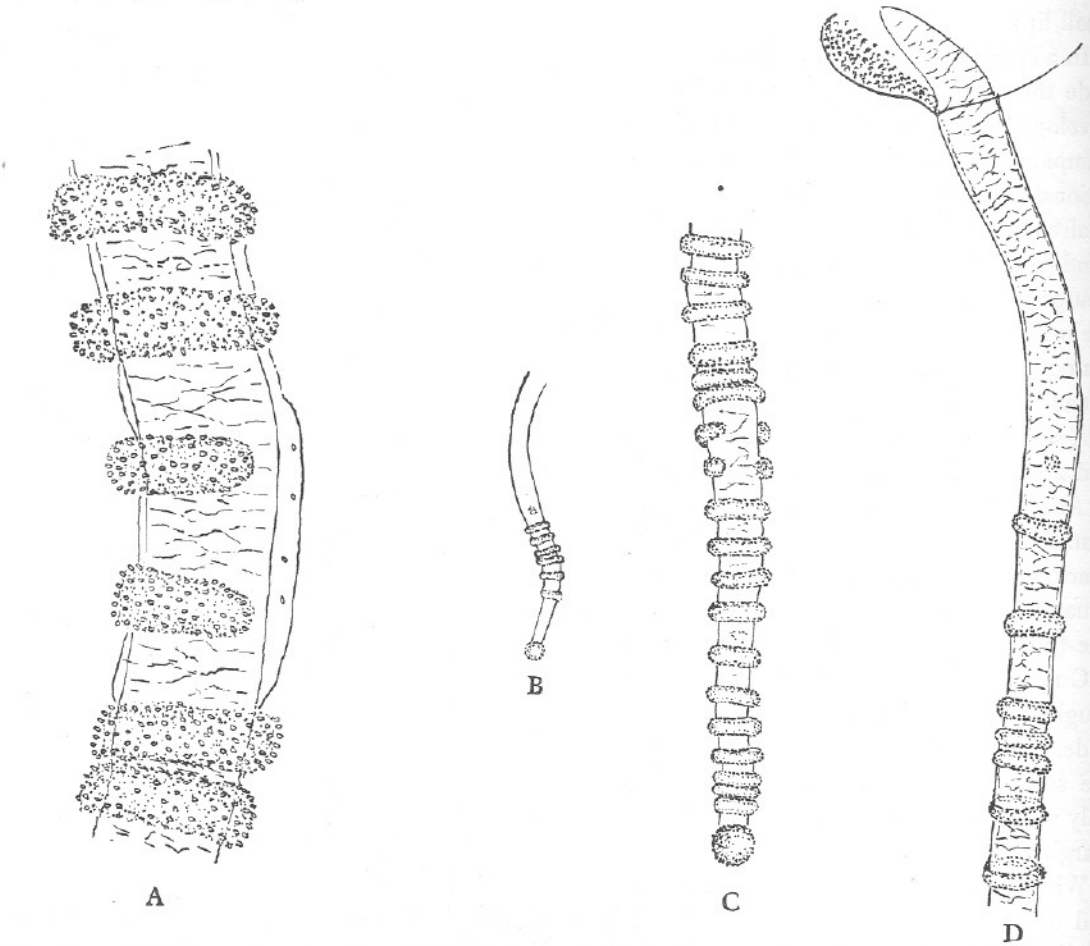
When the medusa has reached a height and diameter of about 5 mm. all the eight small marginal tentacles of the first series have developed; thus, there is one in each adradius. From now onwards the second small marginal tentacles begin to develop in each adradial sector.

The *marginal tentacles* (Text-fig. 266) when fully grown have up to fifty or more bands of nematocysts; most of these are complete rings. These nematocyst rings do not continue quite to the base of the marginal tentacle. The base is thus smooth, and it is also of even width, having no swelling; there is, however, a large adaxial cushion of nematocysts on the umbrella margin at the base of each marginal tentacle. The marginal tentacles have an endodermal core, which sometimes appears to be hollow for a short distance in the basal region. This endodermal core consists of several peripheral rows of cells, and not a single row. The core can be seen to continue into the substance of the umbrella margin to the ring canal.

When studying the distribution of the nematocyst rings on the marginal tentacles I have noticed that about eight or so rings from the end there are often one or two which do not completely clasp the tentacle, and this free portion of tentacle is slightly thickened. It is as though we have

an incipient organ of adhesion. It may be from this point that the twitching movements mentioned under 'Habits' originate.

The small marginal tentacles (Text-fig. 266 B) between the groups are in every respect similar to the large marginal tentacles, differing only in being much smaller and having consequently far fewer nematocyst rings.



Text-fig. 266. *Gossea corynetes*. Details of marginal tentacles of preserved specimen. A, terminal portion of a large marginal tentacle nine rings from the end; B, small marginal tentacle; C, terminal portion of large marginal tentacle; D, basal portion of large marginal tentacle.

The right-hand marginal tentacle in each of the eight groups of large marginal tentacles is always the largest, and the left-hand the smallest.

The *marginal vesicles* are situated in the jelly on the exumbrellar side of the ring canal. In sections, the cellular concretion lies loose in the cavity of the vesicle (Russell, 1939*a*); it is, however, probably attached to the wall of the vesicle normally, and breaks away.

Browne (1900) records as many as twenty-nine marginal vesicles in one specimen.

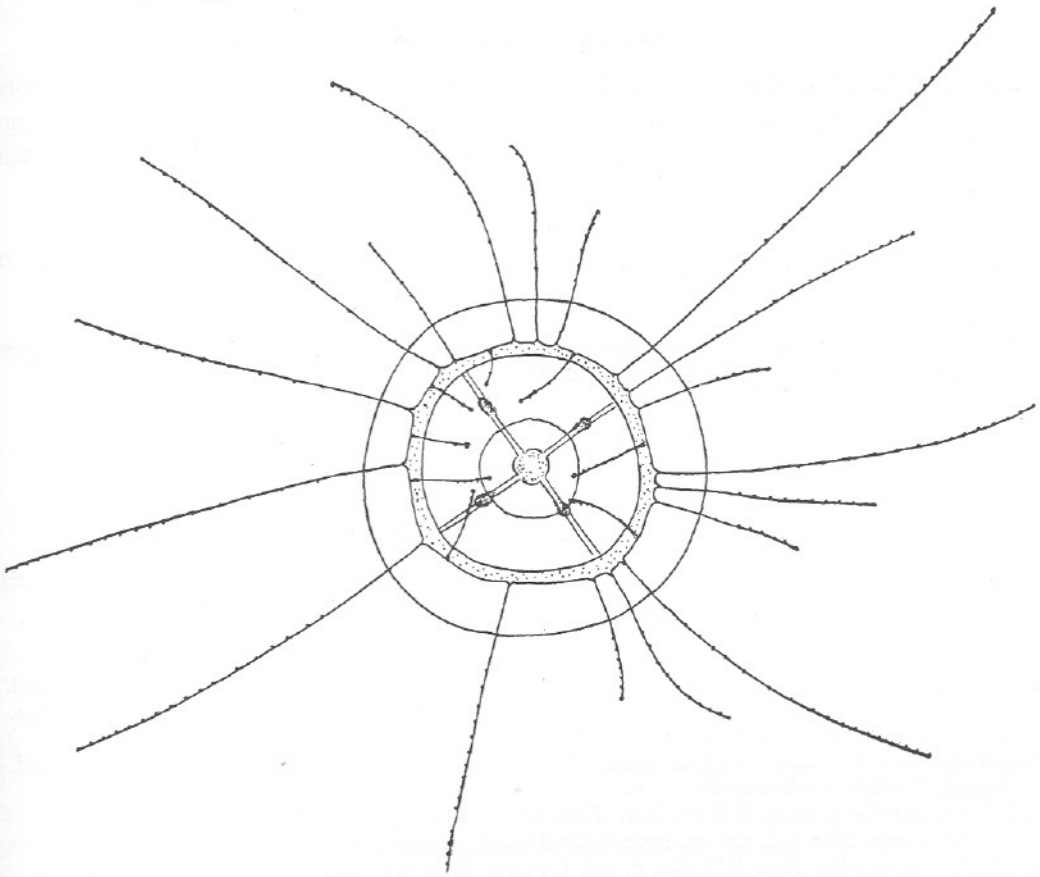
Seasonal occurrence

Gossea corynetes is essentially a medusa of late summer and autumn in British waters. From its known occurrence it appears that it is likely to be found in the plankton in any month from July

to December inclusive. The young medusa is probably liberated from its hydroid in July and August, when most specimens caught are small. Thereafter large specimens may be found (see also Kramp, 1930).

Habits

When the medusa *Gossea corynetes* is poised in still water the large marginal tentacles of the eight groups are held outwards rather stiffly, while the small marginal tentacles hang downwards and are sometimes directed inwards (Text-fig. 267). When contracted the large marginal tentacles have a club-shaped appearance.



Text-fig. 267. *Gossea corynetes*. Living specimen *c.* 7 mm. in diameter seen from above, Plymouth, 15. xi. 35. Showing typical attitudes of marginal tentacles, with small ones pointing downwards and inwards. This specimen is abnormal; one of the groups of three marginal tentacles is missing, and instead there are three large marginal tentacles widely spaced.

The large marginal tentacles have a characteristic twitching movement which was first noted by Gosse (1853). Examination of living specimens at Plymouth showed that this twitching occurs when the marginal tentacles are extended and that the motion is confined to the distal portion of the tentacle. The twitches occurred at periods of one a second or slower.

When fully extended the longest marginal tentacles are about twice the diameter of the umbrella.

A specimen at Plymouth was seen to eat a crab zoea, and when doing this the manubrium was considerably elongated, so that the mouth reached to the umbrella margin.

OLINDIIDAE

HYDROID. Not known.

Historical

Gossea corynetes was first described by Gosse (1853) as *Thaumantias ? corynetes* from specimens collected at Ilfracombe in September and October 1852. Haeckel (1879) described the same species, from South Brittany, as *Gossea circinata*. Browne (1900) pointed out that the two medusae described by Gosse and Haeckel were probably stages of the same species, and this has subsequently been confirmed.

Genus **Craspedacusta** Lankester, 1880

MEDUSAE. Olindiidae without peduncle; with four simple radial canals; without centripetal canals; with hanging pouch-like gonads only on radial canals; with evenly distributed marginal tentacles all of one kind, without organs of adhesion; with sensory clubs in enclosed vesicles in velum.

HYDROID. *Craspedacusta*, without tentacles.

There is one British species of the genus *Craspedacusta sowerbyi* Lankester. It is our only species of freshwater medusae and can be easily identified. Its hydroid is known.

NOTE: As there are so many papers on *Craspedacusta* and it is the only British freshwater species, the references to it are listed separately on pp. 511–15.

Craspedacusta sowerbyi Lankester

Plate XXIV, fig. 1; Text-figs. 268–74

Craspedacusta sowerbii Lankester, 1880*a–e*, *Nature, London*, vol. XXII (17 June), p. 147; *Zool. Anz. Leipzig*, III. Jahrg., no. 59, p. 321; also, *Nature, London*, vol. XXII, pp. 177, 190, 241, 316.
Mayer, 1910, *Medusae of the World*, vol. II, p. 363, fig. 207.
Boulenger & Flower, 1928, *Proc. Zool. Soc. London*, no. LXVI, p. 1005, pl. i, text-figs. 1, 2.
Dejdar, 1934, *Zeit. Morph. Ökol. Tiere, Berlin*, Bd. XXVIII, p. 595, figs. 1–41 (hydroid and medusa).
Limnocodium victoria Allman, 1880*a–c*, *Nature, London*, vol. XXII (24 June), p. 178; and pp. 218, 290.
Allman, 1880*d*, *Journ. Linn. Soc. London*, vol. XV (1881), no. 82, p. 131, figs. 1–3.
Limnocodium (*Craspedacustes*) *sowerbii*, Lankester, 1880*f*, *Quart. Journ. Micr. Sci. London*, N.S. vol. XX, p. 351, pls. XXX, XXXI; text-figs. 1–5.
Microhydra ryderi Potts, 1885, *Science, New York*, vol. V, no. 123, p. V (hydroid only).
Potts, 1897, *Amer. Nat.* vol. XXI, p. 1032 (hydroid and medusa).
Potts, 1898, *Ann. Mag. Nat. Hist.* ser. 7, vol. I, p. 130 (hydroid and medusa).
Potts, 1906, *Quart. Journ. Micr. Sci., London*, N.S. vol. L, p. 623, pl. XXXV, XXXVI (young medusa).
Browne, 1906, *Quart. Journ. Micr. Sci., London*, N.S. vol. L, p. 635, pl. XXXVII (young medusa).
Mayer, 1910, *Medusae of the World*, vol. II, p. 366, figs. 208, 209.
Pottsia ryderi, Ryder, 1885, *Amer. Nat.* vol. XIX, p. 123.
Limnocodium sowerbii, Günther, 1894, *Quart. Journ. Micr. Sci., London*, N.S. vol. XXXV, p. 539, pl. 40.
Hargitt, 1908*b*, *Biol. Bull. Woods Hole*, vol. XIV, p. 304, figs. 1–7.
Limnocodium kawaii Oka, 1907, *Annot. Zool. Jap.* vol. VI, pt. III, p. 219, pl. viii.
Oka, 1908, *Zool. Anz. Leipzig*, Bd. XXXII, no. 23, I. *Wiss. Mitt.* (2), p. 669.
Limnocodium sowerbyi, Douglas, 1912, *Zeit. Wiss. Zool. Leipzig*, vol. CII, p. 92, pl. vi, text-figs. 1, 2.
Limnocodium sowerbyi var. *kawaii*, Oka & Hara, 1922, *Annot. Zool. Jap.* vol. X, pt. IV, Art. 7, p. 83, figs. 1–3.
Microhydra germanica Roch, 1924, *Zool. Anz. Leipzig*, Bd. LVIII, p. 131, figs. 1, 2.
Craspedacusta ryderi, Payne, 1924, *Journ. Morph. Philadelphia*, vol. XXXVIII, no. 3, p. 387, pls. i–x (hydroid and medusa).
Payne, 1926, *Biol. Bull. Woods Hole*, vol. L, no. 6, p. 433, figs. 1–9.

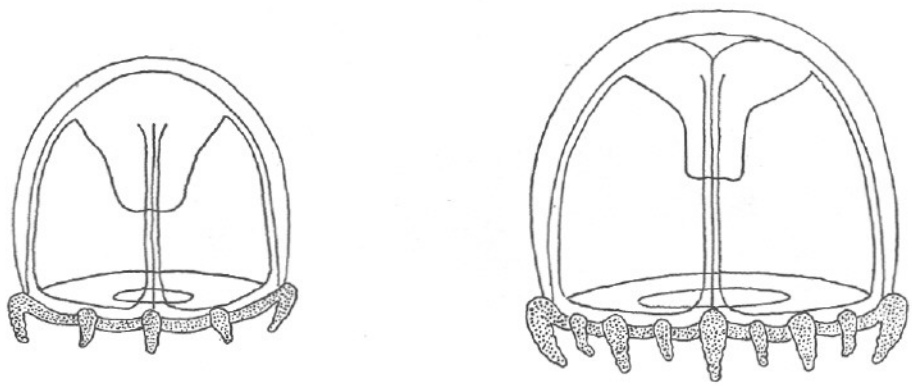
Craspedacusta germanica, White, 1930, ibid. vol. LIX, p. 222, 16 figs.
Non *Craspedacusta marginata* (Modeer), Hummelinck, 1938, *Zool. Anz. Leipzig*, Bd. CXXIV, Heft 11/12, p. 333, fig. 1 (see Hummelinck, 1941, ibid. Bd. CXXXVI, Heft 1/2, p. 9, figs. 1–7).
Craspedacusta sowerbyi, Kramp, 1950, *Proc. Zool. Soc. London*, vol. CXX, pt. 1, p. 166.

Specific Characters

Four perradial marginal tentacles large.*

Description of Adult

Umbrella slightly flatter than a hemisphere; jelly fairly thick; with well developed marginal nematocyst ring. Velum broad and well developed. Stomach large, upper portion conical with broad square base, tapering downwards to cross-shaped distal region. Mouth with four simple or slightly folded lips, extending beyond umbrella margin. Four straight radial canals and ring canal broad and massive. Four large smooth triangular pouch-like gonads, with rounded corners, hanging down into subumbrellar cavity from points of junction of radial canals with stomach.



A B

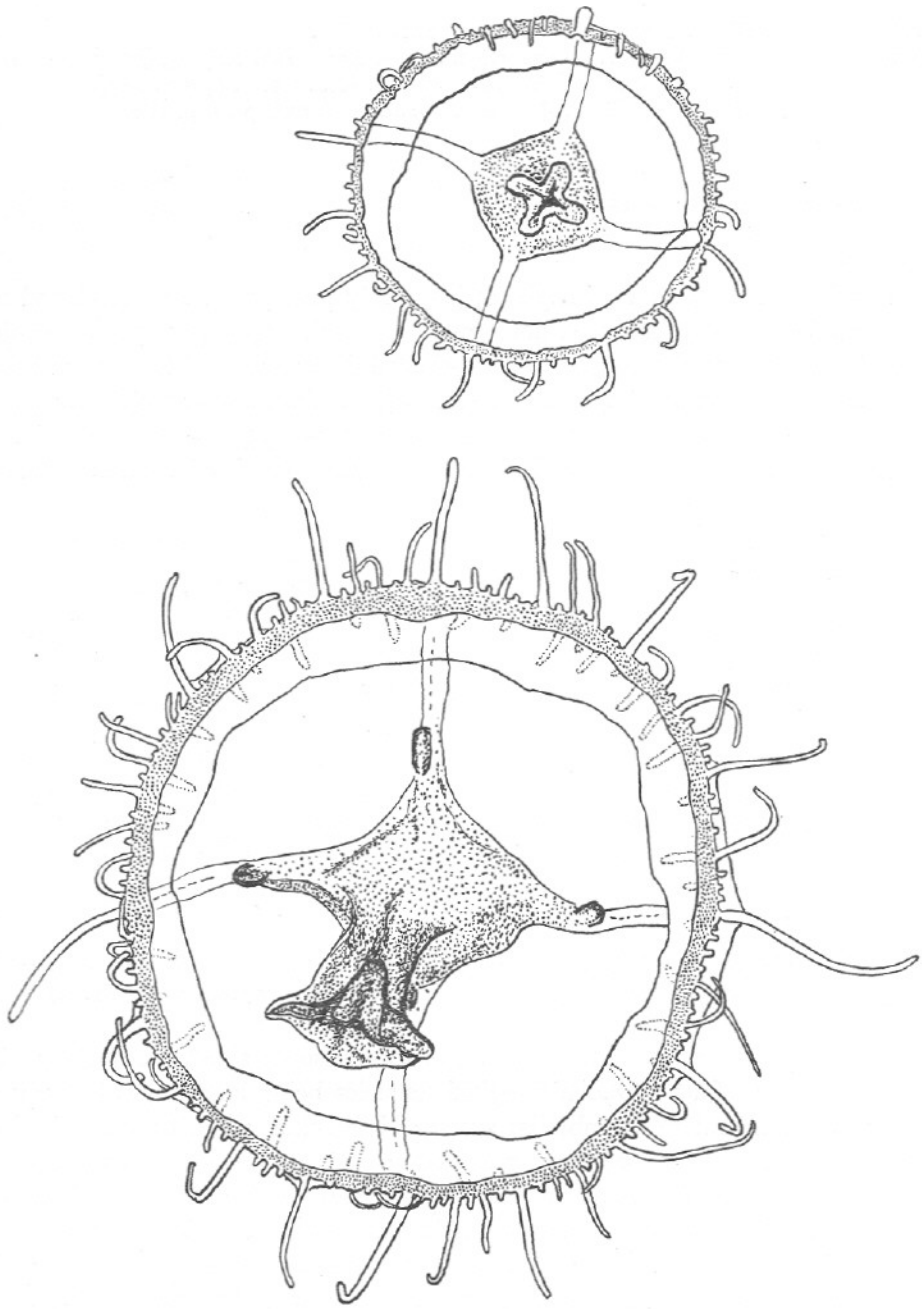
Text-fig. 268. *Craspedacusta sowerbyi*. Young stages. A, with eight marginal tentacles; B, with sixteen marginal tentacles. × *c.* 80. (After Boulenger & Flower, 1928, text-figs. 1, 2.)

Hollow marginal tentacles 200 to 400, or more, in several series situated at different levels on umbrella margin, oldest four perradial marginal tentacles being largest and highest; bases of marginal tentacles adherent to exumbrella; surface of marginal tentacles covered with evenly distributed papillae each with three to ten nematocysts. Marginal vesicles 100 to 200, or more, in number, usually about half number of marginal tentacles; situated in velum, forming centripetal tubes with basal enlargements near umbrella margin each containing single stalked concretion. Diameter of umbrella 10–20 mm. Colour of stomach, nematocyst ring, and gonads yellowish brown, yellowish or sepia; often quite colourless except for greenish tinge.

Distribution

Craspedacusta sowerbyi is a freshwater medusa, which was originally found in 1880 in the giant water-lily (*Victoria regia*) tanks of the Royal Botanical Society's Gardens in Regent's Park,

* Kramp (1950) fully described *C. sinensis* Gaw and Kung from China, differing from *C. sowerbyi* in having no large perradial marginal tentacles, and a much less indented marginal nematocyst ring. He also maintained that in *C. sowerbyi* the papillae are arranged in transverse belts on the marginal tentacles; in *C. sinensis* the papillae are elongated and irregularly distributed.



Text-fig. 269. *Craspedacusta sowerbyi*. Preserved specimens from the Exeter Ship Canal, August 1928. Above, 2·5 mm. in diameter; below, 4·5 mm. in diameter. (E. T. Browne collection, from R. Vallentin.)

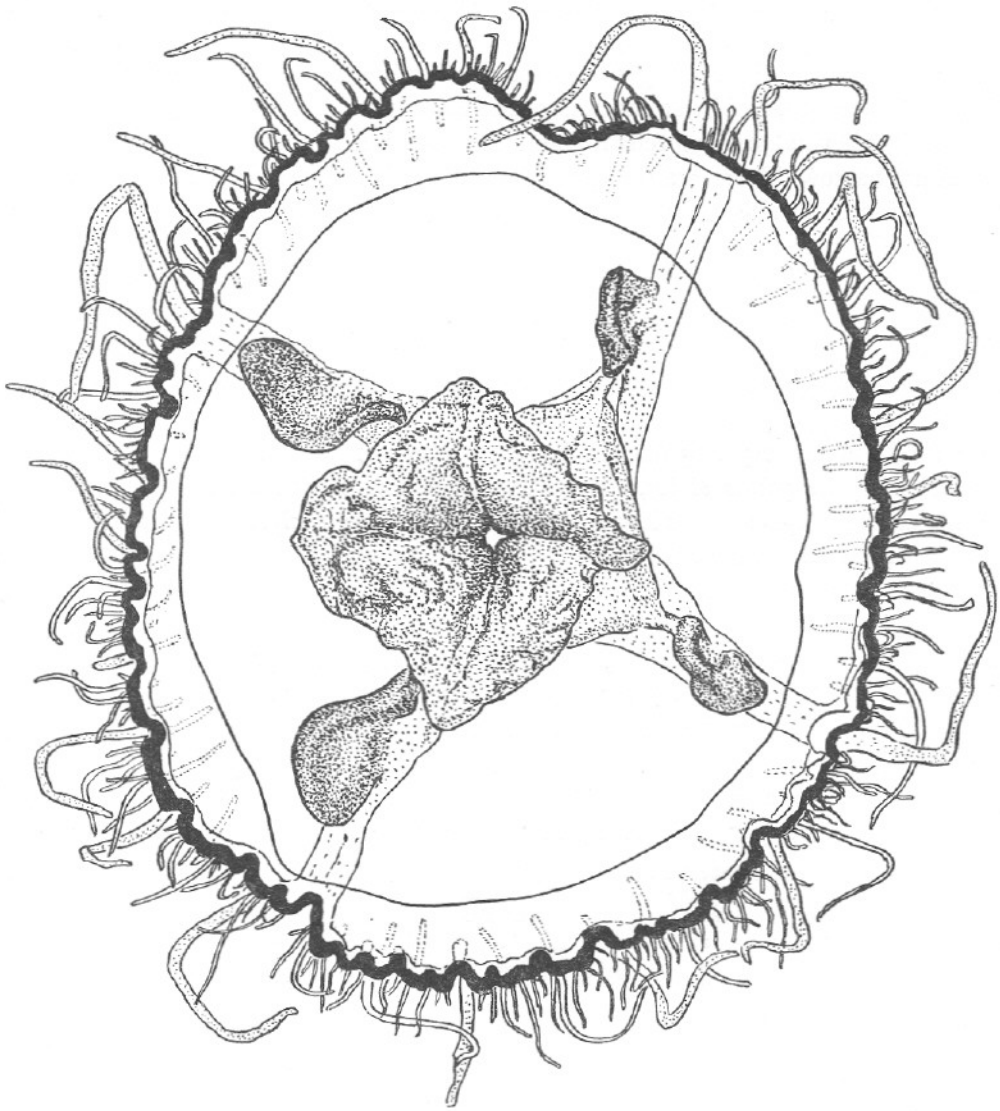
London. It has since been recorded from tanks or aquaria at Sheffield (Lankester, 1893), Birmingham (Boulenger & Flower, 1928), Boscombe (Totton, 1929; Hickson, 1929); Edinburgh (van Someren, 1933).

It has only been recorded in open and more natural waters in the Exeter Ship Canal* (Vallentin,

* Medusae were reported to be present here in 1948 by Mr N. A. Holme.

1930); a colliery reservoir in Monmouthshire (Tattersall, 1933; Jenkins, 1935); and Witcombe Reservoir in Gloucestershire (Bassindale, 1949).

Elsewhere it has been found in France, Holland, Germany, Austria, Czechoslovakia, Russia, China, Japan, Canada, U.S.A., and the Panama Canal zone, and its distribution is such that it can no longer be regarded as so rare as was at first believed.



Text-fig. 270. *Craspedacusta sowerbyi*. Preserved male *c.* 9 mm. in diameter, Exeter Ship Canal, August, 1928. (E. T. Browne collection, from R. Vallentin.)

It is usually observed that when this medusa is found in aquaria or in natural conditions only one sex is represented. The hydroid, *Microhydra ryderi*, is very small and has a resting stage. It may thus easily be transported on water-plants or even on birds' feet. It is usual for an

individual hydroid to produce medusae only of one sex; thus on the transportation of a single hydroid to fresh grounds, a stock of hydroids is produced by asexual budding which will all produce medusae of the same sex.

Developmental Stages and Structural Details

The developmental stages of *Craspedacusta sowerbyi* have been described by a number of workers, the most detailed for British medusae being that by Boulenger & Flower (1928).

The earliest stage (Text-fig. 268A), when just liberated from its hydroid *Microhydra ryderi*, is about 0·45 mm. in height and 0·47 mm. wide. The umbrella is bell-shaped and the jelly rather thin. The velum is broad. The stomach is rather large, with a broad quadrangular base, but it does not project beyond the umbrella margin. The mouth is simple. The four radial canals and ring canal are narrow. There are no signs of gonads. There are eight marginal tentacles, four perradial and four interradial, of which the interradial may sometimes be very slightly the smaller. The bases of the marginal tentacles are attached for a very short distance to the exumbrellar margin. There are as yet no marginal vesicles.

The next stage has sixteen marginal tentacles due to the growth of eight adradial marginal tentacles (Text-fig. 268B). It appears that under some conditions medusae may be liberated from the hydroid at this sixteen-tentacled stage (van Someren, 1933), but the adradial marginal tentacles are then slightly shorter than the others.

The umbrella is now 0·5–0·65 mm. in diameter. The first signs of the gonads are apparent as small pouches at the points of junction of the radial canals with the stomach. The marginal vesicles are also now appearing. They develop somewhat irregularly, but by the time the sixteen marginal tentacles have developed there are typically eight, one on each side of each of the perradial marginal tentacles. The marginal vesicles at this stage are spherical and have no radial prolongations in the velum.

The umbrella becomes more hemispherical in shape as growth proceeds after the stage with sixteen marginal tentacles, and the numbers of marginal tentacles and marginal vesicles quickly increase. A specimen 4 mm. in diameter may have as many as 196 marginal tentacles and sixty-four marginal vesicles.

The stage at which the marginal vesicles may start developing is also variable, as the following figures given by Dejdar (1934) show. These figures refer only to fully developed vesicles:

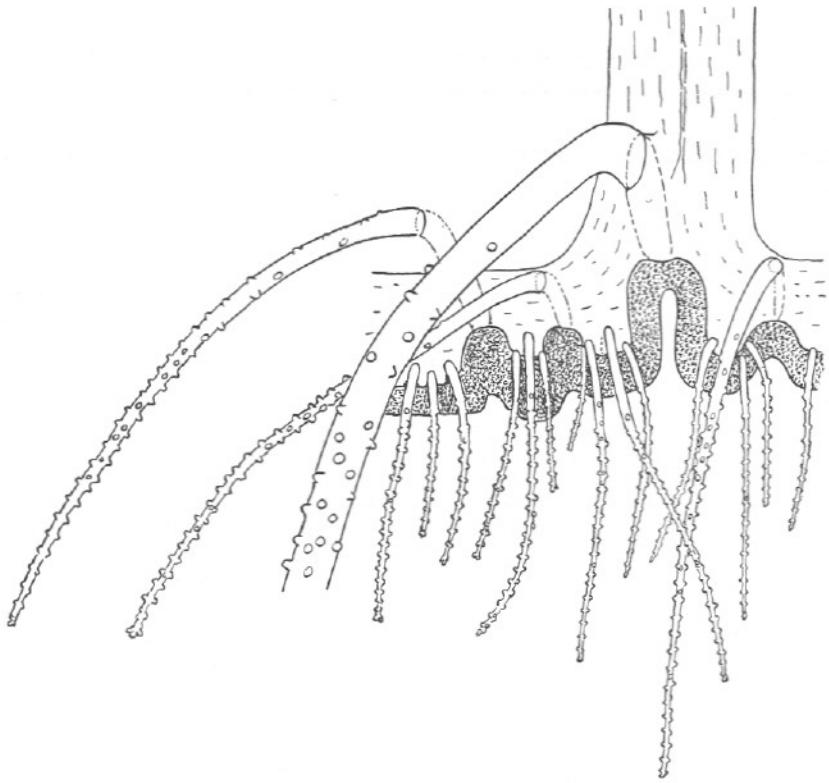
Umbrella diameter (mm.)	No. of marginal tentacles	No. of marginal vesicles
1	16	0
2	40	18
3	56	28
4	80	32
5	104	48
7	188	84
12	270	120
15	340	152
20	480	200

The degree of development of the medusa is no doubt determined by the conditions of the environment, and one might expect medusae in natural waters to develop more slowly and grow larger than those found in heated aquarium tanks. In this respect it should be noted that medusae have been recorded with mature gonads at any size from about 10 mm. in diameter upwards.

The chief structural characters and their histological details have been described in many publications, often with conflicting results. The whole literature has been fully summarized by

Dejdar (1934) and he has added his own observations. Much of the following account has been derived from Dejdar's work.

The form of the *marginal nematocyst ring* is rather characteristic (Text-fig. 271). In young medusae it appears as a continuous smooth ring filling the interspaces between the marginal tentacles, and covering the umbrella margin immediately beneath the points of junction of the tentacles with the exumbrella. Its appearance alters, however, with the growth of the medusa.



Text-fig. 271. *Craspedacusta sowerbyi*. Preserved specimen from Exeter Ship Canal, August 1928. Portion of umbrella margin at the junction of a radial canal with the ring canal, showing marginal nematocyst ring.

As the older marginal tentacles become carried up the exumbrella with the growth of the umbrella margin, that part of the nematocyst ring in the immediate neighbourhood of the base of the marginal tentacle follows. As a result the nematocyst ring has a number of deep cleft-like bays beneath the oldest marginal tentacles. Among the other marginal tentacles the bays are of varying degrees of shallowness according to the ages of the marginal tentacles, the youngest marginal tentacles having no embayments in the nematocyst ring beneath them.

In this way the umbrella margin of a fully grown medusa has a frilled appearance (Text-fig. 270).

The *velum* in young medusae is horizontal. In full-grown medusae it hangs vertically downwards. This is quite an unusual feature among medusae. According to Dejdar the muscle fibres in the velum begin a short distance away from the umbrella margin, so that the velum is rather independent of umbrella movements. It is somewhat thick and gelatinous.

The *stomach* has three endodermal regions. In the lower region near the mouth the cells are cubical and unciliated. In the middle region the cells are ciliated; and in the upper true stomach region there are many secretory cells (Dejdar, 1934).

The four perradial lips of the mouth are smooth, but slightly folded in old medusae.

According to Lankester (1881*a*) the cells of the upper stomach region exhibit intra-cellular digestion. He said that the cells of this region appear, under certain circumstances, as an open meshwork giving off amoeboid processes by means of which solid food particles are taken in.

The *gonads* are very distinctive. They arise on the under surfaces of the radial canals where they merge with the stomach. They appear thus almost as pouches which have grown out from the stomach wall at the four corners of its base. Dejdar records having seen food in the pouches.

Van Auken (1940) states that the male gonad is more elongated at its distal end than that of the female, and hangs down farther into the subumbrellar cavity.

The sperm are 25μ long, of which 18μ is tail. The ripe eggs have a delicate membrane, are opaque, and 0·54–0·58 mm. in diameter (Dejdar, 1934).

The development of the egg has been described by Payne (1926); segmentation is unequal.

The *marginal tentacles*, which are hollow, are covered with small papillae, in the points of which the nematocysts are situated in groups (Text-fig. 272). These groups consist of two to ten nematocysts, though three to seven is the usual number. The basal portions of the older marginal tentacles are frequently almost devoid of nematocysts.

The marginal tentacles are formed as outgrowths of ectoderm and endoderm from the umbrella margin. At first the endodermal core is solid, but later a lumen is formed. The cavities of the marginal tentacles are continuous with the cavity of the ring canal (Payne, 1924).

The *marginal vesicles* are of an unusual form (Text-fig. 273). They are long and tubular, and situated in the velum. The end nearest the umbrella margin forms an enlarged cavity which contains the concretion. This cavity is continued as a narrow tube running towards the margin of the velum where it ends blindly.

The concretion consists of twelve to eighteen refractory cells covered by an outer layer of eight to ten very flat transparent cells. The concretion is attached, by a pedicel of varying length, to the wall of the vesicle nearest to the ring canal. It has thirteen to twenty sensory hairs on its basal region just above the pedicel.

The concretion begins as an endodermal outgrowth from the ring canal. The axis of the concretion is thus endodermal in origin, but it is later covered by a layer of cells which are ectodermal in origin and which also line the vesicle (Douglas, 1912; Dejdar, 1934).

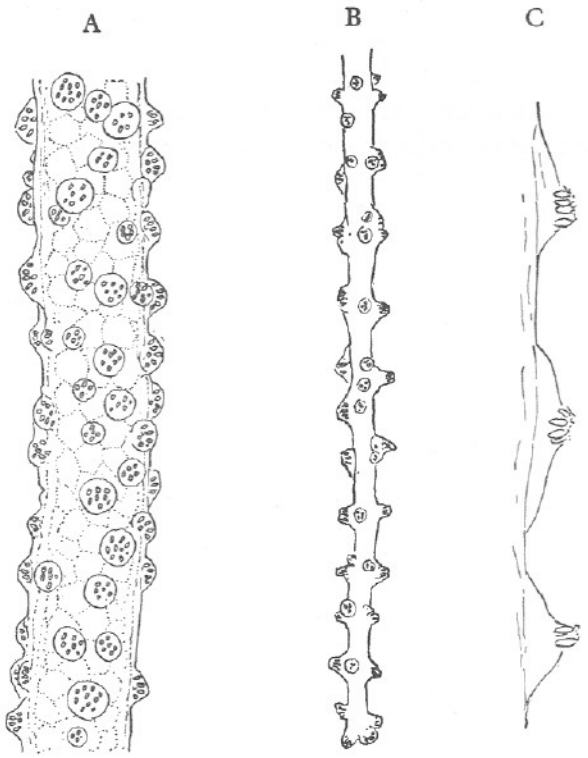
Payne (1924) described what he thought to be another sense organ situated at the junction of the umbrella margin and the velar ectoderm. It consisted of a number of elongated cells set together so as to resemble 'the layers of an onion'. Dejdar (1934) was unable to find these in his material.

Seasonal occurrence

In the two British localities in which *Craspedacusta sowerbyi* was found in natural waters the medusae first appeared in July. In the Exeter Ship Canal (Vallentin, 1930) they were found from July to October; during this period the temperature of the water ranged from 72° to 57° F. In the colliery reservoir in Monmouthshire (Jenkins, 1935) they occurred from July to September, the temperatures being 68–71° F.

In the *Victoria regia* tanks in Regent's Park, which were artificially heated to 85–90° F. the medusae were found at different times between April and August; in similar tanks in Sheffield they occurred from June to October. In a tropical aquarium tank in Edinburgh (van Someren, 1933) heated to 75° F. they appeared in May.

Under natural conditions, therefore, the species might be expected to be found in midsummer, when the temperature is reaching its maximum, until autumn.



Text-fig. 272. *Craspedacusta sowerbyi*. Details of marginal tentacles of preserved specimen from the Exeter Ship Canal, August 1928. A, portion of large marginal tentacle; B, terminal portion of small marginal tentacle; C, nematocyst clusters.

Habits

Much has been written on the habits of *Craspedacusta sowerbyi*.

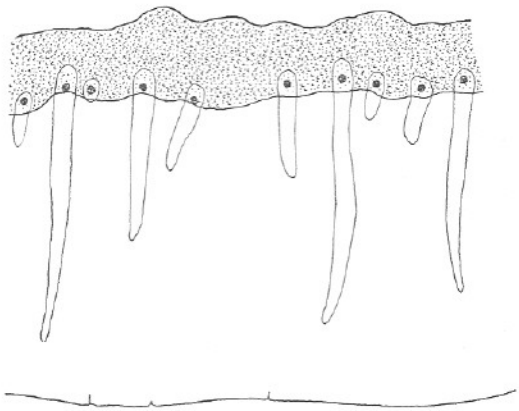
The medusa is an active swimmer. In the young stages the velum apparently acts normally as in other medusae. In older stages, however, it hangs downwards. The swimming attitudes have been described by a number of authors, e.g. Hargitt (1908), Boulenger & Flower (1928), Moser (1930), Ortenburger & Phillips (1931), and Dejdar (1934). The medusa swims actively upwards from the bottom with marginal tentacles contracted and pointing downwards; after reaching the surface it sinks passively downwards with elongated marginal tentacles trailing behind. When the medusa is sinking downwards its umbrella is much flattened, the velum hangs downwards, and the mouth extends well beyond the umbrella margin.

According to Hargitt (1908) in the normal resting attitude on the bottom the medusa lies on its back with marginal tentacles spread out along the bottom and velum pointing upwards. Dejdar (1934) found that the smallest medusae took many minutes to sink through about 24 cm.

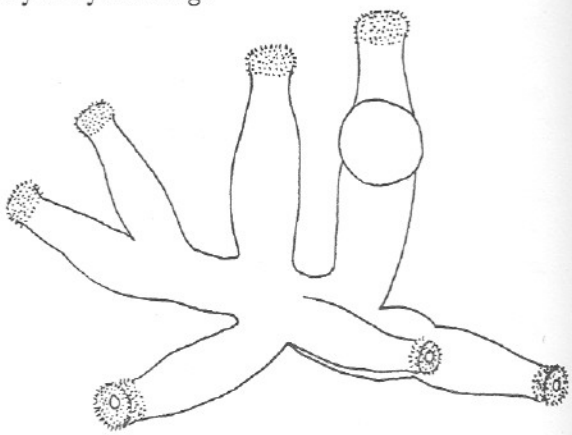
Under natural conditions the medusae tend to be found near the surface in bright sunny weather, but when lying deep down they may be brought to the surface by stirring the water up with an oar or some such object (e.g. Payne, 1924; Garman, 1924; White, 1930; Jenkins, 1935).

Payne (1924) and White (1930) note that the medusa becomes very active in the laboratory when a light is suddenly turned on. Romanes (1880, 1885) also recorded that they seek the unshaded end of a tank and swim at the surface during the daytime, but sink when the sun goes down.

Romanes made a number of observations on the physiology of *C. sowerbyi*. He found that at 65° F. the umbrella contracted at the rate of eighty pulsations a minute, whereas at 85° F. this rate increased to 180 per minute. A temperature of 100° F. was found to be fatal; this is considerably higher than the lethal temperature for marine medusae which Romanes gave as 70° F. The freshwater medusae were completely destroyed by freezing.



Text-fig. 273. *Craspedacusta sowerbyi*. Portion of velum with marginal vesicles, of preserved specimen from Exeter Ship Canal, August 1928.



Text-fig. 274. *Microhydra ryderi*, the hydroid of *Craspedacusta sowerbyi*. (After Payne, 1924, Pl. v, fig. 36.)

They were killed by immersion in sea-water of dilutions from 1 in 4 to 1 in 10, but in 1 in 15–18 the medusae would swim about for days.

In the effect of excising the margin of the umbrella they agree with marine medusae. If a portion of the umbrella is nipped the mouth moves over to that point, as in *Tiaropsis indicans*, but, unlike the latter, these movements cease after the extreme margin has been cut away.

Hargitt (1907) found that in distilled water the power of swimming was considerably lessened.

Maas (1908) experimented on the effects of NaCl and KCl, and of electric stimulation, while Cremer (1907) made observations with an electrogram.

The medusae have been found to feed on a variety of freshwater plankton organisms, among which are *Daphnia* and other small Crustacea, rotifers and Protozoa, including *Arcella*.

Schmitt (1939) gives a rather unusual record of damage done to goldfish by these medusae. The owner of the fish stated that 'apparently whenever one touched the tail of a fish it seemed to cause such an injury that a portion of the fin dropped off'. Kramp (1950, p. 176) records similar attacks on young fish in an aquarium.

HYDROID. *Microhydra ryderi* Potts. (Text-fig. 274.)

(For full description see Payne, 1924, *Journ. Morph. Philadelphia*, vol. XXXVIII, no. 3, p. 393, pl. i, fig. 1; pl. v, fig. 36; pl. x; Dejdar, 1934, *Zeit. Morph. Ökol. Tiere, Berlin*, Bd. XXVIII, Heft 5, p. 598, figs. 1–13.)

Simple polyps, without tentacles; cylindrical, 0·5–2·0 mm. high, with apical mouth surrounded by nematocysts forming a capitulum; basal portion with thin periderm covering; solitary or in small colonies of two to four, rarely seven polyps.

Medusa buds at first lateral; later terminal in position owing to reduction of oral region.

The hydroid was first discovered in the British Isles by Bourne (1884*a*). Payne (1924) records that 'the hydroid contracts during the winter into a solid mass of cells and secretes a chitinous-like covering around it; all traces of the capitulum are lost'. When brought into the laboratory these resting stages may redevelop into hydroids in a few days.

Historical

*Craspedacusta sowerbii** was first recorded and so named by Lankester (1880*a*) in the number of *Nature* published on 17 June. A week later, 24 June, Allman (1880*a*) also published an account of the medusa in *Nature* under the name *Limnocodium victoria*. Allman had, however, proposed his name at a meeting of the Linnean Society on the same day that Lankester's name was published. By mutual agreement it was decided that the name should be *Limnocodium sowerbii*. As this violated the accepted rules of nomenclature Mayer (1910) applied on 28 August 1907 to the International Commission on Zoological Nomenclature asking that the well-known name *Limnocodium* should be retained. The Commission, however, decided that *Craspedacusta sowerbii* Lankester, 1880, 17 June, has clear priority over *Limnocodium victoria* Allman, 1880, 24 June.

* The spelling *sowerbyi* is now preferable.

ORDER

TRACHYMEDUSAE

Hydromedusae with hemispherical or deep bell-shaped umbrella; with thickened marginal nematocyst ring; with gonads usually confined to radial canals; with solid marginal tentacles, or with solid and hollow marginal tentacles; with sense organs in form of sensory clubs with endodermal axes which may be free or enclosed. Without a hydroid stage.

The Trachymedusae are distinguished from the Leptomedusae by the fact that the sense organ or statocyst has an endodermal origin and is not purely ectodermal. Sense organs with a similar endodermal origin occur in some Limnomedusae and in Narcomedusae. The Trachymedusae are, however, distinguished from the Limnomedusae in having solid marginal tentacles with an axis composed of a single row of cylindrical endoderm cells. They are distinguished from the Narcomedusae in that the margin of the umbrella is not lobed or divided by peronial grooves.

A characteristic feature of most Trachymedusae is the heavy musculature of the subumbrella and the great development of the velum. They are also characterized by having direct development without an interposed hydroid stage. They are essentially oceanic.

In most Trachymedusae the marginal tentacles are very fragile and liable to break off at their bases in preserved specimens. Since, therefore, most of our knowledge of the group has been gained from the examination of preserved specimens collected on oceanographical expeditions, the lack of perfect specimens has hindered progress in the identification and classification of these medusae. Owing to their widespread oceanic existence, also, there appears to be considerable variation in any one species and in the past many have been described. As increasing numbers have become available from the different expeditions many intermediate forms have been found and it has become difficult to find hard and fast distinctions. There has, thus, been a tendency on the part of some authors to lump together many of these so-called species, but until more is known it is better not to go too far in this direction.

A satisfactory classification of the Trachymedusae has presented great difficulties. They can for certain be divided into four families, the Geryonidae, the Rhopalonematidae, the Halicreidae, and the Ptychogastridae. Of these, the first and the last two are well defined, but there has been considerable discussion on the Rhopalonematidae. This family has previously been known as the Trachynematidae; since, however, the genus *Trachynema* has now ceased to exist and is sunk as a synonym of *Rhopalonema*, it is necessary that the family should take its name from the latter genus.

Many authors have attempted to divide the family into two subfamilies, the Rhopaloneminae and the Aglaurinae, or have even given these divisions family rank. The division has been based on the rather slight character of the presence or absence of a peduncle. In fact this character might afford a satisfactory division were it not that one genus, *Crossota*, contains species both with and without peduncles. On the whole, therefore, it seems better to retain a single family.

Of the four families of the Trachymedusae the Ptychogastridae are not represented in our

fauna, being cold-water medusae. The remaining three families can be distinguished by the following characters:

Trachymedusae with four or six radial canals; with centripetal canals . . . . **Geryonidae**
Trachymedusae with eight, or rarely more, radial canals; without centripetal canals:
Each marginal tentacle of uniform structure throughout . . . . **Rhopalonematidae**
Each marginal tentacle with flexible proximal portion and stiffer distal portion . **Halicreidae**

Family GERYONIDAE

Trachymedusae with stomach with peduncle; with four or six radial canals; with centripetal canals; with flattened leaf-shaped gonads on radial canals; with marginal tentacles of two kinds, hollow and solid; with marginal sensory clubs enclosed in mesogloea.

The characteristic features of the family Geryonidae are the fact that they are the only Trachymedusae with less than eight radial canals and the presence of centripetal canals. From these characters, and the form of the umbrella, the structure of the marginal tentacles, and the position of the enclosed sensory clubs, the Geryonidae appear to lie on the border line between the Limnomedusae and the Trachymedusae.

The family is represented in British waters by one genus, *Liriope* Lesson.

Genus **Liriope** Lesson, 1843

Geryonidae with four radial canals.

There is probably one British species of the genus, *Liriope tetraphylla* (Chamisso & Eysenhardt). The species is very variable, especially as regards the shape of the gonads, and it is probably the only species of the genus. In general appearance it is quite unmistakable.

Liriope tetraphylla (Chamisso & Eysenhardt)

Plate XXIV, fig. 2; Text-figs. 275–82

Geryonia tetraphylla Chamisso & Eysenhardt, 1821, *Nova Acta K. Leop. Carol. Deutsche Akad. Naturforsch. Bonnae*, Bd. x, p. 357, pl. xxvii, fig. 2.
Dianaea exigua Quoy & Gaimard, 1827, *Ann. Sci. nat. Paris*, tome x, pl. vi, figs. 5–8.
Geryonia bicolor Eschscholtz, 1829, *System der Acalephen*, p. 89, pl. xi, fig. 1.
Geryonia rosacea Eschscholtz, 1829, ibid. p. 89, pl. xi, fig. 2.
Geryonia exigua, Eschscholtz, 1829, ibid. p. 89.
Liriope cerasiformis Lesson, 1843, *Hist. Nat. Zooph. Acalèphes*, p. 332.
Maas, 1893, *Ergebn. Plankton Expedit. Humboldt-Stift.* Bd. II, K.c., p. 35, pl. ii, figs. 5, 6; pl. iii, figs. 1–3, 8–10.
Geryonia appendiculata Forbes, 1848, *Monogr. Brit. Medusae*, p. 36, pl. v, fig. 2.
Liriope tetraphylla, Gegenbaur, 1856, *Zeit. Wiss. Zool. Leipzig*, Bd. VIII, p. 257.
Vanhöffen, 1902, *Wiss. Ergebn. 'Valdivia'*, Bd. III, p. 82, pl. x, fig. 14.
Mayer, 1910, *Medusae of the World*, vol. II, p. 418, pl. liii, fig. 4.
Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 112, pl. iii, figs. 6, 7; pl. iv, figs. 2, 3.
Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, no. 1946, p. 55.
Browne, 1916, *Trans. Linn. Soc. London*, ser. 2 (Zool.), vol. XVII, pt. II, p. 198.
Bigelow, 1919, *Bull. U.S. Nat. Mus.* 100, vol. I, pt. III, p. 325.
Uchida, 1928, *Japan. Journ. Zool.* vol. II, no. 1, p. 82, fig. 3.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 518, fig. 26.
Thiel, 1936, *Zool. Jahrb. Jena*, Abt. Syst., Ökol. Geogr. Bd. LXIX, Heft 1, p. 45, fig. 10.
Bigelow, 1938, *Zoologica, New York*, vol. XXIII, pt. II, p. 127.

Liriope bicolor, Gegenbaur, 1856, *Zeit. Wiss. Zool. Leipzig*, Bd. VIII, p. 257.
Liriope rosacea, Gegenbaur, 1856, ibid. p. 257.
Maas, 1897, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXIII, no. 1, p. 26, pl. iii, figs. 7, 8.
Hartlaub, 1909*b*, *Zool. Jahrb. Jena, Abt. Syst.* Bd. XXVII, Heft 5, p. 466, pl. xxii, figs. 28, 31, 32.
Mayer, 1910, *Medusae of the World*, vol. II, p. 417, pl. lii, fig. 1.
Liriope appendiculata, Gegenbaur, 1856, *Zeit. Wiss. Zool. Leipzig*, Bd. VIII, p. 257.
Liriope exigua, Gegenbaur, 1856, ibid. p. 257.
Mayer, 1910, *Medusae of the World*, vol. II, p. 413, pl. lii, figs. 2–4; pl. liii, fig. 4.
Kramp, 1924, *Rep. Danish Oceanogr. Expedit.* 1908–10, vol. II, Biol. H. 1, p. 30, fig. 25.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 516, fig. 25.
Liriope mucronata Gegenbaur, 1856, *Zeit. Wiss. Zool. Leipzig*, Bd. VIII, p. 257, pl. viii, fig. 17.
Mayer, 1910, *Medusae of the World*, vol. II, p. 414, text-fig. 267.
Kramp, 1924, *Rep. Danish Oceanogr. Expedit.* 1908–10, vol. II, Biol. H. 1, p. 31, fig. 26.
Liriope scutigera McCrady, 1857, *Proc. Elliott Soc. Nat. Hist. Charleston*, vol. I, p. 208.
Fewkes, 1881*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. VIII, no. 8, p. 162, pl. vi, figs. 7, 10, 11.
Brooks, 1886*a*, *Mem. Boston Soc. Nat. Hist.* vol. III, no. 12, p. 373, pls. 41, 42.
Mayer, 1910, *Medusae of the World*, vol. II, p. 421, text-fig. 278; pl. l, figs. 7–10; pl. li, fig. 1.
Liriope catharinensis F. Müller, 1859, *Arch. Naturgesch. Berlin*, 25. Jahrg. Bd. I, pp. 310, 316; pl. xi, 25 figs.
Maas, 1893, *Ergebn. Plankton Expedit. Humboldt-Stift.* Bd. II, K.c., p. 37, pl. ii, figs. 7, 9.
Mayer, 1910, *Medusae of the World*, vol. II, p. 421, pl. l, figs. 1–6.
Xanthea tetraphylla, L. Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 365.
Glossocodon catharinensis, Haeckel, 1864, *Jena Zeit. Naturw.* Bd. I, p. 461.
Liriope eurybia Haeckel, 1864, ibid. Bd. I, pp. 329, 462, pl. xii, figs. 11–25.
Maas, 1893, *Ergebn. Plankton Expedit. Humboldt-Stift.* Bd. II, K.c., p. 35, pl. ii, figs. 2, 3.
Mayer, 1910, *Medusae of the World*, vol. II, p. 420, pl. li, figs. 3, 4.
Kramp, 1924, *Rep. Danish Oceanogr. Expedit.* 1908–10, vol. II, Biol. H. 1, p. 31, fig. 27.
Liriope ligurina Haeckel, 1864, *Jena Zeit. Naturw.* Bd. I, p. 457.
Haeckel, 1865*b*, *Rüsselquallen*, p. 23.
Glossocodon eurybia, Haeckel, 1866, *Jena Zeit. Naturw.* Bd. II, pp. 93–128, 129–43.
Haeckel, 1865*b*, *Rüsselquallen*, pp. 28, 33, pls. ii, iii.
Glossocodon mucronatum, O. & H. Hertwig, 1878, *Das Nervensystem der Medusen*, p. 48, pl. iv, fig. 4.
Liriantha tetraphylla, Haeckel, 1879, *System der Medusen*, p. 286.
Liriantha appendiculata, Haeckel, 1879, ibid. p. 287.
Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 495.
Liriantha scutigera, Haeckel, 1879, *System der Medusen*, p. 287.
Liriantha catharinensis, Haeckel, 1879, ibid. p. 287.
Liriantha mucronata, Haeckel, 1879, ibid. p. 288.
Liriope cerasus Haeckel, 1879, ibid. p. 289, pl. xviii, fig. 15.
Liriope crucifera Haeckel, 1879, ibid. p. 290.
Liriope conirostris Haeckel, 1879, ibid. p. 291.
Mayer, 1910, *Medusae of the World*, vol. II, p. 419, pl. li, fig. 2.
Glossocodon canariensis, Haeckel, 1879, *System der Medusen*, p. 292.
Glossocodon lütkenii Haeckel, 1879, ibid. p. 293, pl. xviii, fig. 5.
Glossocodon agaricus Haeckel, 1879, ibid. p. 293.
Glossocodon tenuirostris Fewkes, 1882*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. IX, no. 7, p. 278, pl. vii, figs. 1–9.
Glossocodon haeckelii Goette, 1886, *Math. naturw. Mitth. Akad. Wiss. Berlin*, p. 599; *SitzBer. preuss. Akad. Wiss.* Bd. VII, p. 833.
Liriope distanogona Maas, 1893, *Ergebn. Plankton Expedit. Humboldt-Stift.* Bd. II, K.c., p. 36, pl. iii, figs. 4–7.
Liriope compacta Maas, 1893, ibid. p. 37, pl. ii, fig. 11.
Maas, 1905*a*, *Siboga-Expedit.* Monogr. X, p. 62, pl. ix, figs. 55–9.
Liriope minima Maas, 1893, *Ergebn. Plankton Expedit. Humboldt-Stift.* Bd. II, K.c., p. 37, pl. ii, figs. 8, 10; pl. iv, figs. 1, 2.
Liriope hyperbolica Maas, 1893, ibid. p. 38, pl. ii, fig. 4.
Liriope hyalina Agassiz & Mayer, 1899, *Bull. Mus. Comp. Zoöl. Harvard*, vol. XXXII, p. 166, pl. ix, fig. 32.
Liriope agaricus, Vanhöffen, 1902, *Wiss. Ergebn. 'Valdivia'*, Bd. III, p. 79.
Liriope canariensis, Vanhöffen, 1902, ibid. p. 79.
Liriope lütkeni, Vanhöffen, 1902, ibid. p. 79.
Liriope indica Bigelow, 1904, *Bull. Mus. Comp. Zoöl. Harvard*, vol. XXXIX, p. 258, pl. v, figs. 17, 18.
Mayer, 1910, *Medusae of the World*, vol. II, p. 421, text-fig. 279.

Liriope hemisphericus Bigelow, 1904, *Bull. Mus. Comp. Zoöl. Harvard*, vol. xxxix, p. 259, pl. iv, figs. 15, 16.
Liriope haeckeli, Hartlaub, 1909*b*, *Zool. Jahrb. Jena, Abt. Syst.* Bd. xxvii, Heft 5, p. 464, pl. xxii, figs. 29, 30, 33.
Liriope sp., Browne, 1926, *Trans. Zool. Soc. London*, vol. xxii, pt. 1, no. 14, p. 109.

Specific Characters. Here regarded as the only species of the genus.

Description of Adult

Umbrella hemispherical, or slightly flatter or higher than a hemisphere; jelly thick, especially in apical region; marginal nematocyst ring present, with four perradial and four interradial short exumbrellar nematocyst tracks. Velum well developed. Stomach small, situated on elongated tapering peduncle of varying shape; length of peduncle very variable, from one to three times umbrella height. Mouth with four simple or slightly crenulated lips, with nematocyst clusters along margin. Four straight radial canals and ring canal broad; one to three, or sometimes more, short blind centripetal canals in each quadrant. Four flattened leaf-like gonads, one on subumbrellar portion of each radial canal, very variable in shape and size, circular, oval, egg-shaped, heart-shaped, triangular, or kite-shaped, sometimes covering almost entire subumbrellar surface. Four large hollow perradial marginal tentacles with nematocyst rings; four small solid interradial marginal tentacles with adaxial nematocyst clusters. No cirri. Eight closed marginal vesicles, embedded in umbrella jelly, four interradial vesicles just left of interradial marginal tentacle bases, four perradial vesicles immediately beneath bases of perradial marginal tentacles; each with one concretion. Diameter of umbrella 10–30 mm. Colour of stomach, gonads and marginal tentacles rose-red or green.

Distribution

Liriope tetraphylla is a warm-water oceanic medusa and has only been recorded on the south-western coasts of the British Isles. It may thus be carried into the English Channel by the flow of Atlantic water, having been recorded at Portland, Dartmouth and Plymouth. Its occurrence is, however, dependent upon the hydrographic conditions.

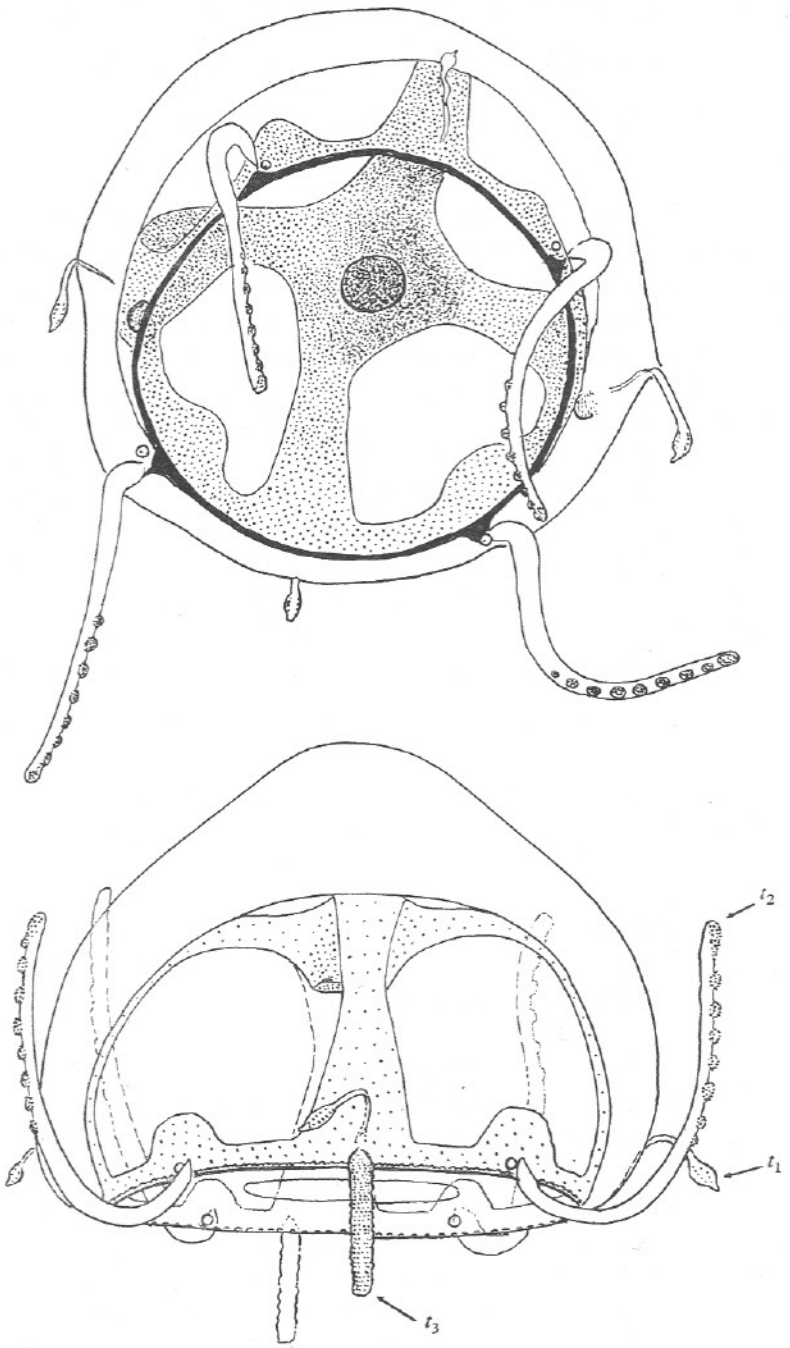
The medusa has a world-wide distribution and occurs in all three oceans and in the Mediterranean. It is confined mainly to the warm waters of the oceans between the north and south isotherms of about 20° C. (Thiel, 1936, p. 52, fig. 10).

Developmental Stages and Structural Details

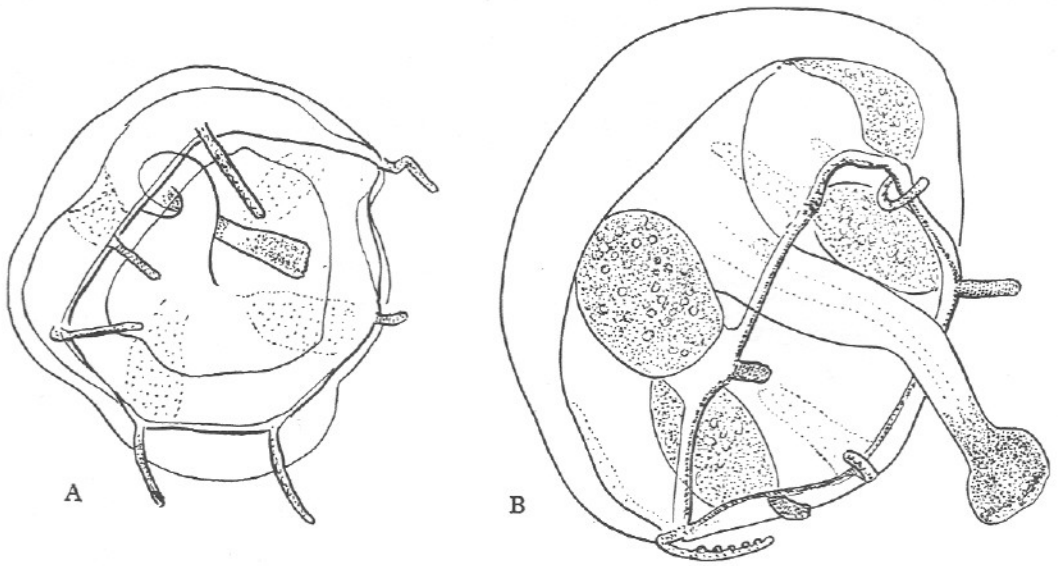
Liriope tetraphylla is a Trachymedusa with direct development, fully described by Metschnikoff (1886*a*) and Brooks (1886*a*). Metschnikoff described the development of Mediterranean *Liriope* from the egg (Text-fig. 282). The eggs were 0·135 mm. in diameter; they were laid between 3 and 4 p.m., from December to March. Segmentation is regular. After the sixteen-celled stage has been reached, each cell divides transversely, an endodermal layer thus being produced inside the layer of ectoderm by delamination. The endoderm cells migrate inwards to form a closed sac, and jelly is developed between the two layers. The ectoderm cells become ciliated and the larva swims actively.

The jelly increases in thickness until the larva is almost spherical and the endoderm sac becomes closely applied to the ectoderm on that side which is to be the oral pole, or subumbrellar surface.

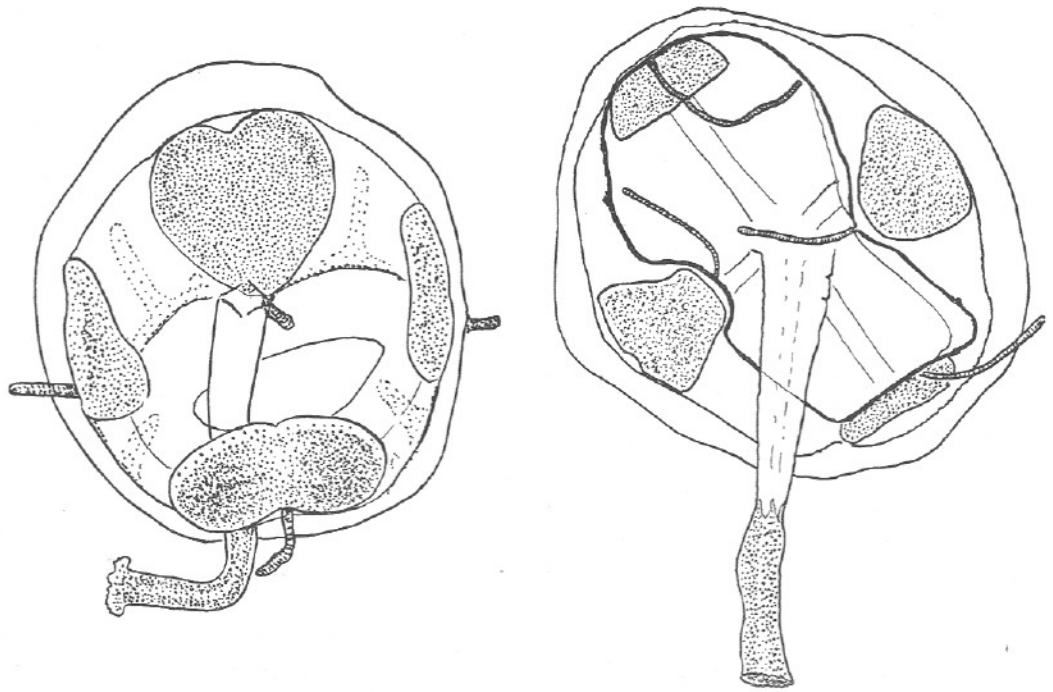
The mouth develops as an opening from the endodermal sac, which is to form the gastric cavity, and four short marginal tentacles grow out from this primary stomach. These have endodermal



Text-fig. 275. *Liriope tetraphylla*. Young specimen 1·7 mm. in diameter. Above, subumbrellar view; below, lateral view. t_1, primary perradial marginal tentacle; t_2, solid interradial marginal tentacle; t_3, secondary hollow perradial marginal tentacle.



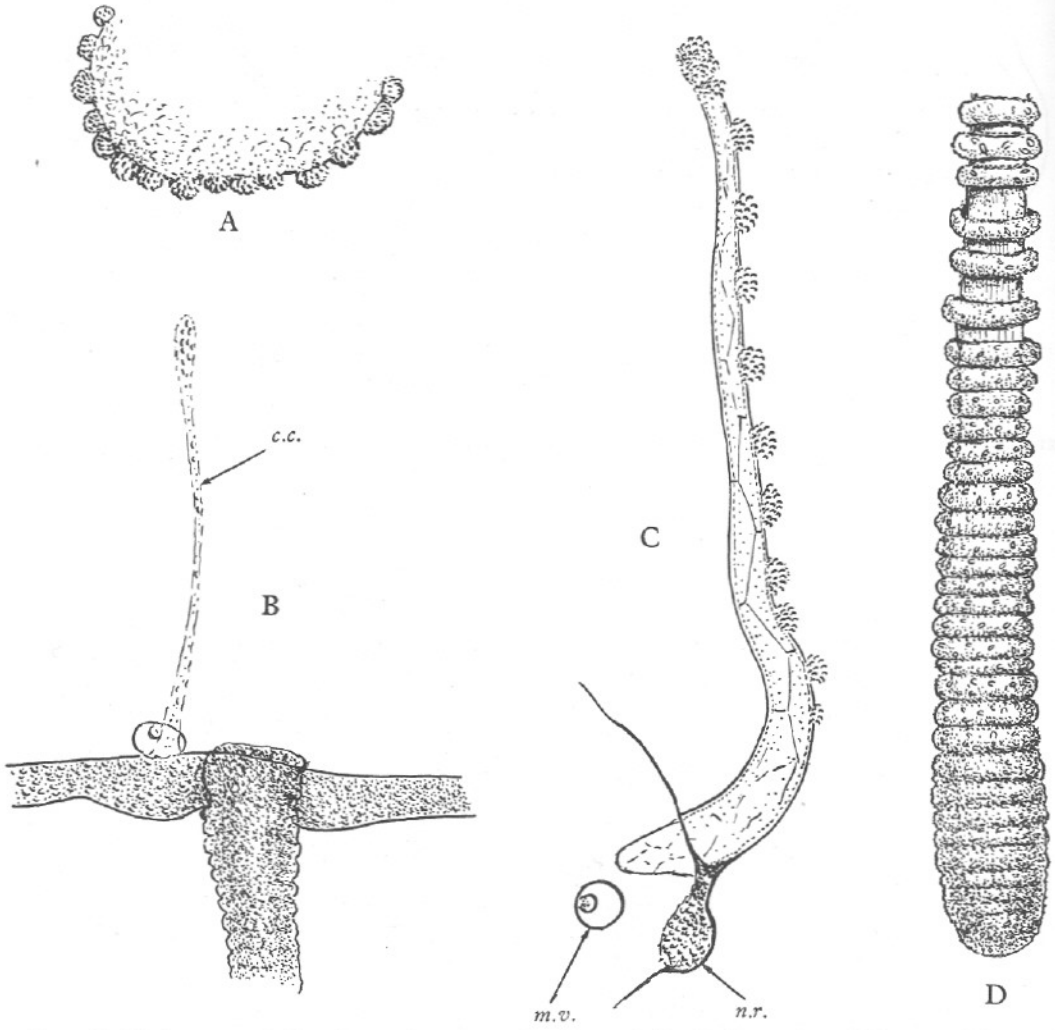
Text-fig. 276. *Liriope tetraphylla*. Preserved specimens, Plymouth, 26. x. 33. A, *c.* 2.5 mm. in diameter; B, *c.* 4.5 mm. in diameter.



Text-fig. 277. *Liriope tetraphylla*. Preserved specimens *c.* 9 mm. in diameter, Plymouth, 26. x. 33 and 25. x. 13. (Latter from E. T. Browne collection.)

cores derived from the endoderm of the stomach wall. The velum now develops and by the sixth day a spherical medusa-like larva is thus formed.

The medusa now becomes more flattened and the lower surface is arched to form the sub-umbrellar cavity. The upper and lower walls of the stomach fuse over four somewhat heart-shaped interradial areas, leaving unfused portions which form the four radial canals, the ring



Text-fig. 278. *Liriope tetraphylla*. A, portion of margin of mouth-lip; B, base of a solid interradial marginal tentacle, with a centripetal canal and a marginal vesicle; C, lateral view of a solid interradial marginal tentacle, showing a marginal vesicle (*m.v.*), and the marginal nematocyst ring (*n.r.*) of the umbrella; the tentacle is in the erect position; D, terminal portion of a hollow perradial marginal tentacle.

canal, and the first beginnings of the four larger interradial centripetal canals. All the canals are wide, the radial canals becoming slightly narrower as they approach the stomach.

The radial canals are formed on the same radii as the four marginal tentacles. These primary marginal tentacles are therefore perradial.

When the medusa is between 1 and 2 mm. in diameter the umbrella is nearly hemispherical (Text-fig. 275). The jelly is fairly thick, especially in the apical region. The stomach is short and

the mouth has four simple lips. There is no peduncle. The four radial canals and ring canal are broad, the radial canals being widest at their distal ends. The four interradial centripetal canals show as wide embayments from the ring canal. There are no signs of gonads. There are four small perradial primary marginal tentacles, situated on the exumbrella a short distance above the umbrella margin. These primary marginal tentacles consist of a large nematocyst swelling at the end of a short stalk. At the apex of this swelling is a small whip-like extension. Browne (1896*a*, p. 495) says that this whip-like tongue is contained within the bulb containing the nematocysts. He says that he has seen it 'occasionally protruded and after moving rapidly about in every direction withdrawn again inside the bulb'.

On the margin of the umbrella there are four solid interradial marginal tentacles, with batteries of nematocysts on their adaxial sides (Text-fig. 278C). These marginal tentacles are short, and usually carried in an upright position alongside the exumbrella, extending upwards for about half or slightly more than half of the height of the umbrella. When the marginal tentacles are in this position the adaxial nematocyst clusters are directed outwards. In some specimens the secondary perradial marginal tentacles are just appearing on the umbrella margin beneath the small primary marginal tentacles. At this stage the four interradial marginal tentacles are much the largest. There are four marginal vesicles situated in the jelly of the umbrella, one just to the left of the base of each of the four large interradial marginal tentacles (Text-figs. 278B, C). Each vesicle has a single concretion. The medusa is colourless.

With the further growth of the medusa the four secondary perradial marginal tentacles are developed and increase in size. These marginal tentacles differ from the interradial marginal tentacles. They are hollow and have numerous rings of nematocysts (Text-fig. 278D). They are not carried in an upright position, but hang down or trail behind the umbrella when the medusa is swimming. They can be extended to a considerable length. At the same time one or two of the small primary marginal tentacles may be lost. In fact they are usually all lost before the medusa is full grown.

When the medusa is about 3 mm. in diameter the peduncle begins to develop, but the mouth does not extend beyond the umbrella margin. The peduncle lengthens, however, very rapidly and at quite a small size the medusa already has the appearance typical of the adult.

The gonads do not start to appear until the medusa is about 4 mm. in diameter.

There is no marked alteration in structural appearance during the further growth of the medusa. The four remaining marginal vesicles are developed at the bases of the perradial marginal tentacles; the centripetal canals (Text-fig. 278B) increase in number. Thus the four interradial marginal vesicles are situated just to the left of their corresponding marginal tentacles, while the four perradial vesicles are immediately beneath the bases of the radial marginal tentacles.

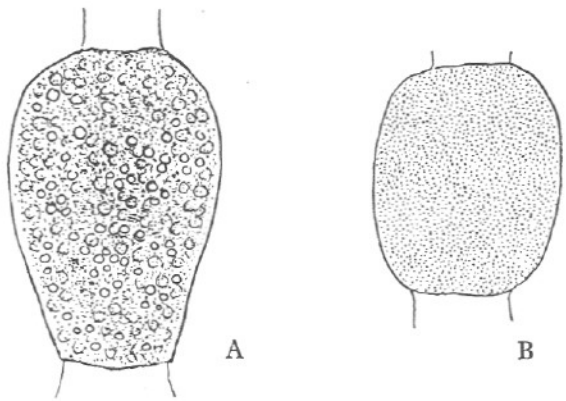
The number of centripetal canals and the stage at which they are developed appear to be somewhat variable. Three is the usual number in each quadrant, of which the central interradial canal is always the longest. Yet there may sometimes be more than three, or only one, in each quadrant.

It is in the gonads, however, that most variation is shown. Not only does the shape of the gonad change with growth, but its final form is also extremely variable (Text-figs. 279, 280, 281). As a result, a great number of species have been erected according to the shape of the gonad (see pp. 426–7).

The outline of the gonad may be circular, oval, egg-shaped, heart-shaped, triangular, or somewhat kite-shaped. It is convenient to indicate the shape of the gonad by the specific name given to the medusa bearing that shaped gonad. This classification is as follows:

Circular	*scutigera* McCrady, 1858
Oval	*catharinensis* F. Müller, 1859
Egg-shaped	*eurybia* Haeckel, 1864
Heart-shaped	*exigua* Quoy & Gaimard, 1827
Triangular	*agaricus* Haeckel, 1879
Kite-shaped	*lütkenii* Haeckel, 1879

The area of the subumbrella occupied by the gonad may also vary and in the medusae in which they are largest the subumbrellar surface may be almost entirely covered. In the form with triangular gonads the upper corners of the gonads may be almost confluent as in *L. compacta* Maas.



Text-fig. 279. *Liriope tetraphylla*. Gonads of preserved specimens, Valencia, 29. xi. 01. (E. T. Browne collection.) A, female; B, male.

Mayer (1910) records having seen gonads of different shapes present in one and the same medusa. While it is possible approximately to place the majority of the gonad shapes into categories, it is found that so many intermediate shapes may occur that all the gaps between the categories are bridged.

The gonads may be small, leaving both ends of the radial canal free, or they may be so large that they merge practically with the ring canal and reach the base of the peduncle. When the two ends of the radial canals are free the distal end near the ring canal is usually broader than the end near the peduncle.

While this range in gonad shape is shown by the species over the whole geographical area of its distribution, it is not usual to find great variation in any one place at one time. For instance, the medusae that appear off the mouth of the English Channel seem to conform mostly to the *exigua* type, with heart-shaped gonads, nevertheless they still show a certain amount of variation; outlines of some gonads from different specimens collected off Plymouth are shown in Text-fig. 280. Indeed, considerable variation may be found in the shapes of the gonads of a single individual (Text-fig. 281), thus confirming the observation of Mayer (1910) recorded above.

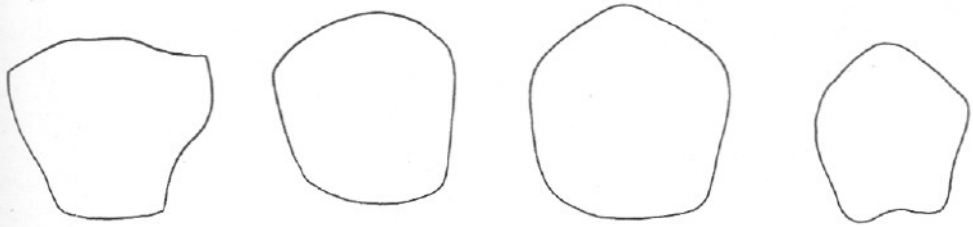
The central mass of jelly in the peduncle terminates in an elongated point in the stomach. This may sometimes project, if the mouth-lips are turned back, giving the appearance of a tongue.

Seasonal occurrence

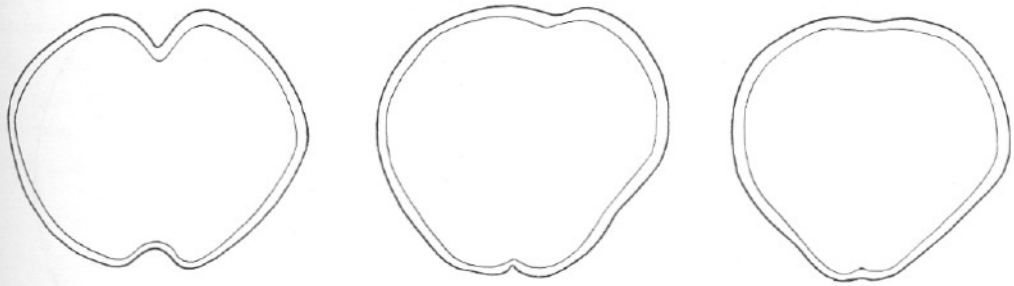
Since *Liriope tetraphylla* is an oceanic medusa with direct development it may be found in any month of the year. Actually its occurrence off the south-western coasts of the British Isles is controlled by hydrographic conditions and its appearance is therefore liable to be irregular. Off Plymouth, for instance, although it was extremely abundant in the latter half of 1930, it then became very scarce (Russell, 1938*a*) until 1948 when it was again abundant.

During the period of its abundance off Plymouth it was found in the months of May to December and January and February, the period of greatest abundance being August to December.

At Valencia it has been recorded in August and November.



Text-fig. 280. *Liriope tetraphylla*. Outlines of gonads from different preserved specimens, Plymouth, 25. x. 13. (E. T. Browne collection.)



Text-fig. 281. *Liriope tetraphylla*. Outlines of three gonads from an individual preserved specimen, Plymouth, 26. x. 33.

Habits

McCrady (1858, p. 209) records that *Liriope* is bold and rapid in its movements and very rapacious. He describes the capture by the medusa of a fish three times its size.

Forbes (1848) states that the medusa is phosphorescent.

I have noticed that the marginal tentacles, of young medusae at any rate, twitch in the manner characteristic of *Gossea* (see p. 407).

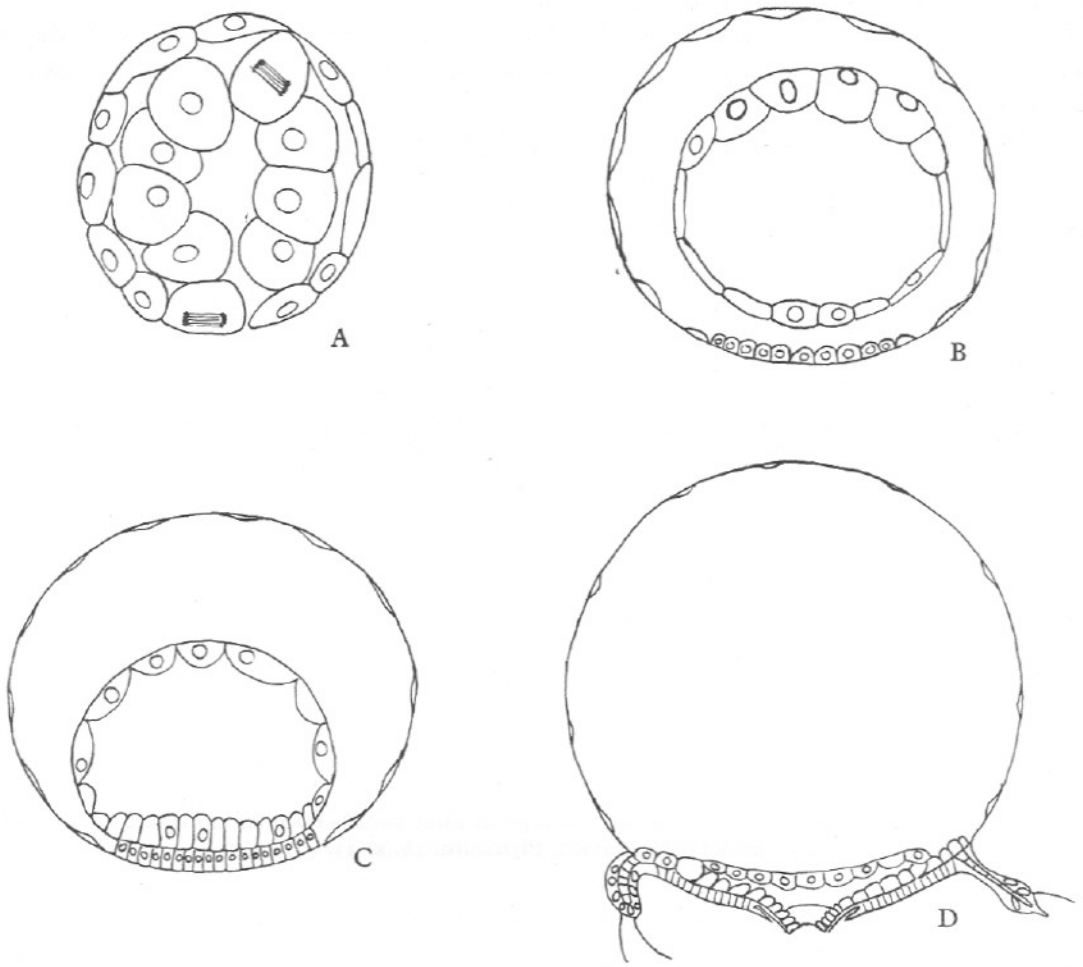
Experiments on developing eggs were made by Maas (1908); complete medusae were developed from half blastomeres, but not from quarter blastomeres.

Historical

Liriope tetraphylla was first described by Chamisso & Eysenhardt (1821). Since that date many species of *Liriope* have been described, based chiefly on the differences in the shape of the gonads. So many have now been described that it has become impossible to separate any of them

satisfactorily and they have been merged into one variable species. The position has been well put by Browne (1926):

Liriope ranges throughout the tropical and warm regions of all the oceans, including the Mediterranean. Many species have been described, some reduced to synonyms after much shuffling, but still the genus baffles those who try to identify the species.



Text-fig. 282. *Liriope tetraphylla*. Development of embryo. A, × 280; B, × 200; C, 5-day old larva × 160; D, 7-day old larva, optical section, × 160. (After Metschnikoff, 1886*a*, pl. v, figs. 18, 21, 22; pl. vi, fig. 2.)

Liriope floats about the ocean in great shoals usually near the surface. Specimens from a particular shoal, often covering a large area, have characters in common. Specimens from another shoal, far away, have also characters in common, but often differ so much from those of the other shoal that they could be regarded as distinct species, and have, in fact, been described and figured as such. But if a collection covers several adjacent areas then trouble begins. The extremes can be isolated and regarded as distinct species, but if the specimens are sufficiently numerous the extremes can be bridged by intermediate stages and so blend the whole lot together. A *Liriope* with cylindrical gonads can be linked by gradual changes in shape of the gonads with one which has distinctly triangular gonads. Specimens showing the extreme characters look

absolutely different, but given sufficient specimens they can be bridged without a break to show where the one ended and the other began. The shape and thickness of the umbrella, the length of the peduncle of the stomach, the number of centripetal canals, and the positions of the gonads upon the radial canals are all involved in these changes. Any extremes of these organs can be blended, and the whole acts like a kaleidoscope.

There are many races of *Liriope* in the oceans, and these on meeting and intermingling probably interbreed and give rise to new races; so there must be a constant change going on, but kept within the limits of the genus so far as the characters are concerned, and such characters are wanted for fixed specific characters. After all, there may be only one species of *Liriope*, and that a very variable one.

Thiel (1936) and Bigelow (1938) have agreed with Browne's final conclusion, which was already foreshadowed by Vanhöffen (1902). Bigelow says:

Granting, however, that the various forms of *Liriope* cannot be considered 'species', in the sense in which the term is generally employed in zoological nomenclature, it still remains an interesting question how they are to be interpreted, and how recorded in scientific literature. While it is now established that intergrades can be found with regard to every character which has been suggested as specific, we have still to recognise that the representatives of different swarms, or of different populations (seasonal or regional), often do differ so widely in many respects, as Browne has vividly described, that they would be referred without hesitation to different species had not the existence of intermediates been proved.

These variations in form thus remain to be explained and to this end therefore the type to which the specimens conform should be stated when the species is recorded.

More recently Ranson (1936) retains at least three Atlantic species, *exigua*, *eurybia*, and *tetraphylla*. Kramp (1947) prefers to leave the question open pending examination of more collections. Whichever is the final verdict, I have thought it most convenient to bring all under one species in this monograph in order that the reader may be able to identify any variety or species as the case may be.

Family RHOPALONEMATIDAE

Trachymedusae with stomach with or without peduncle; with usually eight, rarely more, radial canals; without centripetal canals; with gonads on radial canals or hanging as pouches into subumbrellar cavity; with numerous marginal tentacles, evenly distributed round umbrella margin or arranged in groups, sometimes of two kinds, each marginal tentacle of uniform structure throughout; with free, rarely enclosed, marginal sensory clubs.

The family Rhopalonematidae is represented by five genera which may be included in the British fauna; *Rhopalonema* Gegenbaur, *Colobonema* Vanhöffen, *Pantachogon* Maas, *Crossota* Vanhöffen, and *Aglantha* Haeckel.

For purposes of distinguishing these genera in British* waters the following characters may be used:

Without peduncle:
- With two kinds of marginal tentacles . . . . . **Rhopalonema**
- With one kind of marginal tentacle. . **Colobonema**, **Pantachogon**, and **Crossota**

With peduncle . . . . . **Aglantha**

* It is necessary to state that this key is only suitable for British genera since there is a Pacific species of *Crossota* which has a peduncle, *C. pedunculata* Bigelow.

This at once eliminates those genera except *Colobonema*, *Pantachogon*, and *Crossota*. These can now be distinguished by the following characters:

With thirty-two marginal tentacles	**Colobonema**
With more than thirty-two marginal tentacles:	
Gonads along radial canals	**Pantachogon**
Gonads in form of pouches hanging into subumbrellar cavity . .	**Crossota**

Genus **Rhopalonema** Gegenbaur, 1856

Rhopalonematidae with flattened or hemispherical umbrella; without peduncle; with mouth with four lips; with gonads on restricted portions of radial canals; with eight large marginal tentacles with swollen ends and eight to twenty-four smaller stiff marginal tentacles also with swollen ends; with enclosed sensory clubs.

The essential characteristics of the genus *Rhopalonema* are the possession of two kinds of marginal tentacles, and the fact that in the adult the sensory clubs are enclosed.

There are two species of the genus that may occur in deep western British waters, *R. velatum* Gegenbaur and *R. funerarium* Vanhöffen. They are quite distinctive, and can be separated by the presence of an apical process to the umbrella in the former and its absence in the latter, and by the much greater length of the gonads in the latter.

Rhopalonema velatum Gegenbaur

Text-figs. 283–4

Rhopalonema velatum Gegenbaur, 1856, *Zeit. Wiss. Zool. Leipzig*, Bd. VIII, p. 251, pl. ix, figs. 1–5.
Haeckel, 1879, *System der Medusen*, p. 264.
Maas, 1893, *Ergebn. Plankton Expedit. Humboldt-Stift.* Bd. II, K.c., p. 14, pl. i, figs. 9–11.
Vanhöffen, 1902, *Wiss. Ergebn.* '*Valdivia*', Bd. III, p. 59, pl. x, figs. 16, 23; pl. xi, fig. 32.
Maas, 1905*a*, *Siboga-Expedit.* Monogr. x, p. 50, pl. x, fig. 60.
Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 129, pl. ii, fig. 8; pl. xlv, fig. 11.
Mayer, 1910, *Medusae of the World*, vol. II, p. 378, text-figs. 213–19.
Neppi & Stiasny, 1913*a*, *Arb. Zool. Inst. Univ. Wien u. Zool. Stat. Triest*, Tom. XX, p. 79, pl. iv, fig. 38.
Browne, 1916, *Trans. Linn. Soc. London*, ser. 2 (Zool.), vol. XVII, pt. II, p. 193.
Kramp, 1924, *Rep. Danish Oceanogr. Expedit.* 1908–10, vol. II, Biol. H. 1, p. 23, fig. 21.
Uchida, 1928, *Japan. Journ. Zool.* vol. II, no. 1, p. 77, fig. 1.
Ranson, 1936, *Rés. Camp. Sci. Monaco*, Fasc. XCII, p. 137.
?*Sminthea globosa* Gegenbaur, 1856, *Zeit. Wiss. Zool. Leipzig*, Bd. VIII, p. 246, pl. IX, fig. 17 (?young).
?*Sminthea tympanum* Gegenbaur, 1856, ibid. p. 246, pl. ix, fig. 18 (?young).
Calyptra umbilicata Leuckart, 1856, *Arch. Naturg.* 22. Jahrg. p. 14, pl. i, figs. 9, 10.
Trachynema octonarium Haeckel, 1879, *System der Medusen*, p. 260.
?*Marmanema tympanum*, Haeckel, 1879, ibid. p. 262 (?young).
Marmanema clavigerum Haeckel, 1879, ibid. p. 263, pl. xvii, figs. 1, 2.
Marmanema umbilicatum, Haeckel, 1879, ibid. p. 263.
Rhopalonema coeruleum Haeckel, 1879, ibid. p. 264, pl. xvii, figs. 3–6.
Browne, 1906*a*, *Trans. Linn. Soc. London*, ser. 2 (Zool.), vol. X, pt. VI, p. 172.
Mayer, 1910, *Medusae of the World*, vol. II, p. 380 (in part), text-fig. 222.
Rhopalonema polydactylum Haeckel, 1879, *System der Medusen*, p. 265, pl. xvii, figs. 7–11.
Marmanema velatoides Maas, 1893, *Ergebn. Plankton Expedit. Humboldt-Stift.* Bd. II, K.c., p. 13, pl. i, fig. 6.
Rhopalonema striatum Maas, 1893, ibid. p. 15, pl. i, fig. 3.
Mayer 1910, *Medusae of the World*, vol. II, p. 381, text-fig. 224.
Rhopalonema typicum Agassiz & Mayer, 1902, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXVI, no. 3, p. 152, pl. v, figs. 21, 22.
Rhopalonema clavigerum, Mayer, 1910, *Medusae of the World*, vol. II, p. 382, pl. xlix, fig. 1; text-fig. 225.

Specific Characters

Umbrella with conical apical process; gonads on middle third of radial canals; eight to sixteen enclosed marginal sensory clubs each on right-hand side adjacent to the base of a marginal tentacle.

Description of Adult

Umbrella flatter than a hemisphere, with fairly thin, stiff, jelly, and conical apical thickening or process. Velum broad and very well developed. Stomach narrow, elongated quadrilateral with octagonal base; contractile, extending sometimes nearly to umbrella margin. Mouth with four simple or somewhat elongated lips. Eight straight radial canals and ring canal narrow. Eight gonads in form of elongated pouches situated along middle third of each radial canal. Eight large solid marginal tentacles with swollen ends, situated one at end of each radial canal. One to three very short stiff solid marginal tentacles, with swollen ends, in each octant. Eight or sixteen enclosed marginal sensory clubs. Diameter of umbrella 8–10 mm. Gonads and stomach colourless, or milky white; marginal tentacles colourless or with rose-red tips.

Distribution

Rhopalonema velatum is a warm-water oceanic species and in British waters it is only likely to be found far out off the mouth of the English Channel and the western coasts of Ireland and Scotland bathed by Atlantic waters. Its presence in other areas round the British Isles would be an indication of rather unusual hydrographic conditions.

Elsewhere the medusa occurs in all three oceans and in the Mediterranean, being confined between the isotherms of 15° C. (Thiel, 1936).

Developmental Stages and Structural Details

Rhopalonema velatum is a Trachymedusa with direct development. The development of the egg has been described by Metschnikoff (1886*a*) in the Mediterranean. The eggs are 0·24 mm. in diameter; they remain suspended in the water. Segmentation is regular and a morula is formed which is ciliated rather earlier than is usual among medusae. Metschnikoff was unable to take the development beyond the morula stage.

The youngest stage (Text-fig. 283) of a medusa which might be attributed to this species is figured by Mayer (1910, p. 379, text-fig. 216). This is less than 2 mm. in diameter. The umbrella is bell-shaped, slightly wider than high. The jelly is thin and there is no apical process. The velum is well developed. The stomach is very short, with a broad octagonal base; the eight straight radial canals and ring canal are narrow. There are no signs of gonads. There are eight short marginal tentacles, one opposite each radial canal, each having a spherical terminal swelling. There are eight similar but shorter marginal tentacles, one midway between adjacent radial canals. There are four marginal sensory clubs, one on the right-hand side of each alternate short marginal tentacle. The sense organ is in the form of an unenclosed sensory club with a single concretion (Text-fig. 283). Later an ectodermal capsule grows out from the umbrella margin surrounding the sensory club, so that eventually a closed vesicle is formed (Text-fig. 284 C).

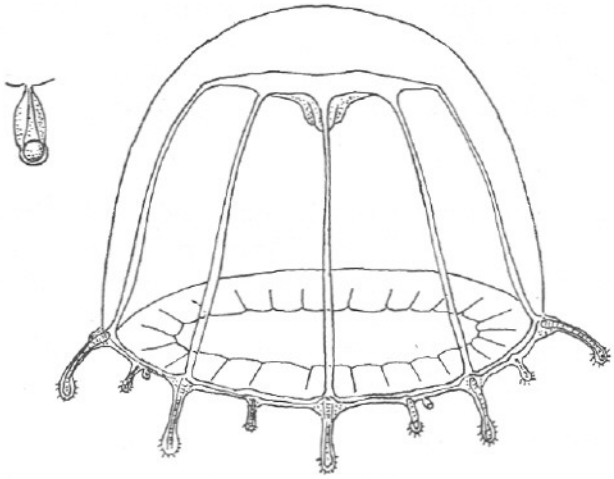
In small specimens less than 3 mm. in diameter caught far west of the mouth of the English Channel in April 1938, the four marginal sensory clubs were already enclosed.

During the further growth of the medusa the umbrella becomes more hemispherical and the apical process is developed. The stomach becomes elongated. The eight marginal tentacles

opposite the radial canals increase considerably in length, and two additional small short marginal tentacles may develop in each octant. Medusae may be found therefore with from sixteen (eight large and eight small) to twenty-four (eight large and sixteen small) or thirty-two (eight large and twenty-four small) marginal tentacles. The marginal tentacles are, however, extremely delicate and fragile, and only in the best preserved material are they to be found intact. Usually they are broken off at their roots.

The number of marginal sensory clubs increases from four to eight, one on the right-hand side of each of the first short marginal tentacles to develop in each octant. Later there may be sixteen in all, an additional club developing on the right-hand side of each of the eight large marginal tentacles.

The gonads first develop when the medusa is about 4 mm. in diameter.



Text-fig. 283. Probably a young stage of *Rhopalonema velatum*, *c.* 2 mm. in diameter, with enlarged view of marginal sensory club. (After Mayer, 1910, fig. 216, from life, Stazione Zoologica, Naples.)

The conical process on the summit of the umbrella is a constant feature distinguishing the species from *R. funerarium*. In preserved specimens it usually appears to be marked off from the rest of the umbrella by a transverse circular furrow or depression. In shape and size it varies considerably.

The velum is unusual in that it hangs downwards (Text-fig. 284).

As with other oceanic species the slight variations in form from place to place have resulted in the description of a number of species and these have later been merged together as variants of a single species. There is, for instance, the *R. striatum* type in which the umbrella is very flat and the gonads are situated on the inner third of the radial canals, as they are also in the *R. clavigerum* type which is, however, more normal in shape.

Seasonal occurrence

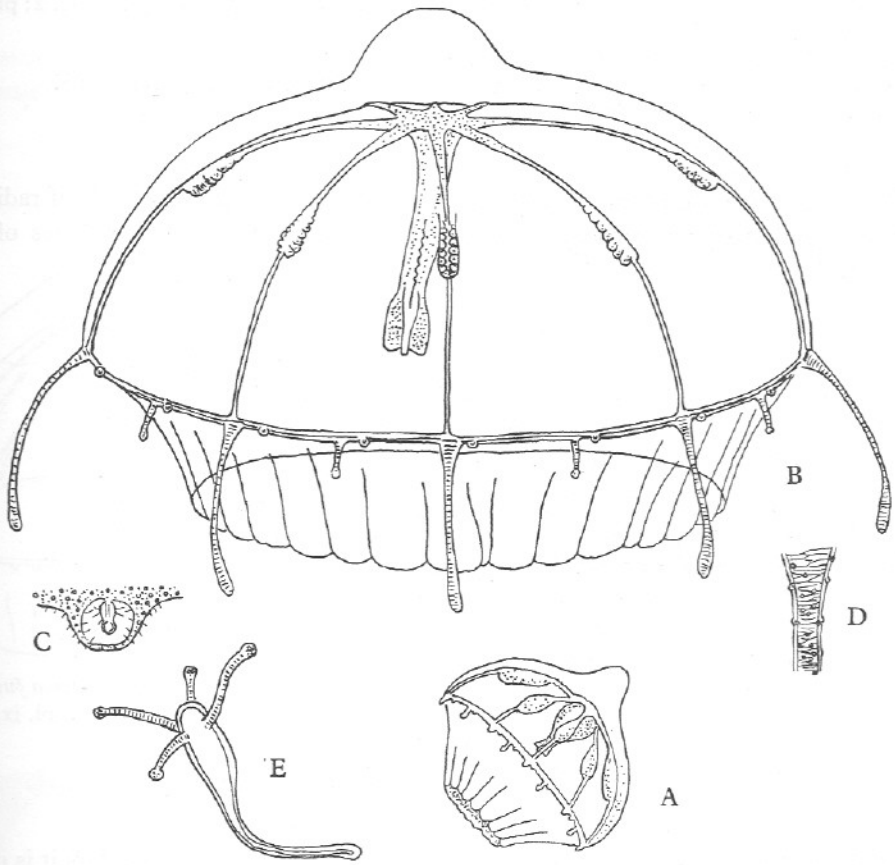
Since *Rhopalonema velatum* is an oceanic medusa with direct development it may be found at any season of the year, though it is probably less numerous in winter than in summer.

Habits

As regards its swimming, Agassiz & Mayer (1902) say: 'The bell-walls are very thin but are remarkably stiff and rigid, swimming being accomplished by means of the strokes of the powerful

velum which is exceedingly flexible.' 'The velum is large, and the contractions of its powerful muscles cause it to vibrate with remarkable rapidity.'

Mayer (1910) states that a larval *Cunina* is often found attached to the subumbrella of this medusa at Naples (Text-fig. 284E).



Text-fig. 284. *Rhopalonema velatum*. A, mature medusa; B, enlarged view of half-grown medusa; C, marginal sensory club, within its wall-like capsule; D, portion of marginal tentacle; E, *Cunina* larva ectoparasitic on subumbrella of *Rhopalonema*. (After Mayer, 1910, from life, Stazione Zoologica, Naples, December, 1907.)

Kramp (1924) has made a detailed study of the biology of *Rhopalonema velatum* in the Mediterranean where 'it is perhaps the most common of all the medusae'. The medusae were most frequent in hauls taken with 65–800 m. of wire out, but they rose nearer the surface in coastal waters. Small individuals were mostly present in the upper water layers, while the large ones predominated in the deeper layers.

Historical

Rhopalonema velatum was first described by Gegenbaur (1856) from the Mediterranean. As already stated on p. 432 a large number of species have been described, but they are now generally regarded as a single species, with the exception of the *R. funerarium* described by Vanhöffen (1902).

Rhopalonema funerarium Vanhöffen

Text-figs. 285–6

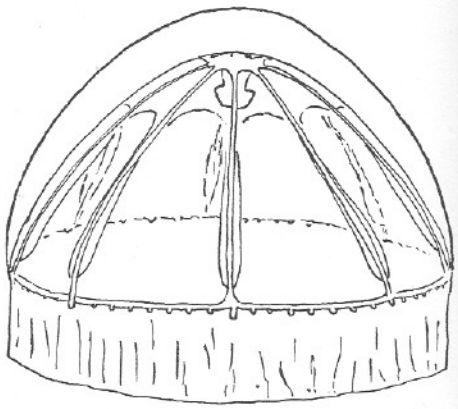
Non *Dianaea funeraria* Quoy & Gaimard, 1827.
Rhopalonema funerarium Vanhöffen, 1902, *Wiss. Ergebn.* '*Valdivia*', Bd. III, p. 61, pl. ix, fig. 2; pl. x, fig. 17; pl. xi, fig. 31.
Kramp, 1947, *Danish Ingolf-Expedit.* vol. v (14), p. 14, pl. ii, figs. 4–5.
Rhopalonema coeruleum Maas, 1905*a*, *Siboga-Expedit.* Monogr. x, p. 51, pl. x, figs. 67, 68.
Mayer, 1910, *Medusae of the World*, vol. II, p. 380 (in part), text-figs. 221, 223.

Specific Characters

Umbrella without conical apical process: gonads occupying outer two-thirds of radial canals; thirty-two enclosed marginal sensory clubs each situated midway between bases of adjacent marginal tentacles.

Description of Adult

Umbrella hemispherical with fairly thin, stiff, jelly without conical apical thickening or process. Velum broad and very well developed. Stomach narrow, elongated quadrilateral with octagonal base; contractile, probably extending sometimes nearly to umbrella margin. Mouth with four simple lips. Eight straight radial canals and ring canal narrow. Eight gonads in form of elongated pouches situated along outer two-thirds of each radial canal. Eight large solid marginal tentacles with swollen ends, situated one at end of each radial canal. Three very short stiff solid marginal tentacles with swollen ends in each octant. Thirty-two enclosed marginal sensory clubs. Diameter of umbrella 9–17 mm.



Text-fig. 285. *Rhopalonema funerarium*. (After Vanhöffen, 1902, pl. ix, fig. 2.)

Distribution

Rhopalonema funerarium is a warm-water oceanic species and in British waters it is only likely to be found far out off the mouth of the English Channel and south-west of Ireland, which is the farthest north it has yet been recorded (Kramp, 1947).

Elsewhere the medusa occurs in all three oceans and in the Mediterranean.

Developmental Stages and Structural Details

Owing to confusion that has existed on the identity of the species of *Rhopalonema* it is not possible to give descriptions of the early stages of *R. funerarium*. It seems likely, however, that it would be very similar to the description given under *R. velatum*.

As regards the structural details of the adult Kramp (1947) has recently given additional information. In four of the specimens he examined the stomach (Text-fig. 286A) was only about one-quarter the height of the subumbrellar cavity, while in one it was more than half the height. The small marginal tentacles have cores consisting of one row of elongated cylindrical endoderm cells, and these are surrounded by an ectodermal epithelium of large, flat cells. These small interradial marginal tentacles are terminated by almost spherical knobs (Text-fig. 286B).

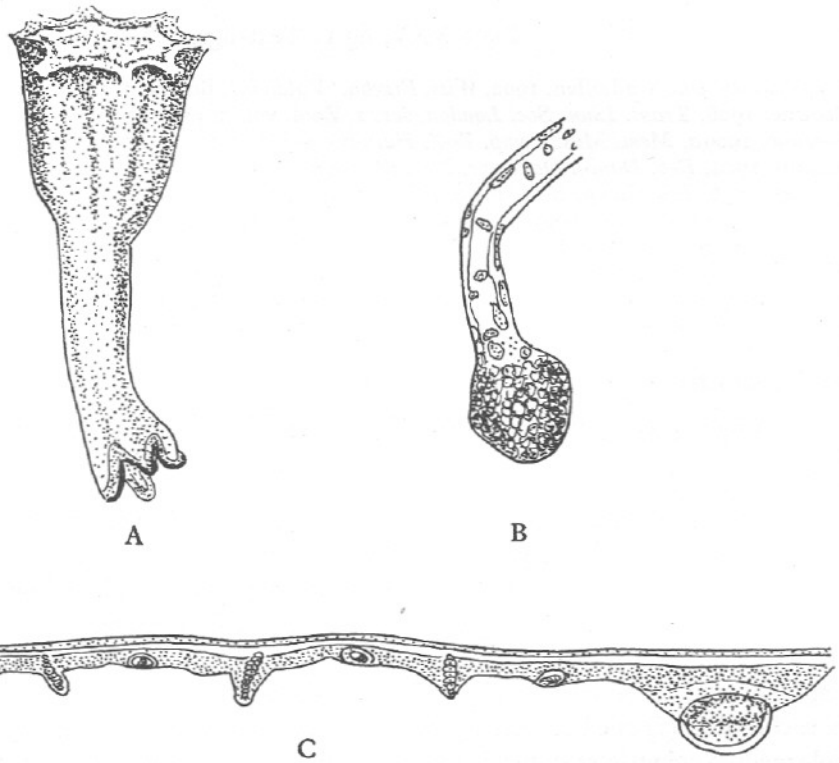
The apex of the umbrella may be somewhat thickened in some specimens, but it never has the distinct knob characteristic of *R. velatum*.

Seasonal occurrence

Since *Rhopalonema funerarium* is an oceanic warm-water species it is probably likely to be found at any time of year.

Habits

This species appears on the whole to live at deeper levels than *R. velatum*, of which Ranson (1936) considered it to be a deep-water race.



Text-fig. 286. *Rhopalonema funerarium*. A, stomach and mouth; B, small interradial marginal tentacle (after Kramp, 1947, pl. ii, figs. 4, 5); C, portion of umbrella margin (after Vanhöffen, 1902, pl. xi, fig. 31).

Historical

Rhopalonema funerarium was first described by Vanhöffen (1902). It has been considered by some authors to be a variety of *R. velatum* (see Thiel, 1936, and Ranson, 1936), but Bigelow (1909*a*, 1919), Broch (1929) and Kramp (1947) regard it as a distinct species.

Genus **Colobonema** Vanhöffen, 1902

Rhopalonematidae with bell-shaped umbrella; without peduncle; with mouth with four lips; with eight narrow radial canals; with elongated linear gonads along radial canals; with thirty-two evenly spaced marginal tentacles, all of one kind, of which eight interradials are youngest; with free sensory clubs.

RHOPALONEMATIDAE

The essential character which distinguishes the genus *Colobonema* is the sequence of development of the thirty-two marginal tentacles among which the eight interradial marginal tentacles are the last to develop. This genus is also distinguished from the following genus, *Pantachogon*, by the fact that the number of marginal tentacles apparently never exceeds thirty-two.

There is one British species of the genus, *Colobonema sericeum* Vanhöffen.

Colobonema sericeum Vanhöffen

Plate XXV, fig 1; Text-figs. 287–9

Colobonema sericeum Vanhöffen, 1902, *Wiss. Ergebn.* '*Valdivia*', Bd. III, p. 57, pl. ix, fig. 1; pl. xii, figs. 39–42.
Browne, 1906, *Trans. Linn. Soc. London*, ser. 2, Zool. vol. x, pt. VI, p. 172.
Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 133, pl. ii, figs. 4, 5; pl. xlv, fig. 12.
Kramp, 1924, *Rep. Danish Oceanogr. Expedit.* 1908–10, vol. II, Biol. H. 1, p. 28, fig. 22.
Ranson, 1936, *Rés. Camp. Sci. Monaco*, Fasc. XCII, p. 152, pl. ii, figs. 14, 15.
Colobonema typicum, Maas, 1905*a*, *Siboga-Expedit.* Monogr. x, p. 53, pl. x, figs. 62–5.
Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, p. 46.
Bigelow, 1919, *Bull. U.S. Nat. Mus.* 100, vol. I, pt. V, p. 322.
Homoeonema typicum, Mayer, 1910, *Medusae of the World*, vol. II, p. 385, figs. 230, 231.
Homoeonema (*Colobonema*) *sericeum*, Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 500, fig. 12.

Specific characters

Gonads extending along proximal two-thirds of radial canals; thirty-two marginal tentacles.

Description of Adult

Umbrella bell-shaped, as broad as high, or slightly broader; jelly very firm, but fairly thin; no apical process. Velum very well developed. Stomach four-sided, of varying length but not extending beyond umbrella margin. Mouth with four short simple pointed lips. Eight straight narrow radial canals widening slightly towards apex of subumbrella. Eight narrow linear gonads, without folds, one extending along proximal two-thirds of each radial canal. Thirty-two short stump-like solid marginal tentacles, of which eight interradials are youngest. Marginal sense organs club-like, (?) one between adjacent marginal tentacles. Umbrella up to 40 mm. in height. Whole medusa colourless; stomach, marginal tentacles, and gonads less transparent; subumbrellar musculature iridescent.

Distribution

Colobonema sericeum is a deep-sea oceanic medusa, and has only been recorded in the British area over deep water west of Ireland.

It is a warm and temperate water species occurring in all three oceans, but not in the Mediterranean (Kramp, 1947). It is therefore likely that it may be found in any deep-water collections west and north of the British Isles.

Structural Details

The early development of *Colobonema sericeum* has not been described, but the sequence of development of the marginal tentacles is known and is described below.

The substance of the umbrella is quite stiff, e.g. Kramp (1924) says that 'the shape will keep astonishingly well and the bell hardly ever collapses as in most of the similar forms'.

The velum is very broad and may reach a width of 7 mm.

The length of the stomach is very variable. For instance, Bigelow (1919) records a specimen 26 mm. high in which the stomach was only 1 mm. long, and two others, 27 and 29 mm. high, in which it reached the umbrella margin. He also found intermediate lengths.

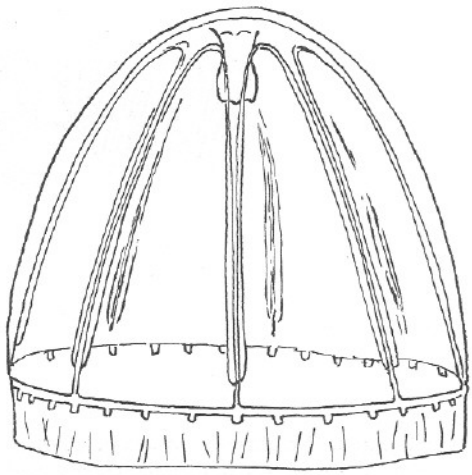
Some observations on umbrella and stomach dimensions in millimetres are as follows:

Umbrella		Stomach		
Height (mm.)	Diameter (mm.)	Length (mm.)	Breadth (mm.)	
18	.	.	2	(Browne, 1906*a*)
18	19	2	4	(Vanhöffen, 1902)
24	27	10	3	
30	30	5	5	
9	12	3	.	(Maas, 1905*a*)
22	32	12	.	
25	35	12	.	
25	27	20	.	
35	45	16	.	
16	24	4	.	(Vanhöffen, 1912*a*)
18	22	3	.	
20	30	3	.	
25	36	6	.	
28	40	7·5	.	

The conditions in the apical region of the subumbrella deserve mention, and attention was first called to them by Ranson (1936).

In *Pantachogon haeckeli* (p. 441) there is a circular transparent region, free of musculature, at the apex of the subumbrella. The eight interradial muscular fields are thus each transversely truncated at the boundary of this region (Text-fig. 290).

But in *Colobonema sericeum* the apex of each interradial muscle field has the shape of a paraboloid curve. This form results from the widening of the radial canals until their walls become contiguous near the subumbrella apex (Text-fig. 288). The whole apex of the subumbrella thus becomes roofed by the radial canal tissue, but the canals themselves remain distinct, their walls converging more or less to a point over the centre of the stomach. The dorsal wall of the stomach is thus formed by the openings of the radial canals.

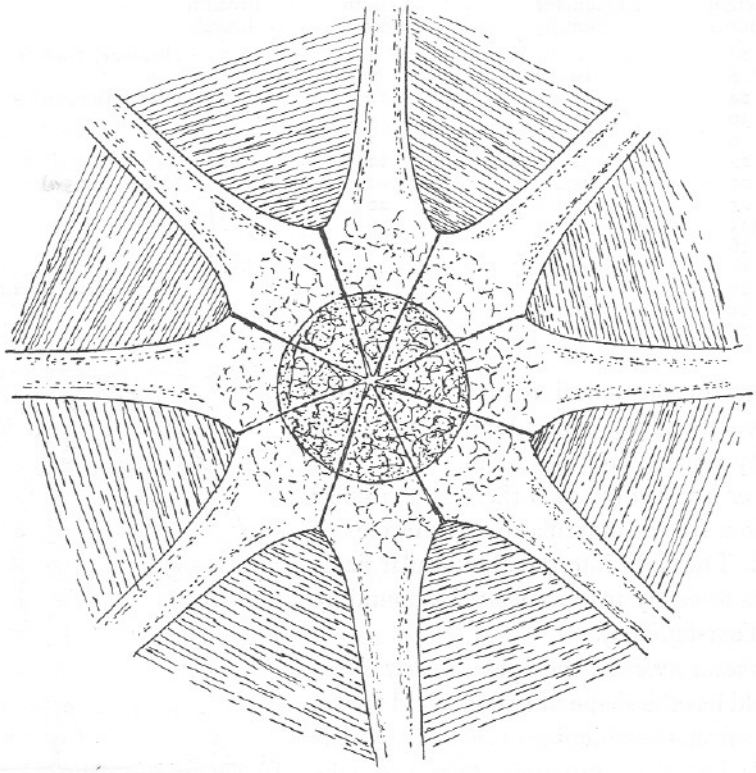


Text-fig. 287. *Colobonema sericeum*. × 2. (After Vanhöffen, 1902, pl. ix, fig. 1.)

The sequence of development of the marginal tentacles (Text-fig. 289) is remarkable, the interradial tentacles being the last to appear. The youngest stage at which details have been recorded is that figured by Maas (1905, pl. x, fig. 63). In this there are eight perradial marginal tentacles and eight adradial marginal tentacles, one on each side of each alternate perradial marginal tentacle. The next stage is the development of the remaining adradial marginal tentacles, giving eight perradial plus sixteen adradial = twenty-four. In the final stage the eight interradial marginal tentacles are developed, making thirty-two in all. This number appears to be constant.

There are few observations as to the sizes of the medusae at the different stages of marginal tentacular development. Presumably the youngest stage figured by Maas (1905) was about 12 mm. in diameter, since that was the smallest size listed by him in his collection. Vanhöffen (1902) recorded a specimen 13 mm. high in which the interradial marginal tentacles were only

weakly developed, and another, 18 mm. high, in which they were still small. Browne (1906) recorded a specimen from the Bay of Biscay about 18 mm. in height in which the interradial marginal tentacles were just beginning to develop. Bigelow (1938) recorded a specimen from Bermuda, *c.* 20 mm. high, in which the interradial marginal tentacle in one octant had not appeared, those in six other octants being represented by rudimentary knobs only, the margin of the eighth octant being torn off.



Text-fig. 288. *Colobonema sericeum.* Apical view of the summit of the umbrella in a preserved specimen, showing the stomach, radial canals, and muscle fields. (E. T. Browne collection, 'Thor', 1906.)

These observations may be summarized as follows:

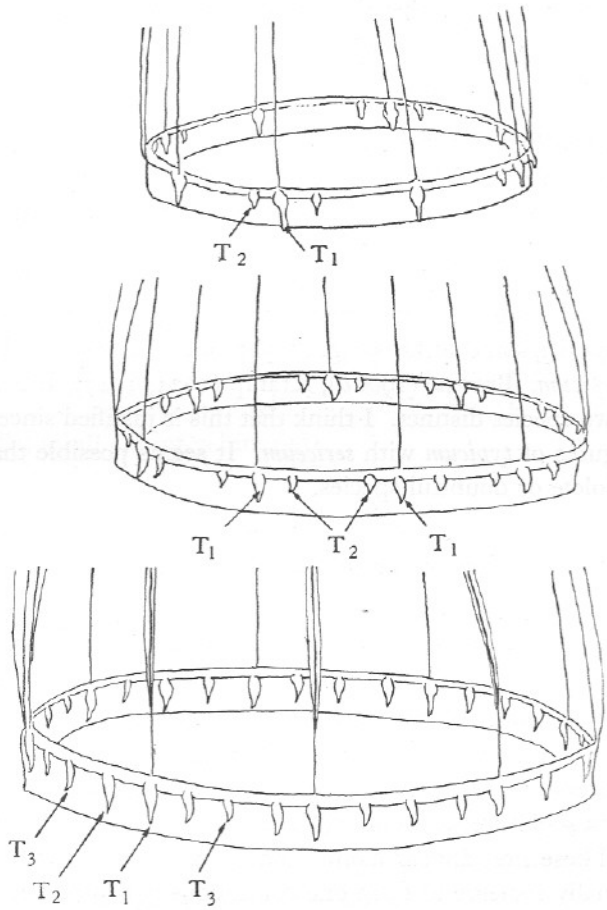
Umbrella size (mm.)	No. of marginal tentacles	
	Adradial	Interradial
? 12	8	None
13	16	8 weakly developed
18	16	8 just beginning
18	16	8 still small
20	16	6 (? 7) rudimentary knobs

It thus appears that the interradial marginal tentacles are not fully developed until after the medusa has reached a height of 20 mm. Even in large specimens, however, the interradial marginal tentacles remain much the smallest (Bigelow, 1909*a*).

The short stump-like form of the marginal tentacles is apparently normal; and this appearance is not due to their having been broken off short, since in better preserved specimens the tips

are rounded and the ectodermal coverings complete* (Bigelow, 1938); Bigelow also suggests that since the perradial and adradial marginal tentacles appear all about the same length they are but little extensible.

For some time no marginal sense organs were found in any medusae and it was thought that perhaps there was normally none present. Bigelow (1919, 1938), however, records that he found one sense organ, between a perradial and an adradial marginal tentacle, in each of two specimens.



Text-fig. 289. *Colobonema sericeum*. Umbrella margin of young specimens to show disposition of the perradial (T 1), adradial (T 2) and the interradial (T 3) marginal tentacles. (After Maas, 1905*b*, pl. x, figs. 63–5.)

The sense organ is a 'free club much like that of *Aglantha*, standing free on the margin, midway between two tentacles. Its structure is not remarkable, there being an endodermal core with a terminal mass of concretions.' 'It stands on a slight elevation of the margin.' Bigelow found these elevations, alternating with the marginal tentacles, in several specimens, though he could find no more sense organs. It is thus possible that normally the sense organs alternate with the marginal tentacles but are easily lost.

Most authors state that the medusa is completely colourless, but Maas (1905) says that the stomach, canals and gonads appear bright brown.

* This view, however, is not thought to be correct by Kramp (1947).

Seasonal occurrence

Since *Colobonema sericeum* is a deep-sea oceanic medusa it seems likely that specimens may be found at any time of year.

Habits

Nothing is known of the habits of the living medusa beyond that it is a deep-water form. Kramp (1947) gives some indications that the younger medusae do not live so deep down as the older ones.

Historical

Colobonema sericeum was first described and figured by Vanhöffen (1902), and all subsequent descriptions have agreed in essentials with his. Maas (1905*a*), however, identified undoubted specimens of *C. sericeum* with a medusa he had previously described (Maas, 1897) as *Homoeonema typicum*. The latter species was described as having more than thirty-two marginal tentacles and distally placed gonads. In view of the fact that Maas (1905*a*) himself considered that the two species were the same and that he expressed a possible doubt as to the correct interpretation of structure in his description of *typicum*, some authors, e.g. Mayer and Bigelow, have followed him in giving priority to the name *typicum*. Browne (1906*a*), Kramp (1924, 1947), Broch (1929), and Ranson (1936) have kept the two species distinct. I think that this is justified since it is quite impossible to reconcile Maas's figures of *typicum* with *sericeum*. It seems possible that it would be best to sink *typicum* as an obsolete or doubtful species.

Genus **Pantachogon** Maas, 1893

Rhopalonematidae with bell-shaped umbrella; with apical region of subumbrella truncated and without musculature around base of stomach; without peduncle; with mouth with four lips; with eight narrow radial canals; with elongated linear gonads along radial canals which at first develop as a number of discontinuous elements; with numerous, more than thirty-two, marginal tentacles, uniformly distributed and all of one kind; with free sensory clubs.

The essential characters of the genus *Pantachogon* are the truncated apex of the subumbrella which lacks the usual musculature surrounding the base of the stomach, and the mode of development of the gonads. These first appear along each radial canal as a number of discontinuous elements which eventually coalesce to form one continuous gonad on each radial canal.

There is one British species in the genus, *P. haeckeli* Maas.

Pantachogon haeckeli Maas

Plate XXV, fig. 2; Text-figs. 290–2

Pantachogon haeckeli Maas, 1893, *Ergebn. Plankton Expedit. Humboldt-Stift.*, Bd. II, K.c., p. 17, pl. i, fig. 2.
Mayer, 1910, *Medusae of the World*, vol. II, p. 389, fig. 239.
Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, no. 1946, p. 44, pl. iii, figs. 4–8.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 503, fig. 15.
Bigelow, 1938, *Zoologica, New York*, vol. XXIII, pt. II, no. 5, p. 115.
Kramp, 1947, *Danish Ingolf-Expedit.* vol. V (14), p. 19, pl. ii, figs. 7, 8.
Pantachogon rubrum Vanhöffen, 1902, *Wiss. Ergebn.* '*Valdivia*', Bd. III, p. 63, pl. ix, fig. 9; pl. x, figs. 19, 20; pl. xi, fig. 25.
Maas, 1905*a*, *Siboga-Expedit.* Monogr. X, p. 55, pl. x, fig. 66.

Mayer, 1910, *Medusae of the World*, vol. II, p. 389, figs. 240, 241.
Kramp, 1913*b*, *Vidensk. Medd. Dansk. naturh. Foren. Kbh.* Bd. LXV, p. 274.
Kramp, 1924, *Rep. Danish Oceanogr. Expedit.* 1908–10, vol. II, Biol. H. 1, p. 22, fig. 19.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 504, fig. 16.
Ranson, 1936, *Rés. Camp. Sci. Monaco*, Fasc. XCII, pp. 147, 153, pl. ii, fig. 16.
Thiel, 1936, *Zool. Jahrb. Jena, Abt. Syst., Ökol. Geogr. Tiere*, Bd. LXIX, Heft 1, p. 24, fig. 4 (in part).

Specific Characters. Sixty-four marginal tentacles.

Description of Adult

Umbrella bell-shaped, about as broad as high, sometimes slightly broader; jelly fairly thin; without apical process; with thirty-two fine exumbrellar furrows; summit of subumbrella transversely truncated and devoid of musculature, remainder of subumbrellar musculature well developed. Velum very broad. Stomach rather short, of somewhat varying length, eight-sided at base; no peduncle. Mouth with four simple pointed lips. Eight straight uniformly narrow radial canals. Gonads at first form discontinuous linear swellings along each side of each radial canal which eventually coalesce and become folded transversely; covering distal two-thirds or whole of radial canal from base of stomach to ring canal. Sixty-four solid marginal tentacles in one row, all of same size and structure, probably short and stumpy; seven in each octant and eight approximately perradial in position. Sixty-four marginal sense organs, one between every two marginal tentacles. Height of umbrella up to 15 mm. Whole medusa colourless with iridescent subumbrella, or all except velum red.

Distribution

Pantachogon haeckeli is a deep-sea oceanic species which has only been recorded from the British region from deep water off south-west and west Ireland. I have found two specimens in Mr Browne's collection taken from 1000 fathoms, 50 miles north-west of Eagle Island on the west coast of Ireland.

The medusa is widespread in all three oceans and the Mediterranean. It is thus liable to be taken over deep water anywhere to the west and north of the British Isles.

Developmental Stages and Structural Details

The only observations on the early development of *Pantachogon haeckeli* are those given by Kramp (1947). In a specimen 2 mm. in height there were two marginal tentacles and one interradial sensory club between every two radial canals, except in one octant where there was one interradial tentacle and a sensory club close beside it.

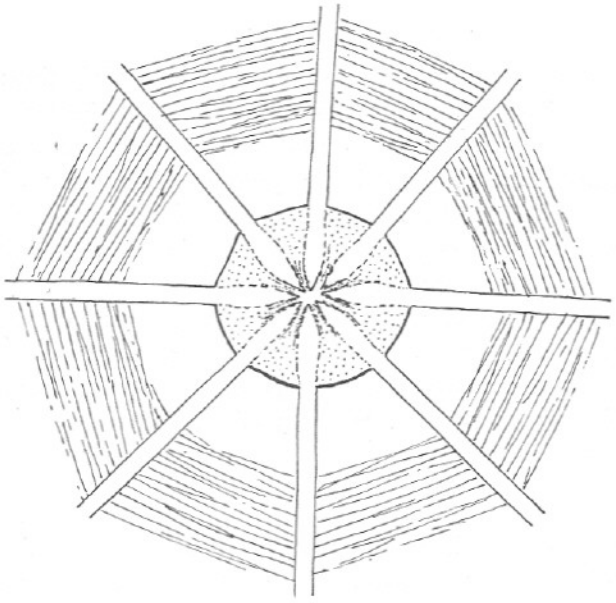
In the adult the flat circular area at the apex of the subumbrella (Text-figs. 290, 291), which is devoid of musculature, seems to be a characteristic feature of this medusa. This was first pointed out by Ranson (1936). This transparent region is traversed by the eight radial canals, which open into the dorsal surface of the stomach through spear-shaped apertures (Text-fig. 290). Over the remainder of the subumbrella the musculature is highly developed.

The thirty-two longitudinal exumbrellar furrows are also a marked feature. They do not quite reach the summit of the umbrella (Text-fig. 291).

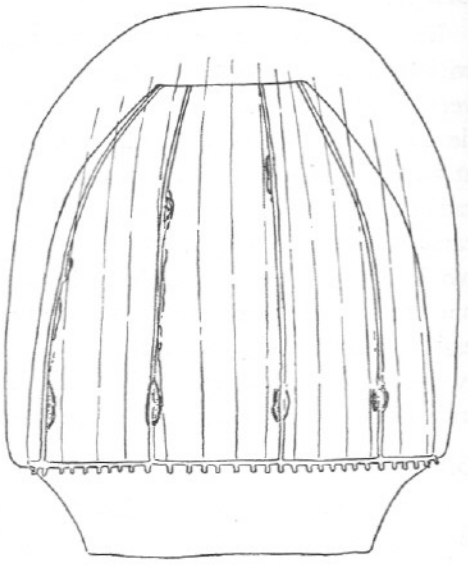
The gonads first appear as two to four swellings on the radial canals. As they grow and become more massive, gonadial tissue is developed in the intervening spaces, so that eventually the gonadial mass on each radial canal becomes continuous. At the same time as the gonads increase in size and thickness they become thrown into transverse folds which may be as many as six in number. The size of the medusa at which the gonads develop is very variable. Ranson

(1936), for instance, records specimens of 5 and 6 mm. in height in which the gonads were already very well developed and folded. On the other hand, in other specimens of about the same size the gonads were only just beginning to appear, and this may be so in larger specimens. The gonads are, however, often lost on preservation.

The sequence of development of the marginal tentacles is not fully known. Kramp (1947) states that in some specimens 3 mm. high there were three marginal tentacles between adjacent



Text-fig. 290. *Pantachogon haeckeli.* Apical view showing clear region at the summit of the umbrella. Preserved specimen, 50 miles N.W. of Eagle Island, Ireland, 11. viii. 04. (E. T. Browne collection.)



Text-fig. 291. *Pantachogon haeckeli.* Damaged preserved specimen, without stomach showing flattened apex of subumbrella, and the ex-umbrella furrows, 50 miles N.W. of Eagle Island, Ireland, 11. viii. 04. (Near side of umbrella only drawn.) (E. T. Browne collection.)

radial canals, but he could not decide which of these tentacles were the youngest. In specimens 4·0–4·5 mm. high the number of marginal tentacles between adjacent radial canals appeared usually to be five, though in some the middle, interradial, marginal tentacle was only a rudiment. In a specimen 5 mm. high there were six marginal tentacles between adjacent radial canals and these were all alike; in three octants there were also rudiments of the seventh marginal tentacle, and this was always the third one from the left. Kramp says: 'In the course of the development of the tentacles *Pantachogon haeckeli* thus really seems to differ from *Colobonema sericeum*, in which an interradial tentacle does not appear until four other tentacles have been developed.'

Bigelow (1938) has remarked that it is suggestive that the perradial marginal tentacles are not always exactly opposite their respective radial canals and may not therefore be strictly perradial. These marginal tentacles also appear to be no larger than the others. Kramp (1947) states that it is exceptional for a perradial marginal tentacle not to be exactly opposite a radial canal, and then it only happens opposite the 'secondary' canals which issue from the stomach between the four mouth-lips.

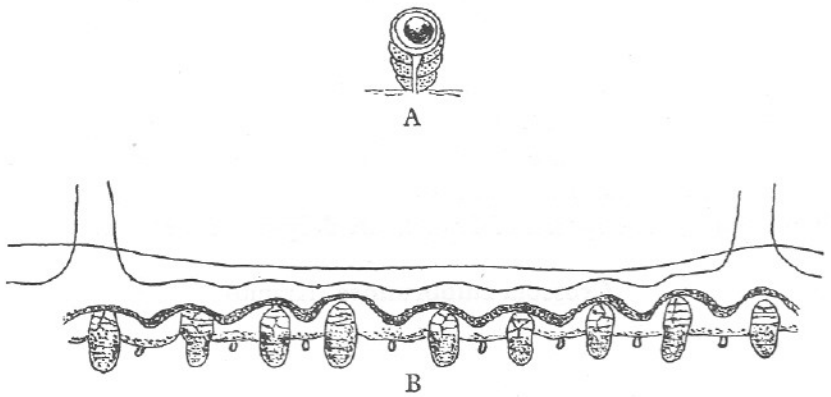
The number of marginal tentacles appears to be determinate and a greater number than sixty-four has not been recorded.

There is some doubt as to the actual structure of the marginal tentacles. In all specimens so far seen they appear to be stump-like (Text-fig. 292 B), but it is not certain whether this is their normal form or whether they have been broken off short. Bigelow (1938) is inclined to favour the latter view, but in the two specimens I have seen some of the longer marginal tentacles are definitely rounded at their ends and one at least has its tip covered with nematocysts. It is thus possible that the complete tentacles are short and stump-like, though the length they can attain in life is not known.

Between the bases of the marginal tentacles the margin of the umbrella is thickened, forming prominences crowded with nematocysts (Text-fig. 292 B).

The marginal sense organs are typical sensory clubs (Text-fig. 292 A).

Pantachogon haeckeli appears to occur in two forms, the one colourless and the other bright red and described under the name of *P. rubrum*. Most authors appear now to consider that these



Text-fig. 292. *Pantachogon haeckeli*. A, marginal sense organ; B, portion of umbrella margin. (After Vanhöffen, 1902, pl. x, fig. 19; pl. xi, fig. 25.)

are merely forms of the same species since colourless and red medusae may occur together, as well as specimens having colourless umbrellas but red bases to the stomach (Kramp, 1942). It is possible that the coloration is related to the depth at which the medusae have been living. A similar colour variation occurs in *Aglantha digitalis*. Vanhöffen (1902) records that while in the adult the whole medusa is red, except for the whitish velum, in young specimens the stomach and canals are red, or only the stomach.

Seasonal occurrence

Since *Pantachogon haeckeli* is such a widespread oceanic medusa it seems likely that it may occur at any time of year. The specimens here recorded from 50 miles north-west of Eagle Island were taken in August.

Habits

There is no information on the habits of the living medusae. The species is an inhabitant of deep water, the majority of records having been from hauls from 500 m. or deeper. Kramp (1947) could find no evidence of differences in vertical distribution according to the size of the medusa.

RHOPALONEMATIDAE

Historical

Pantachogon haeckeli was first described by Maas (1893) from a single specimen caught south-west of Iceland. Later (1904*a*) he recorded another specimen from Spitsbergen. The red form was described by Vanhöffen (1902) as *P. rubrum*.

Genus **Crossota** Vanhöffen, 1902

Rhopalonematidae with bell-shaped or hemispherical umbrella; with or without peduncle; with mouth with four lips; with eight or more radial canals; with gonads on radial canals in form of elongated pouches hanging into subumbrellar cavity; with numerous evenly spaced marginal tentacles, all of one kind; with free sensory clubs.

In its general characters the genus *Crossota* comes very near to *Aglantha*, and the two genera cannot be really satisfactorily demarcated. The differences are that in some species of *Crossota* there is no peduncle, or only a trace of one, and that in one species the number of radial canals is more than eight.

As far as can be stated at present the only species likely to be included in the British fauna is *C. rufobrunnea* Kramp. Another species, *C. brunnea* Vanhöffen, may possibly occur in the North Atlantic west of the British Isles since Bigelow (1938) has recorded specimens which may have been this species from Bermuda. For recent discussions on the genus see Bigelow (1938), Thiel (1936) and Kramp (1947). The species of *Crossota* are deep-water medusae.

Crossota rufobrunnea (Kramp)

Text-figs. 293–6

Aglantha rufobrunnea Kramp, 1913*b*, *Vidensk. Medd. Naturh. Foren. Kbh.* Bd. LXV, p. 273, figs. 1, 2.
Crossota norvegica, Kramp, 1920*b*, *Bergens Mus. Aarb.*, 1917–18, no. 8, p. 5.
Crossota rufobrunnea, Kramp & Damas, 1925, *Vidensk. Medd. Naturh. Foren. Kbh.* Bd. LXXX, p. 317.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 506, fig. 17.
Kramp, 1942, *Medd. Grønland*, Bd. LXXXI, no. 1, p. 79.
Kramp, 1947, *Danish Ingolf-Expedit.* vol. V (14), p. 22, pl. ii, figs. 9–10; pl. iii, figs. 1–8; pl. iv, figs. 1–4; pl. vi, fig. 5; and text-figs. 8, 9.

Specific Characters

Stomach without peduncle; with eight radial canals; 200–250 marginal tentacles.

Description of Adult

Umbrella slightly higher than a hemisphere, with or without trace of apical process; jelly moderately thin. Velum moderately broad. Stomach short, pyriform, quadrangular in section, without peduncle. Mouth with four short lips. Eight comparatively broad, straight, ribbon-like radial canals; ring canal narrow. Eight sausage-shaped gonads hanging down into subumbrellar cavity from junctions of radial canals with stomach. About 200 to 250 short solid marginal tentacles. ? Marginal sense organs. Diameter of umbrella 10–15 mm. Colour of umbrella, velum, stomach, and marginal tentacles deep reddish brown.

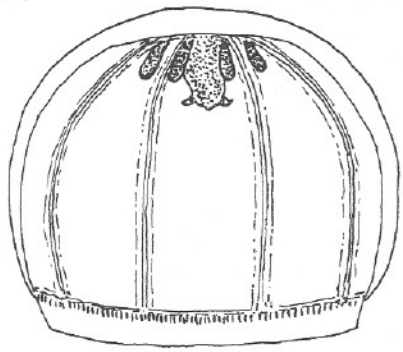
Distribution

Crossota rufobrunnea is widely distributed in the depths of the boreal Atlantic, but not in the Norwegian nor polar seas. It has been taken in deep water south-west of Ireland and west of north Scotland (Kramp, 1947).

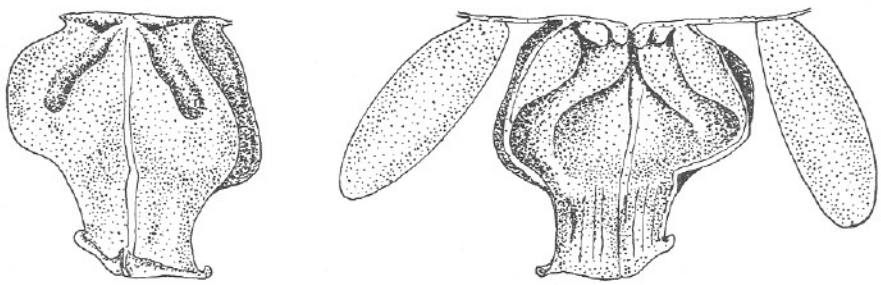
Structural Details

There have been no accounts of the early stages of this medusa. Kramp (1947) describes the structural details of the adult.

The umbrella, when moderately contracted, is somewhat higher than a hemisphere, up to 15 mm. in diameter and 10 mm. in height. The jelly is about 1·5 mm. thick at the apex of the umbrella, becoming gradually thinner towards the margin. The exumbrella has about twenty meridional grooves in each octant running upwards from the margin to the level of the base of the stomach, but leaving the apex smooth.



Text-fig. 293. *Crossota rufobrunnea*. Davis Strait, 1928. (After Kramp, 1947, pl. vi, fig. 5, coloured sketch from life.)



Text-fig. 294. *Crossota rufobrunnea*. Stomach: A, external view; B, internal view showing the two whorls of invaginated pouches and one of the longitudinal grooves; a gonad is shown on either side. (After Kramp, 1947, pl. iii, figs. 1, 2.)

The circular musculature of the subumbrella is weakly developed, and the velum has weak muscles.

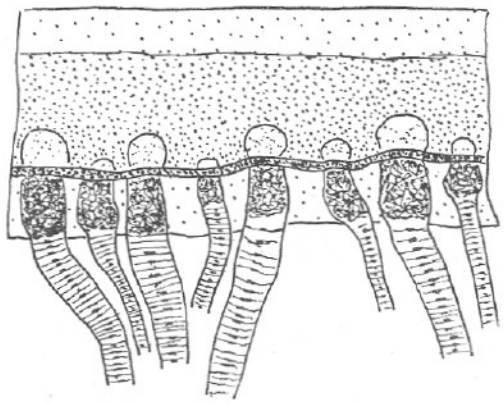
The stomach (Text-fig. 294) is about one-third of the height of the subumbrellar cavity in length. It has a star-shaped base, with eight points corresponding to the radial canals. The stomach walls are fairly thin and thrown into two whorls of deep folds. The upper whorl consists of eight small narrow folds hanging down into the stomach cavity, with their inner edges almost meeting in the centre. Their cavities communicate with the subumbrellar cavity through eight small radiating fissures in the upper wall of the stomach between the radial canals. The lower whorl consists of eight large elongated folds lying separate from and immediately below the upper folds, and gradually tapering towards the mouth. On the outer side of the stomach there are eight deep, open grooves corresponding with the anterior folds. The endoderm of the pouches is slightly thickened and its surface is papillose.

Four strings of large, vacuolated endoderm cells run from the points of the four mouth-lips upwards to the base of the stomach. These are covered by thin ectoderm and appear externally on the stomach as prominent edges, which are indicated internally as sharp grooves.

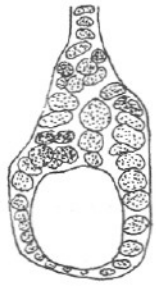
Although the stomach has no peduncle, in certain states of contraction the apical portion of the jelly forms a slight conical projection into the base of the stomach resembling the peduncle in *Aglantha*.

Kramp gives histological details of the radial canals, which, although broad and ribbon-like in appearance, in fact have fairly narrow internal cavities.

The gonads (Text-fig. 294) are hollow and communicate with the radial canals.



Text-fig. 295. *Crossota rufobrunnea*. Portion of umbrella seen from adaxial side with the velum removed. (After Kramp, 1947, pl. iv, fig. 2.)



Text-fig. 296. *Crossota rufobrunnea*. Marginal sense organ in longitudinal section. (After Kramp, 1947, pl. iv, fig. 3.)

The marginal tentacles are probably rather long, and each has a large, broad endodermal spur projecting into the umbrella jelly in front of the ring canal (Text-fig. 295). The marginal tentacles are in different stages of development, but are not regularly alternating. Each marginal tentacle is usually separated from its neighbour by a distance of about its own width.

Since the radial canals are not exactly evenly spaced the number of marginal tentacles varies somewhat from octant to octant. Kramp records that in a specimen 10 mm. high with 240 marginal tentacles the number per octant varied from sixteen to thirty-seven. He gives two other counts as follows:

$$27+22+23+26+28+25+28+26=205.$$
$$36+34+35+26+34+31+33+25=254.$$

The marginal sense organs (Text-fig. 296) are readily lost.

Seasonal occurrence

Being a deep-water oceanic species this medusa is likely to occur at all times of the year.

Habits

Nothing is known of the habits of *Crossota rufobrunnea* beyond that it is a deep-water species.

Historical

Crossota rufobrunnea was first described by Kramp (1913*b*) as *Aglantha rufobrunnea*. Vanhöffen thought that Kramp's specimens were probably identical with his *Crossota norvegica*, but later by an examination of Vanhöffen's original specimens Kramp (1947, p. 21) was able to prove that they were distinct species.

Genus **Aglantha** Haeckel, 1879

Rhopalonematidae with deep bell-shaped umbrella; with well-developed peduncle; with mouth with four lips; with eight narrow radial canals; with gonads on radial canals or in form of elongated pouches hanging from radial canals near base of peduncle into subumbrellar cavity; with numerous evenly spaced marginal tentacles, all of one kind; with four or eight free sensory clubs.

Essential characteristics of the genus *Aglantha* are the deep cylindrical bell-shaped form of the umbrella, the well-developed peduncle, and the form and position of the gonads.

There is one British species of the genus, *Aglantha digitale* (O. F. Müller) var. *rosea* (Forbes). On account of its shape it cannot be confused with any other British species. Care, however, should be taken in identifying small specimens to see that they are not *Aglaura hemistoma*, a warm-water species that has not yet been taken in the British region.

Aglantha digitale (O. F. Müller) var. **rosea** (Forbes)

Plate XXVI, figs. 1–10; Text-figs. 297, 298

Circe rosea Forbes, 1848, *Monogr. British Medusae*, p. 34, pl. i, fig. 2.
Agassiz, 1862, *Contr. Nat. Hist. U.S.* vol. IV, p. 349.
Aglantha digitalis, Haeckel, 1879, *System der Medusen*, p. 272 (in part).
Hartlaub, 1894, *Wiss. Meeresuntersuch.* N.F., Bd. I, Abt. Helgoland, Heft 1, IV, p. 79.
Sverdrup, 1922, *Skrift. Vidensk. Kristiania*, 1921, Bd. I, Mat.-Nat. Kl. p. 27, pl. iv, fig. 16.
Uchida, 1928. *Jap. Journ. Zool.*, vol. II, p. 79.
Aglantha rosea, Browne, 1897*a*, *Proc. Zool. Soc. London*, p. 833, pl. xlix, fig. 1.
Bigelow, 1909*b*, *Proc. U.S. Nat. Mus.* vol. XXXVII, p. 312.
Russell, 1938*a*, *Journ. Mar. Biol. Assoc.* vol. XXII, p. 433, fig. 5.
Aglantha digitale var. *intermedia* Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 122, pl. xxix, figs. 4–10.
Aglantha digitale, Mayer, 1910, *Medusae of the World*, vol. II, p. 402 (in part), pl. xlix, fig. 2.
Bigelow, 1915*a*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. LIX, no. 4, p. 314.
Kramp, 1924, *Danish Oceanogr. Exped.* 1908–10, no. 8, vol. II, H. 1, p. 29, fig. 24.
Aglantha digitale var. *rosea* Kramp, 1927, *K. danske vidensk. Selsk. Skr.* natur. og math. Afd., 8. Raekke, XII, p. 152.
Aglantha digitale forma *rosea* Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 513, fig. 23.

N.B. The above is the synonymy of *Aglantha digitale* var. *rosea*; for the synonymy of the aggregate species *A. digitale* see Mayer (1910) and Kramp (1947).

Specific Characters

Gonads situated on radial canals near junction of peduncle to subumbrella; pendent.

Description of Adult

Umbrella deep cylindrical bell-shaped, with small conical apical process; about twice as high as wide; jelly thin. Velum broad and well developed. Stomach small, situated at end of long conical peduncle, reaching nearly to umbrella margin. Mouth with four simple lips. Eight straight radial canals and ring canal narrow. Eight sausage-shaped gonads hanging freely in subumbrellar

cavity from radial canals close to base of peduncle. Eighty or more solid smooth marginal tentacles in single row, each with core of single columnar endoderm cells. Eight naked marginal sensory clubs situated singly about midway between adjacent radial canals on inner side of ring canal near velum; each with single concretion. Height 5–18 mm. according to season. Colour of stomach, mouth and marginal tentacles sometimes delicate or bright pinkish red; often quite colourless.

Distribution

Aglantha digitale var. *rosea* is an oceanic species and is thus, as a general rule, found only on the Atlantic coasts of the British Isles and in the northern North Sea. In certain years, however, according to the flow of Atlantic water, the medusa may be carried into the English Channel and southern North Sea.

Elsewhere it is a cosmopolitan species in the northern hemisphere, but, as a variety of *Aglantha digitale*, it is limited to the warmer and temperate waters.

Owing to its oceanic habit the species can be used as a valuable indicator of the occurrence of Atlantic water in the English Channel and North Sea (Russell, 1938*a*) and the western Baltic (Künne, 1937*b*).

Developmental Stages and Structural Details

Aglantha digitale is a Trachymedusa with direct development. The variety *rosea* differs from the typical form in its smaller size and in having eight marginal sensory clubs. The typical form reaches a height of 30–40 mm. and is reputed to have only four marginal sensory clubs (but see p. 451).

The earliest stage of the variety *rosea*, seen at Plymouth in March 1936, was 0·3 mm. in diameter. It was saucer-shaped and had two long and two short marginal tentacles, and two tentacular rudiments. These were arranged irregularly round the margin. There were four marginal sensory clubs, each with a single concretion. The longer marginal tentacles were tinged with pink at their ends.

Medusae with a diameter of 0·4 mm. had eleven to twelve marginal tentacles, and four marginal sensory clubs (Pl. XXVI, fig. 1).

In these early stages the medusae agree very closely in appearance with the earliest stages of *Aglaura hemistoma* Péron & Lesueur as described by Metschnikoff (1886*a*, p. 93, pl. vii, figs. 29, 30), except that apparently they are slightly larger (Text-fig. 297).

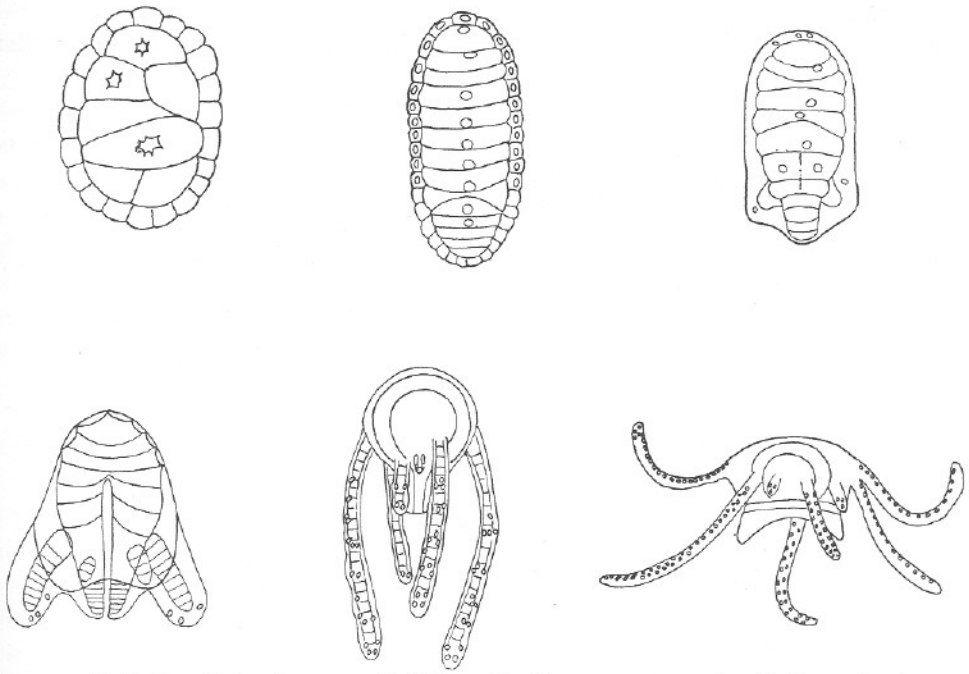
The marginal tentacles have a core of a single row of columnar endodermal cells, and are covered with long cilia (Pl. XXVI, fig. 7). There are many nematocysts in the ectoderm, and these are most numerous on the abaxial sides and at the ends of the marginal tentacles. Round the margin of the umbrella is a thickened region thickly beset with nematocysts.

The medusa soon becomes more bell-shaped and at a height of 0·9 mm. has fourteen marginal tentacles, and the mouth has four distinct lips (Pl. XXVI, figs. 2, 3).

When the medusa has reached a height of 2·1 mm. it has the elongated bell-shape typical of the adult and the apical process of the umbrella is fully developed (Pl. XXVI, fig. 4). There are now sixteen marginal tentacles, but still only four marginal sensory clubs. The umbrella margin is thickly beset with nematocysts, and it has a number of marginal lobes, which later develop into marginal tentacles by the outgrowth of an endodermal core from the wall of the ring canal. The marginal tentacles are ciliated.

In a specimen 2·8 mm. in height the first signs of the eight gonads were apparent on the radial canals near the base of the peduncle (Pl. XXVI, fig. 6). There were now twenty-four marginal tentacles.

Specimens of nearly 4 mm. in height had between twenty and thirty marginal tentacles, but still only four marginal sensory clubs.



Text-fig. 297. Early larval development of *Aglaura hemistoma*, an example of direct development as is found in *Aglantha digitale* var. *rosea*. (After Metschnikoff, 1886*a*, pl. vii, cilia omitted.)

The details of slightly older specimens were as follows:

Umbrella height (mm.)	No. of marginal tentacles	No. of marginal sensory clubs
4·4	34	5
5·0	37	8
6·0	36	8

It is thus evident that when the medusa is somewhere between 4 and 5 mm. in height the number of marginal sensory clubs increases from four to eight. It should, however, be noted that this refers to medusae caught early in the year. In the summer, when the medusae do not grow to so large a size (see p. 451), it is possible that corresponding stages of development will also be smaller.

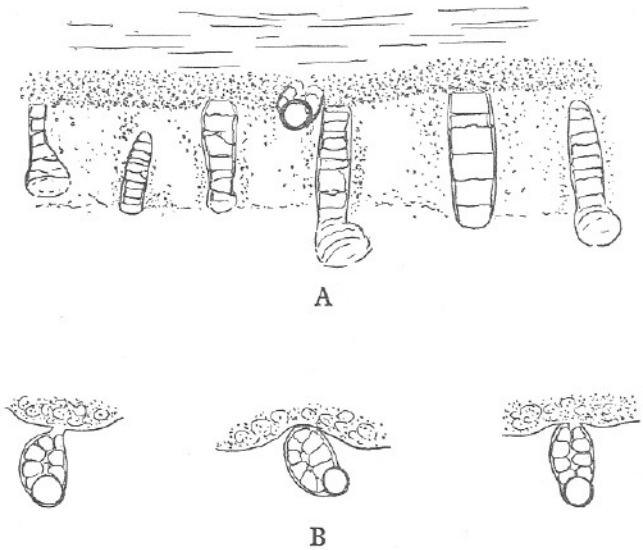
The gonads in adult medusae hang down as hollow sausage-shaped sacs into the subumbrellar cavity (Pl. XXVI, fig. 9); they are formed by evagination from the walls of the radial canals (G.T. Hargitt, 1917, p. 597). In mature individuals 16–18 mm. in height the gonads are 5–7mm. long. When the medusae are mature at a height of 5–6 mm. the gonads are *c.* 0·75–1·0 mm. in length. But in both small and large adults there may be considerable variation in the size of the gonads, which may be much smaller than the maximum sizes given above.

There are numerous nematocysts on the mouth-lips.

The medusa is very delicate and its marginal tentacles are easily broken off (Text-fig. 298A). It is thus unusual to find many specimens with perfect marginal tentacles in tow-net catches. When the marginal tentacles are broken the ectoderm becomes torn off their basal regions, but stumps of the endodermal core may remain.

The marginal sensory clubs are short and oval, and the single concretion is situated distally (Text-fig. 298B).

The eggs of specimens from Plymouth, liberated in May 1936, were transparent and colourless, and 0·36–0·39 mm. in diameter.



Text-fig. 298. *Aglantha digitale* var. *rosea*. A, portion of umbrella margin with broken marginal tentacles and a marginal sense organ, viewed from the adaxial side with the velum removed; B, marginal sense organs. (Preserved specimen.)

A histological study of the gonads has been made by G. T. Hargitt (1917). The eggs mature at different times and are liberated from the ovary a few at a time. 'The entire process of growth and maturation is carried on and completed within the gonad, and the eggs have formed both polar bodies and are ready for fertilization as soon as they are liberated from the ovary.' Hargitt states that the eggs of *Aglantha* are most favourable for the study of the maturation process, since this all takes place in the ovaries and the chromosomes are very large. He states that the germ cells are ectodermal in origin.

NEMATOCYSTS. Stenoteles and microbasic euryteles (Russell, 1940*a*).

Seasonal occurrence

Since it has direct development *Aglantha digitale* var. *rosea* occurs in the plankton all the year round. As already mentioned, however, its presence in some regions is due to hydrographic conditions, and its appearance from time to time may therefore seem to be seasonal.

Habits

Aglantha digitale var. *rosea* is an exceedingly active medusa. With its elongated shape it can go a considerable distance through the water with a single contraction of the umbrella.

In perfect living specimens it can be seen that the marginal tentacles are often carried with their ends wound in a loose coil of a single whorl (Pl. XXVI, fig. 4).

The medusa passes through several generations in one year (Russell, 1938*a*, p. 433). The annual sequence in south-western regions of the British Isles appears to be as follows. The year starts with large individuals, 12–18 mm. in height, which were produced by the last spawning of the previous year. These large medusae spawn in late March and their offspring mature in May, after which there are three, or possibly four, successive generations produced in the summer. These summer medusae only grow to a height of about 5–7 mm.

M'Intosh (1890*c*) also noted that off St Andrews the medusae were large in April, while in November they were small.

A somewhat similar difference in size is found in medusae in Danish waters (Kramp, 1927). It is possible that the medusa retires to deeper waters during the winter (see Kramp, 1913*a*, and Russell, 1938*a*). Fowler (1898) stated that it was found in the Faeroe-Shetland channel in the surface water, in contrast to the deeper living var. *digitale*.

Hansen (1951) gives *c.* 15° C. as the maximum temperature that the medusae will tolerate in the Oslo Fjord in summer.

Historical

The specific name *digitale* is derived from that first given by O. F. Müller (1776) to the medusa, which he called *Medusa digitale*. The first description of the variety *rosea* was given by Forbes (1848) who named it *Circe rosea*.

Haeckel (1879) redescribed *Aglantha digitale* stating clearly that it always has four marginal sensory clubs, and that the umbrella is 30–40 mm. in height. Hartlaub (1894) found specimens of a small *Aglantha* off Helgoland which had eight marginal sensory clubs. He briefly described them under the name *A. digitalis*, giving *Circe rosea* as a synonym. Browne (1897*a*) considered that the possession of eight marginal sensory clubs instead of four was a specific distinction. He redescribed the variety, from Valencia, under the name of *Aglantha rosea*. Most authors, including Kramp (1927) and Bigelow (1926) have considered that these differences are only varietal; that *A. digitale* (O. F. Müller) forma *typica* is large and has four marginal sensory clubs, and that var. *rosea* is small and has eight marginal sensory clubs. This conclusion is strengthened by the fact that it is not known for certain that four marginal sensory clubs is the normal number for the typical form. Bigelow (1909*b*) records specimens from the Labrador coast up to 29 mm. in height in which the gonads first appear at a height of 7–10 mm. These medusae had eight marginal sensory clubs; the largest, which was 29 mm. in height, had 214 marginal tentacles.

It seems reasonable to suppose that we have here a single species which, owing to its very wide distribution, shows considerable variation in the size to which it grows under different environmental conditions (see also Kramp, 1942).

The development of the typical form has been described by Fewkes (1881*a*) and Le Danois (1913).

Family HALICREIDAE

Trachymedusae with stomach without peduncle; with eight or more broad radial canals; without centripetal canals; with gonads on radial canals; marginal tentacles distributed evenly or in groups round umbrella margin, all of one kind; each marginal tentacle with flexible proximal portion and stiff distal portion; with free marginal sensory clubs.

HALICREIDAE

The distinctive characters of the family Halicreidae lie in the structure of the marginal tentacles, in which the proximal portion differs from the distal portion, and in the rudimentary flattened form of the manubrium.

The family is represented in British waters by three genera, *Halicreas* Fewkes, *Haliscera* Vanhöffen, and *Botrynema* Browne.

Genus **Halicreas** Fewkes, 1882

Halicreidae with eight radial canals; with a continuous row of marginal tentacles; with perradial gelatinous papillae on the exumbrella.

There is probably one British species in the genus, *Halicreas minimum* Fewkes.

Halicreas minimum Fewkes

Text-figs. 299, 300

Halicreas minimum Fewkes, 1882*b*, *Bull. Mus. Comp. Zoöl. Harvard*, vol. IX, no. 8, p. 306.
Bigelow, 1938, *Zoologica, New York*, vol. XXIII, pt. II, no. 5, p. 122.
Kramp, 1947, *Danish Ingolf-Expedit.* vol. V (14), p. 7, pl. vi, fig. 3.
Halicreas papillosum Vanhöffen, 1902, *Wiss. Ergebn.* '*Valdivia*', Bd. III, p. 68, pl. ix, figs. 7, 8; pl. xi, fig. 30.
Maas, 1905*a*, *Siboga-Expedit.* Monogr. X, p. 57, pl. x, fig. 70; pl. xi, fig. 71.
Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 138, pl. iii, fig. 3; pl. xxxiii, figs. 8, 9; pl. xxxiv, figs. 1–3, 5, 8, 10, 11.
Mayer, 1910, *Medusae of the World*, vol. II, p. 391, figs. 242, 243.
Vanhöffen, 1912*a*, *Deutsche Südpolar-Expedit.* 1901–3, Bd. XIII, Zool. V, p. 378.
Ranson, 1936, *Rés. Camp. Sci. Monaco*, Fasc. XCII, p. 164.
Thiel, 1936, *Zool. Jahrb. Jena*, Abt. Syst., Ökol. Geogr. Tiere, Bd. LXIX, Heft 1, p. 34 (in part).
Halicreas papillosum var. *antarcticum* Browne, 1908, *Trans. Roy. Soc. Edinb.* vol. XLVI, pt. II (no. 10), p. 237.
Halicreas (*Halicreas*) *papillosum*, Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 508, fig. 18.

Specific Characters

Exumbrella with eight perradial lateral processes, each with five to ten or more small conical papillae.

Description of Adult

Umbrella hemispherical or somewhat flattened; jelly thick in upper region, with conical apical process of varying size which may be completely absent; subumbrellar cavity shallow, with thin jelly at sides and margin; eight rounded perradial lateral exumbrellar processes, each with five to ten or more small conical papillae. Velum well developed. Stomach broad and flat; mouth simple and circular. Eight straight radial canals and ring canal broad. Gonads oval, each situated on radial canal in positions varying from proximal to middle region. About 200 to 600 solid marginal tentacles of which eight perradial are largest; each marginal tentacle flexible proximally and stiffer distally. Three to four marginal sensory clubs in each octant. Diameter of umbrella up to 44 mm. Colour of radial canals and gonads bright scarlet red; stomach somewhat lighter red; basal portions of marginal tentacles bright red.

Distribution

Halicreas minimum is a deep-sea oceanic medusa which has not been recorded actually in the close vicinity of the British Isles, but occurs in deep water off the Slope (Kramp, 1947). I have

found four specimens in a collection sent me by the late Mr G. P. Farran from the west coast of Ireland (S.R. 1850, 27. v. 14, M.O.T., 0–1200 fm.).

The medusa occurs widespread in all three oceans, except in Arctic seas. It has, however, not yet been recorded from the Mediterranean.

Developmental Stages and Structural Details

The complete life history of *Halicreas minimum* is not known. Stages as small as 1 mm. in diameter have been recorded by Thiel (1936) as belonging to this species.

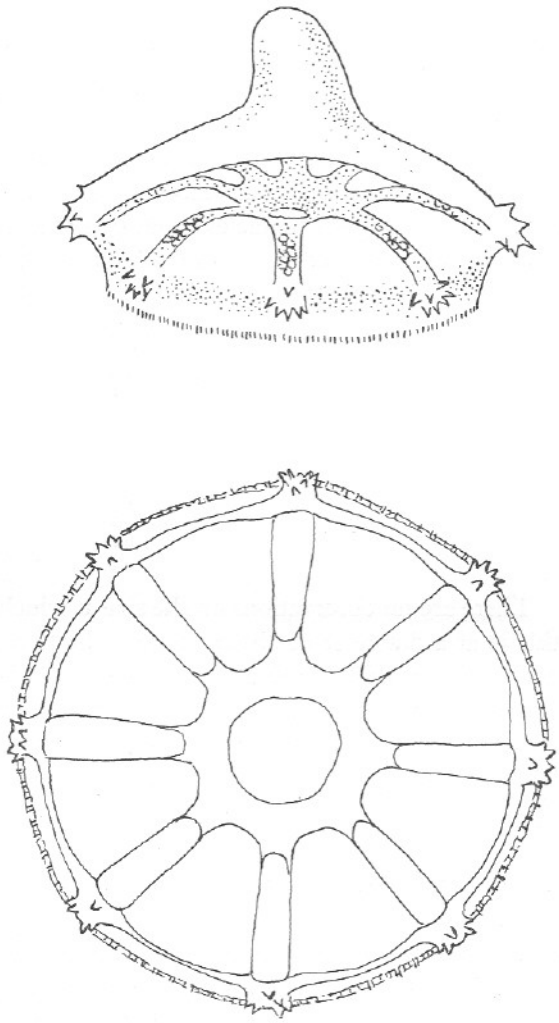
In the smallest specimens the umbrella is bell-shaped. The jelly is fairly thick, but the eight perradial exumbrellar processes are not yet developed. In their stead there are many nematocyst clusters irregularly scattered over the whole surface of the exumbrella. There is no apical process. The stomach is wide and circular and the mouth simple. The eight radial canals are fairly broad. There are no signs of gonads. There are only eight perradial marginal tentacles and no signs of interradial marginal tentacles. The marginal tentacles have a basal thickening at the umbrella margin. Thiel did not mention the marginal sensory clubs.

The interradial marginal tentacles have already developed when the medusa is 3 mm. in diameter, but Thiel gives no information as to their numbers.

The perradial exumbrellar processes are recognizable when the medusa is at least 6 mm. in diameter.

The further growth of the medusa consists of the increase in the numbers of marginal tentacles and the development of the gonads.

Detailed descriptions of later stages have been given by Vanhöffen (1902, 1912*a*), Maas (1905*b*) and Bigelow (1909*a*).



Text-fig. 299. *Halicreas minimum*. Above (after Vanhöffen, 1902, pl. ix, fig. 7, × 2); below (after Kramp, 1947, pl. vi, fig. 3, coloured sketch from life, Davis Strait, 1928).

The form of the apical process varies considerably from a very tall pyramid to an inconspicuous knob. The summit of the umbrella may even be rounded, with no trace of a process. According to Vanhöffen (1912*a*) the apical process is usually high and pointed in younger individuals and flatter in older ones, although this is not always so.

The eight perradial exumbrellar processes (Text-fig. 300A, B) are the most characteristic feature of this medusa, and they are more prominent in large than in small individuals. They are situated on the sides of the exumbrella near the umbrella margin and each has five to ten or more*

* Up to at least 16 in specimens I have seen.

small rounded conical papillae or tubercles. They give the umbrella an octagonal appearance when viewed from above. The jelly is very solid.

An abnormal specimen which had a similar process, with about nine papillae, situated at the umbrella apex was described by Browne (1908) as var. *antarcticum*. Bigelow (1913) showed that this was merely an individual variation, having found among three specimens two with a smooth apical process and a third with a tuberculated apical process.

The subumbrella has radial ridges and there may be a rounded prominence situated interradially between the bases of each of the radial canals.

The marginal tentacles increase in numbers with the size of the medusa. A comparison of the numbers of marginal tentacles in an octant in medusae of different sizes is given below. These observations are taken from Vanhöffen (1902), Maas (1905*b*) and Bigelow (1909*a*).

Diameter of umbrella (mm.)	No. of marginal tentacles in an octant
12	*c.* 20
21	23–27
23	28–31
24	20–33
26	19–26
27	30–40
29	29–35
30	40–50
42	17–31
44	58–80

There are no observations on the size at which the medusa becomes mature, but assuming that this is at a diameter of about 20 mm. the numbers of marginal tentacles will vary from about 200 to 600 in this size and larger specimens. It is evident from the last two specimens quoted above that the numbers may vary considerably in specimens of the same size. There may also be considerable differences in the numbers of marginal tentacles in the different octants in a single specimen, e.g. a specimen 42 mm. in diameter recorded by Bigelow which had seventeen to thirty-one marginal tentacles in its octants.

The structure of the marginal tentacles was first described in detail by Bigelow (1909*a*). Each marginal tentacle has a flexible proximal portion in which the endodermal core consists of cubical cells and a stiffer distal portion in which the endoderm cells are flattened and disk-shaped (Text-fig. 300C). The whole marginal tentacle is covered with ectoderm crowded with nematocysts. This ectodermal layer is often completely missing in preserved specimens, or left adhering only in small patches. In many preserved specimens all the marginal tentacles are broken off short at the base with only basal stumps remaining.

Apparently the eight perradial marginal tentacles are always the largest, being about twice as long as the others.

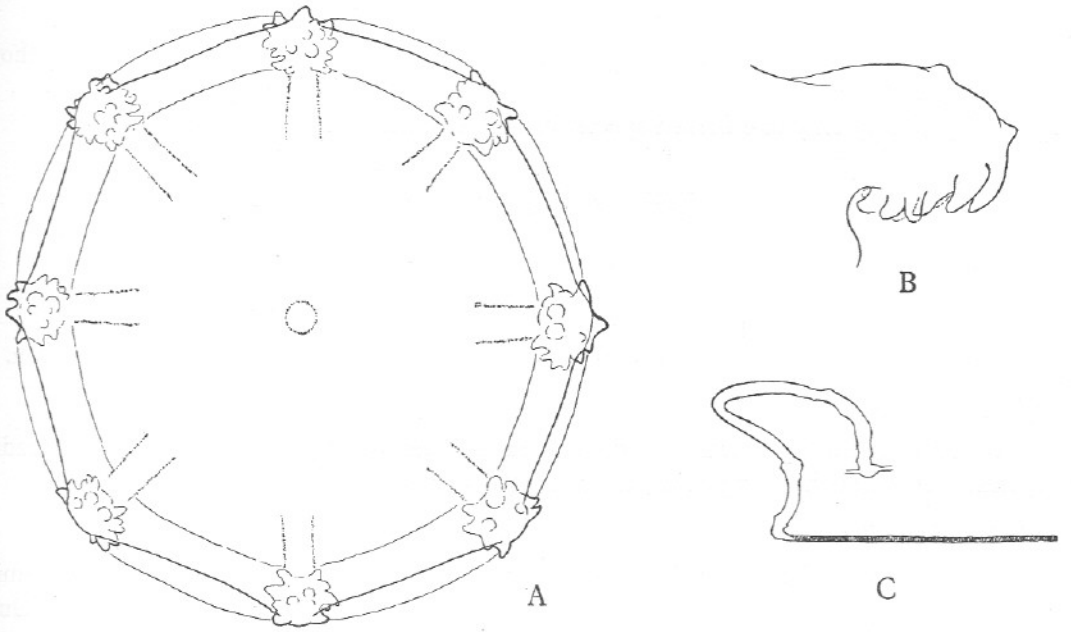
The marginal sensory clubs are elongated and consist of an ectodermal sheath and a core of chordate endoderm cells. From the large size of the distal endoderm cells Bigelow (1909*a*) thought it probable that there should be one or two concretions in the living medusa. The concretions have never been seen in preserved material.

Preserved specimens often have no traces of marginal organs or gastric tissue, these parts having been lost and the medusa consisting of a mere shell of the umbrella. Even in this condition the perradial exumbrellar processes are available as a diagnostic character (Text-fig. 300).

Kramp (1942) describes abnormal specimens in which the numbers of radial canals were five, seven and nine respectively, and one in which two of the eight radial canals were united distally.

Seasonal occurrence

Since *Halicreas minimum* is a deep-sea oceanic species it may probably be found at any time of year. The four specimens from the west of Ireland were taken in May; and Bigelow (1938) found it off Bermuda in all months in which collections were made, from April to September inclusive. He found a 'somewhat greater abundance in spring'.



Text-fig. 300. *Halicreas minimum*. A, umbrella of damaged preserved specimen 30 mm. in diameter seen from above, west of Ireland, 27. v. 14 (sent by G. P. Farran); B, lateral view of exumbrellar process of same specimen; C, tracing of photograph of marginal tentacle, showing stiff distal portion. (After Bigelow, 1909*a*, pl. xxxiv, fig. 11.)

Habits

Nothing is known of the habits of the living medusa except that it is a deep-sea species. In the North Atlantic specimens occur chiefly below 650 m. and do not become numerous at less than 2000 m. (Kramp, 1947). The *Meteor* Expedition (Thiel, 1936) obtained specimens* from about 75 m. down to 900 m., and the *Atlantis* (Bigelow, 1938) caught them in horizontal closing net hauls at depths between 600 and 2200 m.

Off Bermuda, Bigelow recorded one specimen from the surface, but the chief centre of distribution appeared to lie at least as deep as 1400–1800 m. Since many of the medusae are colourless Bigelow quotes this as an exception to the general rule that medusae from very deep water are densely pigmented.

Thiel (1936) showed that the younger stages appear to live nearer the surface than do the older.

Historical

Halicreas minimum was first described by Fewkes (1882*b*) from two specimens, from the coast of New England, which consisted merely of the shells of the umbrella. The eight perradial processes, however, were conspicuous and it was on these that Fewkes based his genus *Halicreas*.

* Including two other species (see Kramp, 1947).

Subsequently the species was re-described in detail by Vanhöffen (1902) under the name of *H. papillosum*. All authors have considered it most probable that Vanhöffen's species was really the same as that described by Fewkes. This opinion was finally confirmed by Bigelow (1938) who was able to find one of Fewkes's original specimens in the Museum of Comparative Zoology, Harvard.

Genus **Haliscera** Vanhöffen, 1902

Halicreidae with eight radial canals; with a continuous row of marginal tentacles; without exumbrellar papillae.

There is probably only one British species in the genus, *Haliscera bigelowi* Kramp.

Haliscera bigelowi Kramp

Plate XXVII, fig. 2; Text-figs. 301, 302

Homoeonema alba, Bigelow 1909*a*, *Mem. Mus. Comp. Zöol. Harvard*, vol. XXXVII, p. 142, pl. iii, figs. 1, 2; pl. xxxiii, figs. 6, 11; pl. xxxiv, fig. 9.
Haliscera bigelowi Kramp, 1947, *Danish Ingolf-Expedit.* vol. v (14), p. 8, pl. i, figs. 5–8; pl. ii, figs. 1, 2.

Specific Characters

Umbrella almost hemispherical; gonads oval, each situated along two-fifths of length of radial canal, nearer stomach than ring canal; about ninety-six marginal tentacles.

Description of Adult

Umbrella almost hemispherical; jelly very thick in upper region, with dome-shaped summit; subumbrellar cavity shallow with thin jelly at sides and margin; no exumbrellar papillae. Velum very broad. Stomach broad and flat; mouth simple and circular. Eight straight radial canals and ring canal broad. Gonads oval, each situated along two-fifths of length of radial canal nearer stomach than ring canal. About ninety-six solid marginal tentacles; each marginal tentacle flexible proximally and stiffer distally; distribution of large and small marginal tentacles rather irregular. Three marginal sensory clubs in each octant. Diameter of umbrella 15–19 mm. Colourless.

Distribution

Haliscera bigelowi is a deep-sea oceanic medusa whose distribution in the North Atlantic is such that it might be expected to occur in deep water west and south-west of the British Isles, from which region it has indeed been mentioned by Kramp (1947). It is probably the same species as that recorded by Bigelow (1909*a*) from the eastern tropical Pacific.

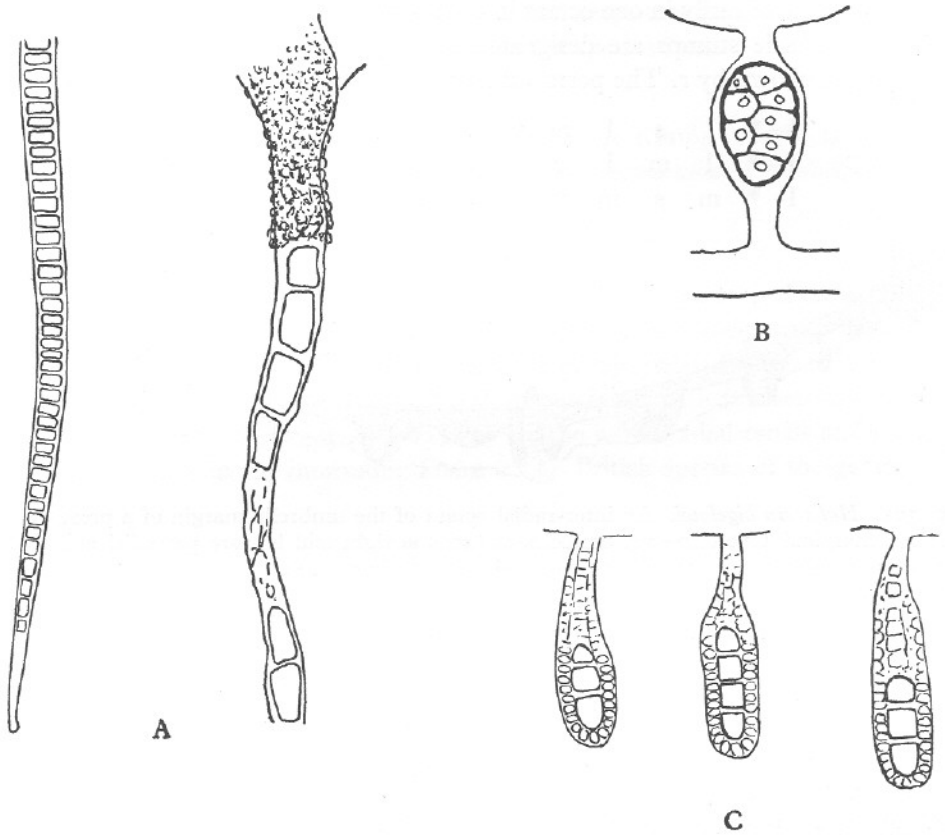
Developmental Stages and Structural Details

The complete development of *Haliscera bigelowi* is not known. The smallest specimen that has been recorded was 5 mm. in diameter (Kramp, 1947); this had about eighty marginal tentacles. Another, 6 mm. in diameter, had about ninety-six marginal tentacles; and in the largest, 19 mm. in diameter, the number of marginal tentacles did not exceed 100.

I have myself seen four specimens among Mr Browne's material collected by the *Thor*.

The form of the umbrella is characteristic, the sides of the subumbrella being thin and separated by a slight constriction from the massive, highly domed summit, which comprises nearly two-thirds of the height of the medusa.

The gonads form elongated, oval, and rather flat swellings on the radial canals. Each female gonad contains about seven large eggs (Text-fig. 301 B). At the proximal end of the gonad the sides of each radial canal flare outwards suddenly and then run in slightly converging lines towards the ring canal. A well-marked angle is thus formed on each side of a radial canal at the proximal end of the gonad (Pl. XXVII, fig. 2).



Text-fig. 301. *Haliscera bigelowi*. A, left, stiff distal end of marginal tentacle; right, flexible proximal portion of marginal tentacle, with all the ectoderm rubbed off except at the base; B, female gonad; C, three marginal sense organs. (Preserved specimens, A and C from E. T. Browne collection, 'Thor' 1906; B, after Kramp, 1947, pl. i, fig. 6.)

The marginal tentacles (Text-fig. 301 A) are all of the same structure, though varying in size according to age. They resemble those of *Halicreas minimum* in having flexible proximal portions with an axis of cubical endoderm cells and a stiffer distal portion in which the endoderm cells are flatter and disk-shaped. The whole marginal tentacle is clothed in ectoderm crowded with nematocysts, but in preserved specimens this ectodermal layer is frequently completely missing, or left adhering only in small patches. In most preserved specimens almost all the marginal tentacles are broken off short at their bases and represented only by basal stumps (Text-fig. 302).

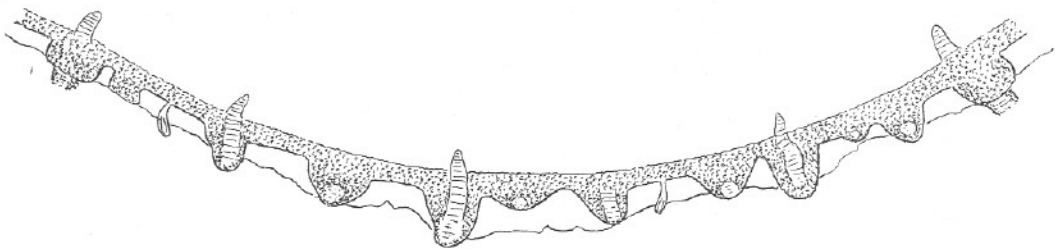
At the base of each marginal tentacle there is a thickening of the marginal nematocyst tissue.

In the specimens I have examined the perradial stumps are certainly always among the largest, but there is considerable difference in size among the stumps of the interradial marginal tentacles and some of these appear quite as large as those of the perradial marginal tentacles. In one

specimen, however, in which some of the marginal tentacles were intact a perradial marginal tentacle was considerably longer than a large interradial marginal tentacle. This agrees with what Kramp finds (1947).

In the specimens I have seen, 12–14 mm. in diameter, it is, as I have said, rather difficult to discriminate between the different sizes of the marginal tentacle stumps. But I have attempted to do so somewhat arbitrarily in one octant in each of three specimens with the following results. The marginal tentacle stumps are designated large (l), medium (m), and small (s), and the sensory clubs are shown by *c*. The perradial stumps are indicated by asterisks (*).

l * l s l m *c* m s l l s *c* s l *
l * l m l *c* s l m l m s l m l *
l * m s m m *c* m s l m l *c* m l *



Text-fig. 302. *Haliscera bigelowi*. An inter-radial octant of the umbrella margin of a preserved specimen with broken marginal tentacles—the tentacles at extreme right and left are perradial and there are two marginal sense organs shown. (E. T. Browne collection, 'Thor' 1906.)

In the second octant described above one of the sensory clubs was missing, and it appears that there are normally two in each octant. Kramp (1947), however, states that there are three in each octant distributed as follows:

To the right-hand side of a perradial tentacle we first see another tentacle and then a statocyst followed by three tentacles, one statocyst, three more tentacles, and again one statocyst; but between this third statocyst and the first one in the next octant there are six tentacles! A statocyst in the middle of this group of six tentacles would result in a completely symmetrical and regular position of statocysts round the umbrella margin, with three tentacles between each successive pair of statocysts, but I have never seen a statocyst on the left-hand side of a perradius. I do not think that the absence of a statocyst in this place is due to its being broken off; though the statocysts are small and delicate organs, they are astonishingly resistant, and even in badly preserved specimens most of them are retained and always as described here; variations are only observed when the number of tentacles in an octant is another than twelve.

The marginal sensory clubs are large and elongated, narrowing into a short stalk at the base (Text-fig. 301 C). Distally there are three to four very large endoderm cells, which probably contain concretions when the medusa is alive, no concretions being present in preserved specimens. According to Kramp (1947) the endodermal core consists of about ten cells; and the ectoderm consists of two different kinds of cells, two lateral rows of rectangular cells in the distal half or two-thirds, and large flattened cells on the proximal portion and abaxial and adaxial sides of the distal portion.

Bigelow (1909*a*) states that 'the majority of specimens were entirely colourless in life; but in one individual the entire entodermic system was of a very pale orange'.

Seasonal occurrence

Since *Haliscera bigelowi* is a deep-sea oceanic species it may probably be found at any time of year. In the Atlantic it has been recorded in May, June, July and August (Kramp, 1947).

Habits

Nothing is known of the habits of the living medusa except that it is a deep-sea species, but there is little satisfactory information as to how deep the species lives.

Historical

Haliscera bigelowi was first described and figured as such by Kramp (1947). It is probably the same species as that referred by Bigelow (1909*a*) to *Homoeonema alba* of Vanhöffen.

Genus **Botrynema** Browne, 1908

Halicreidae with hemispherical umbrella with thick jelly; without peduncle; with simple circular mouth; with eight broad radial canals; with broad oval flattened gonads on radial canals; with eight solitary perradial marginal tentacles, and two groups each of seven to twelve marginal tentacles in each interradius; marginal tentacles all of one kind; with free sensory clubs.

The essential characters of the genus *Botrynema* are the broad radial canals and the grouping of the marginal tentacles in the interradii. There is one British species of the genus, *B. brucei* Browne.

Botrynema brucei Browne

Plate XXVII, fig. 1; Text-figs. 303, 304

Botrynema brucei Browne, 1908, *Trans. Roy. Soc. Edinb.* vol. XLVI, pt. II (no. 10), p. 239; pl. i, figs. 8, 9; pl. ii, fig. 1.

Vanhöffen, 1912*a*, *Deutsche Südpolar Expedit.* 1901–3, Bd. XIII, Zool. V, p. 382, pl. ii, fig. 5; text-figs. 18, 19.

Kramp, 1947, *Danish Ingolf-Expedit.* vol. V (14), p. 11, pl. i, fig. 9; pl. ii, fig. 3; pl. vi, fig. 4.

Botrynema ellinorae, Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, p. 53, pl. iv, figs. 1–4.

Specific Characters. Umbrella with apical knob.

Description of Adult

Umbrella hemispherical or slightly higher than wide, with smooth margin; jelly thick, especially in apical region, with rounded apical knob. Velum very broad. Stomach wide, circular, and short; with eight-cornered base; no peduncle; mouth simple. Eight broad straight radial canals, and very broad ring canal. Eight broad oval gonads situated on proximal or central halves of each radial canal. Eight solid perradial marginal tentacles; sixteen adradial groups of seven to twelve solid marginal tentacles; all marginal tentacles without basal swellings. Three to four marginal sense organs in each perradial space between adradial groups of marginal tentacles(?). Diameter of umbrella up to 20 mm. Colour of stomach, canals and gonads red or bright scarlet red; pale reddish brown (Bigelow, 1913) or whitish in formalin.

Distribution

Botrynema brucei is a deep-sea oceanic species recorded here for the first time in the vicinity of British coasts. I have found two specimens in Mr Browne's collection taken 50 miles north-west of Eagle Island on the west coast of Ireland on 11 August 1904, in a D-net from 1000 fathoms.

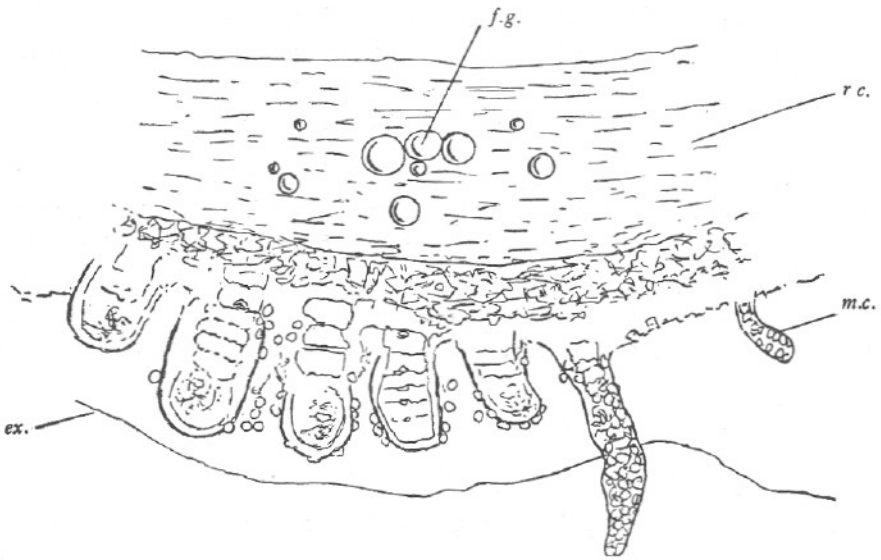
Elsewhere the species is probably widely distributed in deep water, except in Arctic seas.

Developmental Stages and Structural Details

The earliest stages of *Botrynema brucei* are not known. Specimens have been recorded between 3 and 20 mm. in diameter. In the smallest specimen seen by Vanhöffen (1912*a*) the marginal tentacle groups were only just indicated, but already in those 5 mm. in diameter there were as many as eight tentacles in a single marginal group.

The umbrella is not especially muscular, but the breadth of the velum is noteworthy.

According to Bigelow (1913) the Pacific specimens ranging between 8 and 13 mm. in diameter were apparently all immature, for the walls of the radial canals in the sexual regions were but



Text-fig. 303. *Botrynema brucei*. Portion of the umbrella margin showing a group of marginal tentacles all of which are broken off except the smallest which is on the extreme right; a marginal sense organ is shown on the right. (Preserved specimen, off Eagle Island, Ireland, 11. viii. 04, E. T. Browne collection.) *f.g.*, fat globule; *r.c.*, ring canal; *m.c.*, marginal sensory club.

little thickened. One of the specimens in Mr Browne's collection, which was 20 mm. in diameter, had lost most of the gonadial tissue except for that of one gonad which was more or less complete in outline. In the other, which was 8 mm. in diameter, the gonads were just appearing. The gonads may start a short distance from the stomach and reach only to about the middle of the radial canal, or they may occupy the middle region of the canal.

The radial canals and ring canal contain large numbers of fat globules.

In nearly all specimens so far recorded the marginal tentacles appear to have been broken off short at their bases, the basal portions being embedded in the jelly between the ring canal and the exumbrellar margin. In one of the specimens from off Eagle Island three of the younger marginal tentacles were intact; they were quite short and tapered (Text-fig. 303). Kramp (1947) saw a few very young marginal tentacles and stated that they have the same structure as in other species of Halicreidae.

The disposition of the groups of marginal tentacles is very distinctive. In each group the tentacles are apparently ranked in the order of their development, the basal portions decreasing regularly in length from one side of a group to the other (Text-fig. 303). This is probably because

the older marginal tentacles have their embedded roots lengthened as the margin of the umbrella grows. Vanhöffen (1912*a*) was only able to notice an indication of this ranking in one of his specimens.

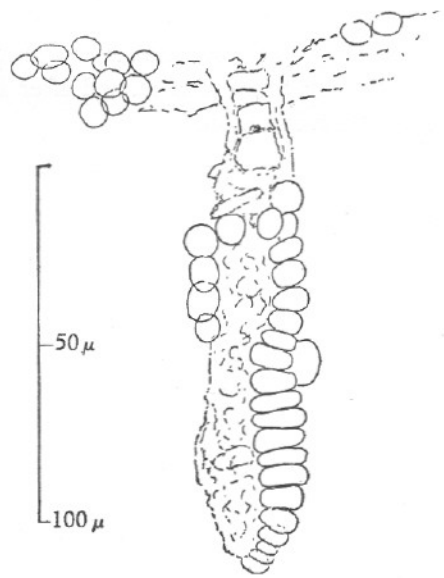
The sequence of development of the marginal tentacles, however, alternates from octant to octant. In four alternate perradii the youngest marginal tentacles are at the sides of the groups nearest the adjacent radial canal. In the remaining four perradii the oldest marginal tentacles are in that position. Thus in any one octant the sequence of development in the two groups runs in the same direction, but the direction alternates from octant to octant.

The marginal tentacle groups are equally spaced round the umbrella margin, the eight single marginal tentacles being situated in the centre of each perradial space, opposite a radial canal.

The number and position of the marginal sense organs need further verification. Vanhöffen (1912*a*) found sixteen sensory clubs, one between each group of marginal tentacles; these were so disposed in relation to the radial canals that the number in each octant alternated between three and one.

Bigelow (1913) said that the sensory clubs 'are grouped, lying in the perradial regions in the space between the two tentacle groups which flank each radial canal, three in each group'. He says that each club consists of an ectodermal sheath and a clear endodermal core. None of his specimens had concretions.

Kramp (1942) stated that there were usually three sensory clubs in each interradial space, and only one, sometimes two, on either side of the perradial marginal tentacles.



Text-fig. 304. *Botrynema brucei*. Marginal sense organ of preserved specimen, off Eagle Island, Ireland, 11. viii. 04. (E. T. Browne collection.)

The sensory clubs are apparently easily lost and I could find none in one of the specimens I examined, but in the other there was one club (Text-fig. 304) in each of several of the spaces between the marginal tentacle groups, both perradial and interradial. Browne (1908) could find none in his specimen from the Antarctic.

Seasonal occurrence

The two specimens recorded above from the west coast of Ireland were caught in August. Other records have been June and July in the North Atlantic and March in the Antarctic.

Habits

Nothing is known of the habits of the living medusa. The species evidently lives normally in deep water, all specimens having been recorded in hauls from 300 to 3000 m.

Historical

Botrynema brucei was first described by Browne (1908) from a single specimen in the Scottish National Antarctic Expedition collections, and he raised the genus *Botrynema* for it.

The species was next recorded by Vanhöffen (1912*a*) who saw nine specimens from the Antarctic. The next year Bigelow (1913) gave a further description of specimens from the North Pacific under the name *B. ellinorae*, thinking that it was the same as *Alloionema ellinorae* described by Hartlaub (1909*c*) from the Arctic. Kramp (1942) considered it highly probable that Hartlaub's species was distinct. He found that specimens from the Arctic had no apical knob to the umbrella whereas those from the Atlantic always had knobs. Also the stomach and radial canals in the former were light roseate and the umbrella margins orange, while in the latter these were bright scarlet red.

Kramp (1947) thinks that *Botrynema brucei* may be the same species as *Halicreas glabrum* of Vanhöffen (1902), but the latter was insufficiently described for certain identification.

Botrynema brucei was named after Dr William S. Bruce, the leader of the Scottish National Antarctic Expedition.

ORDER

NARCOMEDUSAE

Hydromedusae with sides of umbrella divided by peronial grooves so that umbrella margin may be lobed; with broad stomach with entire circular periphery or with rectangular peripheral pouches; without radial canals, and with or without a peripheral canal system; with gonads on stomach walls; with solid marginal tentacles leaving umbrella some distance above margin, and sometimes small secondary tentacles on margin itself; with sense organs in form of free sensory clubs with endodermal axes.

Without true hydroid stage, but sometimes with parasitic larval development.

The Narcomedusae are distinguished from all other medusae by the structure of the umbrella. This has a central lens-shaped mass of jelly below which the sides of the umbrella are very thin. The large solid marginal tentacles leave the umbrella some distance above its margin and from their bases the peronial grooves or peronia run vertically downwards to the margin. At the junction the margin itself is often cleft, giving the umbrella a lobed appearance.

The stomach is very broad and circular, its base covering the lower surface of the lens-shaped mass of jelly. Around the periphery of the stomach there may or may not be rectangular marginal pouches. A ring canal may be present, but this does not form a continuous ring round the umbrella margin as in the other orders of Hydromedusae. It runs along the margin of each umbrella lobe and vertically along both sides of each peronium, thus forming a number of loops. The whole canal is known as the peripheral canal system.

The marginal tentacles have solid axes consisting of a single row of disk-shaped endoderm cells.

Narcomedusae are mostly rather fragile organisms and preserved specimens are often considerably damaged. They are entirely oceanic. For mention of life histories see pp. 23, 25.

The Narcomedusae are best classified according to the presence or absence of stomach pouches, and the position of these pouches, when present, in relation to the marginal tentacles. For purposes of orientation the marginal tentacles are regarded as being perradial. The Narcomedusae can thus be divided into three families, the Cuninidae, the Aeginidae, and the Solmaridae; there is also a fourth family, the Halammohydridae, which contains an aberrant form considered to be a Narcomedusa.

The above three families can be distinguished by the following characters:

With stomach pouches:	
Pouches perradial	**Cuninidae**
Pouches interradial	**Aeginidae**
Without stomach pouches	**Solmaridae**

All three families are represented in the British fauna, by four genera with four species.

FAMILY CUNINIDAE

Narcomedusae with perradial and undivided stomach pouches; with or without peripheral canal system; with marginal tentacles leaving umbrella opposite centre of each stomach pouch, equal in number to that of pouches; pouches not extending beyond points of origin of tentacles; without secondary tentacles on umbrella margin; with or without otoporpae.

CUNINIDAE

The distinctive character of the family Cuninidae is the position of the marginal tentacles in relation to that of the stomach pouches, both being perradial so that a tentacle arises opposite the middle of the distal margin of a pouch.

The family is represented in British waters by one genus, *Solmissus* Haeckel.

Genus **Solmissus** Haeckel, 1879

Cuninidae without peripheral canal system; without otoporpae.

There is one British species of the genus, *Solmissus incisa* (Fewkes).

Solmissus incisa (Fewkes)

Text-figs. 305–7

Solmaris incisa Fewkes, 1886, *Rep. U.S. Comm. Fish and Fisheries*, pt. XII (1884), p. 954, pl. ix.
Solmissus incisa, Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 67, pl. xxi, figs. 1–3, 5.
Mayer, 1910, *Medusae of the World*, vol. II, p. 483.
Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, no. 1946, p. 57.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 527, fig. 33*a*, *b*.
Ranson, 1936, *Rés. Camp. Sci. Monaco*, Fasc. XCII, p. 206.
Solmaris rhodoloma Vanhöffen, 1908, *Wiss. Ergebn. 'Valdivia'*, Bd. XIX (1925), Heft 2, p. 60, pl. vii, fig. 5.

Specific Characters

Twenty to forty marginal tentacles; two to five marginal sense organs; umbrella up to 100 mm. diameter.

Description of Adult

Upper portion of umbrella flat and disk-like; jelly fairly thick, but very soft and fragile; lower marginal portion of umbrella thin and flexible with twenty to forty marginal lappets about as long as wide. No otoporpae. Velum ? well developed. Stomach large and circular, covering subumbrellar surface of upper portion of umbrella, with twenty to forty marginal pouches slightly wider than long; septa between pouches alternating with tentacle roots. No peripheral canal system. Gonads? Twenty to forty stiff tapering marginal tentacles, slightly longer than diameter of umbrella, with solid endodermal axes; attached to exumbrella at upper ends of peronia separating marginal lappets; endodermal roots only about half as long as septa between marginal gastric pouches. Two to five marginal sense organs on each marginal lappet. Diameter of umbrella up to 100 mm. Colourless, or ? with red gastric pouches (Vanhöffen, 1909).

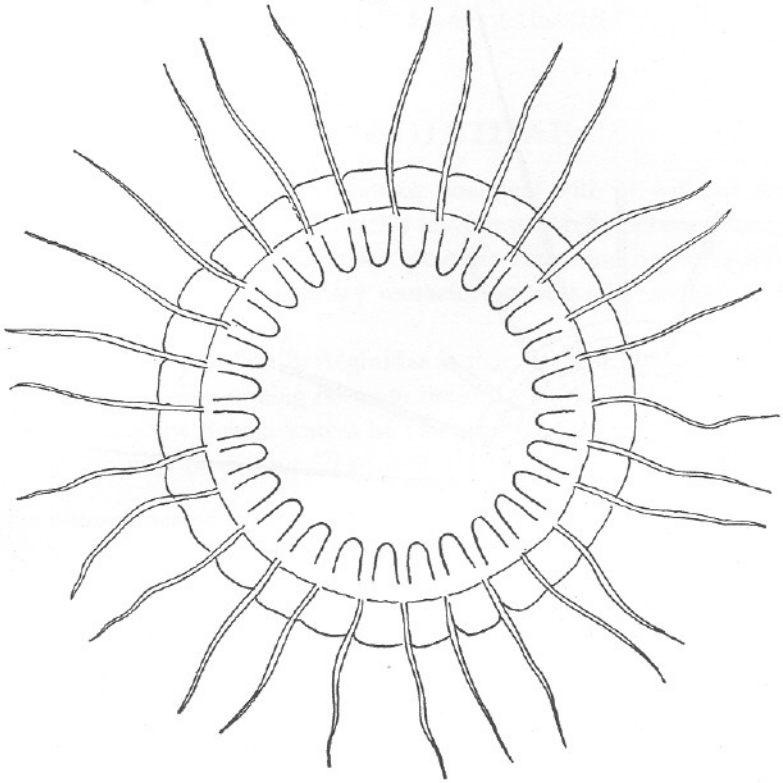
Distribution

Solmissus incisa is a deep-water oceanic medusa and is only likely to be found off the western coasts of the British Isles over very deep water. It has not previously been recorded in British waters, but, in March 1939, Mr P. G. Corbin gave me several specimens caught at night far out west of the mouth of the English Channel (50° 07′ N., 12° 12′ W. and 50° 25′ N., 11° 35′ W.).

The species has also been recorded from several localities in the North Atlantic (Kramp, 1948*a*) and in the Mediterranean (Ranson, 1936), from Bermuda ? (Bigelow, 1938); the South Atlantic? (Vanhöffen, 1908); and the Pacific as far north as Bering Sea and Kamchatka (Bigelow, 1909*a*, 1913; Uchida, 1928; Bigelow & Leslie, 1930).

Developmental Stages and Structural Details

Solmissus incisa is so fragile a medusa that no fully complete specimens have yet been obtained. In all so far seen the greater part of the stomach is torn away, so that all that remains to determine the identity of the species are the portions of the gastric wall which persist in the regions of the septa between the marginal pouches. The gonad structure has therefore not been seen.



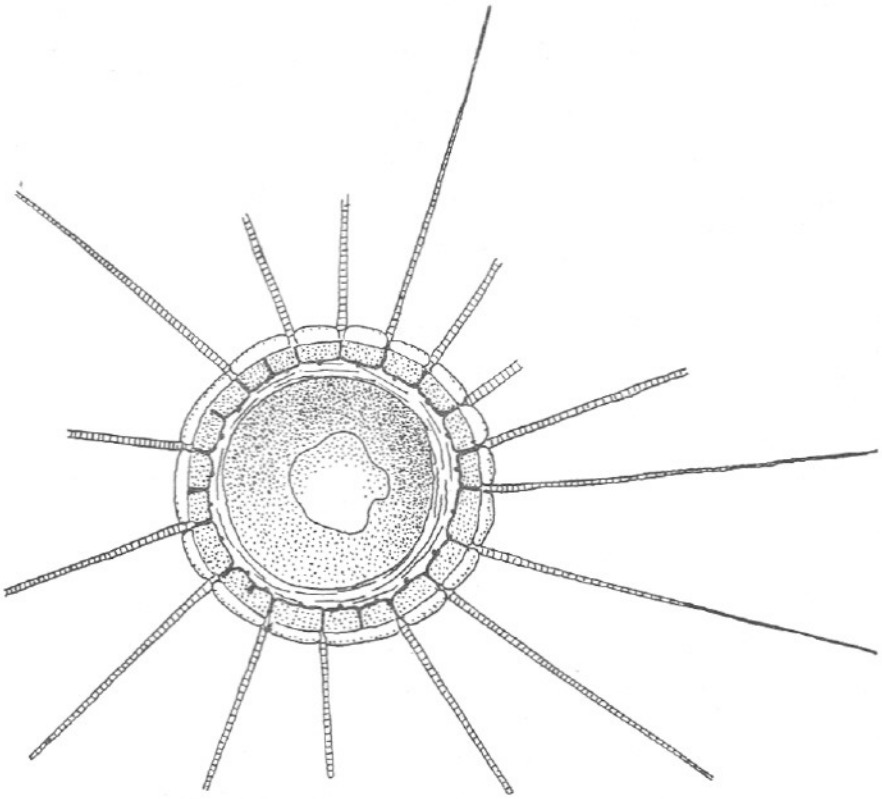
Text-fig. 305. *Solmissus incisa.* × *c.* ¾. (After Vanhöffen, 1908, pl. vii, fig. 5.)

The life history of the medusa is not known, and very small stages have not been described. In the following table the diameter of the umbrella and the numbers of marginal tentacles are given for specimens of different sizes. These figures refer to specimens from the Pacific (Bigelow, 1909*a*, 1913) and to those collected off the mouth of the English Channel by Mr Corbin.

Pacific		Pacific		British	
Diameter of umbrella (mm.)	No. of marginal tentacles	Diameter of umbrella (mm.)	No. of marginal tentacles	Diameter of umbrella (mm.)	No. of marginal tentacles
10	16 (+3 developing)	60	31	13	? 17
		65	34	20	? 14
17	21	68	31	25	? 9
40	20	70	27	30	19
40	20 or 21	75	29	30	20
43	19	75	35	35	? 15
43	24	76	40	35	20
44	23	80	32	40	*c.* 19
44	23	*c.* 100	32	45	21
45	19	103	35	48	19
48	22	112	35	55	17
50	23	—	—	55	20
c. 50	20–25				

It is evident that *S. incisa* is very nearly related to *S. albescens* of the Mediterranean. In fact Ranson (1936) has suggested that it is merely a giant form of *S. albescens*.

S. albescens is a smaller species 25–30 mm. in diameter and appears almost invariably to have no more than sixteen marginal tentacles; it also has a greater number of marginal sense organs, viz. five to eight on each marginal lappet.



Text-fig. 306. *Solmissus incisa.* Oral view of a small specimen 10 mm. in diameter. There are only one or two marginal sensory clubs per lappet; a few of the marginal tentacles are shown in their entire length. (After Bigelow, 1909*a*, pl. xxi, fig. 1.)



Text-fig. 307. *Solmissus incisa.* Optical section of a marginal sensory club stained in borax carmine; the bristles have all been destroyed by preservation. × 300. (After Bigelow, 1909*a*, pl. xxi, fig. 5.)

The sensory clubs (Text-fig. 307) arise from large and somewhat triangular supporting cushions; each contains a single large rounded concretion (Bigelow, 1909*a*, p. 68).

The margin of the umbrella in preserved specimens is often split along the peronia.

Seasonal occurrence

It is probable that *Solmissus incisa* is to be caught in deep water all the year round. The occurrence recorded above off the mouth of the English Channel was in March 1939.

Habits

Nothing is known of the habits of *Solmissus incisa* in life.

It is a deep-water medusa and probably mesoplanktonic, only rarely being taken at the surface in the daytime. The specimens taken off the mouth of the English Channel were caught at night, between 2318 hr. and 0018 hr.

Historical

Solmissus incisa was first described by Fewkes (1886) as *Solmaris incisa*. Bigelow (1909*a*) pointed out that the species was actually a *Solmissus*.

The possibility that the species may be the same as *S. albescens* has already been mentioned. If in the future it should be decided that this is so, the specific name *albescens* has priority.

It has also been suggested that *S. faberi* and *S. bleekii* of Haeckel (1879) are the same species.

Family AEGINIDAE

Narcomedusae with interradial, divided stomach pouches; with or without peripheral canal system; with primary perradial marginal tentacles leaving umbrella between marginal pouches, in number at least half that of stomach pouches; pouches extending beyond points of origin of primary tentacles; with or without secondary tentacles on umbrella margin; with or without otoporpae.

The distinctive character of the family Aeginidae is that the stomach pouches are interradial in position, the marginal tentacles arising between them.

The family is represented in British waters by two genera, *Aegina* Eschscholtz and *Aeginura* Haeckel. The two genera may be distinguished as follows:

Typically with eight primary stomach pouches; with three to six, typically four, marginal tentacles and no secondary tentacles . . . . . **Aegina**

With sixteen primary stomach pouches; with eight primary marginal tentacles and with secondary marginal tentacles . . . . . **Aeginura**

In *Aegina* the number of marginal tentacles may vary from three to six, the numbers of stomach pouches varying accordingly. The most pronounced character distinguishing the two genera is the presence of secondary tentacles actually on the umbrella margin in *Aeginura*. Since, however, the umbrella margin is often badly damaged it is necessary to use the other characters alone sometimes for identification. An additional diagnostic character is the peripheral canal system which is present in *Aegina* but is absent, or at least in a degenerate state, in *Aeginura*.

Genus **Aegina** Eschscholtz, 1829

Aeginidae typically with eight, occasionally ten or twelve, stomach pouches, which may or may not have secondary divisions; with peripheral canal system; with typically four, occasionally three, five or six, primary marginal tentacles; without secondary marginal tentacles; without otoporpae.

There is one British species of the genus, *Aegina citrea* Eschscholtz.

Aegina citrea Eschscholtz

Plate XXVIII, fig. 1; Text-figs. 308–10

Aegina citrea Eschscholtz, 1829, *System der Acalephen*, p. 113, pl. xi, fig. 4.
Haeckel, 1879, *System der Medusen*, p. 338.
Maas, 1905*a*, *Siboga-Expedit.* Monogr. x, p. 71, pl. xi, fig. 72; pl. xiii, figs. 79–82.
Vanhöffen, 1908, *Wiss. Ergebn.* '*Valdivia*', Bd. xix (1925), Heft 2, p. 50.
Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. xxxvii, p. 73, pl. i, fig. 5; pl. xiv, fig. 5.

Mayer, 1910, *Medusae of the World*, vol. II, p. 451, text-figs. 299, 300.
Browne, 1916, *Trans. Linn. Soc. London*, ser. 2, Zool. vol. XVII, pt. II, p. 200.
Bigelow, 1919, *Bull. U.S. Nat. Mus.* 100, vol. I, pt. V, p. 330.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 530, fig. 35.
Ranson, 1936, *Rés. Camp. Sci. Monaco*, Fasc. XCII, p. 209, pl. ii, fig. 22.
Bigelow, 1938, *Zoologica, New York*, vol. XXIII, pt. II, p. 131.

Aegina rosea Eschscholtz, 1829, *System der Acalephen*, p. 115, pl. x, fig. 3.
Haeckel, 1879, *System der Medusen*, p. 338.
Vanhöffen, 1908, *Wiss. Ergebn.* '*Valdivia*', Bd. XIX (1925), Heft 2, p. 48, pl. vii, figs. 1, 2; pl. ix, figs. 16, 17.
Maas, 1909, *Abh. Akad. Wiss. München*, Suppl. Bd. I, p. 35.
Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, no. 1946, p. 59.
Bigelow, 1919, *Bull. U.S. Nat. Mus.* 100, vol. I, pt. V, p. 330.
Thiel, 1936, *Zool. Jahrb. Jena*, Abt. Syst., Okol. Geogr. Tiere, Bd. LXIX, Heft 1, p. 73, fig. 15.
Uchida, 1928, *Japan Journ. Zool.* vol. II, no. 1, p. 91, fig. 8.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 530, fig. 34.

Cunarcha aeginoides Haeckel, 1879, *System der Medusen*, p. 315.
Haeckel, 1881, *Rep. Sci. Res. Challenger, Zool.* vol. IV (1882), p. 24, pl. ix.

Aegina rhodina Haeckel, 1879, *System der Medusen*, p. 338, pl. xx, figs. 11–13.
Mayer, 1904, *Mem. Nat. Sci. Brooklyn Inst. Arts Sci.* vol. I, p. 27, pl. iv, figs. 28, 29.
Mayer, 1910, *Medusae of the World*, vol. II, p. 452, pl. lii, fig. 5; pl. liv, fig. 11.

Aegina canariensis Haeckel, 1879, *System der Medusen*, p. 339.

Aegina eschscholtzii Haeckel, 1879, ibid. p. 339.
Mayer, 1910, *Medusae of the World*, vol. II, p. 453.

Solmundus tetralinus Haeckel, 1879, *System der Medusen*, p. 351, pl. xix, fig. 10.

Aegina lactea Vanhöffen, 1908, *Wiss. Ergebn.* '*Valdivia*', Bd. XIX (1925), Heft 2, p. 50, pl. vii, fig. 3.

Aegina brunnea Vanhöffen, 1908, ibid. Heft 2, p. 51, pl. vii, fig. 4.

Aegina alternans Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 74, pl. xvii, fig. 1.

Aegina pentanema Kishinouye, 1910, *Journ. Coll. Sci. Imp. Univ. Tokyo*, vol. XXVII, Art. 9, p. 32, pl. v, fig. 34.

Aegina aeginoides, Mayer, 1910, *Medusae of the World*, vol. II, p. 454.

Specific Characters. Here regarded as the only species of the genus.

Description of Adult

Umbrella hemispherical; jelly thick in upper half of umbrella, thin at sides of lower half and margin; with four peronia. Velum well developed. Stomach large, circular, and flattened or dome-shaped dorsally, with typically eight rectangular marginal pouches, of which some or all may or may not have slight median clefts or notches; lower portion of stomach conical, mouth simple and circular, not extending beyond umbrella margin. Peripheral canal system present. Gonads on walls of stomach pouches, sometimes extending on to main body of stomach. Typically, four large solid marginal tentacles issuing from umbrella at upper ends of peronia in deep exumbrellar furrows at level of top of stomach; with root-like endodermal continuations in substance of apical jelly; length of each marginal tentacle up to twice diameter of umbrella. No secondary marginal tentacles. Up to ? 100 marginal sensory clubs. No otoporpae. Umbrella up to 50 mm. in diameter. Colour of stomach, stomach pouches, and marginal tentacles yellow, yellowish brown, brown, pink or colourless.

Distribution

Aegina citrea is a deep-sea oceanic species which has only once been recorded in the vicinity of the British Isles, from between Scotland and Rockall (Kramp, 1920). I have found a specimen in Mr Browne's collection taken 50 miles north-west of Eagle Island on the west coast of Ireland, and one in a collection made by R.R.S. *William Scoresby* about 90 miles south-west of the Fastnet (Stat. W.S. 963, 19. i. 50).

The species is world-wide in its distribution and has been recorded from all three oceans and the Mediterranean, as far south as 54° S., and as far north as 63° N. (Kramp, 1947). It is thus likely to be found anywhere in very deep water west of the British Isles.

Developmental Stages and Structural Details

The complete life history of *Aegina citrea* is not known. Very small specimens, however, have been recorded and Thiel (1936) lists specimens as small as 1 mm. in diameter. There is probably little change in general appearance as the medusa grows.

Apparently a certain amount of structural variation is shown by the species and as a result a number of species have been described. The medusa has not yet been captured in sufficient numbers over a wide area to decide whether these 'species' should be regarded as distinct or merely varieties of a single species. The indications are at present that they should be regarded provisionally as a single species. The species does, however, tend to split into two forms, namely *citrea* and *rosea*. The difference lies in the form of the distal margins of the stomach pouches: in the typical *citrea* form these are slightly cleft or notched (Text-fig. 309), but in the *rosea* form they are smooth (Text-fig. 308). Recent evidence points to the fact that this is not really a consistent character. Thus, Bigelow (1938) records specimens in which some of the pouches are notched and others have entire margins in a single specimen. This is also shown in the specimen from 50 miles north-west of Eagle Island (Pl. XXVIII, fig. 1). Bigelow points out another possible difference. In the *citrea* form the gonads usually form two swellings on the oral surface of each pouch, whereas in the *rosea* form a single swelling involves the whole oral surface of each pouch. This character, however, he also shows to be inconsistent, in that the double gonadial swellings may be found in unnotched pouches of the *rosea* form and vice versa.

In preserved specimens the umbrella may appear considerably flattened or hemispherical.

The mouth opening is simple and circular. In the specimen in Mr Browne's collection recorded above there are several distinct thickenings running radially towards the opening. The tissue can be easily torn along these lines to give the impression of pointed lips. Such lips have indeed been mentioned by Haeckel (1879, p. 339 under *A. eschscholtzii*) and by Uchida (1928).

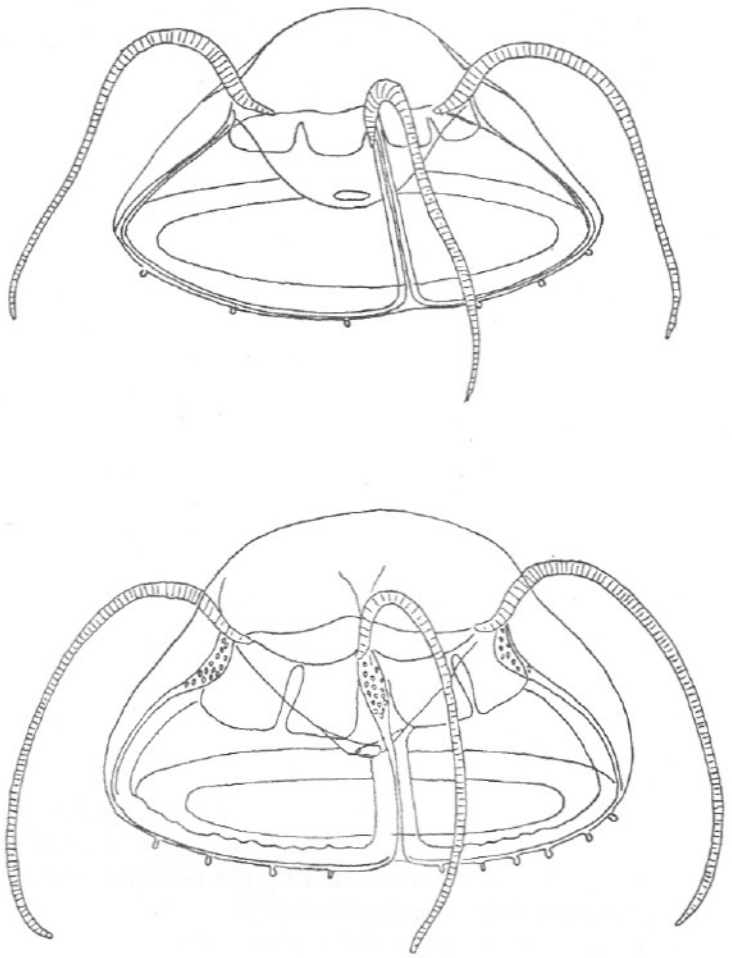
The peripheral canal system forms four loops, each consisting of a canal running down one side of a peronium, along the umbrella margin, and up the side of the next peronium. There are thus two canals, one on either side of each peronium.

The peronia lie in deep exumbrellar furrows and continue upwards to the root of each marginal tentacle.

The endodermal root-like extensions of the marginal tentacles deserve special mention. In the specimen I have seen from the west of Ireland (Pl. XXVIII, fig. 1) they are relatively enormous. While basally they are attached to the dorsal wall of the stomach, their large ends are free and project upwards in the jelly reaching nearly to the summit of the umbrella. A similar formation is shown by Ranson (1936, pl. ii, fig. 22).

In a specimen kindly given me by Dr H. B. Moore from Bermuda, which was of the *rosea* form and had five marginal tentacles, these endodermal roots were quite small and had little or no free end portion projecting upwards in the jelly; in this they agreed with many previously published figures. As Ranson (1936) points out, the large tentacle roots were specifically mentioned by Eschscholtz (1829) in his original description of *citrea* and he gives a figure of them. Eschscholtz also mentions and figures the smaller root in his description of *rosea*.

While admitting that the upward projection of the tentacle roots may be due to lateral contraction of the umbrella, I think that the size of the root appears to be a good character. This should be examined in future to see whether the roots are always definitely large or small, or whether intermediate sizes occur, for this may be a character for deciding whether there are in reality more than one species.



Text-fig. 308. *Aegina citrea*. Above, living specimen *c.* 7 mm. in diameter, Bahamas, 20. vi. 03; below, specimen *c.* 8·5 mm. in diameter, Bahamas, 21. iv. 07. (After Mayer, 1910, pl. lii, fig. 5, and pl. liv, fig. 11, as *A. rhodina*.)

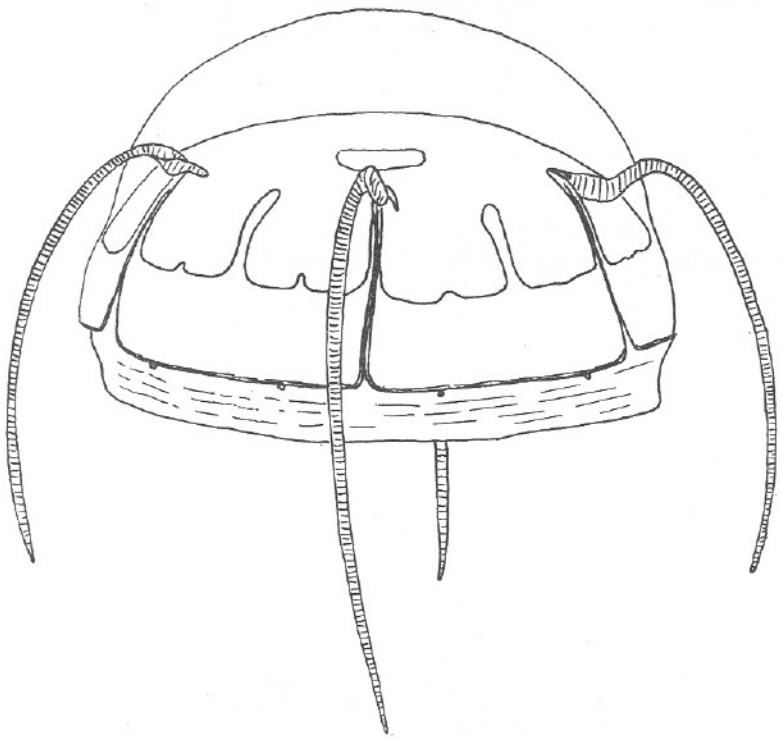
Eschscholtz's figure of *rosea* (1829, pl. x, fig. 3*b*) also shows a very wide peronium. In my Bermuda specimen the peronium is very much wider, and the canals of the peripheral canal system are also wider than in the specimen from the west of Ireland. The umbrella is also very much flatter and the wide appearance of the peronium may be due to lateral expansion.

The medusa is apparently liable to certain meristic variations in the numbers of marginal tentacles and stomach pouches. Specimens with three, five, or even six, marginal tentacles have frequently been recorded, five being the more usual variant. The numbers of stomach pouches vary in agreement with the numbers of marginal tentacles. This meristic variation appears to be more usual in specimens of the *rosea* form.

The number of marginal sensory clubs (Text-fig. 310) is uncertain. Many observers have only recorded a few, namely two or three in each quadrant. Vanhöffen (1908) has, however, recorded as many as about 100 in all. He also mentions about twenty in one quadrant in a specimen of the *rosea* form and sixteen in one of the *citrea* form. Bigelow (1938) also states that the spacing of these organs or their basal parts in Bermuda specimens was consistent with Vanhöffen's results. It seems likely that they are easily broken off in preserved material.

Like most Narcomedusae the marginal tentacles in preserved specimens bend at sharp angles and show no signs of curling. According to Uchida (1928) the abaxial surface of the marginal tentacle is thickly armed with nematocysts.

The *rosea* form of medusa seems to grow to a larger size, up to 50 mm. in diameter, than the *citrea* form which does not often exceed 20 mm.



Text-fig. 309. *Aegina citrea*. Preserved specimen. (After Maas, 1905*b*, pl. xi, fig. 72.)



Text-fig. 310. *Aegina citrea*. Marginal sensory club. (After Mayer, 1910, pl. liv, fig. 11′, as *A. rhodina*.)

The medusa shows certain colour variations. The stomach, stomach pouches, and marginal tentacles may be yellow or brownish yellow (*citrea* form) or pink (*rosea* form). In addition Vanhöffen (1908) described a form with brown gastric pouches and whitish marginal tentacles (as *A. brunnea*) and a whitish form with flesh-coloured marginal tentacles (as *A. lactea*).

An apparently abnormal specimen which had only four stomach pouches was described by Bigelow (1909*a*, as *A. alternans*). Subsequently (Bigelow, 1938) he recorded two other specimens from Bermuda which showed abnormalities. In one there were again only four pouches. In the other, which had six marginal tentacles, there were two normal sectors each with two pouches; three sectors with a single pouch; and in the remaining sector the interradial septum dividing the pouches was incomplete distally.

Seasonal occurrence

Being a deep-sea oceanic species it is most likely that *Aegina citrea* may be found at any time of year. The specimen here recorded from 50 miles north-west of Eagle Island was taken in August; and that from south-west of the Fastnet in January.

Habits

Little is known of the habits of *Aegina citrea* beyond that it is a deep-sea species; the specimen collected by R.R.S. *William Scoresby* was in a vertical closing net haul from 1100 to 900 m. The smallest stages tend to be nearer the surface than the large medusae (Thiel, 1936).

While in preserved specimens the marginal tentacles show no signs of curling, a drawing of a living specimen by Haeckel (1879) shows the marginal tentacles in sinuous curves. Eschscholtz (1829) says that the marginal tentacles move much faster than is usual in other jelly-fish.

Historical

Aegina citrea was first described and figured by Eschscholtz (1829) from a single specimen from the North Pacific. At the same time he described and figured his *A. rosea* which came from the same locality. As has already been stated, a number of other species were afterwards described, but recent opinion tends to the view that they may be regarded provisionally as a single species (see, e.g., Bigelow, 1938). The possibility that specific distinctions may yet be found, however, should be borne in mind.

Genus **Aeginura** Haeckel, 1879

Aeginidae with sixteen stomach pouches, which have slight secondary divisions; peripheral canal system degenerate or absent; with eight primary marginal tentacles; with secondary tentacles on umbrella margin itself; without otoporpae.

There is one British species of the genus, *Aeginura grimaldii* Maas.

Aeginura grimaldii Maas

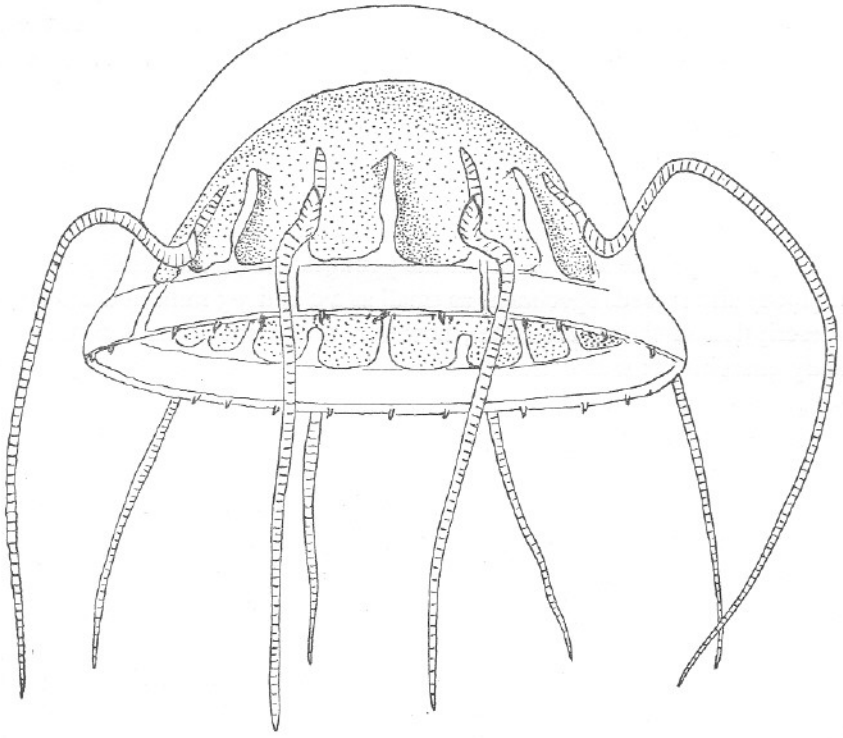
Text-figs. 311, 312

Aeginura grimaldii Maas, 1904*a*, *Rés. Camp. Sci. Monaco*, Fasc. XXVIII, p. 38, pl. iii, figs. 19–28.
Bigelow, 1909*a*, *Mem. Mus. Comp. Zoöl. Harvard*, vol. XXXVII, p. 80, pl. ix, fig. 4.
Mayer, 1910, *Medusae of the World*, vol. II, p. 470, figs. 307–9.
Bigelow, 1913, *Proc. U.S. Nat. Mus.* vol. XLIV, no. 1946, p. 61.
Kramp, 1913*b*, *Vidensk. Medd. Dansk. naturh. Foren. Kbh.* Bd. LXV, p. 276.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 533, fig. 37.
Ranson, 1936, *Rés. Camp. Sci. Monaco*, Fasc. XCII, p. 211.
Bigelow, 1938, *Zoologica, New York*, vol. XXIII, pt. II, p. 132.
Aeginura weberi Maas, 1905*a*, *Siboga-Expedit.* Monogr. X, p. 77, pl. xi, fig. 73; pl. xii, fig. 76; pl. xiv, figs. 90–9.
Cunoctona grimaldii var. *munda* Vanhöffen, 1908, *Wiss. Ergebn. 'Valdivia'*, Bd. XIX (1925), Heft 2, p. 53, pl. viii, fig. 6.
Cunoctona guinensis Vanhöffen, 1908, ibid. p. 53, pl. ix, fig. 29.
Cunoctona obscura Vanhöffen, 1908, ibid. p. 53, pl. viii, fig. 7; pl. ix, figs. 25–8, 30.
?*Aeginura incisa* Mayer, 1910, *Medusae of the World*, vol. II, p. 472, pl. lv, fig. 3 (?young medusa).
Aeginura lanzerotae, Thiel, 1936, *Zool. Jahrb. Jena*, Abt. Syst., Okol. Geogr. Tiere, Bd. LXIX, Heft 1, p. 86, fig. 18.

Specific Characters. Here regarded as the only species of the genus.

Description of Adult

Umbrella hemispherical; jelly thick in upper half of umbrella, thin at sides of lower half and margin; with eight peronia. Velum well developed. Stomach large, circular and flattened dorsally, with sixteen rectangular marginal pouches, with indications of further subdivision by slight median clefts to thirty-two; lower portion of stomach conical. Mouth simple and circular, not extending beyond umbrella margin. Peripheral canal system absent or degenerate. Gonads on walls of stomach pouches; covering whole surface in males; forming irregularly distributed swellings in females. Eight large solid marginal tentacles, issuing from umbrella at upper ends of peronia



Text-fig. 311. *Aeginura grimaldii*. × *c.* 2·5. (After Maas, 1905*b*, pl. xi, fig. 73.)

in deep exumbrellar furrows at level of top of stomach; with root-like endodermal continuations in substance of apical jelly; length of each marginal tentacle up to two or three times diameter of umbrella. Three to five small secondary tentacles on margin of umbrella in each octant. One or two marginal sensory clubs between adjacent secondary marginal tentacles. No otoporpae. Umbrella up to 45 mm. in diameter. Colour of stomach and stomach pouches, chocolate, reddish brown to purplish black, mostly confined to endoderm; marginal tentacles light purple or colourless; jelly of umbrella translucent, marginal region of subumbrella white to pale reddish.

Distribution

Aeginura grimaldii is a deep-sea oceanic species which has not yet been actually recorded from the vicinity of the British Isles.* Its distribution, however, is such that it might be expected in

* I have now seen one specimen in a collection made by R.R.S. *William Scoresby* about 90 miles south-west of the Fastnet in a vertical closing net haul from 900 to 700 m. (Stat. W.S. 963, 19. i. 50).

deep water off the west and north coasts, having been recorded far out in the Atlantic north-west of Ireland and west of Scotland (Kramp, 1920*b*, 1948*a*).

It has been found in all three oceans and as far north as 64° N. in the Davis Strait, but not in Arctic waters.

Developmental Stages and Structural Details

The complete life history of *Aeginura grimaldii* is not known. Thiel (1936) records specimens as small as 1 mm. in diameter, but gives no details of their structure. He states, however, that in a specimen 4·5–5·0 mm. in diameter the eight marginal tentacles and eight divided stomach pouches were clearly recognizable. The numbers of marginal sensory clubs in the octants were 4, 5, 4, 4, 3, 3, 4, 4, i.e. thirty-one in all. He does not mention the presence of secondary marginal tentacles.

A very similar specimen 5 mm. in diameter was described by Mayer (1910) as *A. incisa*, from the surface waters at Tortugas. This resembled the specimen described by Thiel and had three marginal sensory clubs in each octant. But it also had otoporpae, which are always absent in *A. grimaldii*. It is, therefore, possible that Mayer's medusa was another species, although it may also be possible that otoporpae are present in the youngest stages and disappear later.

Vanhöffen (1908) also records specimens as small as 2·0 and 3·5 mm. in diameter, but he gives no detailed description of them. He states, however, that a specimen 8 mm. in diameter had three secondary marginal tentacles in an octant. It is not clear, therefore, at what size the secondary marginal tentacles first appear.

There is little change in the general appearance of the medusa as it grows. The umbrella is, according to Maas (1904*a*), more or less flat in the living medusa. The margin of the umbrella is only very slightly incised perradially, the edges of the incisions being connected by the velum.

The eight perradial incisions dividing the stomach pouches are slightly less deep than the interradial incisions. Bigelow (1913) records a specimen in which the interradial incisions were twice as deep as the perradial, suggesting that the stomach pouches are primarily perradial as in *Cunina*.

The sixteen gastric pouches show slight median divisions on their distal margins.

The peripheral canal system is apparently absent or degenerate. Vanhöffen (1908) could find none in sections across the peronial region or of the margin of the umbrella. Maas (1905*b*), on the other hand, found endodermal tissue in his sections in the regions where the peripheral canal system should be. But this tissue was in the form of a lamella with spaces in it, and without any definite epithelial layer surrounding them to form a true canal. Mayer (1910) suggested that this rudimentary canal system might disappear as the medusa grows.

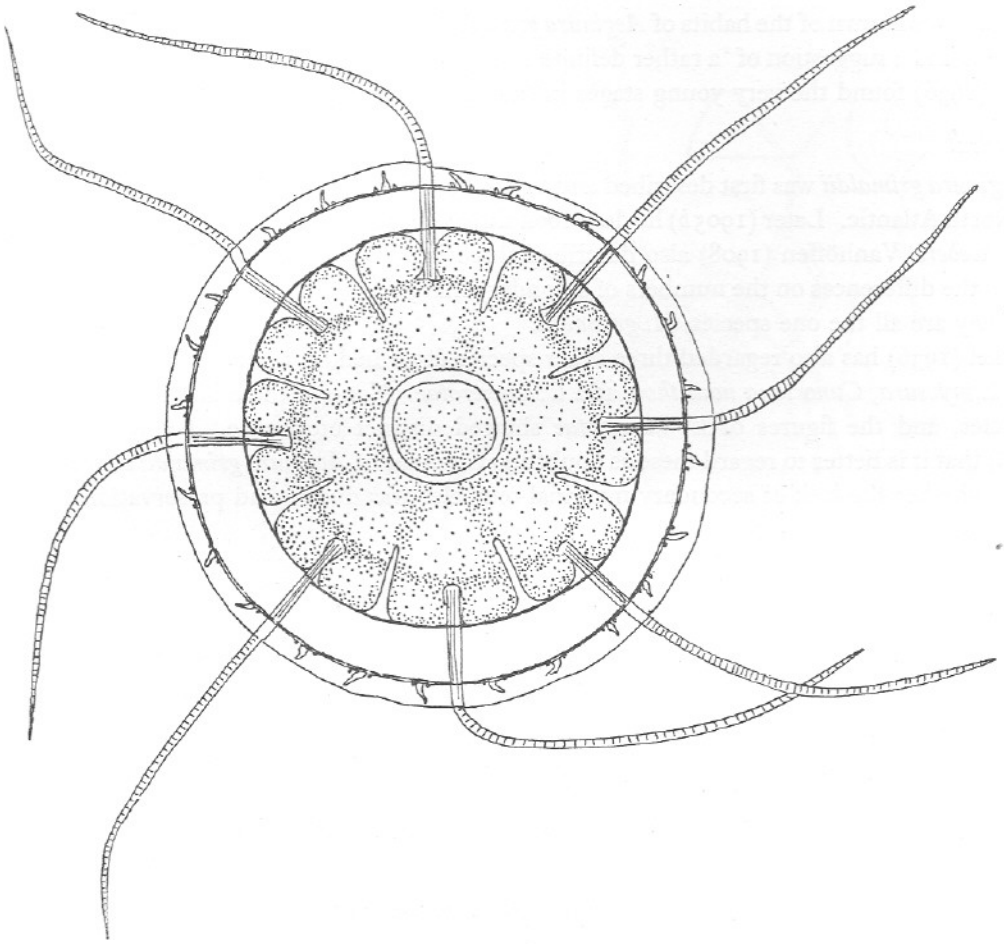
There appears to be sexual dimorphism in the form of the gonads. The whole oral surface of each pouch is uniformly covered by gonadial tissue in the male; but in the female the swellings produced by the very large eggs are irregularly distributed. The eggs are opaque white and show as such when the overlying tissue is torn, or the pigment destroyed (Bigelow, 1913).

The number of secondary marginal tentacles is variable; examples given by Bigelow (1913) are as folows:

Diameter of umbrella (mm.)	No. of sectors	No. of secondary marginal tentacles
15	8	2, 3, 3
22	8	3, 3, 4, 3, 3, 5
27	8	3, 3, 3
32	7	4, 4, 3, 4, 5, 5, 5

There is thus an indication of an irregular increase in number of secondary marginal tentacles with the size of the medusa.

The secondary marginal tentacles are solid, their axes being connected with the endoderm of the umbrella margin. They have a single row of endoderm cells distally, and on the adaxial side there is an ectodermal thickening.



Text-fig. 312. *Aeginura grimaldii*. Preserved specimen, × *c.* 2·2. (After Maas, 1905*b*, pl. xii, fig. 76.)

The marginal sensory clubs are probably easily broken off. One or two are to be found between adjacent secondary marginal tentacles and it is probable that typically there should be two in each interspace, i.e. one on each side of each secondary marginal tentacle.

The pigmentation is very characteristic and is confined mainly to the endoderm. After preservation the stomach and stomach pouches appear almost black. It is a typical deep-sea coloration.

Bigelow (1913) records one specimen with seven instead of the usual eight sectors, and Ranson (1936) records a specimen with only five tentacles; it was 8 mm. in diameter and had eggs.

Seasonal occurrence

Being a deep-sea oceanic species it is most likely that *Aeginura grimaldii* may be found at any time of year. Bigelow (1938) for instance found it off Bermuda in those months in which collections were made, viz. May to September.

Habits

Nothing is known of the habits of *Aeginura grimaldii* except that it is a deep-sea species. Bigelow (1938) found a suggestion of 'a rather definite concentration between, say, 1000 and 1600 metres'. Thiel (1936) found the very young stages in the upper water layers.

Historical

Aeginura grimaldii was first described and figured by Maas (1904*a*) from a single specimen from the North Atlantic. Later (1905*b*) he described three other specimens from the Malay Archipelago as *A. weberi*. Vanhöffen (1908) also described three more species from the Valdivia collections, basing the differences on the numbers of secondary marginal tentacles. It is now generally agreed that they are all the one species, *A. grimaldii*.

Thiel (1936) has also regarded three other species described by Haeckel (1879) as this species, viz. *A. myosura*, *Cunoctona nausithoe*, and *C. lanzerotae*. None of these had secondary marginal tentacles, and the figures of *C. lanzerotae* showed distinct otoporpae. I agree with Bigelow (1938) that it is better to regard these as doubtful synonyms of *Aeginura grimaldii* as we shall never know whether the lack of secondary marginal tentacles was due to bad preservation.

Family SOLMARIDAE

Narcomedusae without stomach pouches; with or without peripheral canal system; with numerous marginal tentacles leaving umbrella opposite periphery of stomach; with or without otoporpae.

The distinctive character of the family Solmaridae is the absence of stomach pouches, the periphery of the stomach being circular and unbroken.

The family is represented in British waters by one genus, *Solmaris* Haeckel.

Genus **Solmaris** Haeckel, 1879

Solmaridae without otoporpae; without peripheral canal system.

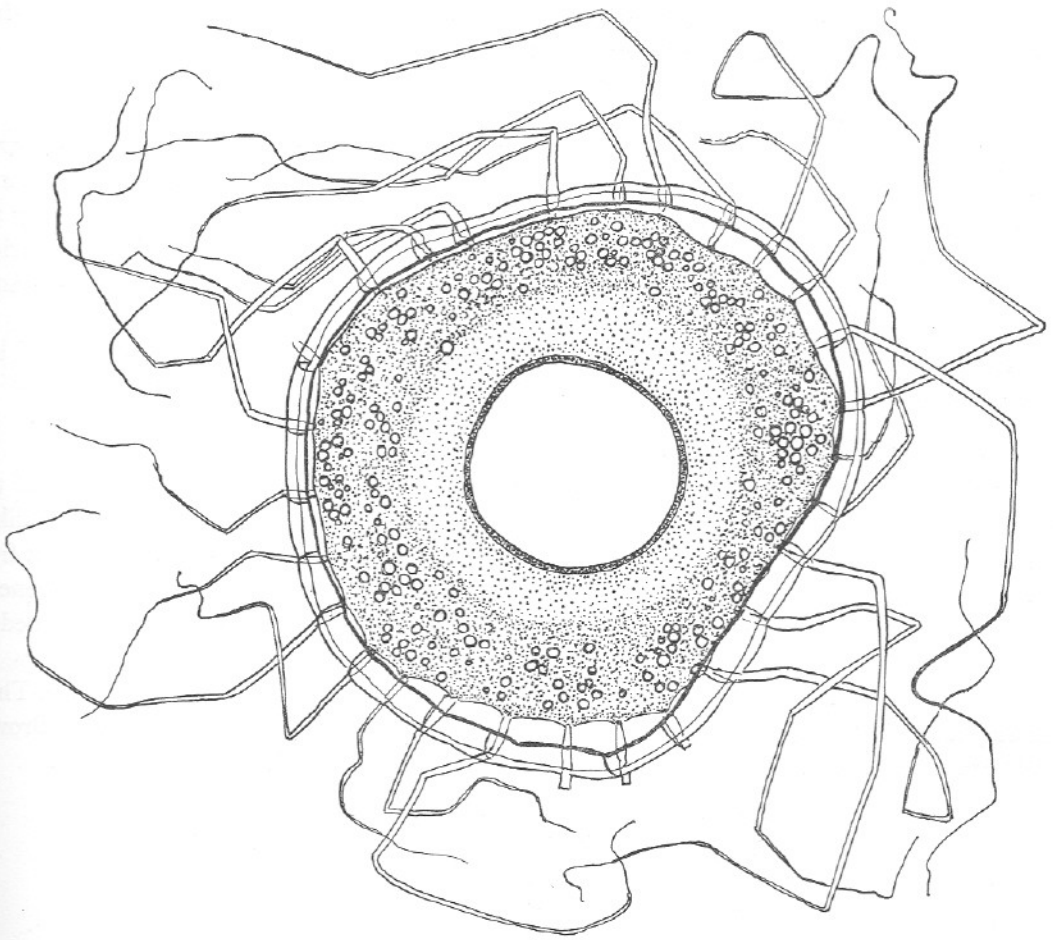
There is one British species of the genus, *Solmaris corona* (Keferstein & Ehlers).

Solmaris corona (Keferstein & Ehlers)

Plate XXVIII, fig. 2; Text-figs. 313, 314

Aegineta corona Keferstein & Ehlers, 1861, *Zool. Beiträge in Neapel u. Messina*, p. 94, pl. xiv, figs. 7–9.
Solmaris corona, Haeckel, 1879, *System der Medusen*, p. 358.
Browne, 1900, *Proc. Roy. Irish Acad.* ser. 3, vol. v, no. 5, p. 732.
Browne, 1903, *Bergens Mus. Aarb.* no. 4, p. 30.
Mayer, 1910, *Medusae of the World*, vol. II, p. 437, text-figs. 288, 289.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 535, fig. 39.
Thiel, 1936, *Zool. Jahrb.* Abt. Syst. Bd. LXIX, Heft 1, p. 60, fig. 12*b*.

?*Solmaris coronantha* Haeckel, 1879, *System der Medusen*, p. 359, pl. xx, figs. 7–10 (as *Aegineta*).
?*Polycolpa forskalii* Haeckel, 1879, ibid. p. 328.
Haeckel, 1882, *Sci. Rep. Challenger*, Zool. vol. IV, p. 31, pl. X, figs. 1–8.
?*Solmaris multilobata* Maas, 1893, *Ergebn. Plankton Expedit. Humboldt-Stift.* Bd. II, K.c., p. 45, pl. iv, figs. 7–13.
Vanhöffen, 1908, *Wiss. Ergebn. 'Valdivia'*, Bd. XIX (1925), Heft 2, p. 61.
Mayer, 1910, *Medusae of the World*, vol. II, p. 438, text-fig. 290.
Broch, 1929, *Nordisches Plankton*, Lief. 21, XII, p. 536, fig. 40.
Solmaris sp. Browne, 1896*a*, *Proc. Zool. Soc. London*, p. 496.
?*Solmaris forskalii*, Mayer, 1910, *Medusae of the World*, vol. II, p. 437.



Text-fig. 313. *Solmaris corona*. Preserved specimen *c.* 6·5 mm. in diameter, Valencia, 1897. (E. T. Browne collection.)

Specific Characters

Umbrella with up to thirty-five rectangular marginal lappets, each up to twice as long as broad; up to thirty-five marginal tentacles; one to three, rarely four, marginal sense organs on each marginal lappet each situated on large cushion with long bristles.

Description of Adult

Upper portion of umbrella with thick flat lens-shaped jelly; lower marginal portion of umbrella thin, with up to thirty-five (or more?) rectangular marginal lappets, each up to twice as long as

broad. No otoporpae. Velum well developed. Stomach circular, without marginal pouches, covering whole lower surface of upper half of umbrella; simple circular mouth opening. No peripheral canal system. Gonad forming broad ring on outer part of subumbrellar stomach wall, one- to two-thirds of stomach radius in width. Up to thirty-five (or more?) stiff marginal tentacles, with solid endodermal axes, attached to exumbrella at upper ends of peronia separating marginal lobes, one and a half to twice diameter of umbrella in length. One to three, rarely four, marginal sense organs on each marginal lappet, each organ situated on large cushion with long bristles. Diameter of umbrella up to 15 mm. (or more?). Colour of marginal tentacles red or yellow; gonads rose-coloured; concretions of sense organs yellowish or rose; whole medusa usually colourless except for sense organ concretions.

Distribution

Round the British Isles *Solmaris corona* has only been recorded from Plymouth (Browne, 1896*a*, two specimens only) and Valencia (Browne, 1900; M. & C. Delap, 1906). It is a purely oceanic species evidently carried northwards in the Atlantic drift, having been recorded in the Faeroe-Shetland Channel (Fowler, 1898); off Norway (Browne, 1903); perhaps off the Hebrides if *S. multilobata* Maas (1893) is the same species; and in deep water west of Scotland (Kramp, 1947).

Elsewhere it has been recorded from the Canary Isles (Haeckel, 1879), the Mediterranean, and possibly the Indian and Pacific Oceans and Red Sea (as *Polycolpa forskalii* Haeckel).

Developmental Stages and Structural Details

Solmaris corona is a Narcomedusa with direct development. The early development of this species has not been described. It probably, however, resembles that of *S. flavescens* (Kölliker) which has been described by Maas (1902). In that species the marginal tentacles grow out from the margin of the planula and the lower half of the umbrella develops as an outgrowth beneath and between the bases of the marginal tentacles. 'The mouth breaks through and the medusa is thus formed from the actinula' (Mayer, 1910, p. 435).

During the course of its development *S. corona* changes very little in general appearance. There is merely an increase in the numbers of marginal lappets, tentacles, and sense organs. Browne (1900) examined a large number of specimens from Valencia with the following results:

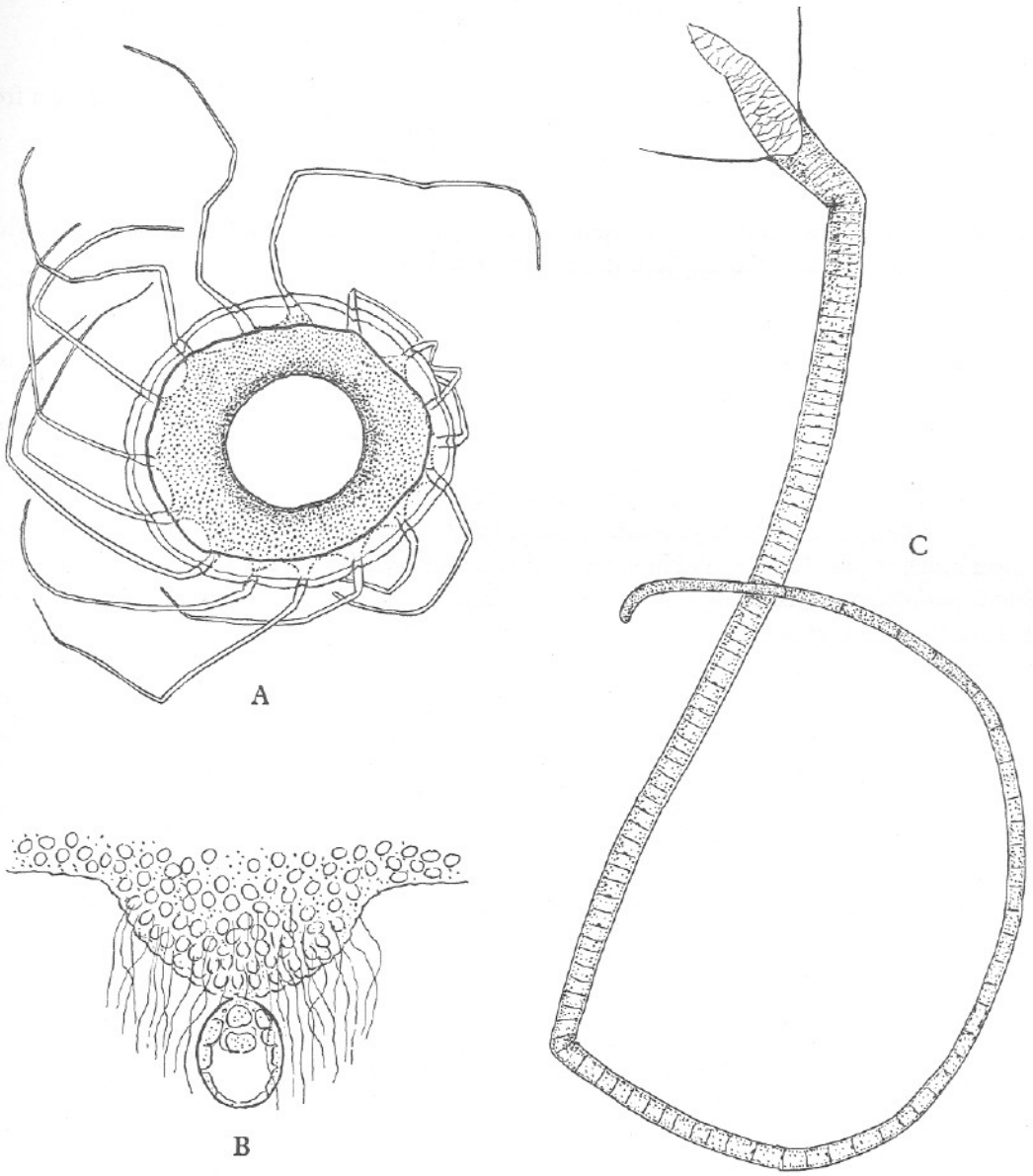
Diameter of umbrella (mm.)	No. of marginal tentacles and lappets	No. of sense organs on each marginal lappet
2–3	12–16	1
4	15–18	—
5	17–29	1–2
6	21–29	1–3
7	22–30	—
8	30	—
10	36	—
12	25–35	—

The marginal lappets of the umbrella increase in number by longitudinal division, so that they are not all of the same shape, some being much broader than others.

In the specimens that Browne examined the sexual cells were just visible in specimens 3 mm. in diameter, and nearly ripe in specimens of about 6 mm. in diameter.

While the maximum number of marginal tentacles found by Browne was thirty-five it is possible that more may be developed. Maas (1893) described a species, *S. multilobata*, which had up to

sixty-four or more; Vanhöffen (1908) describes immature specimens 5–10 mm. in diameter with thirty-four to forty-five marginal tentacles. It seems possible that Maas's medusa may be



Text-fig. 314. *Solmaris corona*. A, small preserved specimen *c.* 2·2 mm. in diameter; B, marginal sensory club; C, marginal tentacle. Valencia, 1897. (E. T. Browne collection.)

a variety of *S. corona*. In preserved specimens the marginal tentacles bend at sharp angles as in other Narcomedusae (Text-fig. 314C).

The sensory clubs (Text-fig. 314B) are borne on large sensory cushions which also bear long bristles according to Mayer (1910), whereas in *S. flavescens* (Kölliker) the bristles are confined to the sensory club itself. Thiel (1936) has suggested that the genus *Solmaris* may consist of only

two variable species which can be distinguished by this difference in the sense organs. Specimens must be examined in future from this point of view. It is to be noted that Haeckel (1879) gave drawings of sensory clubs in *S. coronantha* rather similar to those of *S. flavescens*.

Seasonal occurrence

Solmaris corona has been recorded once off Plymouth in September, and from Valencia from July to November, being abundant in July, August and September.

Habits

Nothing is known of the habits of *Solmaris corona*, except that it is an oceanic medusa which appears to be confined to the upper water layers (e.g. Fowler, 1898).

Historical

Solmaris corona was first described by Keferstein & Ehlers (1861) from Naples. It was next recorded by Browne (1896*a*, 1900) from Valencia.

The synonymy of the species is not yet certain. *S. coronantha* Haeckel (1879) has been considered as the same species. It is, however, noteworthy that Haeckel's drawing of the sense organ (1879, pl. xx, fig. 9) agrees more with that of *S. flavescens*.

It is possible that *Polycolpa forskalii* Haeckel (1879, 1882) is the same species; it differs in having a broader gonadial ring and in having seven marginal sense organs on each marginal lappet. *Solmaris multilobata* Maas (1893) may also be the same species; it has, however, up to sixty-four and more marginal lappets and tentacles, and Vanhöffen (1908) described immature specimens 5–10 mm. in diameter already having thirty-four to forty-five marginal tentacles.

The genus has been reviewed by Thiel (1936), who suggests that there may be two variable species, *S. flavescens* (Kölliker) and *S. corona* (Keferstein & Ehlers). The possible distinguishing features are that in *S. flavescens* the bristles are confined only to the sensory club of the marginal sense organ, whereas in *S. corona* the sensory club rises from a cushion with a broad base which alone has bristles. The genus requires more detailed study.

According to Keferstein & Ehlers (1861) the medusa is known by the Neapolitan fishermen as *sole di mare*.

APPENDIX I

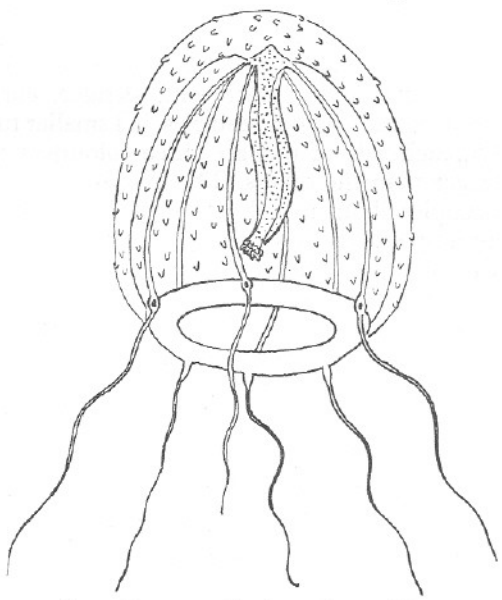
Doubtful species recorded from British waters

Sarsia nodosa Busch (1851, p. 17, pl. ii, figs. 6–8)

Text-fig. 315

'...wir haben ebenfalls an den Küsten von Cornwall eine *Sarsia* gefunden, in der die Zahl aller Organe je sechs betrug, und die ihrer ganzen Organisation nach unzweifelhaft diesem Genus angehört, aber doch genug Unterschiede von den bekannten Arten trägt, um als besondere Species betrachtet zu werden.

Die äussere Gestalt ist sehr ähnlich der der *S. prolifera*, nur ist die Glocke ein wenig mehr gewölbt, wodurch das Ansehen sich dem Kugeligen nähert. Die Grösse beider Arten ist ganz gleich, das Magenrohr wenn geschlossen, hat auch sehr viel Aehnlichkeit, dieselbe Beweglichkeit, dieselbe Länge, Form, dasselbe Hervorragen eines Knopfes über die Kuppel des inneren Schirmes, dieselbe Anordnung der Geschlechtstheile; hingegen statt vier Tentakeln, vier Bulbis, vier Wassergefassen, immer sechs. Die Arme sind bei dieser Art ebenfalls mit kleinen Haftorganen versehen, an denen ich aber keine nesselnden Fäden bemerken konnte; an den Rändern stehen diese kleinen Körner dichter, in der Mitte mehr zerstreut.



Text-fig. 315. *Sarsia nodosa*. (After Busch, 1851.)

Besonders auffallend ist die Struktur der Glocke, welche bei den anderen Arten dieser Gattung vollständig glatt ist, hier hingegen mit Ausnahme kleiner freibleibender Zwischenräume, auf der ganzen Oberfläche mit eigenthümlichen Organen besetzt ist. Diese bestehen aus kleinen Fortsätzen, welche mit einer breiteren Basis aufsitzen und mit einer freien Spitze endigen. Wenn das Thier sich lebhaft bewegt, so kann man sie leicht übersehen, da sie farblos sind und fast dieselbe Durchsichtigkeit haben, wie die Substanz der ganzen Meduse; erst wenn es stille liegt, bemerkt man besonders deutlich an den freien Seitenrändern der Glocke diese kleinen Knöpfchen. An diesen Stellen kann man sich auch am Besten überzeugen, dass sie über das Niveau der anderen Substanz hervorragen, was sich an denjenigen, welche in der Mitte der Glocke liegen, schwerer ermitteln lässt.

Am Eingange des Magenrohres ist ebenfalls eine Verschiedenheit von den anderen bisher betrachteten Arten. Bei den übrigen Sarsien war die Mundöffnung rundlich, und die Haftscheiben waren so angeordnet, dass, wenn sich die Membran auseinanderzog, hier und da ein solches Scheibchen stand. Bei unserer *nodosa* sind die Ränder der Mundöffnung zwar auch noch cirkelartig gebogen, an vier Stellen aber ist eine Unterbrechung des Laufes der Curve, und an diesen stehen die eigenthümlichen Haftorgane, wie auf einem Distelkopf, zusammengedrängt, so dass der obere Theil des Magenrohres bei geöffnetem Munde sich ohnegefähr mit einem Morgensterne vergleichen lässt, an dem die Zinken auf vier Punkten gruppirt wären, während die dazwischen liegenden Flächen frei blieben. Die Haftorgane haben aber hier gar nicht die scheibenartige Gestalt, wie in den anderen, sondern sehen wie einfache Stacheln aus, sie unter-

scheiden sich überhaupt nur durch die Grösse und etwas dunklere Farbe von den kleinen Organen an der äusseren Haut der Meduse; die Form und das strukturlose Verhalten stimmen ganz überein.

Von dieser Medusenspecies kamen fünf Exemplare zur Beobachtung, welche alle dieselben Charaktere darboten, daher kann unmöglich das Vorhandensein von sechs Tentakeln ein rein Zufälliges sein, und wir sind genöthigt die Vierzahl in der Anordnung der Organe als Eigenthümlichkeit der *Sarsia* fallen zu lassen. Es bleiben uns also für diese Gattung nur noch die wenigen aber sehr charakterischen Merkmale: dass der Magen in einem ausdehnbaren, cylindrischen, rüsselförmigen Stiel liegt, und eine einfache Oeffnung hat; dass ferner die Hoden oder Eierstöcke entweder um den ganzen oder nur um einen Theil dieses Stieles rings herum liegen.'

Placed by Hartlaub (1907, p. 68) in the genus *Plotocnide* Wagner.

Modeeria formosa Forbes (1848, p. 70, pl. vii, fig. 1)

Text-fig. 316

'The umbrella is globular, or slightly elliptical, smooth, and transparent. Its inner margin is bordered by a membranous veil. On the outer edge are four conspicuous tubercles, each with two crimson lateral pads, and an ocellus of the same colour between them. From each springs a tentacle, long, translucent, slender, curling, pale, or colourless. Centrally on the margin, between each pair of tentacles, is a smaller tubercle ocellated with crimson, but bearing no tentacle. On each side of this are three colourless tubercles, all very small, but the central one slightly larger than the others. The marginal vessel is rather large and conspicuous. The sub-umbrella occupies about two-thirds of the umbrella, and is slightly conic in form. From its centre hangs an ample balloon-shaped peduncle, obsoletely four-lobed, the lobes of a brilliant crimson hue, the interspaces yellowish-white. I think it probable that the young are produced by gemmation from the crimson spaces. The peduncle terminates in a contracted neck, widening into a campanulate mouth, with four, rather short, lanceolate lips. This orifice is white, with four crimson lines. The peduncle sometimes contracts into a distinctly four-lobed form, and the lips are then more distinct than usual.

The *Modeeria formosa* was taken by Mr M'Andrew and myself off Mull, in the Hebrides, during the autumn of 1845.'

Thought by Haeckel (1879) to be perhaps a young *Turritopsis*, and by Mayer (1910) a young *Oceania armata* Kölliker. Hartlaub pointed out that it had well-developed gonads and thought it was a Pandeid (1914, p. 254).

Oceania pusilla Gosse (1853, p. 384, pl. xiii, figs. 11–14)

'A single specimen occurred in my dip-net the other day of a very tiny Medusa, which I cannot certainly identify, and which I hardly know how to apportion to its proper generic place. It has some resemblance to the lovely little *Modeeria formosa*, but the number and arrangement of its tentacles seem to point out the *Oceanidae* as its allies. I do not see the conspicuous muscular bands which would indicate it as a *Turris*, and I shall therefore call it an *Oceania*. I describe it in the following terms.

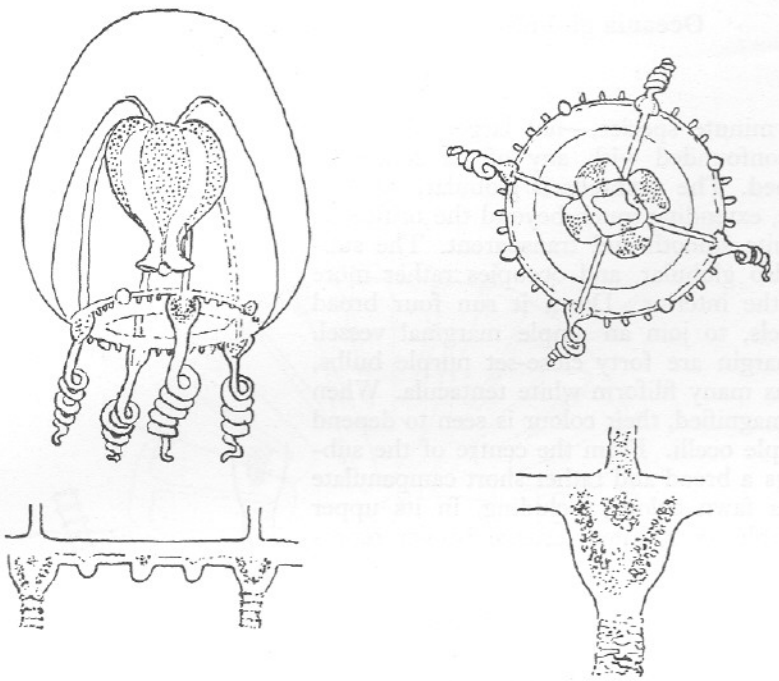
Oceania pusilla. Umbrella mitrate, constricted above the middle, with the summit rounded, one-twelfth of an inch in height. Margin with about twenty-one short tentacles, springing from globose, yellowish bulbs, each of which carries a red ocellus within. The tentacles are usually contracted, and bent upwards.

Subumbrella nearly as large as the umbrella; from its centre depends an ample membranous peduncle, somewhat vase-shaped, but seen vertically to be four lobed, each lobe pyriform in transverse section, the small ends meeting around a minute square central space. These lobes

are marked with delicate veins, as if the structure were irregularly cellular, and are tinged with yellow. The greater part of the peduncle is occupied by the ovaries, four in number, altogether somewhat pear-shaped, the larger end below, and filling the peduncle; they are of an opaque yellow, and each contains a nucleus of dark red. The whole descends into a flexible many-lobed lip, the extremities of which are puckered up, and slightly fimbriated.

This minute species was energetic in swimming, shooting several times its own length at each contraction.'

(? *Pochella polynema* or young *Turritopsis nutricula*—F.S.R.)

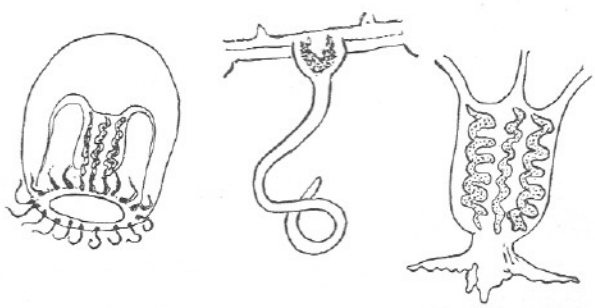


Text-fig. 316. *Modeeria formosa.* (After Forbes, 1848.)

Oceania ducalis Forbes & Goodsir (1851, p. 311, pl. x, fig. 2)

Text-fig. 317

'Umbrella campanulate, subglobose, round above, smooth, colourless, transparent. Subumbrella rather small in proportion, its orifice protected by a conspicuous veil; its margin edged with rose-colour, and bearing 16 ($3 \times 4 + 4$) pinkish tentacula, springing from bulbous bases, each of which is marked by a conspicuous crimson or purple crescentic ocellus: between each pair of tentacles is a minute tubercular process. Down the sides of the subumbrella run the four simple gastrovascular canals, tinged with red. From its centre depends the oblong, massive, reddish-tawny peduncle, in the upper part of which are obscurely seen the convoluted



Text-fig. 317. *Oceania ducalis.* (After Forbes & Goodsir, 1851.)

reproduction glands. The orifice of the peduncle is campanulate, and bordered by four slightly fimbriated lips. The height of the body is less than a quarter of an inch.

It was taken at Tobermory. We had previously met with the same species on the coast of Dorsetshire.'

Placed by Hartlaub (1914, p. 270) in the genus *Tiaranna*. (N.B. If so, its occurrence off the Dorset coast is curious—F.S.R.)

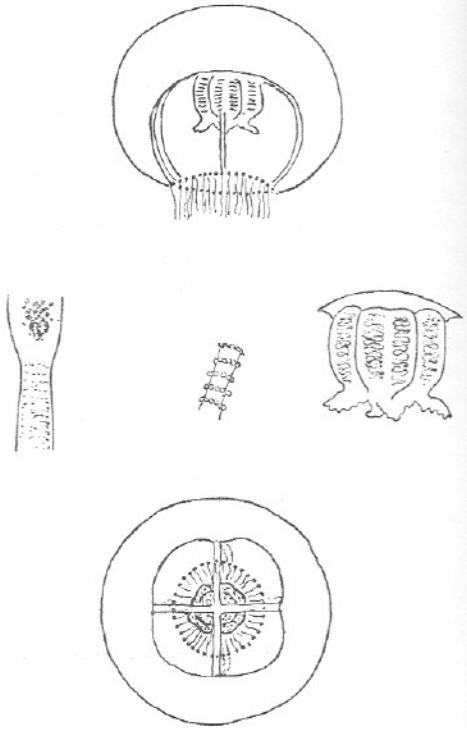
Oceania globulosa Forbes (1848, p. 29, pl. iii, fig. 3)

Text-fig. 318

'This is a minute species,—not larger than a pea,—but so very distinct, that it cannot possibly be confounded with any of its congeners as yet described. The umbrella is globular, inflated, and very wide, extending much beyond the orifice on every side, quite smooth and transparent. The sub-umbrella is also globular, and occupies rather more than half of the interior. Down it run four broad radiating vessels, to join an ample marginal vessel. Round the margin are forty close-set purple bulbs, the bases of as many filiform white tentacula. When the bulbs are magnified, their colour is seen to depend upon rich purple ocelli. From the centre of the sub-umbrella hangs a broad and rather short campanulate peduncle, of a fawn colour, including, in its upper part, four double, convoluted, orange brown reproductive glands. The orifice of the peduncle has four pale, tawny, fimbriated lips.

I procured two specimens of this singular *Oceania* in the Sound of Bressay, in 1835. It differs so much from the other British species of the genus, that I had some hesitation in placing it among the *Oceaniae*. In some respects it approaches more closely *Turris*; but the inconspicuous character of the muscular tissue of the sub-umbrella prevents our assigning it to that highly-developed group.'

Placed by Hartlaub (1914, p. 311) in the genus *Tiaranna*.



Text-fig. 318. *Oceania globulosa*. (After Forbes, 1848.)

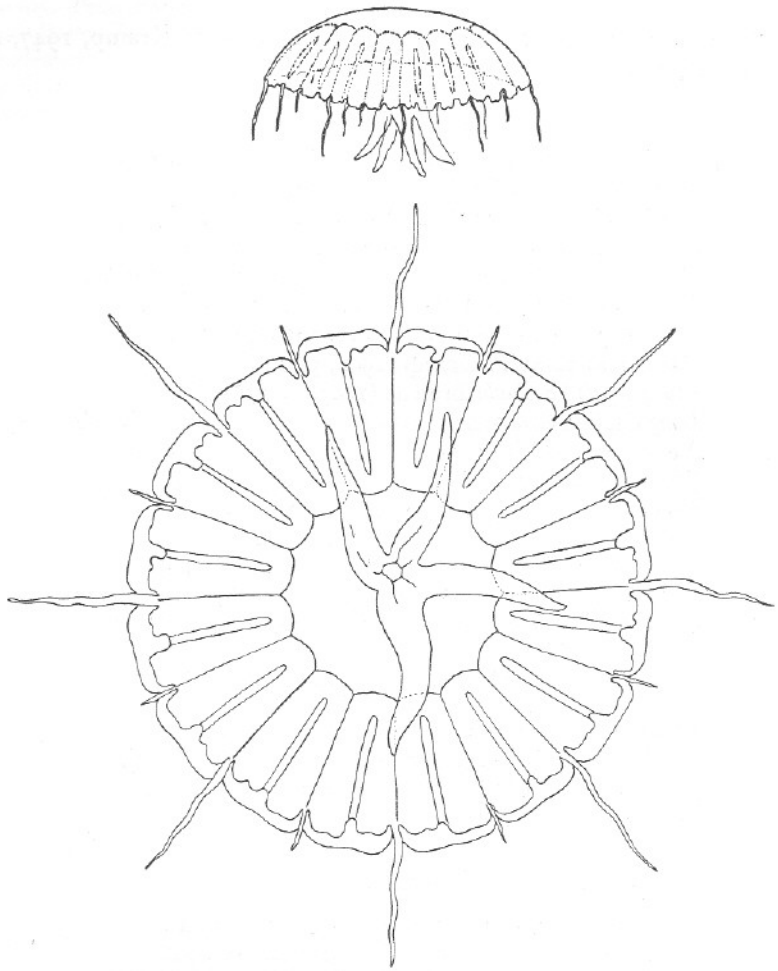
Polyxenia alderi Forbes (1848, p. 32, pl. iv, fig. 2, as *P. cyanostyla*)

Text-fig. 319

Forbes's description is based on a drawing by Mr Alder of a medusa observed on the coast of Devon in 1846.

'The umbrella is expanded, and rather depressed, smooth, and transparent. Its margin is deeply notched by sixteen indentations, out of which spring as many rosy tentacula, alternately longer and shorter. The sub-umbrella is divided into sixteen somewhat triangular spaces, which commence at about two-thirds of its height, and terminate near the margin. In the centre of each

of these spaces is a linear ovary. Each space terminates marginally in two truncated lobes, one on each side of the ovary, and always alternately longer or shorter. Each lobe, especially the shorter one, is slightly lobulated. From the centre of the sub-umbrella springs a short peduncle, very soon terminating in four linear-lanceolate, rather long, arm-like lips, white, tipped with rose colour. They project beneath and lower than the umbrella. The breadth of the disk is about two inches.'



Text-fig. 319. *Polyxenia alderi.* (After Forbes, 1848.)

It is not clear what medusa this can be: it is possibly a Narcomedusa, in which the stomach walls have been torn to give the impression of four lips. It may have been *Solmissus incisa*, although the disposition of tentacles and stomach pouches is wrong for this genus.

APPENDIX II

List of species occurring in the north-east Atlantic outside British waters

(For a summary distribution list of all north Atlantic species see Kramp, 1947, *Danish Ingolf-Expedit.* vol. v (14), pp. 54–7.)

Anthomedusae

Sarsia brachygaster Grönberg (Hartlaub, 1907, p. 11).
Sarsia barentsi Linko (Hartlaub, 1907, p. 14).
Sarsia princeps Haeckel (Kramp, 1926*a*, p. 2).
Plotocnide borealis Wagner (Kramp, 1942, p. 22).
Plotocnide incerta Linko (Kramp, 1942, not a *Plotocnide*).
Euphysa tentaculata (Linko) (Kramp, 1926*a*, p. 22).
Euphysa flammea (Linko) (Kramp, 1926*a*, p. 19).
Paragotoea bathybia Kramp (1942, p. 26).
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Sminthia arctica (Hartlaub) (Broch, 1929, p. 499).
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Crossota norvegica Vanhöffen (Kramp, 1947, p. 26).
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PLATE I

FIG. 1

Sarsia gemmifera. Specimen,
2·8 mm. high, with marginal tentacles and stomach contracted,
Plymouth, 20. vi. 36.

FIG. 2

Sarsia tubulosa.
3·5 mm. high, Plymouth, 3. iv. 36.

FIG. 3

Dipurena halterata.
Valencia, 27. vii. 96. (Del. E.T.B.)

FIG. 4

Sarsia gemmifera.
Specimen in Fig. 1 with marginal tentacles and stomach fully extended.

FIG. 5

Dipurena ophiogaster.
2·5 mm. high, Plymouth, 26. vi. 36.
(Grown in laboratory from specimen in Plate II, fig. 4.)

Plate I

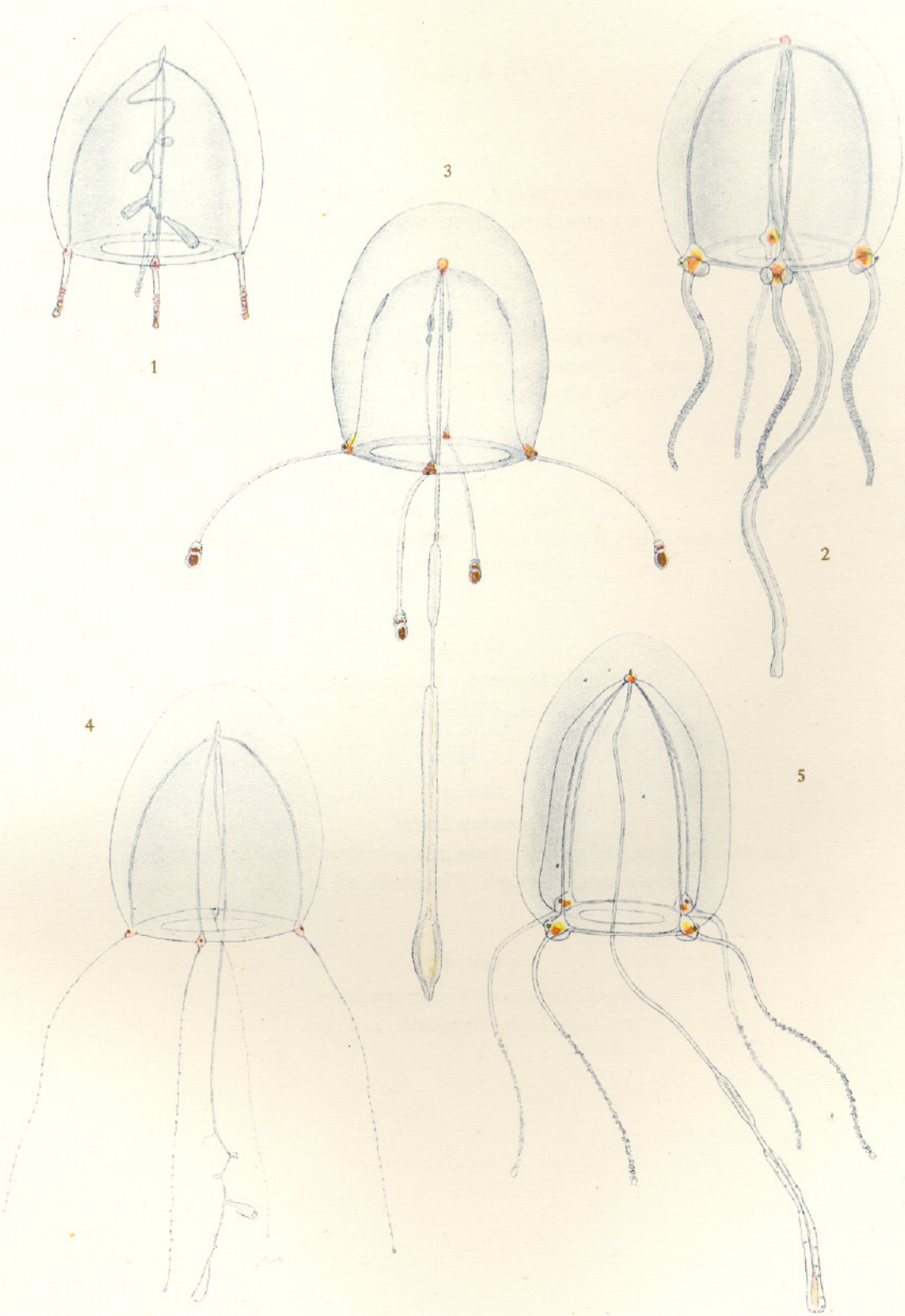

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PLATE II

FIG. 1

Sarsia prolifera. Young specimen,
1·1 mm. high, Plymouth, 17. x. 34.

FIG. 2

Dipurena halterata. Young specimen,
1·4 mm. in diameter, reared from the hydroid in the
Plymouth laboratory by W. J. Rees, 21. v. 38.

FIG. 3

Sarsia eximia. Male,
1·8 mm. high, five days after liberation from the hydroid,
Plymouth, 5. v. 36.

FIG. 4

Dipurena ophiogaster. Young specimen,
1·2 mm. high, Plymouth, 22. vi. 36.

FIG. 5

Syncoryne lovéni.
The medusa attached near the base of the hydranth on the far side is
c. 1·1 mm. in length; Plymouth, 28. iv. 36.

FIG. 6

Sarsia tubulosa. Young specimen.
1·9 mm. high, Plymouth, 4. v. 37.

Plate II

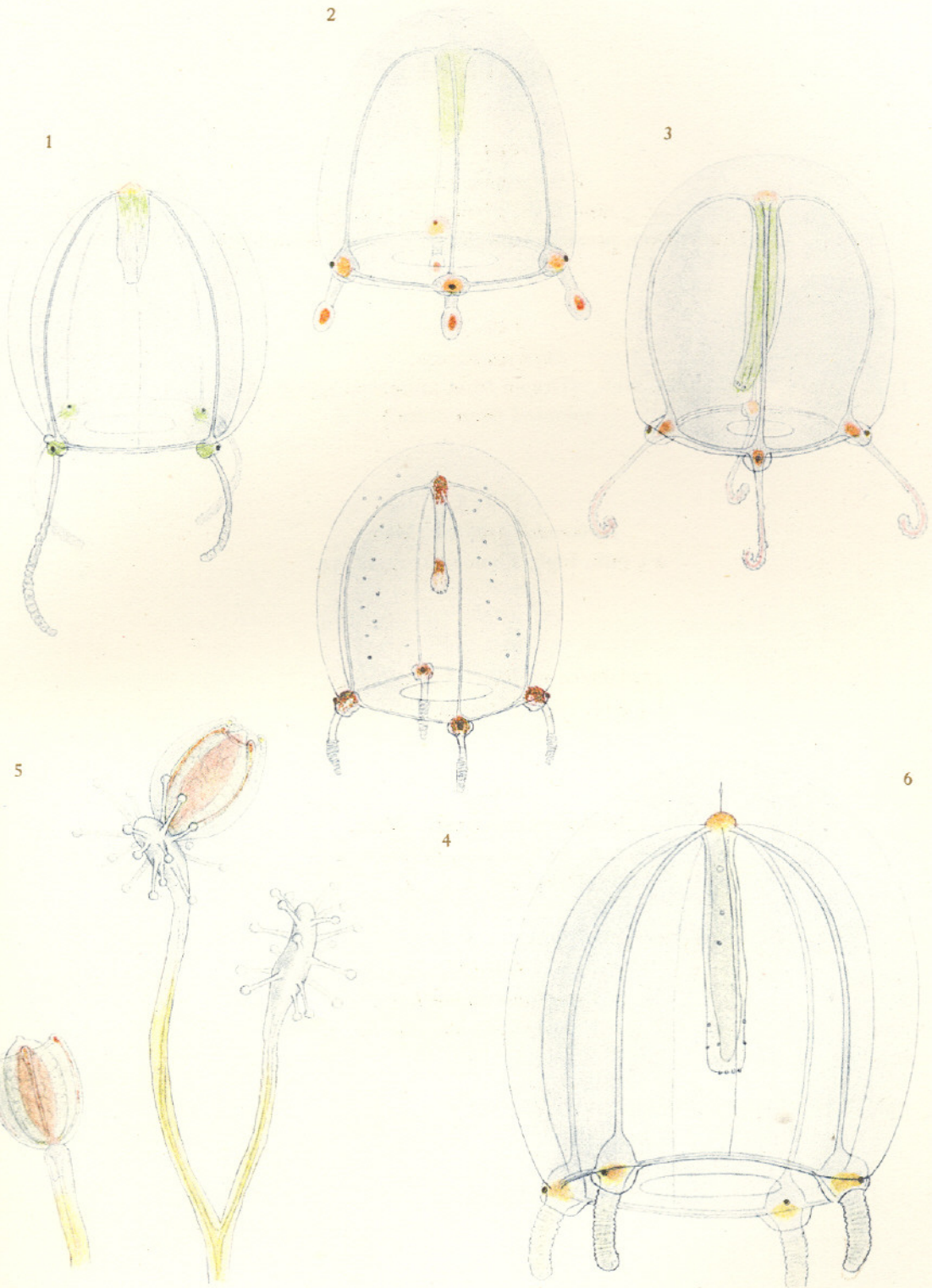

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PLATE III

FIG. 1

Steenstrupia nutans.
c. 5 mm. high, Plymouth, 3. v. 39.
(Drawn from preserved specimen, coloured from life.)

FIG. 2

Euphysa aurata.
c. 4 mm. high. (Drawn from preserved specimen, coloured from notes.)

FIG. 3

Hybocodon prolifer. Male,
2·5 mm. high, Plymouth, 12. iv. 34.

FIG. 4

Hybocodon prolifer. Asexual stage,
2·4 mm. high, Plymouth, 12. iv. 34.

FIG. 5

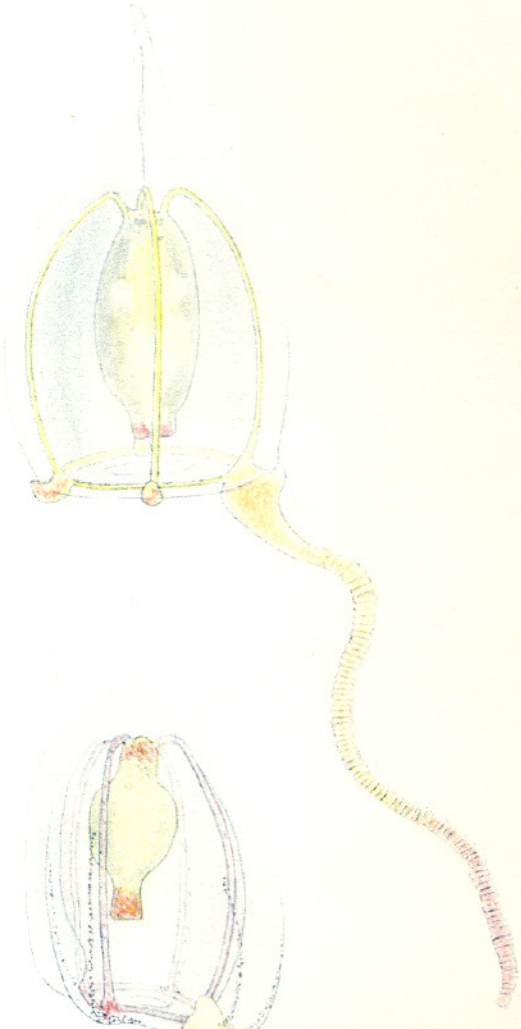
Ectopleura dumortieri. Male,
1·9 mm. in diameter, dorsal view,
Plymouth, 2. x. 34.

FIG. 6

Ectopleura dumortieri.
Lateral view of specimen in fig. 5.

Plate III

1



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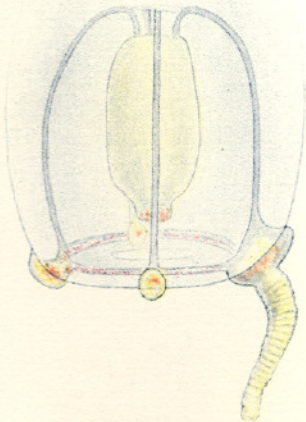

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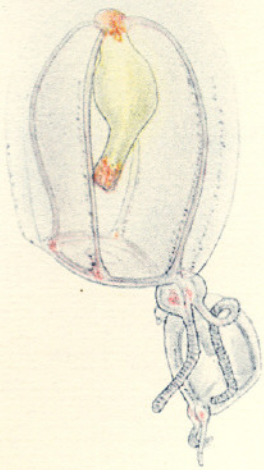

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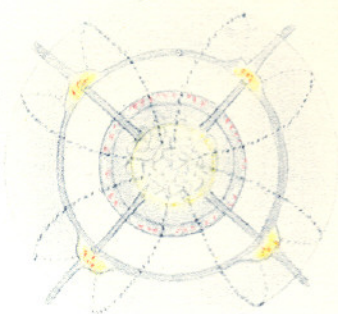

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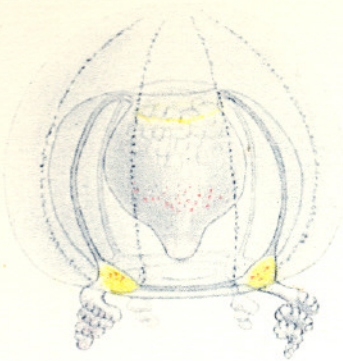

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PLATE IV

FIG. 1

Zanclea costata. Young specimen,
0·68 mm. high, liberated in the Plymouth laboratory on 1. iv. 36
from a hydroid collected near the Eddystone on 3. ii. 36.

FIG. 2

Zanclea costata.
3·1 mm. high, Plymouth, 19. v. 37.

FIG. 3

Zanclea costata. Specimen,
1·4 mm. high reared from the hydroid in the Plymouth laboratory
by W. J. Rees, 28. v. 36.

FIG. 4

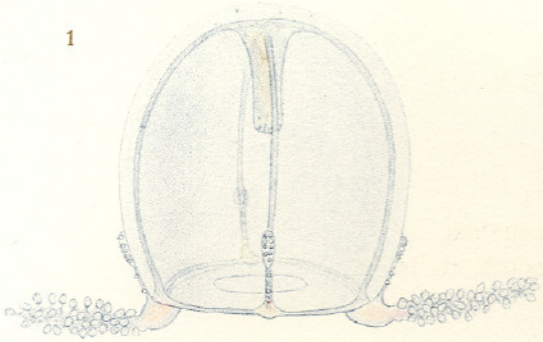
Eleutheria dichotoma.
Collected by P. R. Crimp from Drake's Island, Plymouth, 23. vi. 36.

FIG. 5

Eleutheria dichotoma.
As Fig. 4. Umbrella 0·28 mm. in diameter, with
marginal tentacles somewhat contracted.

FIG. 6

Eleutheria dichotoma.
As Fig. 4. Umbrella 0·57 mm. in diameter.



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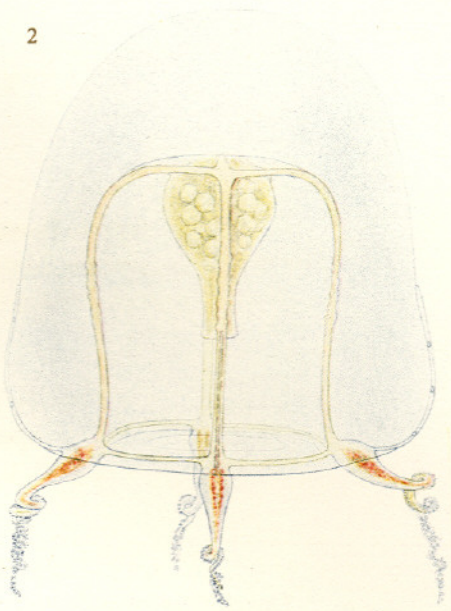

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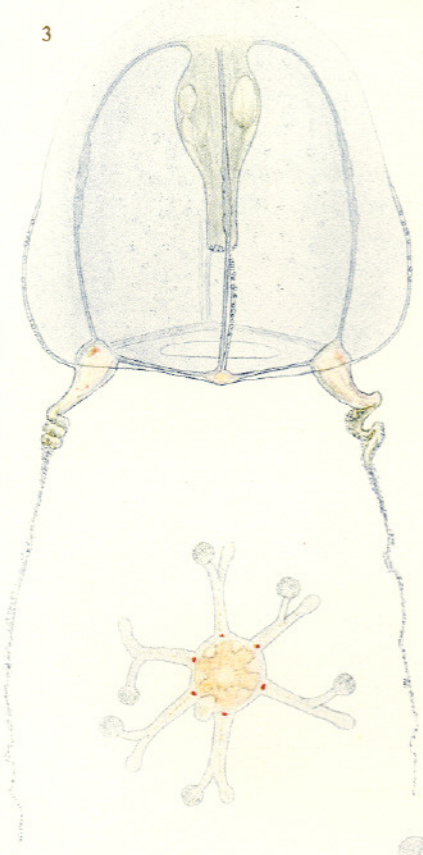

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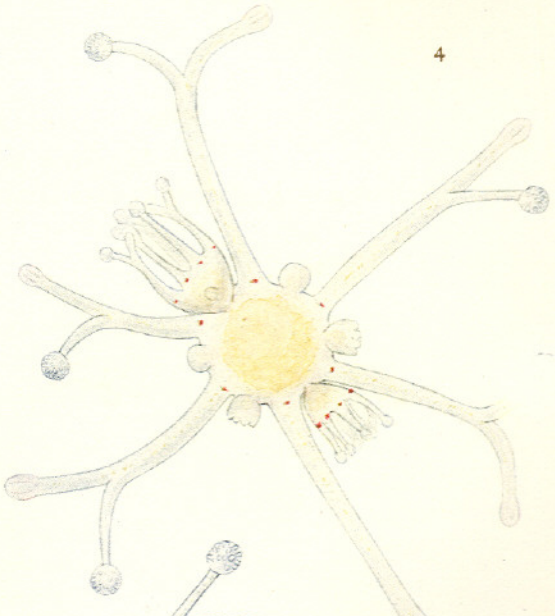

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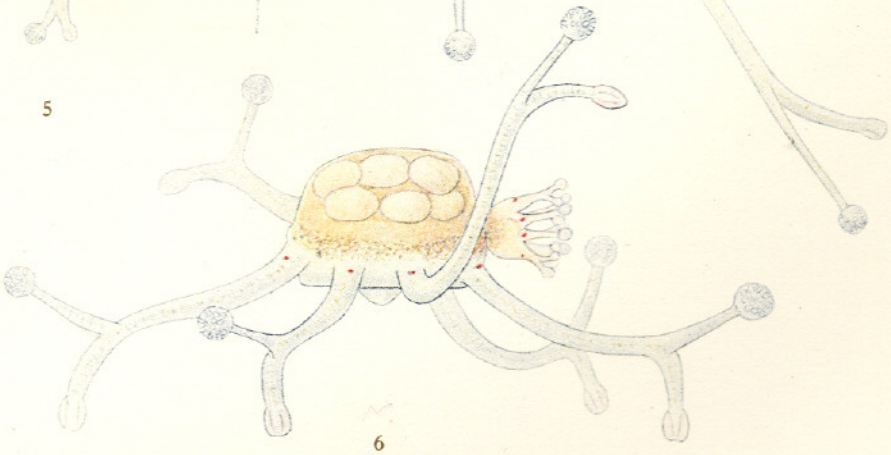

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PLATE V

FIG. 1

Turritopsis nutricula.
4·3 mm. high, Plymouth, 16. ix. 35.

FIG. 2

Planula, 0·2 mm. in length,
liberated from *Turritopsis nutricula*, Plymouth, 31. viii. 37.

FIGS. 3–5

Turritopsis nutricula.
Developing planula and various stages of growth of primary hydranths reared in the Plymouth laboratory, Sept.–Oct. 1937.



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PLATE VI

FIG. 1

Podocoryne hartlaubi.

Probably young specimen of this species, 1·4 mm. in diameter, Plymouth, 18. i. 36.

FIGS. 2, 3

Podocoryne carnea.

Dorsal and lateral views of young specimen, 1 mm. in diameter, a few days after liberation from the hydroid.

FIG. 4

Podocoryne hartlaubi.

3·5 mm. in diameter, mouth of English Channel, 15. iv. 38.

FIG. 5

Podocoryne borealis.

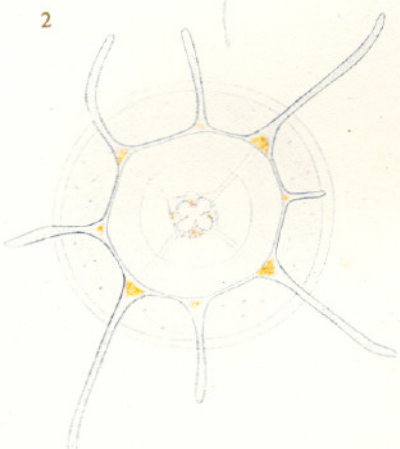
c. 4 mm. high, Plymouth.

Plate VI

1



2



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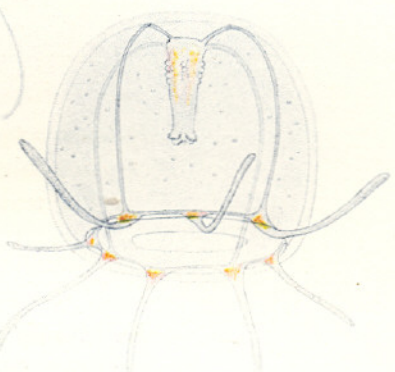

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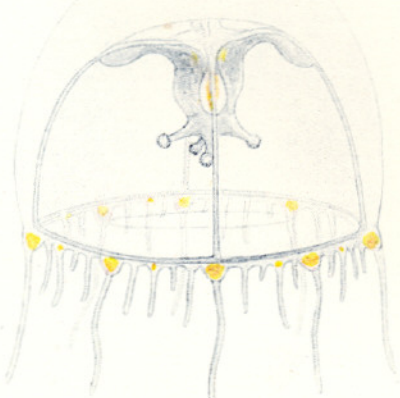

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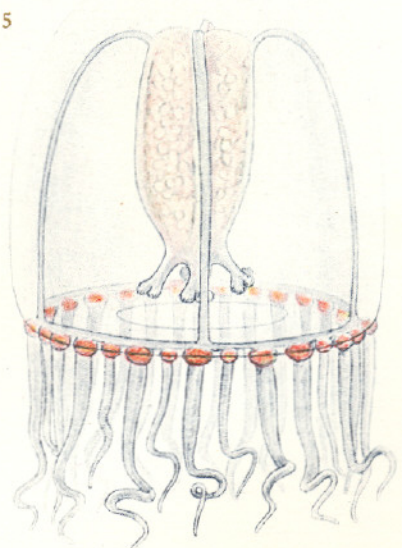

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PLATE VII

FIG. 1

Lizzia blondina. Preserved specimen, 1·7 mm. in diameter, coloured from life, Plymouth, 20. v. 37.

FIG. 2

Lizzia blondina. Preserved specimen, 1·4 mm. in diameter, coloured from life, Penzance, 10. vi. 36.

FIG. 3

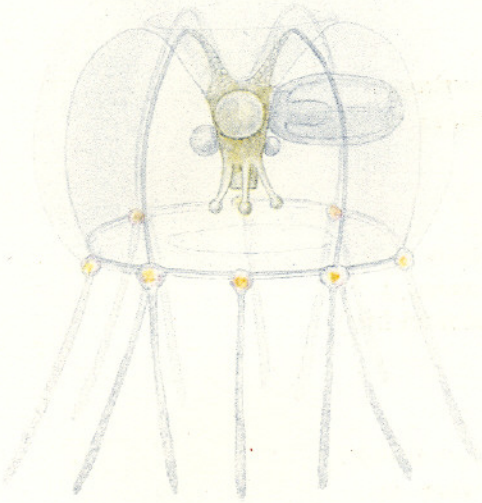
Rathkea octopunctata. Asexual stage, 2·3 mm. high, Plymouth, 14. iv. 37. (Marginal tentacles on far side omitted.)

FIG. 4

Rathkea octopunctata. Mature male, 2·6 mm. high, Plymouth, 3. v. 39.

Plate VII

1



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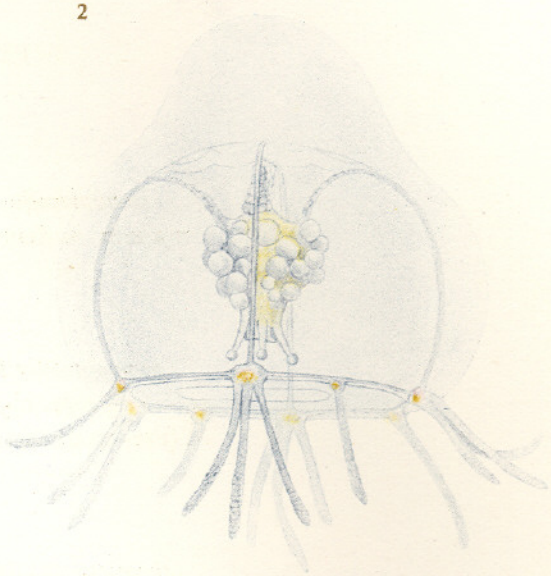

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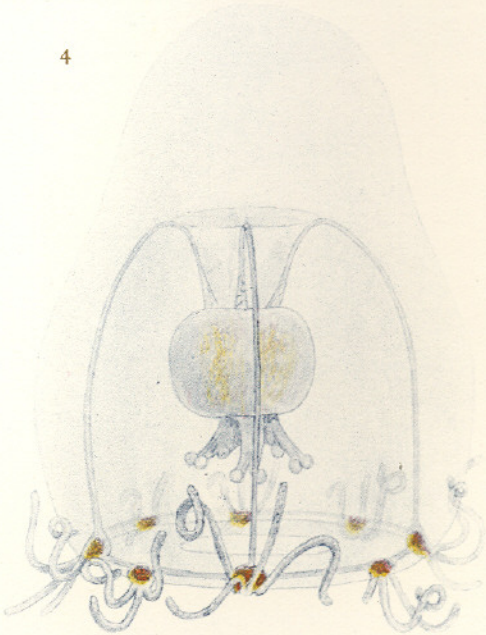

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PLATE VIII

FIG. 1

Bougainvillia ramosa. Mature male, 2·2 mm. in diameter, Plymouth, 14. ix. 38.

FIG. 2

Bougainvillia britannica. Mature male, *c*. 7 mm. high, Plymouth, 25. v. 34. (Preserved specimen, coloured from life.)

FIG. 3

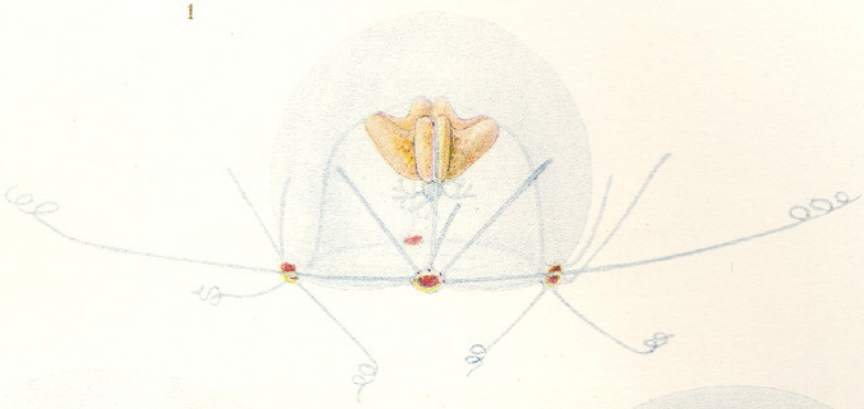
Bougainvillia britannica. Mature female, *c*. 6 mm. high, Plymouth, 22. v. 34. (Preserved specimen, coloured from life.)

FIG. 4

Bougainvillia principis. Mature female, 4·5 mm. high, Plymouth, 20. v. 36. (Preserved specimen, coloured from life.)

Plate VIII

1



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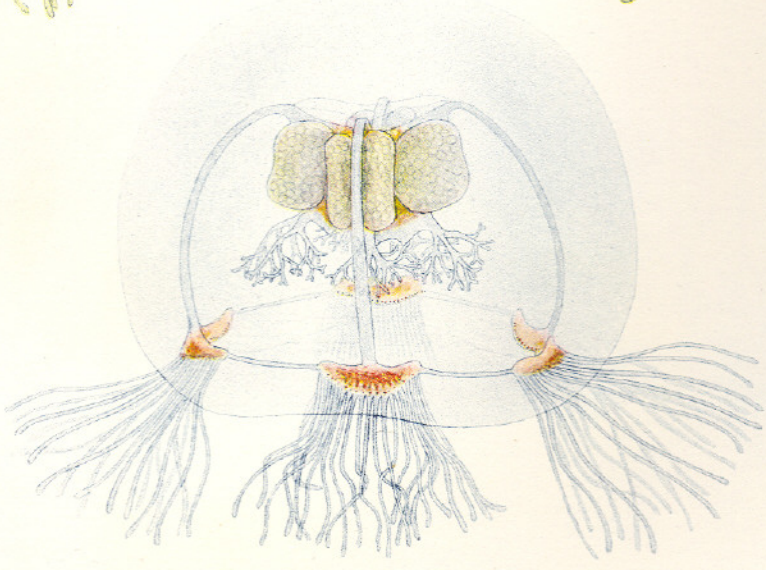

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PLATE IX

FIG. 1

Bougainvillia britannica. Young specimen, 1·6 mm. in diameter, Plymouth, 5. iv. 34.

FIG. 2

Bougainvillia britannica. Young specimen, 3·4 mm. high, Plymouth, 17. iv. 34.

FIG. 3

Bougainvillia britannica. Young specimen, 4·5 mm. high, Plymouth, 3. v. 34. (Preserved specimen, coloured from life.)

FIG. 4

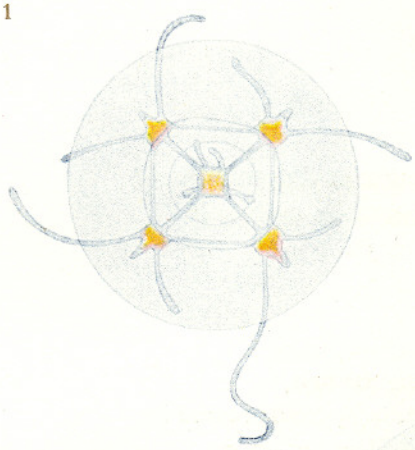
Bougainvillia ramosa. Young specimen, 0·7 mm. in diameter, recently liberated from its hydroid, Plymouth, 2. iv. 36.

FIG. 5

Bougainvillia ramosa. Young specimen, 1·1 mm. in diameter, reared from hydroid, Plymouth, 9. iv. 36.

Plate IX

1



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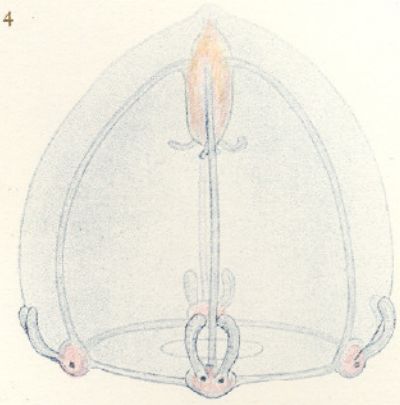

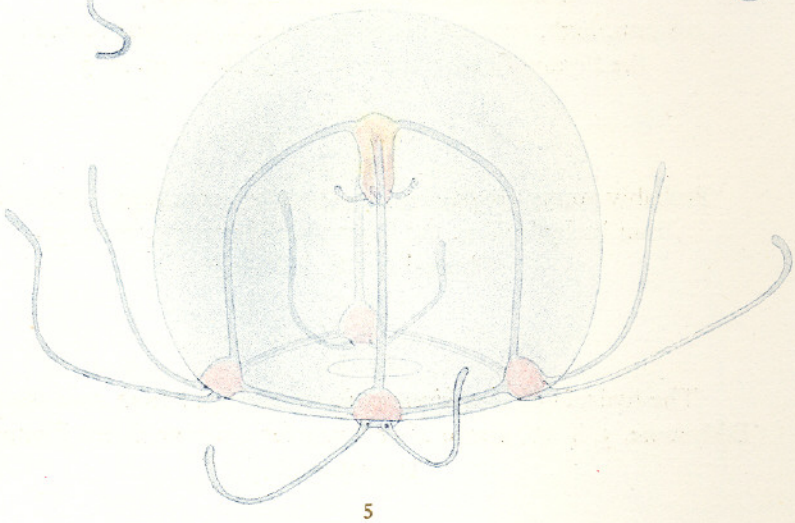

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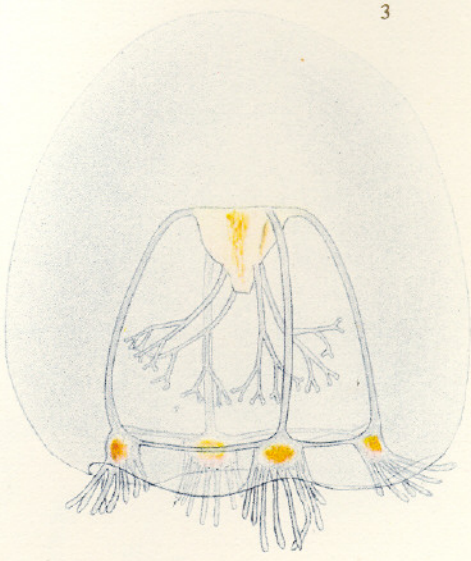

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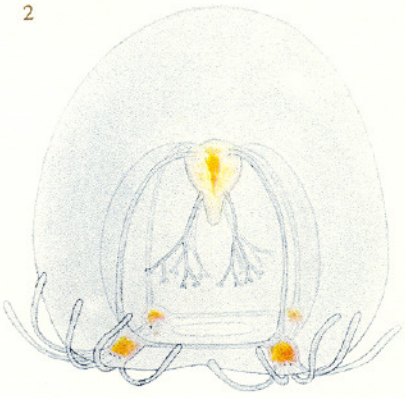

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PLATE X

FIG. 1

The hydroid of *Amphinema dinema* caught in the plankton off Plymouth, 16. xii. 37; this later liberated a medusa in the laboratory, on 6. i. 38.

FIG. 2

Amphinema dinema. Young medusa, 0·8 mm. high, recently liberated from its hydroid; reared in the Plymouth laboratory by W. J. Rees, 19. iv. 37.

FIG. 3

Probably young *Amphinema rugosum*, 0·7 mm. high, liberated from its hydroid in the Plymouth laboratory, 26. v. 37. (Reared by W. J. Rees.)

FIG. 4

The hydroid of *Amphinema dinema*, dredged from near the Eddystone, 3. ii. 36, drawn after living for a month in the Plymouth laboratory.

1



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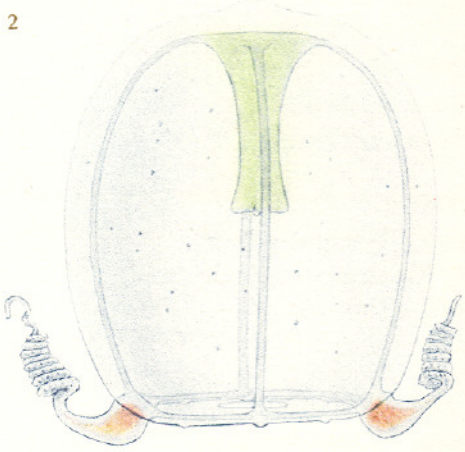

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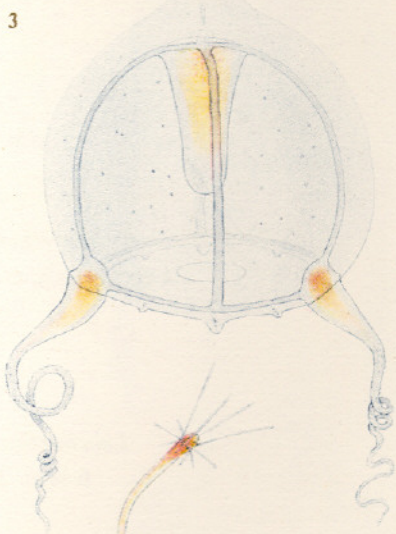

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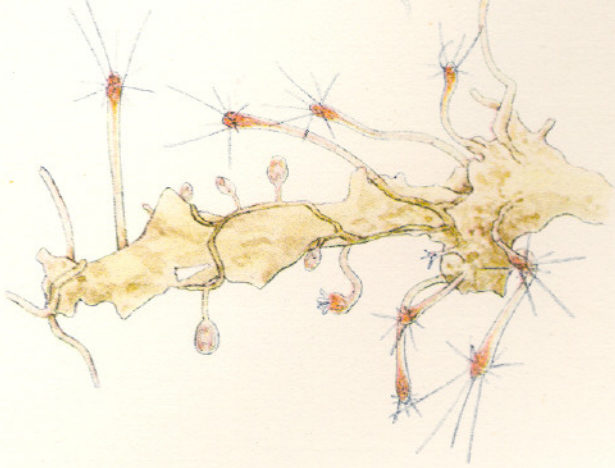

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PLATE XI

FIG. 1

Amphinema dinema. Young female,
2·2 mm. in diameter, Plymouth, 25. ix. 34.

FIG. 2

Amphinema rugosum. Young specimen,
2·4 mm. high, Plymouth, 14. x. 36.

FIG. 3

Amphinema dinema. Mature female,
3 mm. in diameter, Plymouth, 10. x. 35.

FIG. 4

Amphinema rugosum.
3 mm. in diameter, Plymouth.

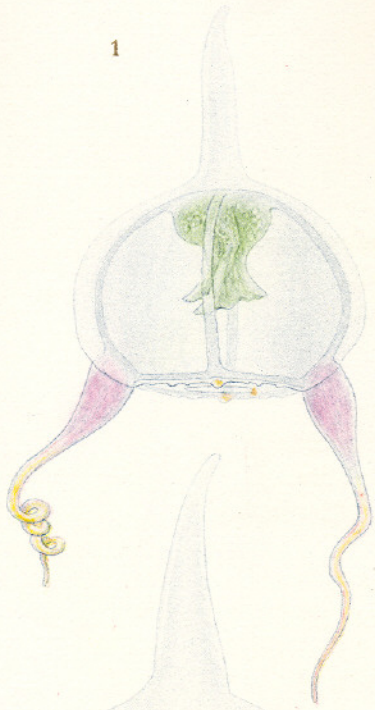
FIG. 5

Leuckartiara octona. Young specimen,
1·2 mm. high, recently liberated from its hydroid,
Plymouth, 20. iii. 36.

FIG. 6

Leuckartiara octona. Young specimen,
6 mm. high, Plymouth, 5. v. 37.

Plate XI



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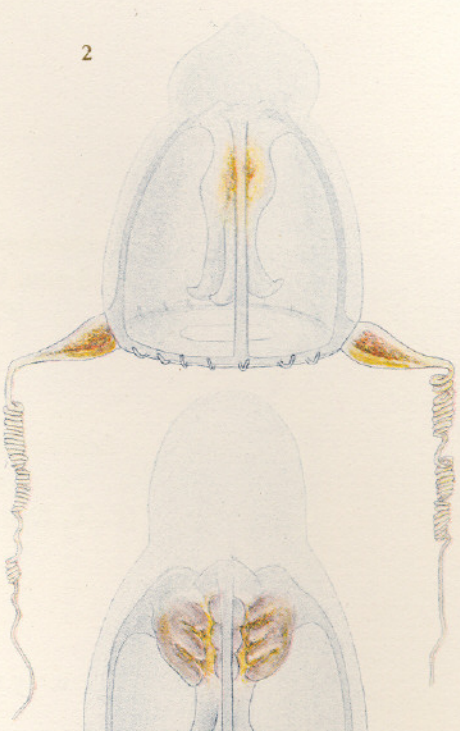

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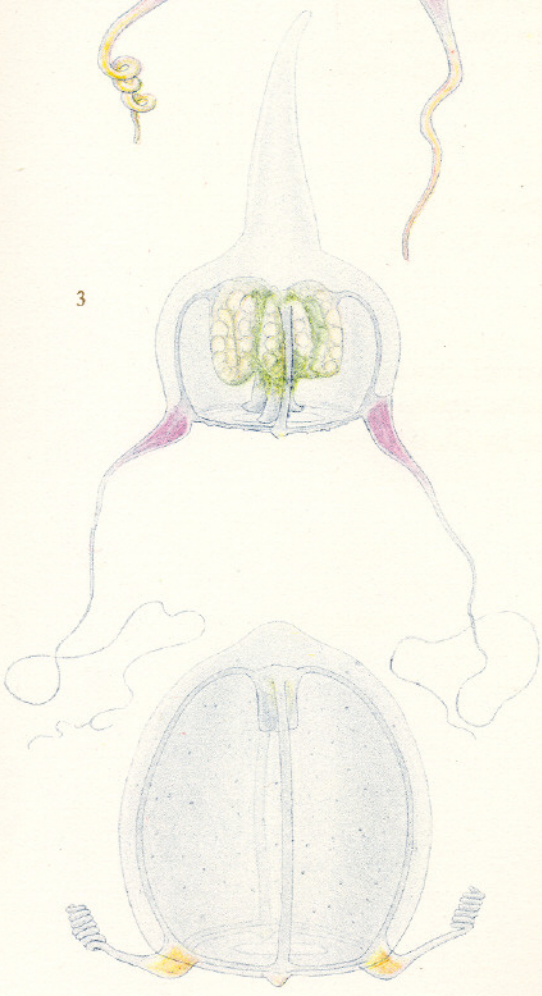

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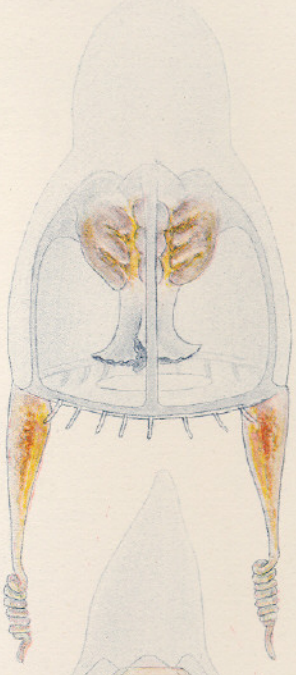

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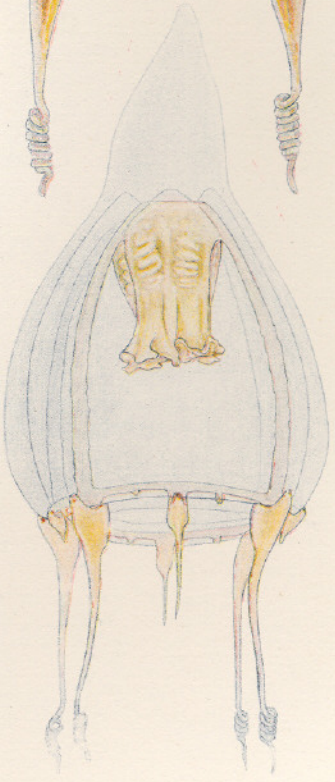


6

Del. F.S.R.

PLATE XII

FIG. 1

Neoturris pileata. Freshly preserved specimen, *c.* 38 mm. high, 50° 36′ N., 9° 33′ W., 3. vi. 38. (Collected by G. A. Steven.)

FIG. 2

Leuckartiara breviconis. Preserved specimen, *c.* 15 mm. high, northern North Sea. (E. T. Browne collection, sent by Cl. Hartlaub.)

FIG. 3

Leuckartiara octona. *c.* 15 mm. high, Plymouth, 23. v. 35.

FIG. 4

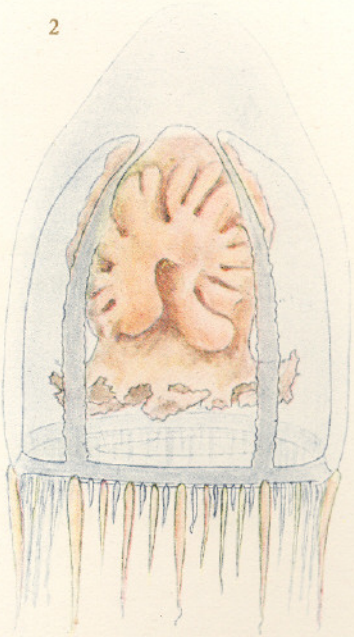
Leuckartiara nobilis. Preserved specimen, *c.* 20 mm. high, Villefranche, 13. iii. 13. (E. T. Browne collection, sent by Cl. Hartlaub.)

Plate XII

1



2



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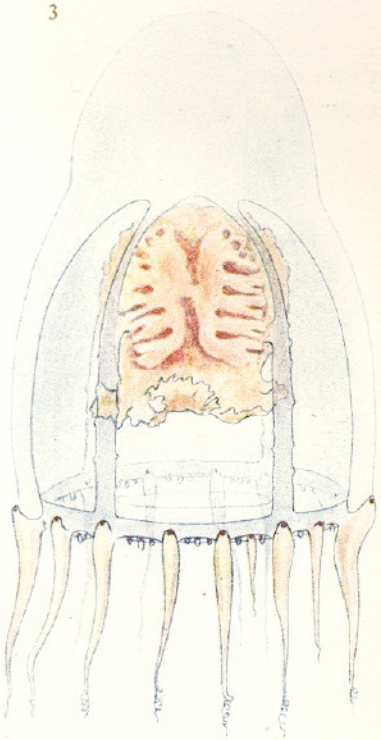

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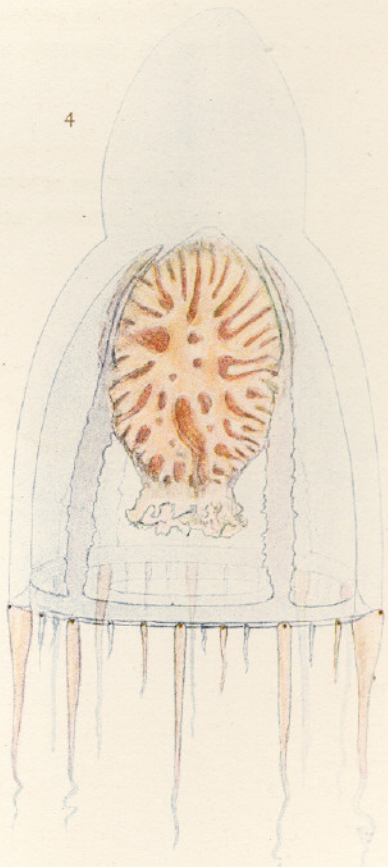


Del. F.S.R.

PLATE XIII

FIG. 1

Bythotiara murrayi. Reconstruction from preserved specimens, *c.* 18 mm. in diameter, 50 miles W.N.W. of Tearaght, Ireland, 3. xi. 04. (E. T. Browne collection.)

FIG. 2

Melicertum octocostatum. Young specimen, 1·5 mm. in diameter, liberated on 16. ii. 36 from hydroid in tanks of Dove Marine Laboratory, Cullercoats, sent to Plymouth by Dr H. O. Bull, drawn 18. ii. 36.

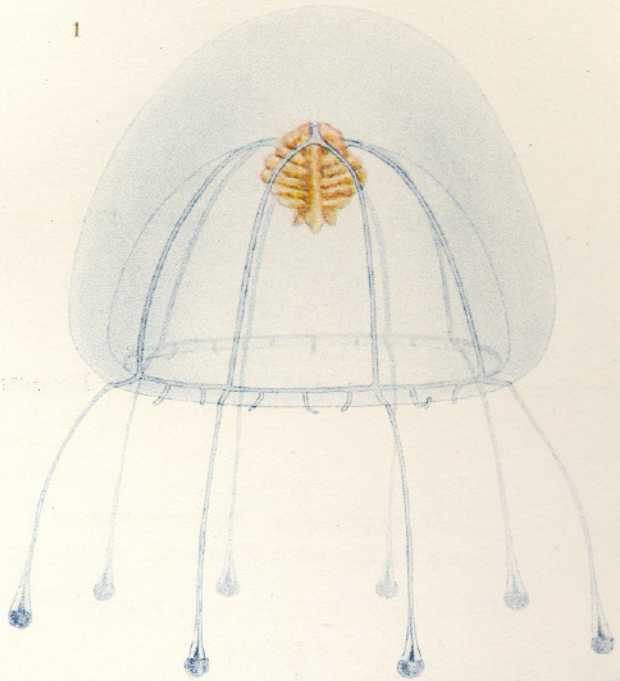
FIG. 3

Melicertum octocostatum. Young specimen, *c.* 2·6 mm. in diameter, same as in Fig. 2, drawn 28. ii. 36.

FIG. 4

Melicertum octocostatum. Young specimen, 2·9 mm. in diameter, same as in Fig. 2, drawn 18. iii. 36.

1



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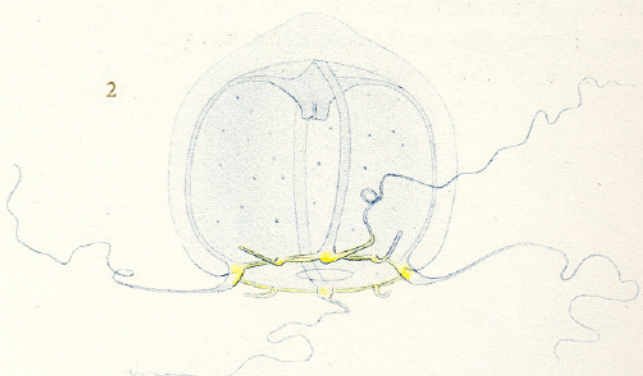

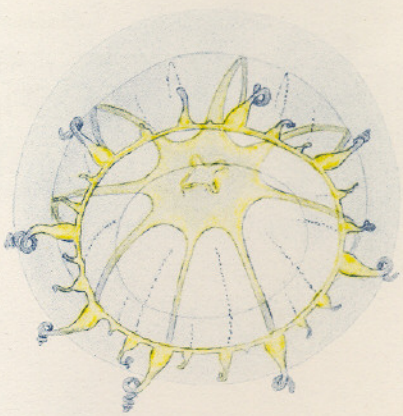

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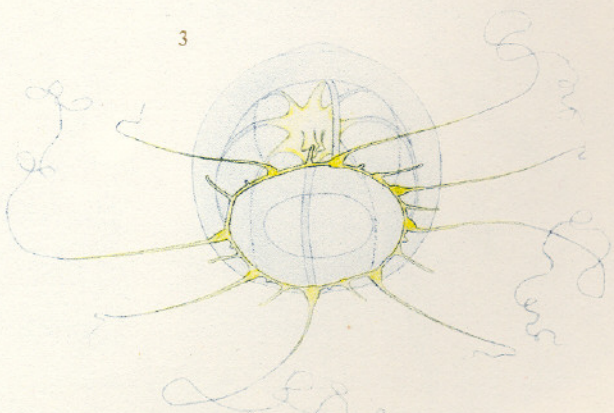


Del. F.S.R.

PLATE XIV

FIG. 1

Laodicea undulata.
c. 20 mm. in diameter, Plymouth, 12. ix. 35.

FIG. 2

Laodicea undulata. Specimen
newly liberated from its hydroid, 0·7 mm. high, Plymouth, 5. v. 36.

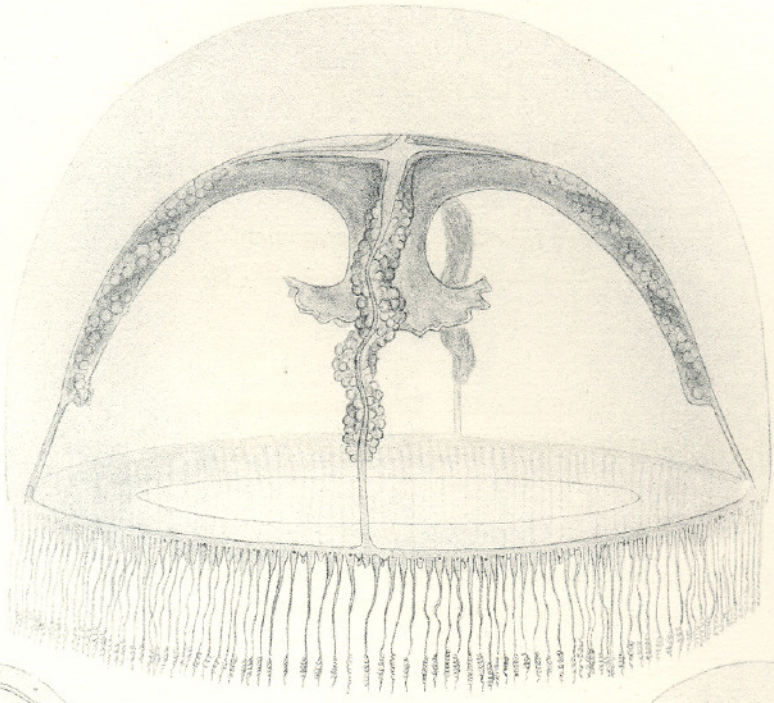
FIG. 3

Laodicea undulata. Young specimen,
c. 6 mm. in diameter, Plymouth, 31. vii. 37.

FIG. 4

Halopsis ocellata. Preserved specimen,
c. 30 mm. in diameter, Faeroe-Shetland Channel, 9. vii. 33.
(Collected on Sir Edward Peel's yacht *St George*.)

1



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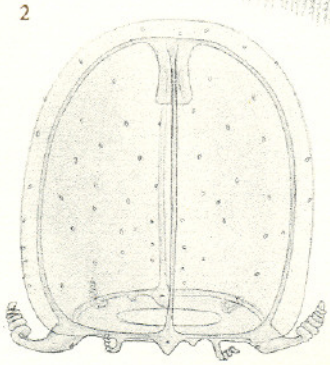

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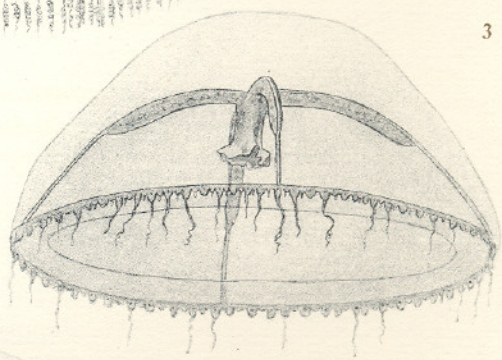
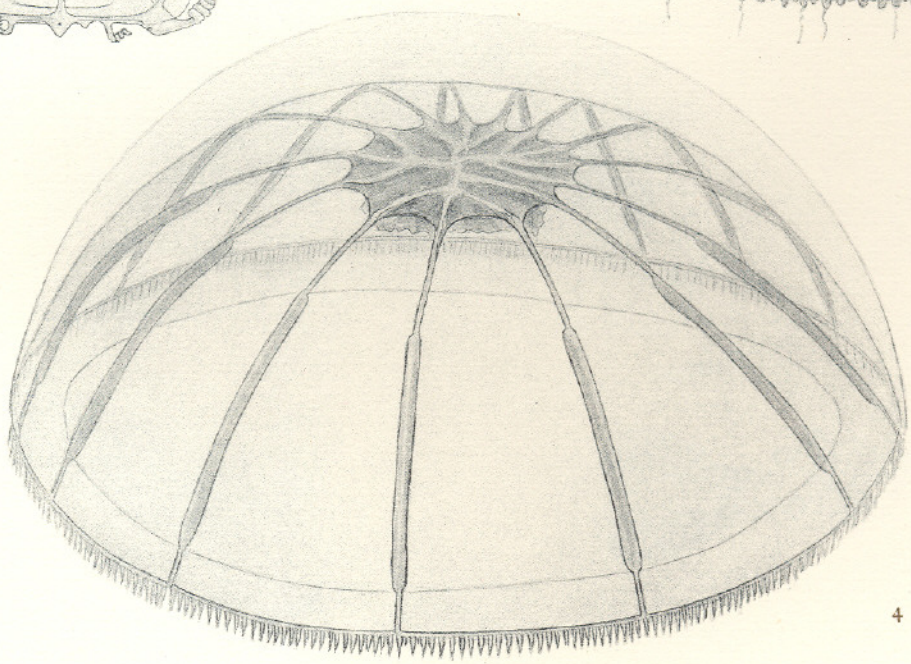




4

Del. F.S.R.

PLATE XV

FIG. 1

Cosmetira pilosella. Young specimen, 1·8 mm. in diameter, Plymouth, 28. iv. 37.

FIG. 2

Cosmetira pilosella. Young specimen, 3·3 mm. in diameter, Plymouth, 28. iv. 37.

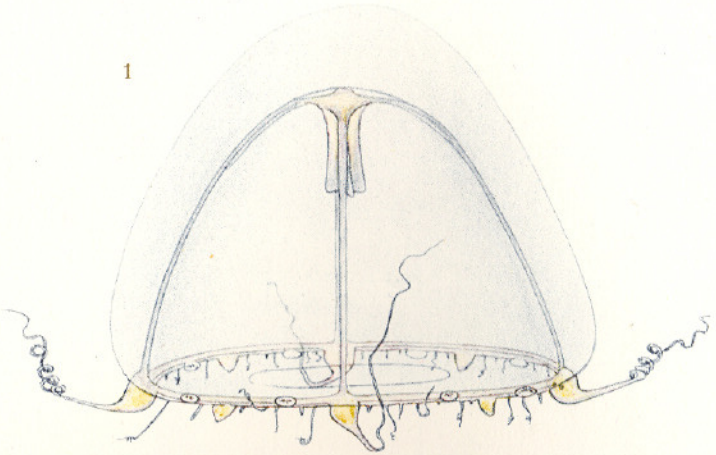
FIG. 3

Cosmetira pilosella. Portion of umbrella margin showing spiral coiling of marginal cirri, Plymouth, 19. v. 37.

FIG. 4

Mitrocomella brownei. Mature female, 5–6 mm. in diameter, Plymouth, 4. v. 37.

1



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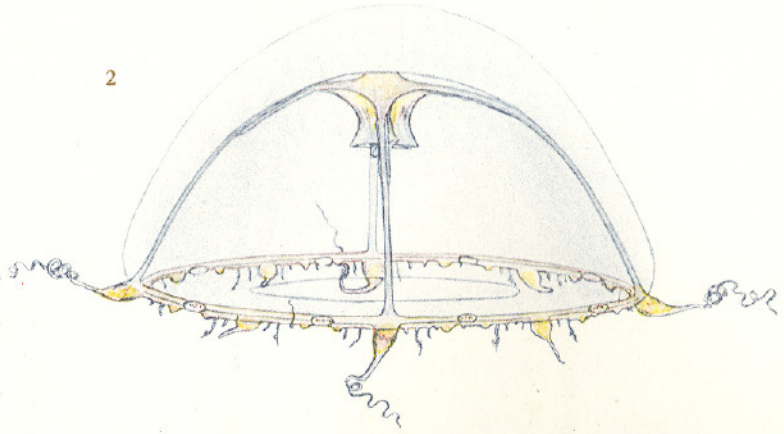

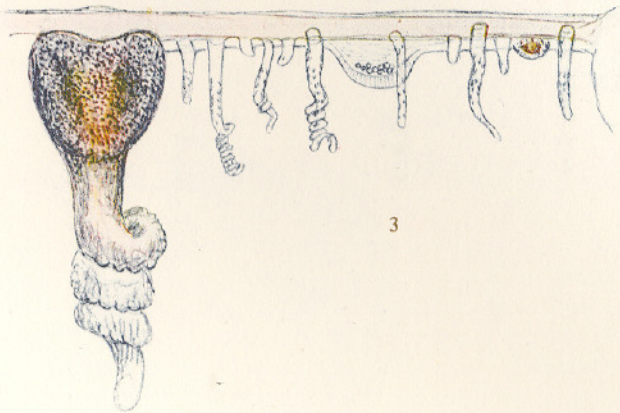

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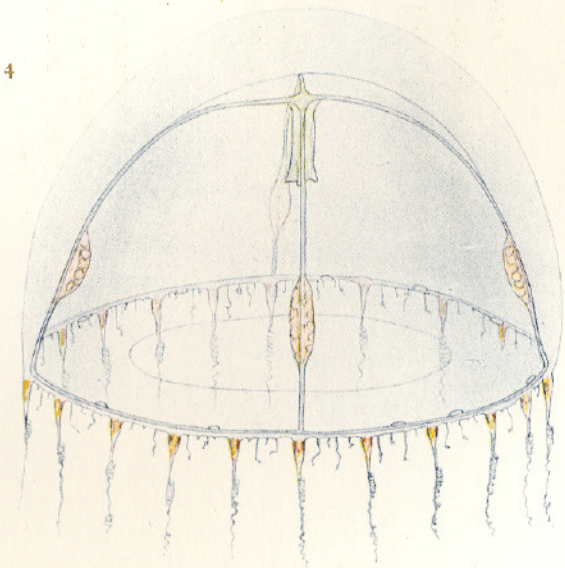


Del. F.S.R.

PLATE XVI

FIG. 1

Phialidium hemisphaericum. Mature female,
c. 10 mm. in diameter, Plymouth, 29. iv. 40.

FIG. 2

Lovenella clausa. Mature male,
c. 7 mm. in diameter, Plymouth.

FIG. 3

Eucheilota maculata. Preserved specimen.
c. 11 mm. in diameter, North Sea.
(E. T. Browne collection.)

FIG. 4

Phialella quadrata. Young specimen,
c. 3·5 mm. in diameter, Plymouth, 25. v. 38.

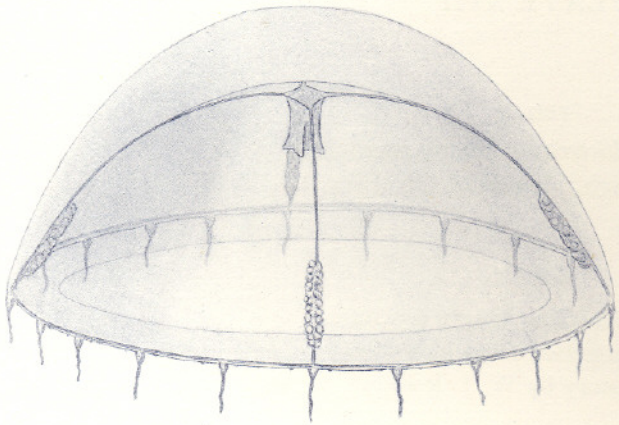
FIG. 5

Phialella quadrata.
c. 5 mm. in diameter, Plymouth, 25. v. 38.

FIG. 6

Phialella quadrata.
c. 4·5 mm. in diameter, Plymouth, 25. v. 38.

1



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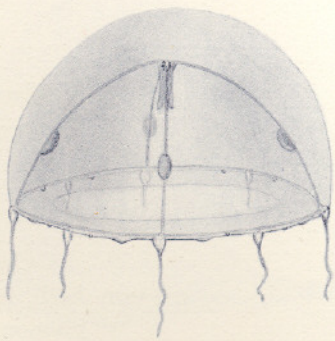

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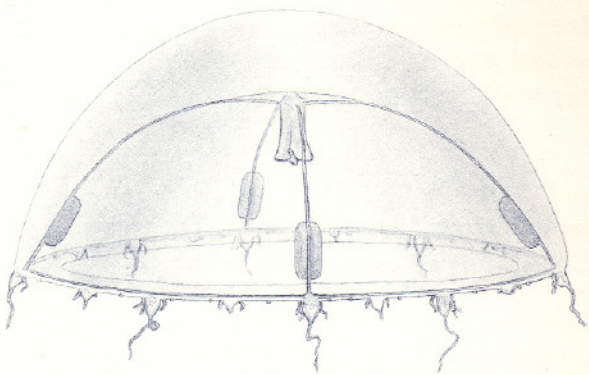

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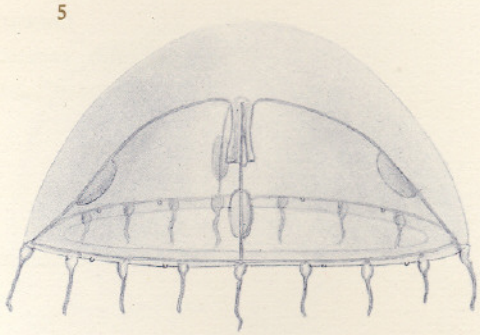

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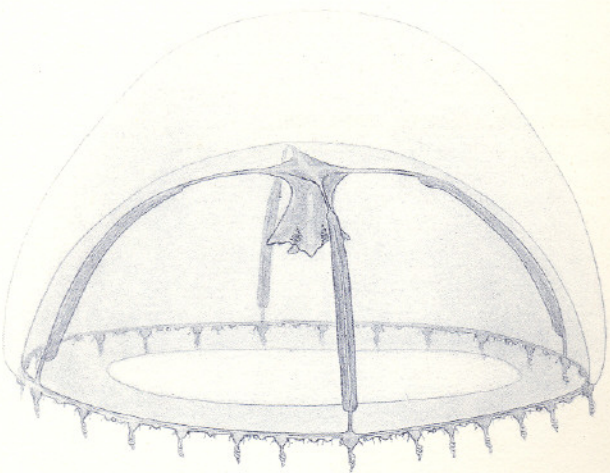

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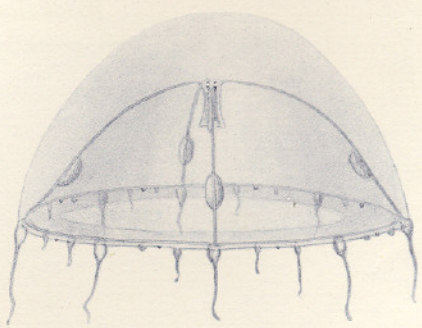


Del. F.S.R.

PLATE XVII

FIG. 1

Tiaropsis multicirrata. Young specimen,
1·4 mm. high, Plymouth, 21. iii. 34.

FIG. 2

Cosmetira pilosella. Young specimen,
0·8 mm. high, recently liberated from its hydroid; reared in the Plymouth laboratory by W. J. Rees, 28. iii. 36.

FIG. 3

Lovenella clausa. Young specimen,
0·75 mm. high, recently liberated from its hydroid; reared in the Plymouth laboratory by W. J. Rees, 10. iii. 36.

FIG. 4

Lovenella clausa.
Same specimen as in Fig. 3, two days later, 0·9 mm. high.

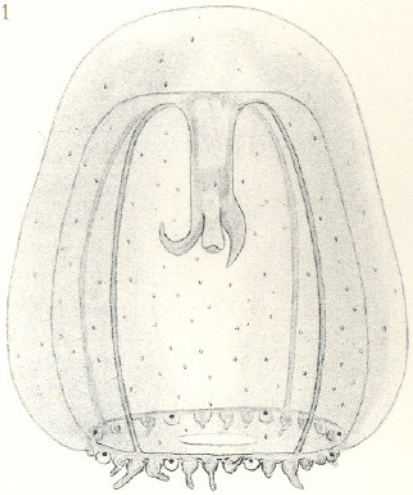
FIG. 5

Phialella quadrata. Young specimen,
c. 2 mm. in diameter, Plymouth, 24. v. 38.

FIG. 6

Phialidium hemisphaericum. Young specimen,
0·7 mm. high, recently liberated from its hydroid, Plymouth, 22. iii. 33.

1



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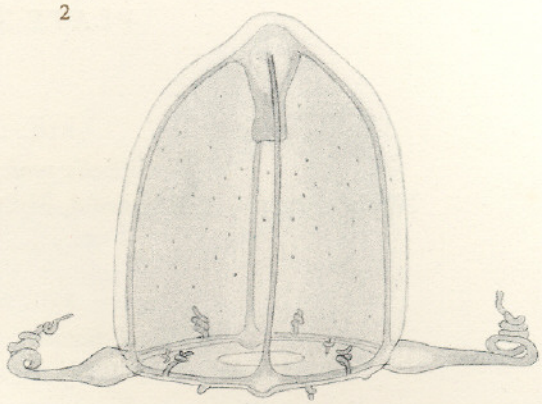

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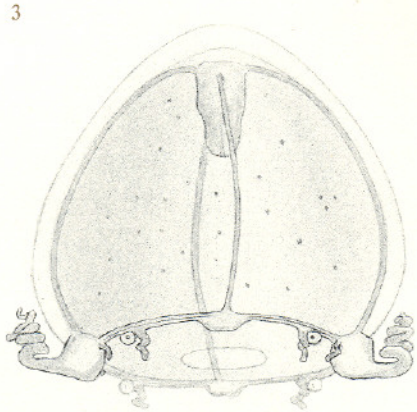

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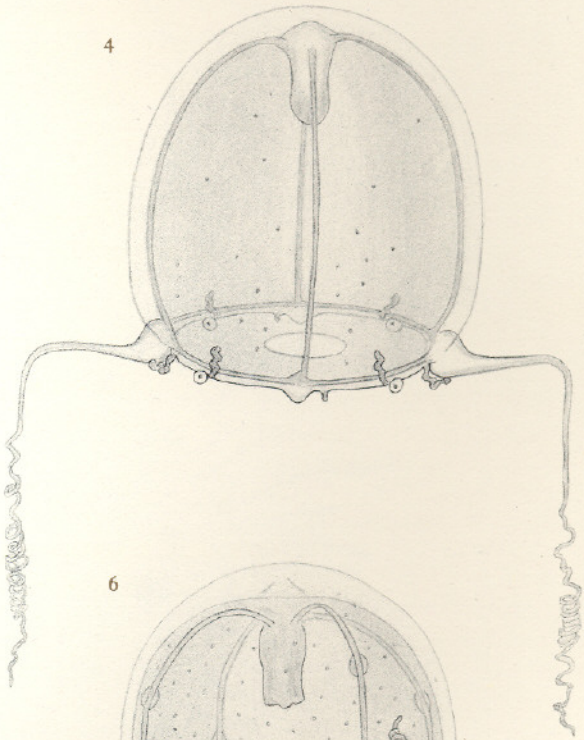

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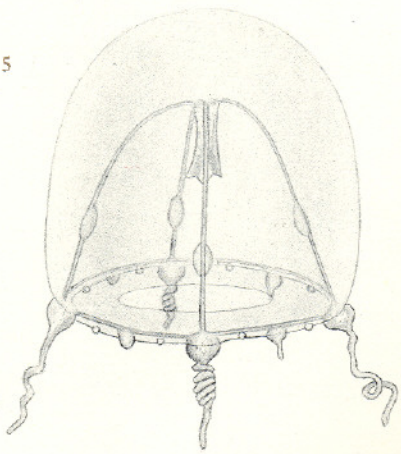

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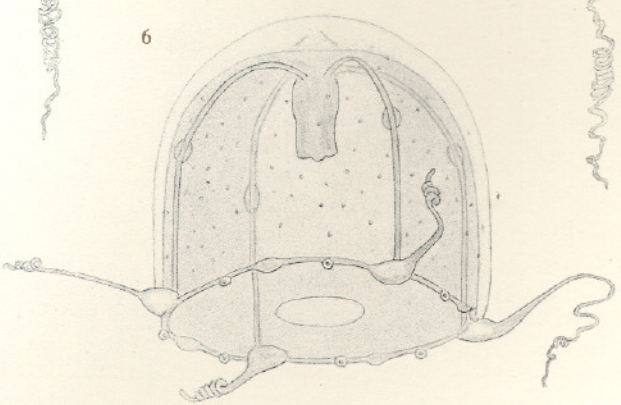


Del. F.S.R.

PLATE XVIII

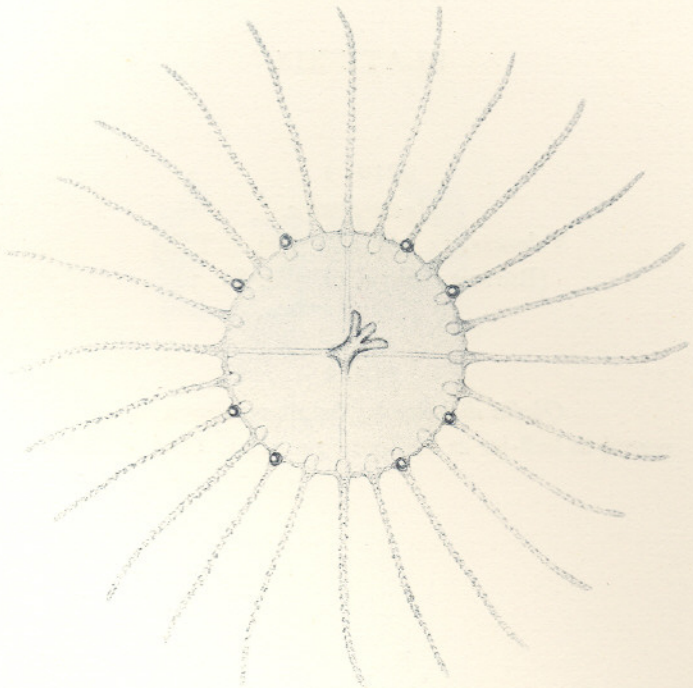
FIG. 1

Obelia geniculata.
Newly liberated from hydroid, Millport, 22. ix. 02. (Del. E.T.B.)

FIG. 2

Obelia dichotoma. Later stage,
reared in bell-jar at Millport, 25. ix. 02. (Del. E.T.B.)

1



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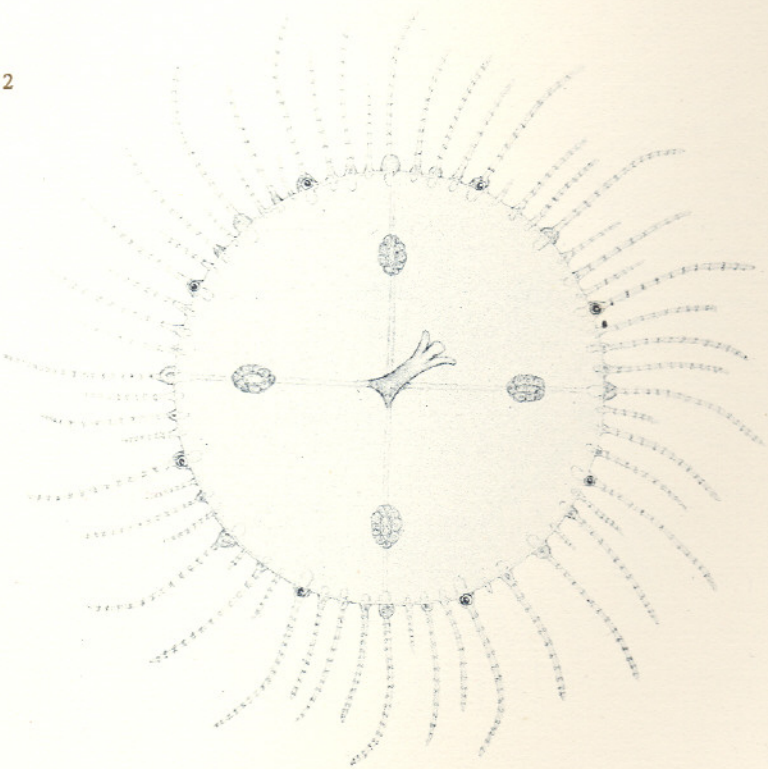


Del. E.T.B.

PLATE XIX

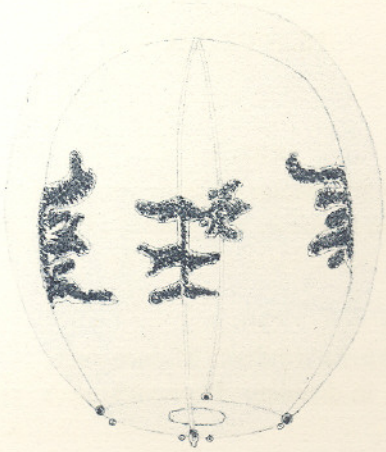
FIG. 1

Agastra mira.
Valencia, 15. viii. 96. (Del. E.T.B.)
(Browne, 1897*a*, pl. xlix, fig. 3.)

FIG. 2

Obelia dichotoma. Adult specimen,
reared in bell-jar at Millport, 14. x. 02. (Del. E.T.B.)

1



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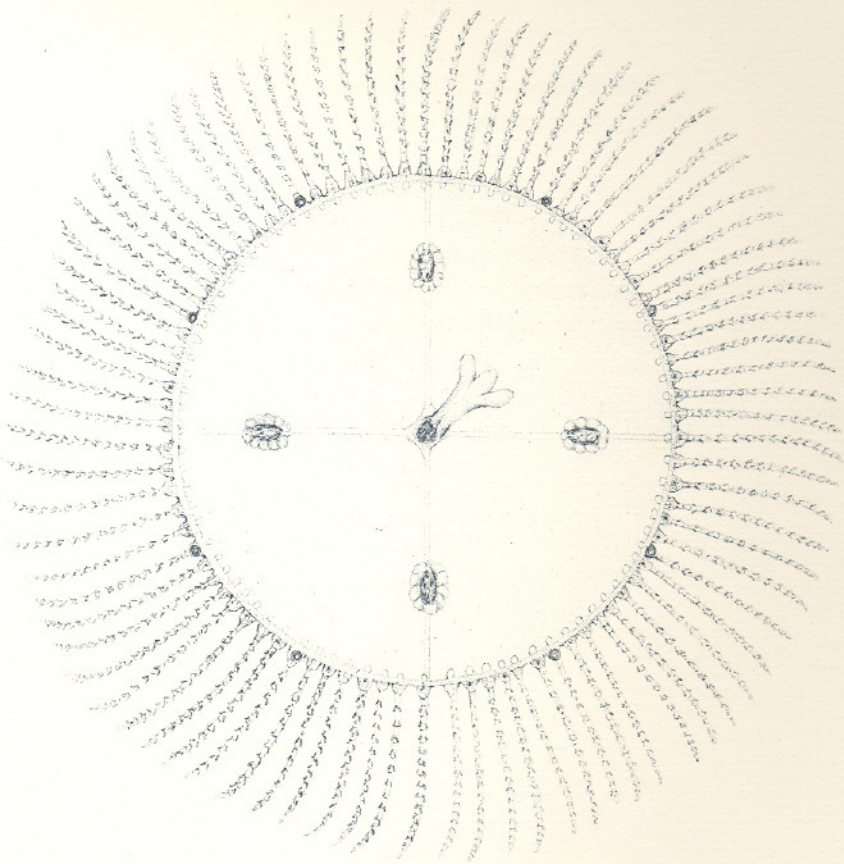


Del. E.T.B.

PLATE XX

FIG. 1

Helgicirrha schulzei. Young specimen,
c. 3 mm. in diameter, Plymouth, 22. vii. 38.

FIG. 2

Helgicirrha schulzei. Mature male,
c. 30 mm. in diameter, Plymouth, 24. x. 34.

FIG. 3

Eirene viridula. Young specimen,
c. 7 mm. in diameter, Plymouth, 24. x. 34.

FIG. 4

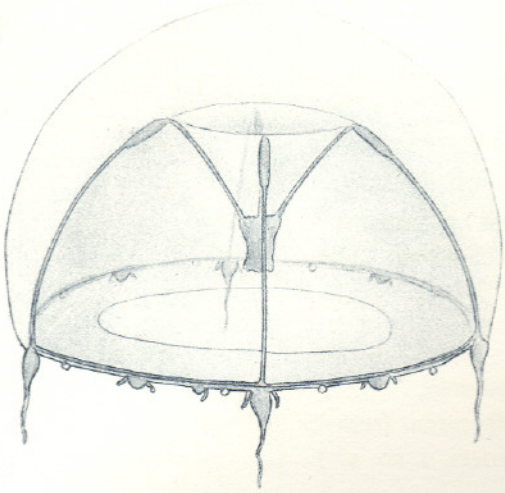
Eirene viridula. Mature female,
c. 18 mm. in diameter, Plymouth, 13. x. 32.

FIG. 5

Phialopsis diegensis.
Drawing constructed from preserved specimens.
(General shape after Bigelow, 1909*a*, pl. xxxvi, fig. 1.)

Plate XX

1



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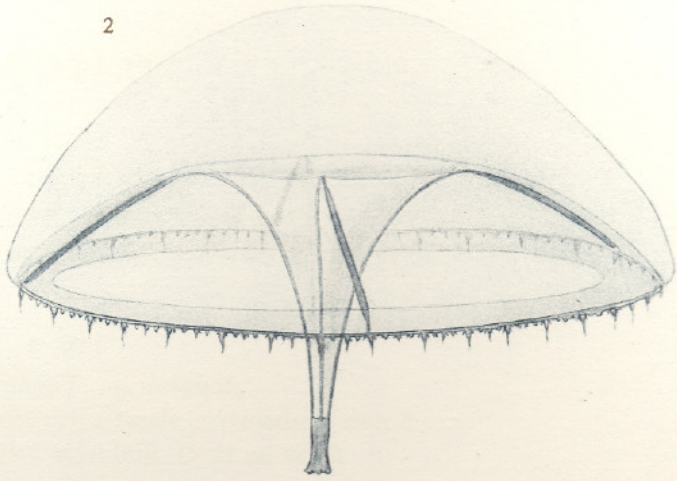

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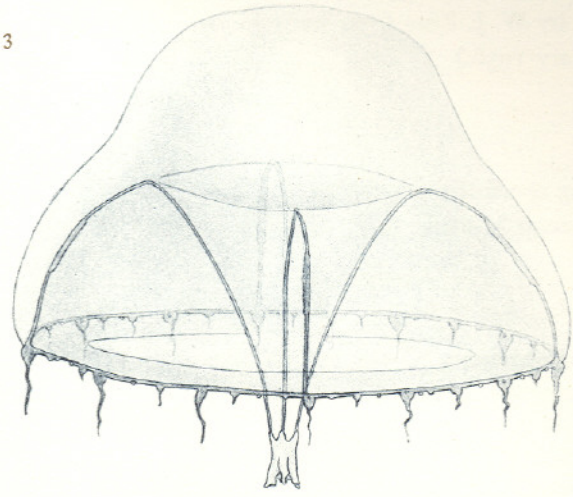

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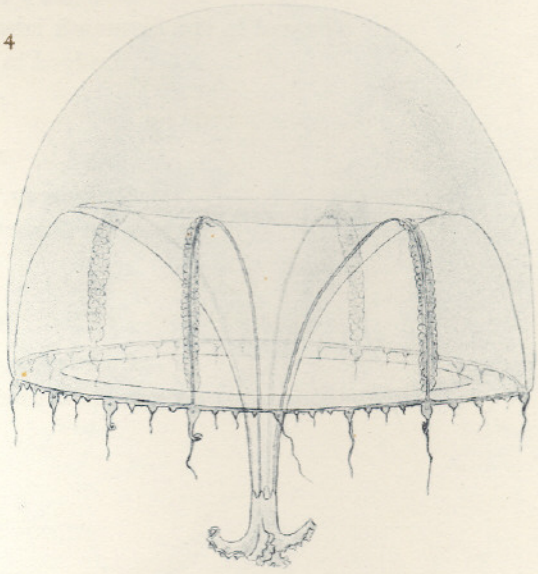

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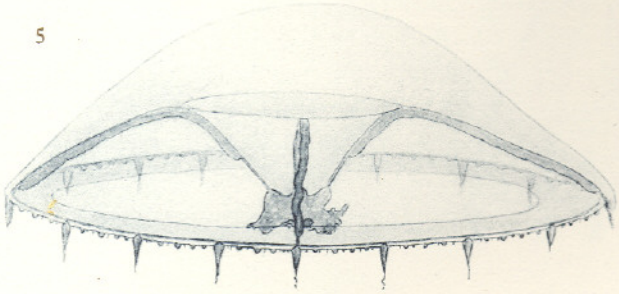


Del. F.S.R.

PLATE XXI

FIG. 1

Octocanna funeraria. Preserved specimen,
c. 30 mm. in diameter. (E. T. Browne collection, 'Thor', 1906.)

FIG. 2

Aequorea sp. Young specimen,
c. 1·6 mm. in diameter, about a day after liberation from its hydroid.
(Sent by H. O. Bull from Cullercoats, 2. xii. 36.)

FIG. 3

Aequorea sp. Young specimen,
1·4 mm. high, 2 or 3 days old, 22. iv. 37.
(Reared in the Plymouth laboratory by W. J. Rees from hydroid
dredged in February 1936.)

FIG. 4

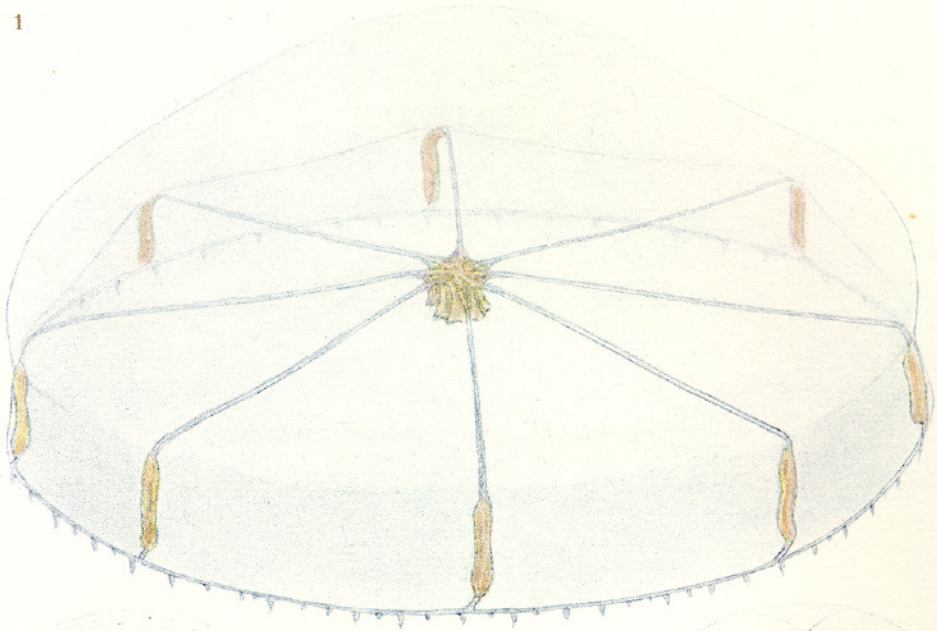
Aequorea sp. Young specimen,
2·5 mm. in diameter, Plymouth, 23. v. 34.

FIG. 5

Aequorea sp. Young specimen,
4·1 mm. in diameter, Plymouth, 7. xi. 35.

Plate XXI

1



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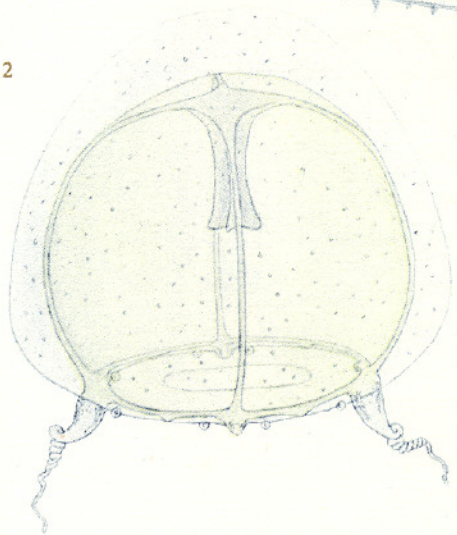

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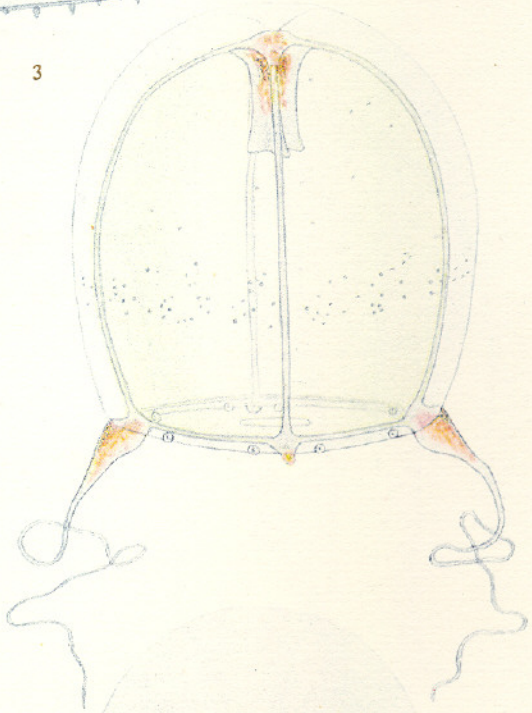

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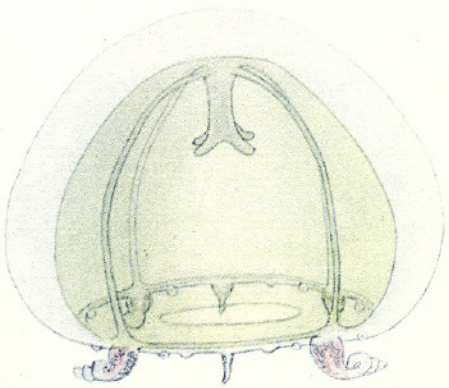

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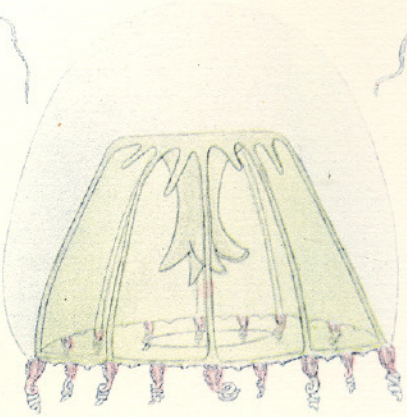


Del. F.S.R.

PLATE XXII

FIG. 1

Eutima gracilis.
Reconstruction from preserved material.

FIG. 2

Eutonina indicans. Preserved specimen.
(E. T. Browne collection.)

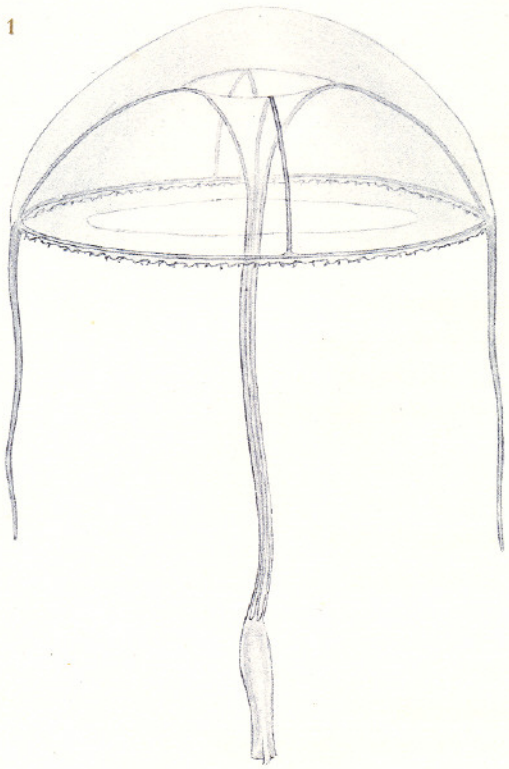
FIG. 3

Tima bairdi. Preserved specimen,
c. 40 mm. in diameter, Firth of Forth,
December, 1908. (E. T. Browne collection.)

FIG. 4

Octorchis gegenbauri.
Reconstruction from preserved material.

1



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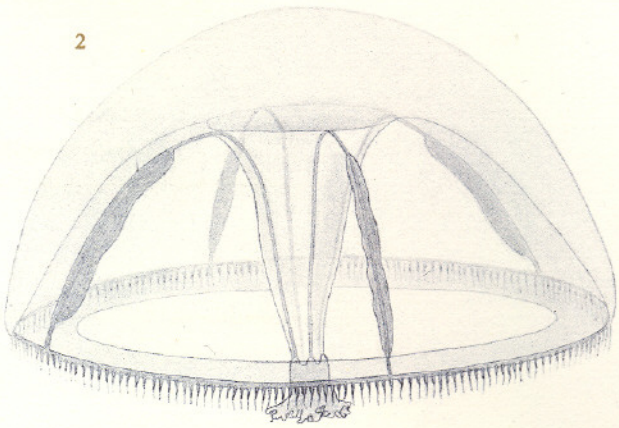

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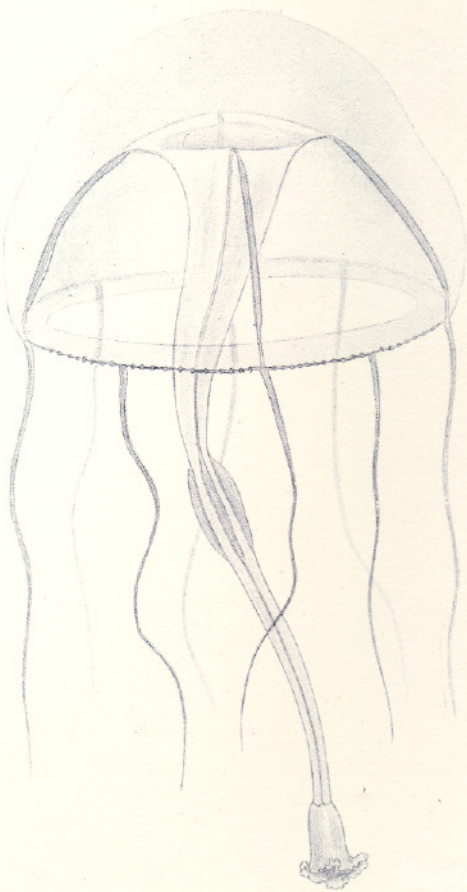

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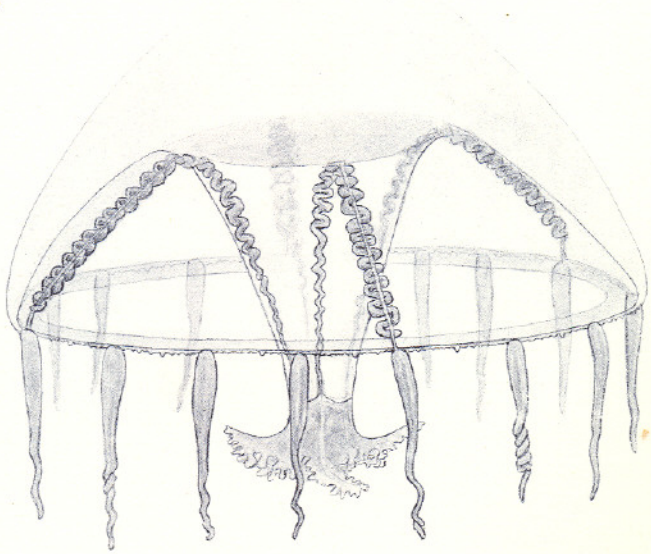

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PLATE XXIII

FIG. 1

Gossea corynetes. Mature male,
c. 10 mm. high, Plymouth, 14. xi. 33.

FIG. 2

Gonionemus vertens. Preserved specimen,
11 mm. high, fish pond at Port Erin, Isle of Man, 1924.
(E. T. Browne collection, sent by H. C. Chadwick.
N.B. The whole subumbrellar surface was yellowish brown.)

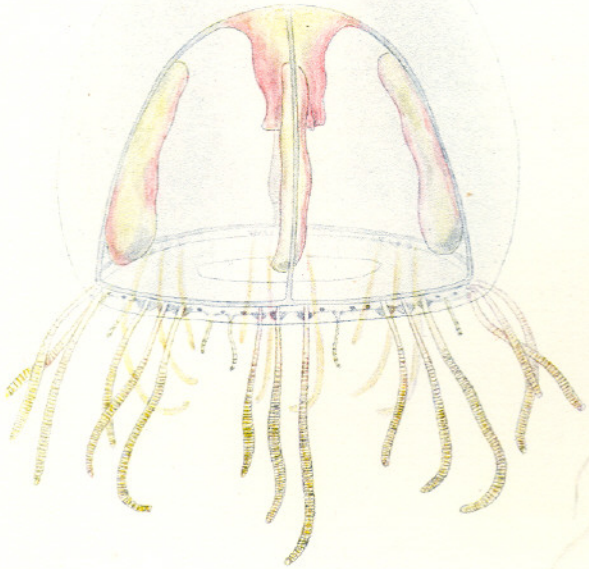
FIG. 3

Proboscidactyla stellata. Mature male,
4·25 mm. in diameter, Plymouth, October 1939.

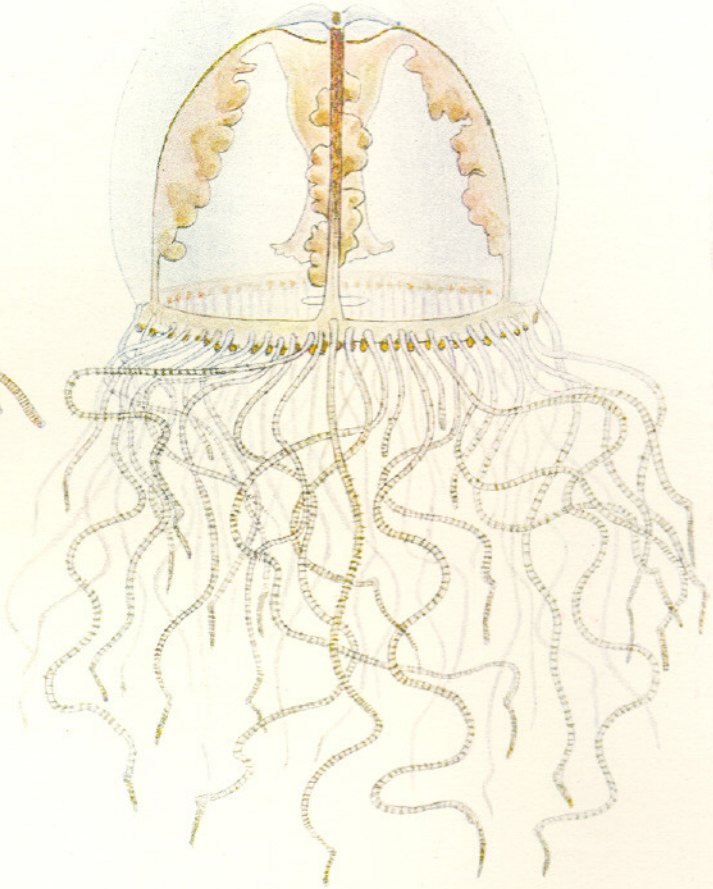
FIG. 4

Proboscidactyla stellata. Young specimen,
1·0 mm. high, recently liberated from its hydroid, Plymouth, 30. iii. 36.

1



2



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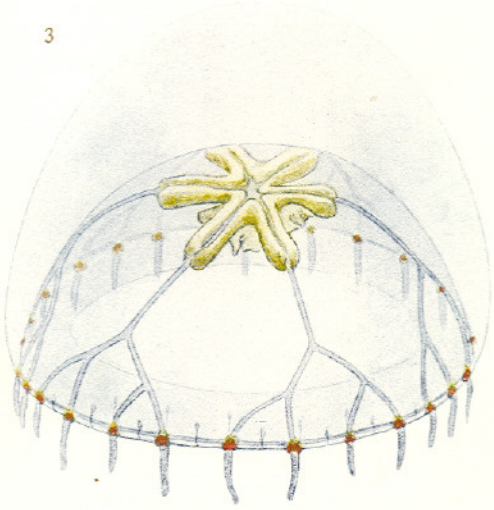

4

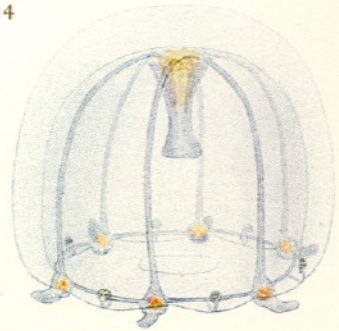

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PLATE XXIV

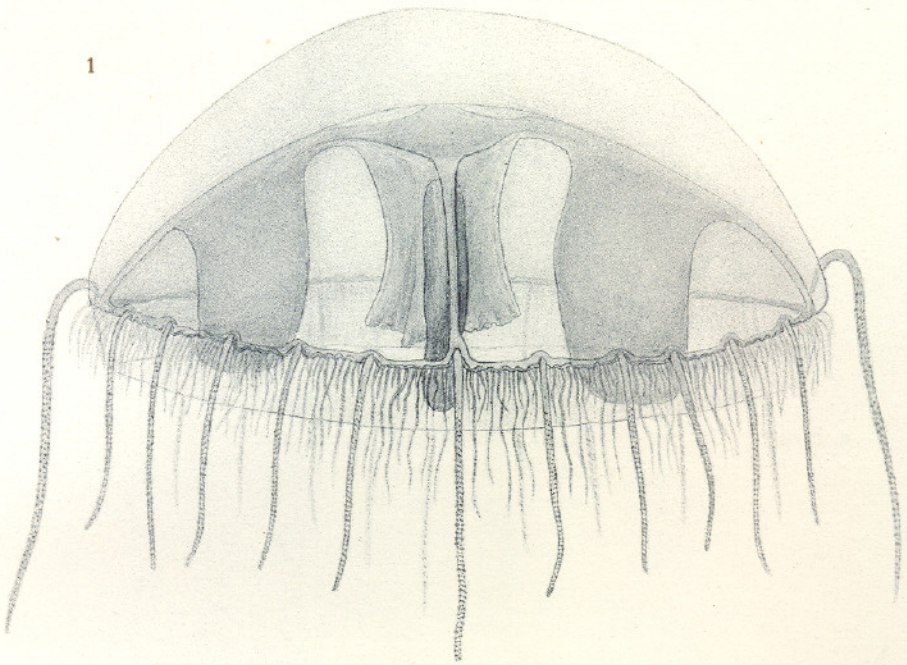
FIG. 1

Craspedacusta sowerbyi. Preserved specimen, *c.* 12 mm. in diameter, Exeter Ship Canal, 29. vii. 28. (E. T. Browne collection, sent by R. Vallentin.)

FIG. 2

Liriope tetraphylla. Preserved mature male, *c.* 12 mm. in diameter, Plymouth, 26. x. 33.

1



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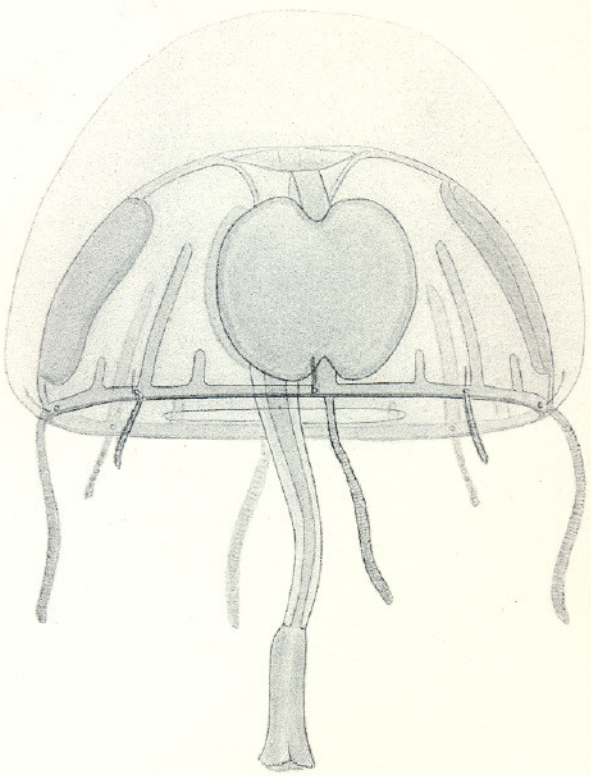

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PLATE XXV

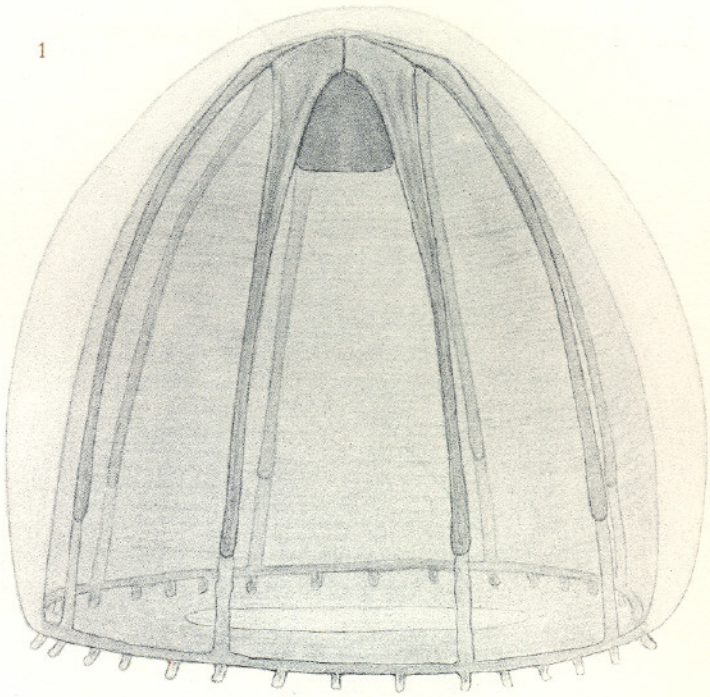
FIG. 1

Colobonema sericeum. Preserved specimen,
c. 21 mm. high. (E. T. Browne collection, 'Thor', 1906.)

FIG. 2

Pantachogon haeckeli. Preserved specimen,
c. 8 mm. high, 50 miles north-west of Eagle Island, Ireland,
11. viii. 04. (E. T. Browne collection.)

1



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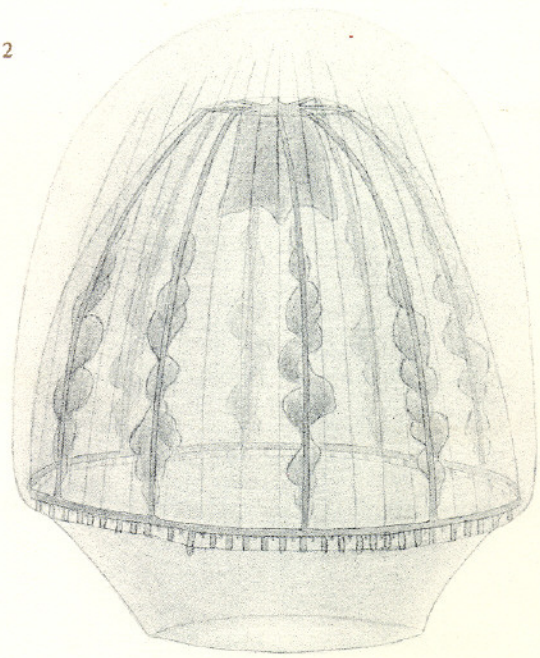

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PLATE XXVI. *Aglantha digitale* var. *rosea*, Plymouth

FIG. 1

Young specimen,
0·4 mm. in diameter, 18. iii. 36.

FIG. 2

Young specimen,
0·9 mm. high.

FIG. 3

Young specimen,
0·85 mm. high, 24. iii. 36.

FIG. 4

Young specimen,
2·1 mm. high.

FIG. 5

Diagrammatic cross-section of adult medusa.

FIG. 6

Developing gonads in young specimen.

FIG. 7

Marginal tentacles of specimen 0·9 mm. high.

FIG. 8

Umbrella margin of specimen 2·1 mm. high, 24. iii. 36.

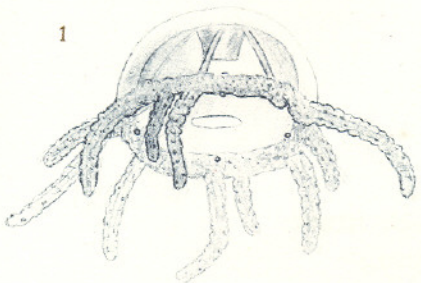
FIG. 9

Diagram to show position of gonad in relation to radial canal.

FIG. 10

Adult medusa, *c.* 13 mm. high.

1



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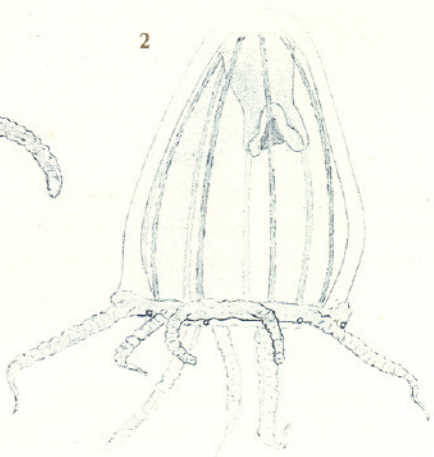

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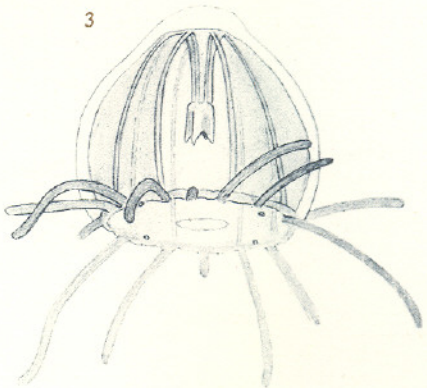

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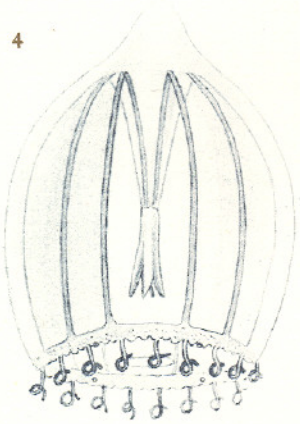

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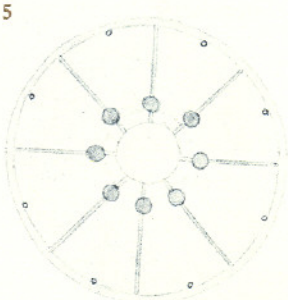

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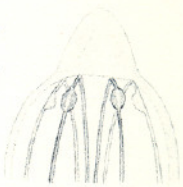

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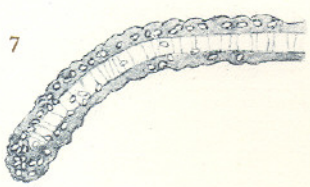

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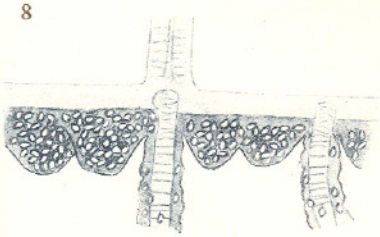

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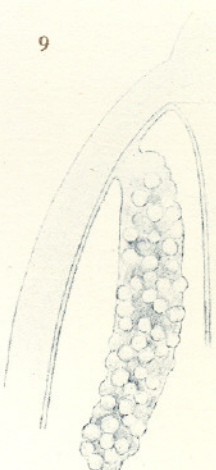

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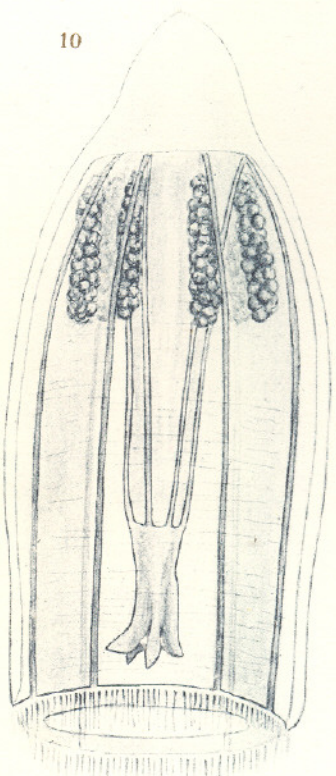

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PLATE XXVII

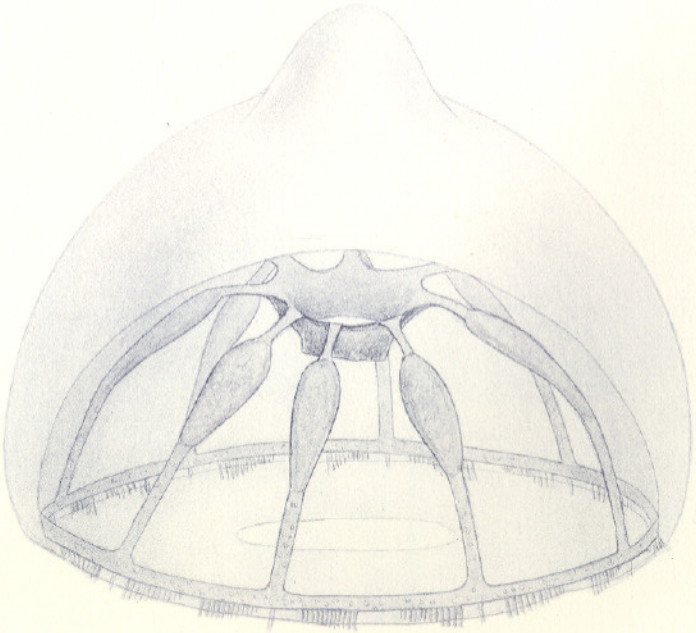
FIG. 1

Botrynema brucei. Preserved specimen,
c. 20 mm. in diameter, 50 miles north-west of Eagle Island,
Ireland, 11. viii. 04. (E. T. Browne collection.)

FIG. 2

Haliscera bigelowi. Preserved specimen,
c. 14 mm. in diameter. (E. T. Browne collection, 'Thor', 1906.)

1



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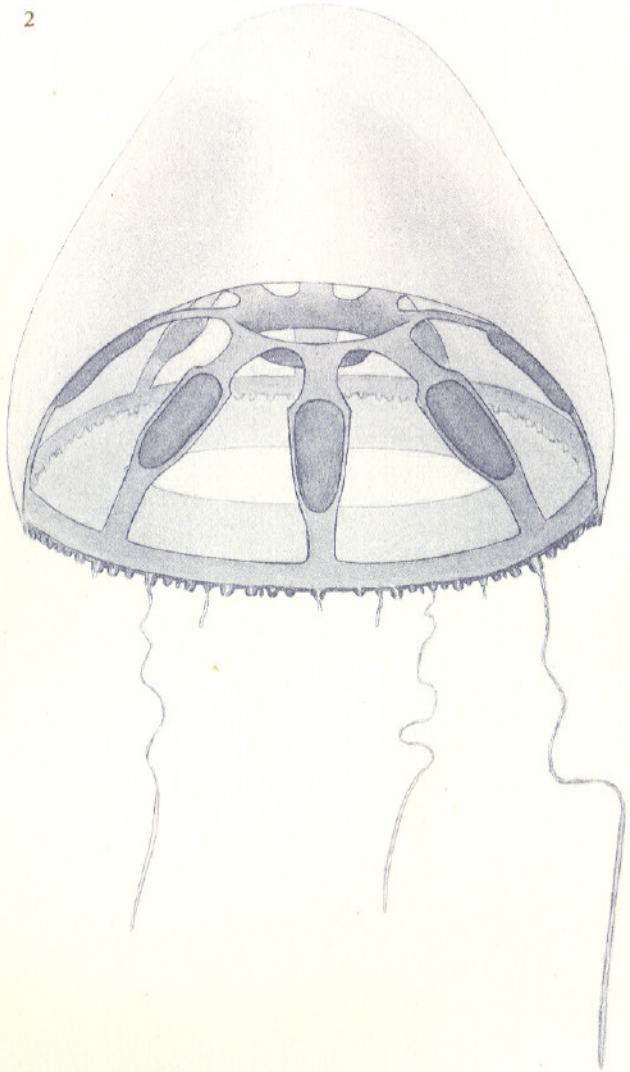

Plate XXVII

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PLATE XXVIII

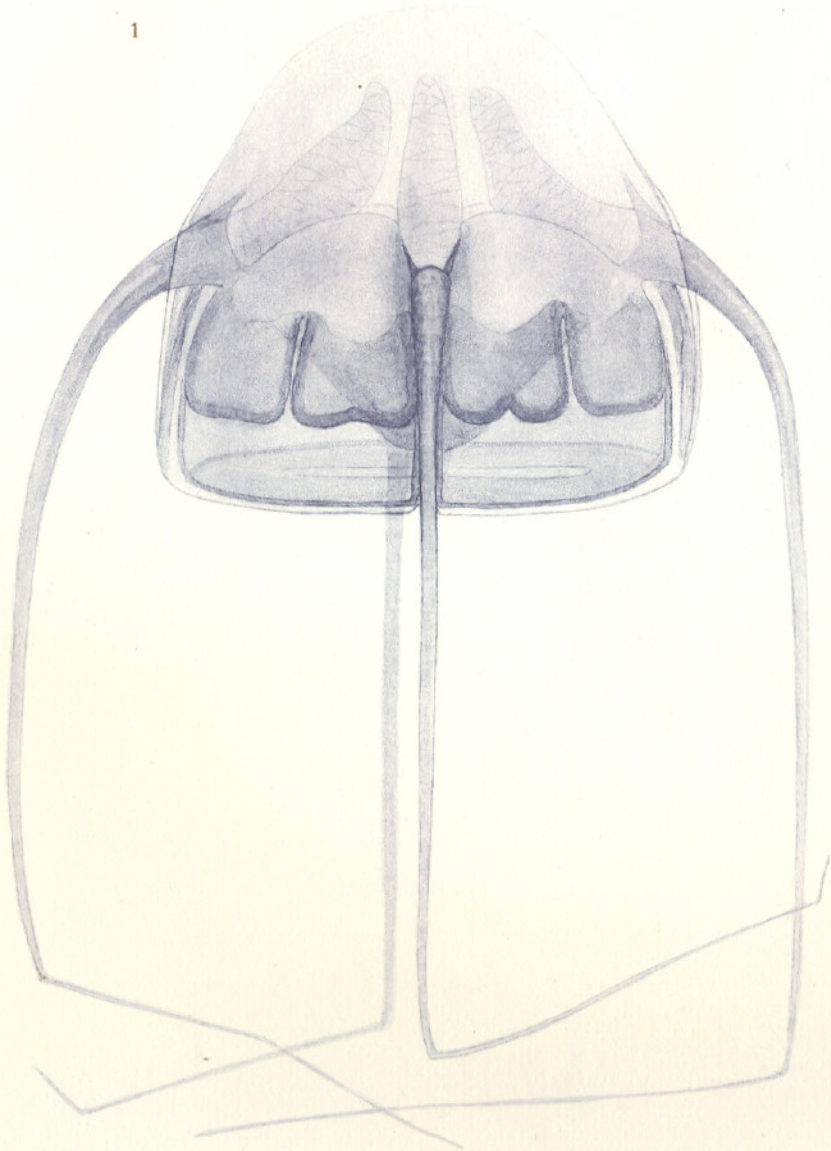
FIG. 1

Aegina citrea. Preserved specimen,
c. 18 mm. wide, 50 miles north-west of Eagle Island, Ireland,
11. viii. 04. (E. T. Browne collection.)

FIG. 2

Solmaris corona. Preserved specimen,
c. 12 mm. in diameter, Valencia, 11. viii. 99.
(E. T. Browne collection.)

1



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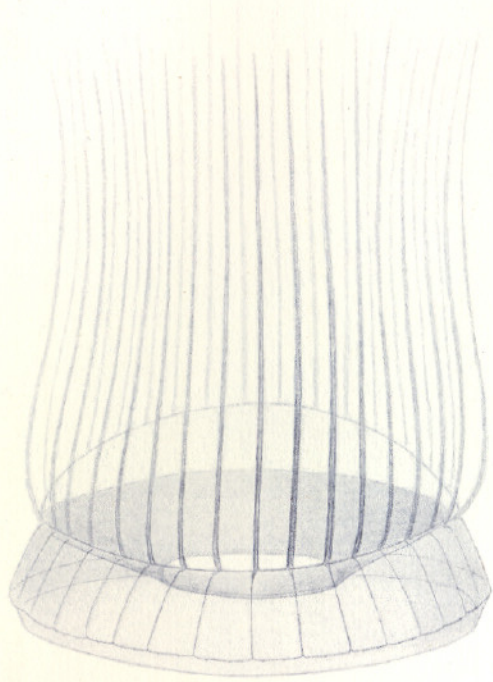

Plate XXVIII

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PLATE XXIX. *Turritopsis nutricula*, Plymouth.

FIG. 1

Preserved specimen, 2·2 mm. high, 3. i. 34.

FIG. 2

Preserved specimen, 3·4 mm. in diameter, 12. x. 36.

FIG. 3

Preserved specimen, 3·6 mm. high,
showing vacuolar spaces and developing planulae, 12. x. 36.

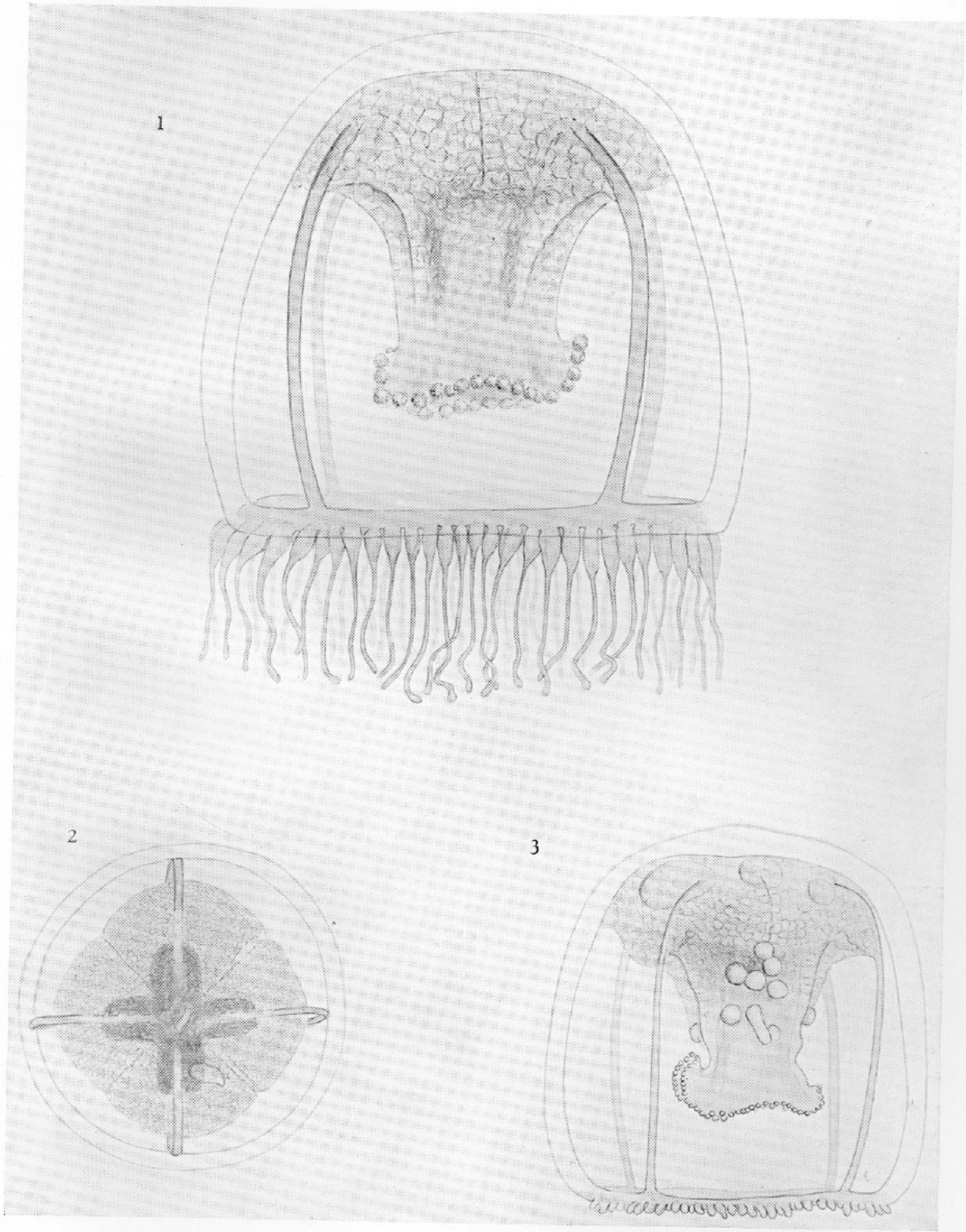

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PLATE XXX. *Leuckartiara octona*, Plymouth.
Form of gonad. Interradius.

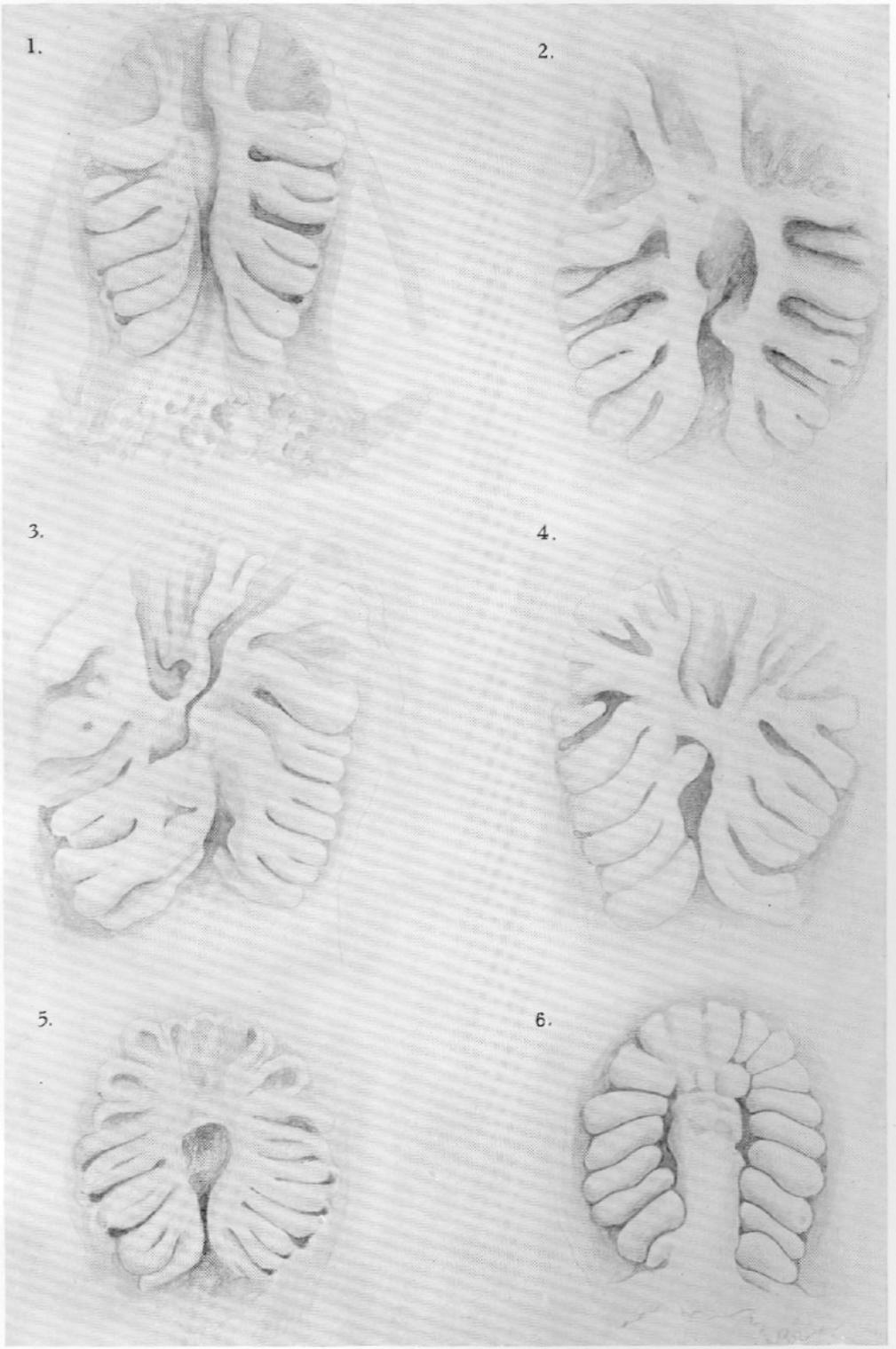
FIG. 1
Showing 'mesenteries'.

FIG. 2
Gonad.

FIGS 3, 4
Two gonads from same specimen.

FIGS. 5, 6
Outer and inner surfaces of same gonad.

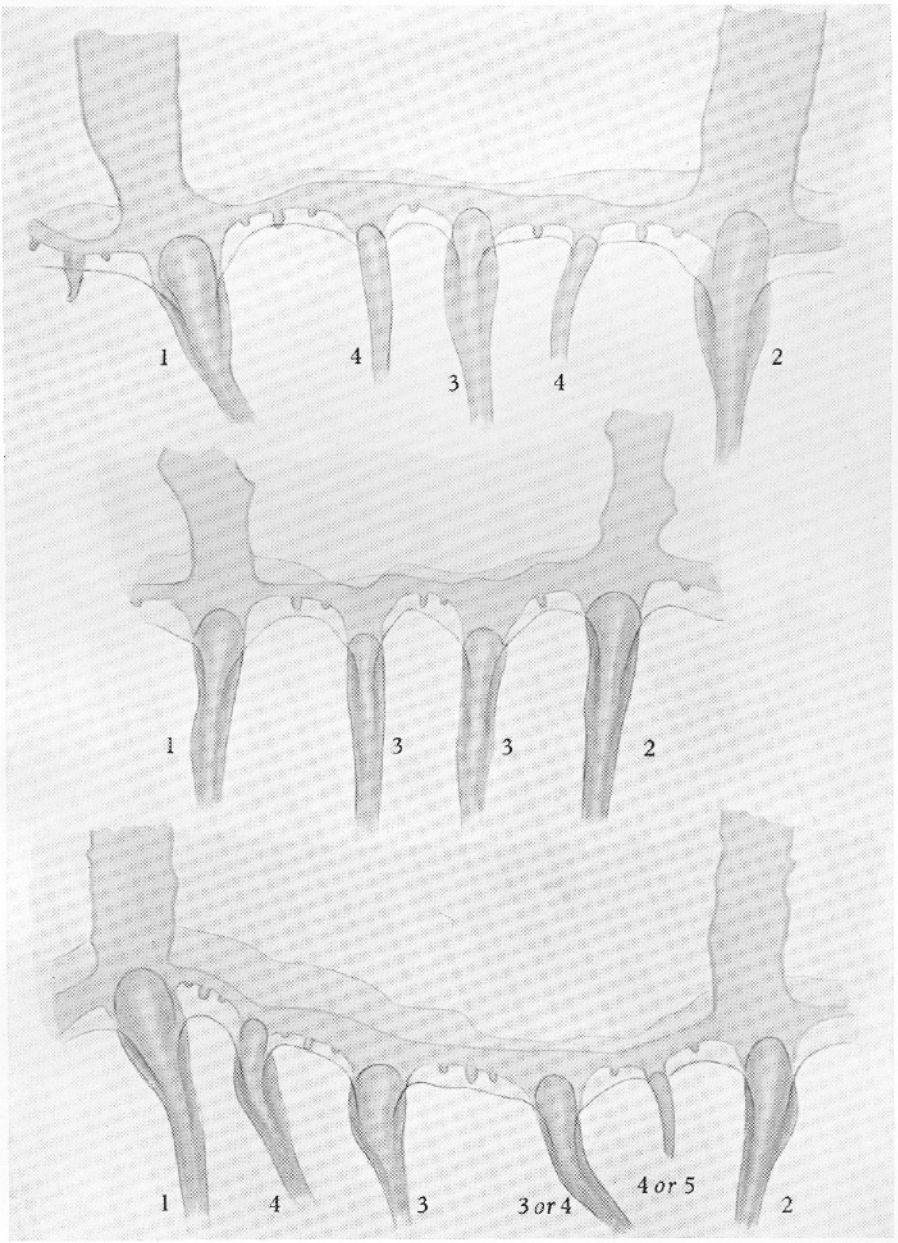
Plate XXX



Del. F.S.R.

PLATE XXXI. *Leuckartiara octona*, Plymouth, 4. vi. 25.
Segments of umbrella margin showing octagonal and duodecimal types of development of marginal tentacles, seen from exumbrellar side, preserved (see p. 191).

Plate XXXI



Del. F.S.R.

PLATE XXXII

FIG. 1

Aequorea forskalea, young preserved specimen, Plymouth.

FIG. 2

Aequorea forskalea, preserved adult medusa, Plymouth.

FIG. 3

Aequorea vitrina, preserved adult medusa, Plymouth.

All slightly enlarged.

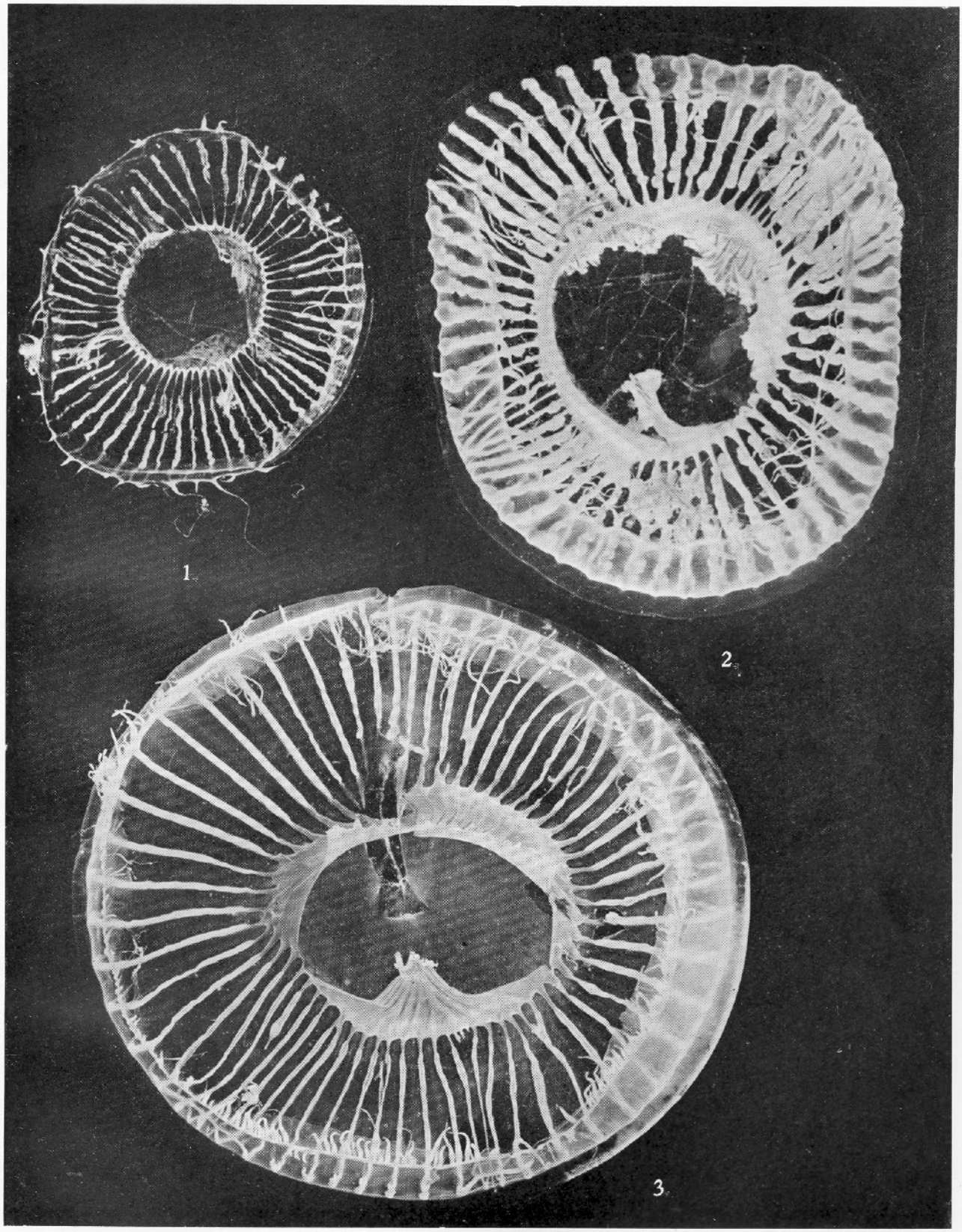


Photo. D. P. Wilson

PLATE XXXIII

FIGS. 1–4

Aequorea pensilis, preserved young specimens, Plymouth.

FIG. 5

Aequorea pensilis, preserved adult medusa, Plymouth.

Plate XXXIII

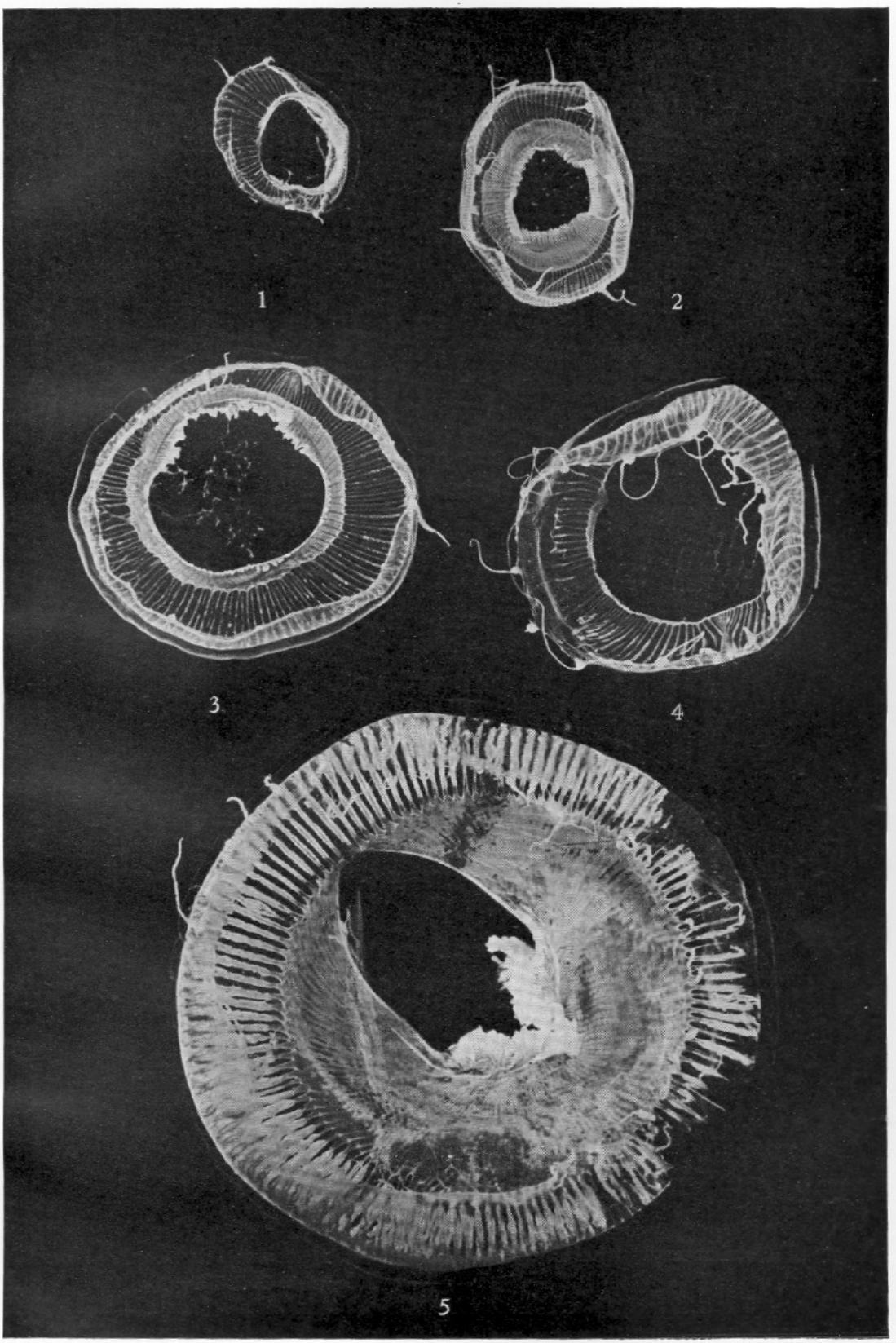


Photo. D. P. Wilson

PLATE XXXIV. Various living Medusae.

FIG. 1

Sarsia gemmifera, × 35. Plymouth.
Photographed 14. vi. 49.

FIG. 2

Steenstrupia nutans, × 23. Plymouth.
Photographed 1. vi. 51.

FIG. 3

Medusa from the hydroid *Trichydra pudica*
sent by Dr H. O. Bull from Cullercoats, × 29. Aboral view.
Photographed 29. v. 51.

FIG. 4

Medusa from the hydroid *Trichydra pudica*
sent by Dr H. O. Bull from Cullercoats, × 32.
Photographed 29. v. 51.

FIG. 5

Lizzia blondina, × 40. Optical section of bell contracting
showing protrusion of velum.
Plymouth. Photographed 9. v. 51.

FIG. 6

Lizzia blondina, × 32.
This is a larger specimen than that shown in Fig. 5.
Plymouth. Photographed 9. v. 49.

FIG. 7

Aequorea sp. newly liberated from the hydroid
Campanulina sent by Dr H. O. Bull from Cullercoats, × 53.
Photographed 25. vi. 51.

Photomicrographs by electronic flash of approx. 1/3,000 sec. duration.

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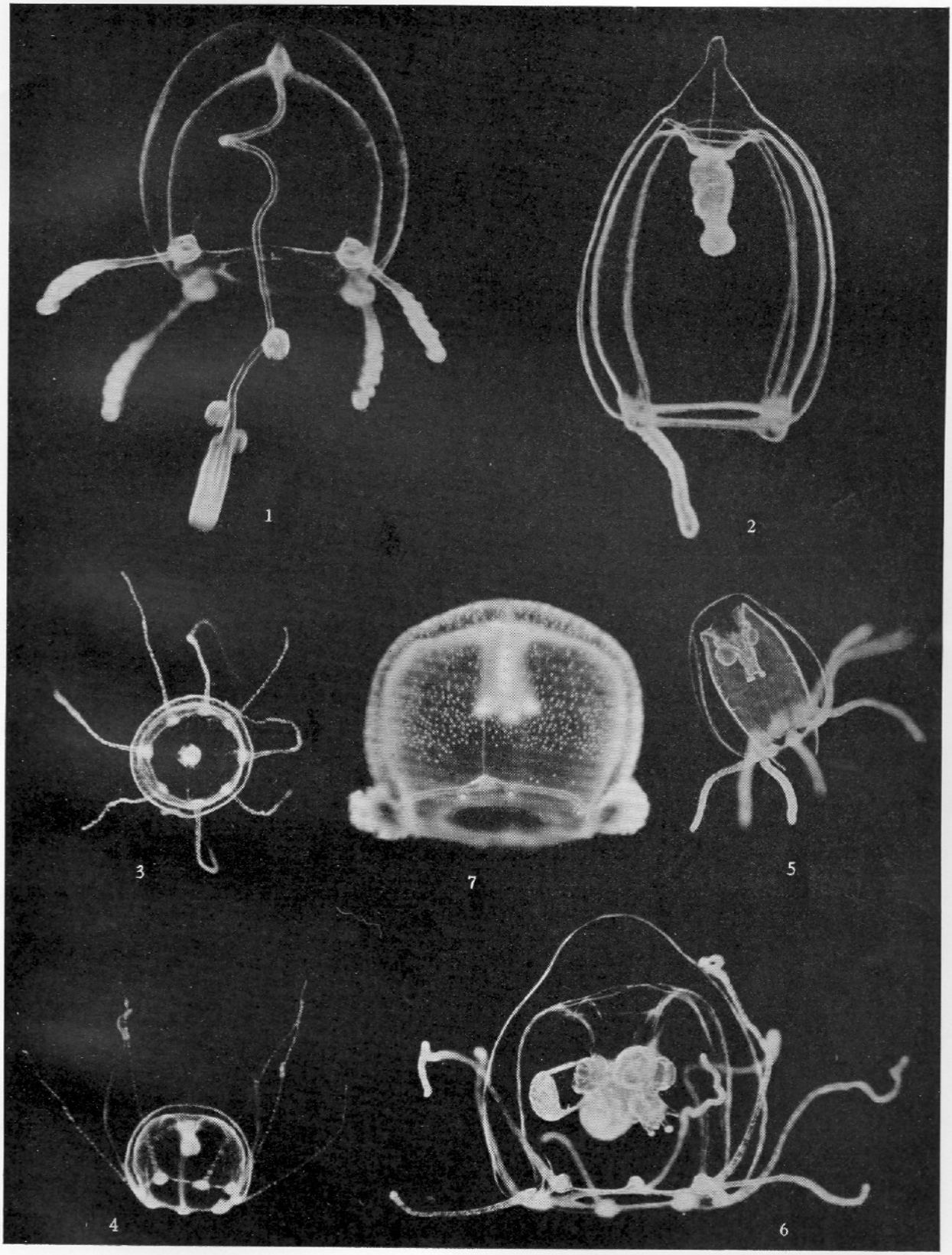

Photo. D. P. Wilson

PLATE XXXV. *Gonionemus murbachi.*

Specimens of medusae sent by Dr H. O. Bull from the Dove Marine Laboratory tanks, Cullercoats, and reared in the Plymouth laboratory, May–July, 1951.

FIG. 1

Young medusa, ×23. Photographed 2. v. 51.

FIG. 2

Oral view of the medusa shown in Fig. 1, ×27.
The marginal vesicles are clearly visible.

FIG. 3

An older medusa, ×9. Photographed 6. vi. 51. This is a characteristic quiescent attitude between pulsations when swimming; the tentacles are contracted and acutely bent.

FIG. 4

A swimming medusa with bell contracting and velum protruding, ×9.
Photographed 11. vi. 51.
The developing gonads are clearly visible.

FIG. 5

Mature medusa in oral view, ×3.
Photographed 4. vii. 51.

FIG. 6

Mature medusa in lateral view, ×3.
Photographed 7. vii. 51.

FIG. 7

Mature medusa in oblique aboral view, ×3.
Photographed 7. vii. 51.
The medusa is slightly heeled over to the right to show the full extent of one mature gonad.

Photomicrographs (Figs. 1–2) and photographs (Figs. 3–7) of living specimens. Exposures by electronic flash of approx. 1/3,000 sec. duration.

(Copyright D. P. Wilson)

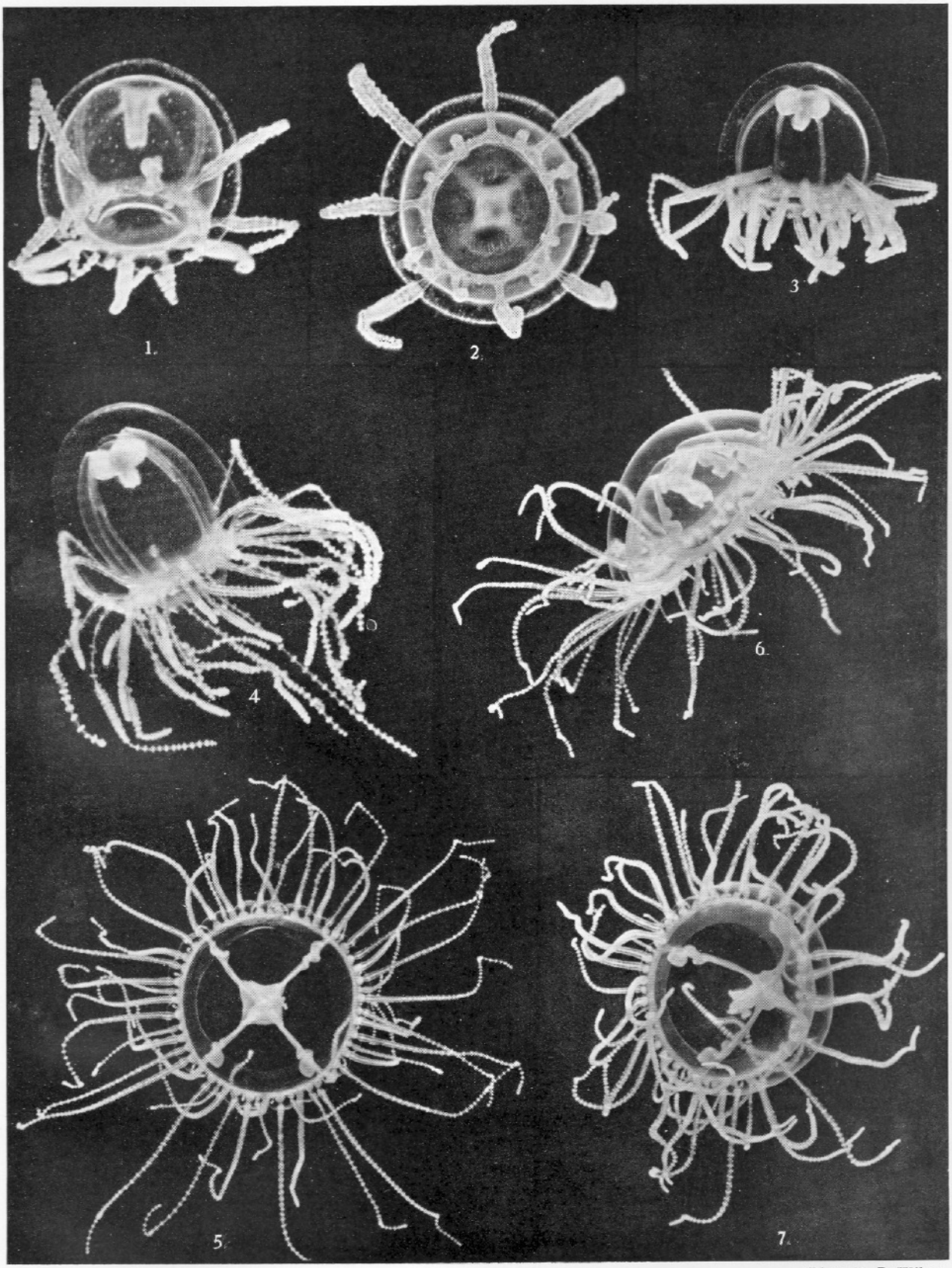

Photo D. P. Wilson.