

THE VIVIPAROUS SCYPHOMEDUSA *STYGIOMEDUSA FABULOSA* RUSSELL

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(Plates I-IV and Text-figures 1-7)

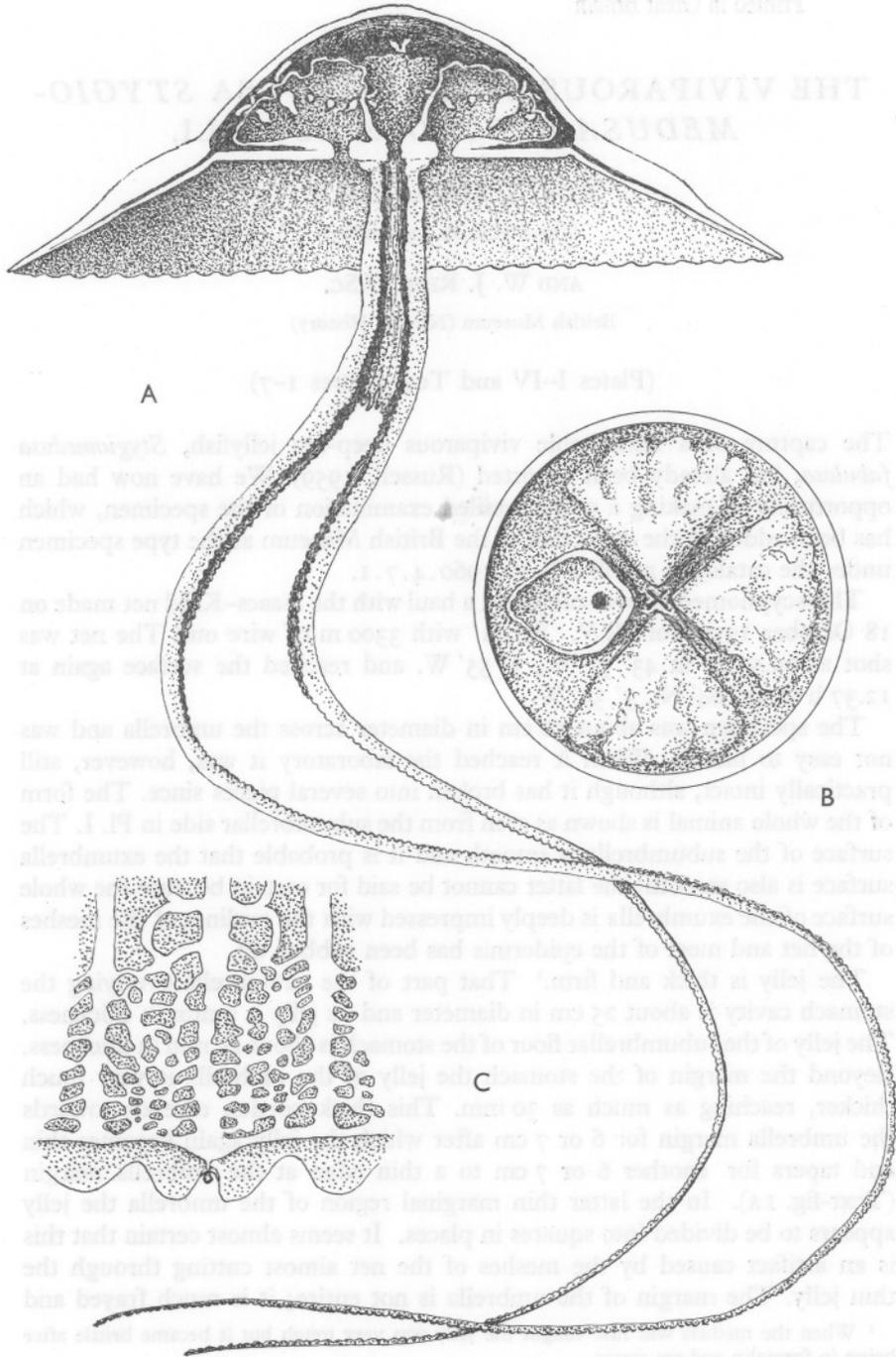
The capture of a remarkable viviparous deep-sea jellyfish, *Stygiomedusa fabulosa*, has already been reported (Russell, 1959). We have now had an opportunity of making a more detailed examination of the specimen, which has been added to the collection of the British Museum as the type specimen under the catalogue number B.M. 1960.4.7.1.

This scyphomedusa was caught in a haul with the Isaacs-Kidd net made on 18 October 1959 from R.V. 'Sarsia' with 3300 m of wire out. The net was shot at 05.53 hr in 43° 51' N., 3° 55' W. and reached the surface again at 12.37 h in 44° 04' N., 3° 39' W.

The specimen was about 50 cm in diameter across the umbrella and was not easy to handle. When it reached the laboratory it was, however, still practically intact, although it has broken into several pieces since. The form of the whole animal is shown as seen from the subumbrellar side in Pl. I. The surface of the subumbrella is smooth and it is probable that the exumbrella surface is also smooth; the latter cannot be said for certain because the whole surface of the exumbrella is deeply impressed with the outlines of the meshes of the net and most of the epidermis has been rubbed off.

The jelly is thick and firm.¹ That part of the exumbrella overlying the stomach cavity is about 25 cm in diameter and its jelly is 9 mm in thickness. The jelly of the subumbrellar floor of the stomach is about 15 mm in thickness. Beyond the margin of the stomach the jelly of the umbrella is very much thicker, reaching as much as 30 mm. This thick portion extends towards the umbrella margin for 6 or 7 cm after which the jelly again becomes thin and tapers for another 6 or 7 cm to a thin edge at the umbrella margin (Text-fig. 1A). In the latter thin marginal region of the umbrella the jelly appears to be divided into squares in places. It seems almost certain that this is an artifact caused by the meshes of the net almost cutting through the thin jelly. The margin of the umbrella is not entire; it is much frayed and

¹ When the medusa was first caught the jelly was very tough but it became brittle after being in formalin and sea water.



Text-fig. 1. *Stygiomedusa fabulosa*: A, half section of complete medusa, the two sectioned brood chambers have been pulled apart to show the one behind; B, vertical view of stomach cavity after removal of exumbrella wall to show arrangement of four brood chambers, one of which has been sectioned near its base to show subumbrellar aperture; C, tracing of enlarged photograph of portion of umbrella margin of young medusa to show gastrovascular canal system (white), marginal lappets and rhopalium. (Del. F. S. R.)

incised, and only in a few places can it be seen that it has shallow rounded lappets. As will be seen later from the description of the young medusa, it is probable that these should have been 60 in number.

There is a weakly developed subumbrellar coronal muscle in the area of the thickened jelly; the muscle fibres are striated.

In the subumbrellar wall of the stomach there are four round interradial apertures each about 15 mm in diameter and situated about 6 cm from the centre of the cross-shaped mouth opening.

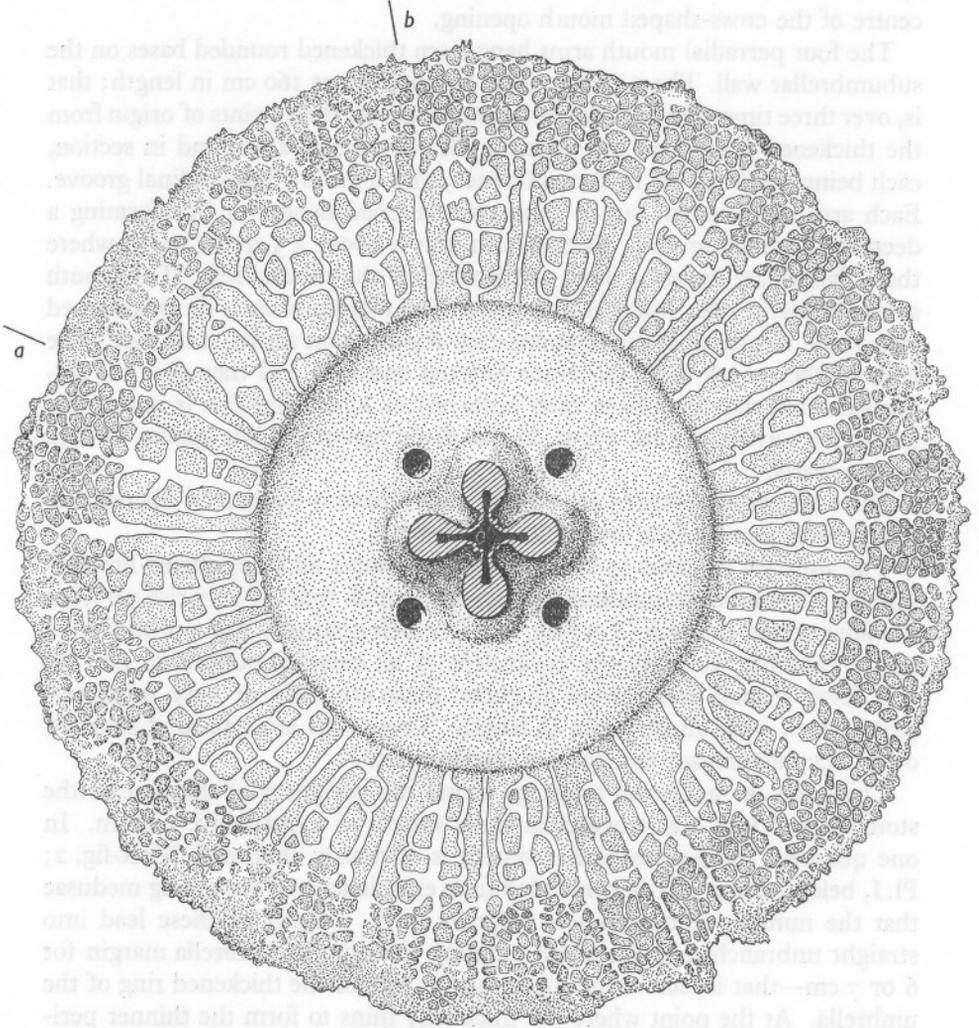
The four perradial mouth arms hang from thickened rounded bases on the subumbrellar wall. These mouth arms are each about 160 cm in length; that is, over three times the diameter of the umbrella. At their points of origin from the thickened pedicel on the subumbrella they are nearly round in section, each being about 11 cm in circumference, with a narrow longitudinal groove. Each arm soon widens out to form two flattened flanges or lips forming a deep longitudinal groove. Each mouth arm is about 4.5 cm in width where these flanges are widest a short distance below the subumbrella. The mouth arms gradually taper towards their ends. The margin of each lip is scalloped with small semicircular crenulations each about 5 mm across at its base. The ends of the mouth arms are much tattered and torn and they give the impression that they may have been branched or lobed, but this is impossible to say for certain. In any event, in this distal region the lips appear to have hollow warts.

For a length of about 15 cm a basal mouth tube is formed by filamentous frilled webs joining each arm to its neighbour.

The stomach is about 25 cm in diameter; almost all its epithelial lining is missing. Round each subumbrellar aperture thick walls of jelly rise up from the floor of the stomach (Text-fig. 1A, B) which gradually thin out to form a brood chamber, possibly the equivalent of an enlarged subgenital pit. At this level around each brood chamber there are rows of very numerous gastric cirri, each about 5 mm in length. These cirri are typical of those of other Scyphomedusae and contain nematocysts.

Thirty-six or more oval openings round the periphery of the base of the stomach lead into a gastrovascular canal system of a distinctive pattern. In one quadrant the gastrovascular system is obviously abnormal (Text-fig. 2; Pl. I, below), but it can be concluded from examination of the young medusae that the number of openings is typically forty. Twenty of these lead into straight unbranched radial canals running towards the umbrella margin for 6 or 7 cm—that is, across the subumbrellar side of the thickened ring of the umbrella. At the point where the thick jelly thins to form the thinner peripheral portion of the umbrella these straight canals start to give off side branches and they continue to do so, giving off seven or eight branches on either side, until the straight canal enters a continuous circular canal at the subumbrella margin. The side branches themselves branch.

Alternating with these twenty straight canals and also passing across the thick part of the umbrella are twenty straight canals which give off three or four successive branches on each side, each of which re-enters the succeeding branch peripheral to it. In this way a characteristic pattern is produced having the appearance of a number of B's placed back to back. On reaching the outer periphery of the thickened part of the umbrella these canal systems



Text-fig. 2. *S. fabulosa*: subumbrellar view of adult specimen to show gastrovascular canal system (white), subumbrellar apertures, and section of base of mouth tube. The inner half of the gastrovascular canal system is accurately drawn; a portion only of the fine peripheral network of canals is exactly as in the specimen, the majority being filled in to give the general appearance. Note abnormal development between a and b. ($\times c. \frac{1}{4}$) (Del. F. S. R.)

give rise to a finer branching system like that of the straight canals and all the branches anastomose round the outer 6 or 7 cm of the umbrella. Many of the areas enclosed by this anastomosis are roughly hexagonal in shape. The central canal of each of the 'B' systems of canals finally enters the marginal ring canal, as do some of the branches of the anastomosing system. Most of the actual margin of the umbrella is missing and the marginal ring canal can be seen in only a few places; but its continuity is confirmed by examination of the young medusa. In the zone of thick jelly the canals are about 5 mm in width.

There are apparently no marginal tentacles, and this is confirmed in the young. Only a few marginal rhopalia are present since so much of the umbrella margin is missing. These appear to be small simple statocysts whose stalks receive canals from the ring canal. The rhopalia, on the basis of the young medusa, are twenty in number and are situated at the ends of the 'B' systems of canals, so that these can now be called rhopalar canals as opposed to the unbranched inter-rhopalar canals.

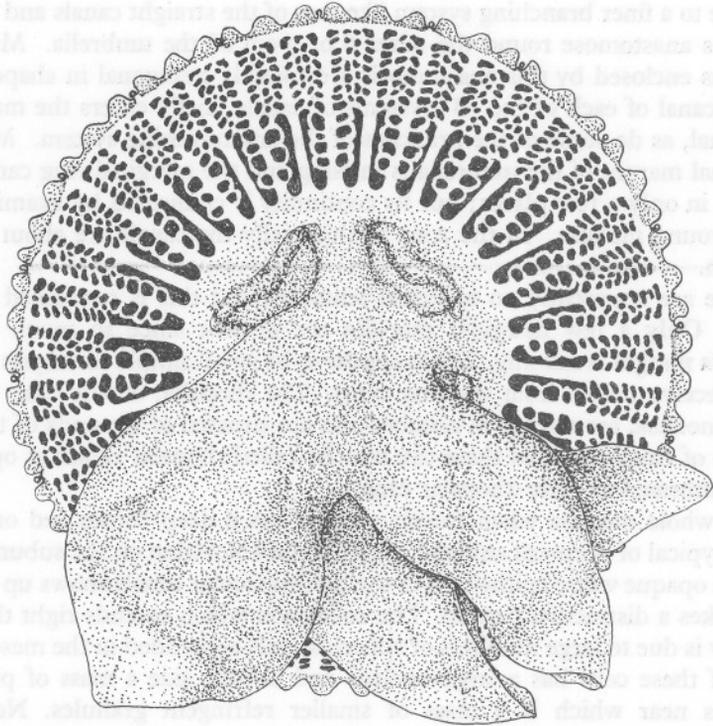
The whole medusa when freshly caught was a deep brown red or plum colour typical of deep-sea animals. Against this coloration on the subumbrella side the opaque white epithelium of the gastrovascular canals shows up clearly and makes a distinctive pattern. The coloration which extends right through the jelly is due to large numbers of spherical cells embedded in the mesogloea. Each of these cells has a large nucleus and on one side a mass of pigment granules near which is a mass of smaller refringent granules. Near the surface of the umbrella there is a thin layer of pigment granules in the mesogloea itself just beneath the surface epithelium.

The colour leaches out, making formalin and sea water pink in colour. Dr G. Y. Kennedy kindly examined the pigment for us, and finds that the bulk of it is a melanin.

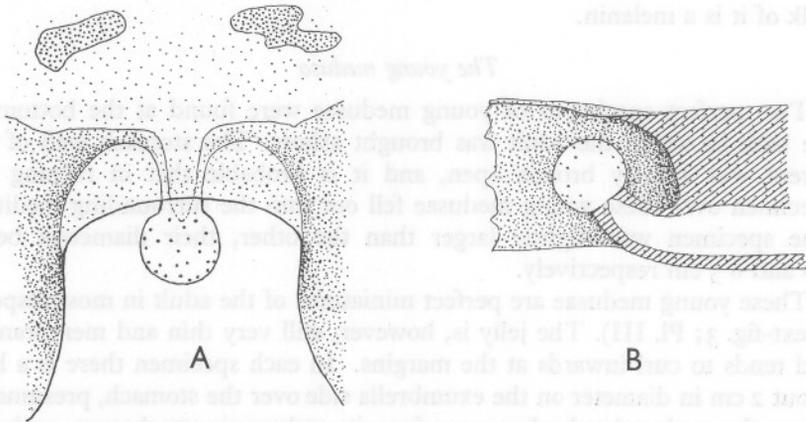
The young medusa

Two perfect specimens of young medusae were found at the bottom of the bath in which the adult was brought ashore. The stomach wall of the parent was already broken open, and it is probable that in turning the specimen over these young medusae fell out into the surrounding medium. One specimen was slightly larger than the other, their diameters being 9.6 and 8.5 cm respectively.

These young medusae are perfect miniatures of the adult in most respects (Text-fig. 3; Pl. III). The jelly is, however, still very thin and membranous and tends to curl inwards at the margins. In each specimen there is a hole about 2 cm in diameter on the exumbrella side over the stomach, presumably where the medusa has broken away from its embryonic attachment, probably prematurely. When lying flat in a dish with the subumbrellar side downwards and drained of surrounding fluid the exumbrella surface shows clearly round



Text-fig. 3. *S. fabulosa*: drawing of young medusa; the gastrovascular system has been drawn semidiagrammatically to indicate the basic pattern. (Nat. size.) (Del. F. S. R.)



Text-fig. 4. *S. fabulosa*: rhopalium of young medusa: A, exumbrellar view; B, semidiagrammatic lateral view half sectioned to show rhopalar canal; the statocyst is not sectioned. (Del. F. S. R.)

its outer half forty radiating ridges corresponding to the septa which lie between the forty main canals of the gastrovascular system. The margin of the umbrella has sixty evenly-rounded lappets and twenty marginal rhopalia. The bases of the two lappets which lie one on each side of a rhopalium together amount to about 8 mm. Between each pair of rhopalar lappets is a single lappet which is situated opposite the end of an inter-rhopalar canal and has a base about 5 mm long. The radial length of each type of lappet is about 3.5 mm. Thus there are forty rhopalar lappets and twenty inter-rhopalar lappets. In the smaller of the two specimens the lappets have not developed to the stage at which they are completely separated to their bases.

The diameter of the stomach is approximately half that of the umbrella. From it radiate forty canals separated by forty clearly seen septa. The gastrovascular canal system is developed exactly as in the adult; there are twenty rhopalar 'B' canals and twenty inter-rhopalar unbranched canals and all run into a complete marginal ring canal after branching to form the peripheral anastomosis of canals.

The mouth arms are very membranous and not yet formed like those of the adult. Their length is not quite as much as the diameter of the umbrella. They are very broad and leaf-shaped, and joined to form a circular basal mouth tube for about half their length.

At the point of origin of each mouth arm from the subumbrella surface the jelly is thickened and this stronger jelly runs radially to the outer margin of the stomach. Between these stiffened areas the subumbrellar wall of the stomach is still very thin and the brood chambers which are already forming push this thin jelly outwards as do the gonads in *Pelagia*. Presumably as the medusa grows the jelly of the stomach wall increases in thickness until only the subumbrellar apertures are left; the condition in *Stygiomedusa* approximates to that indicated by Agassiz & Mayer (1898, plate. viii, fig. 14; pl. x, fig. 23) for *Dactylometra*.

While in external appearance the walls of developing brood chambers give the impression that they might be similar to the gonads of *Pelagia*, a microscopic examination shows no obvious signs of sexual cells. The chamber has a wall of mesogloea from which tapering projections of mesogloea run towards the centre and themselves give rise to branches. The lining epithelium consists mainly of columnar cells, and interspersed at regular intervals are round cells with larger granules, and there are also nematocysts in various stages of development.

There are no marginal tentacles. There are twenty rhopalia, each consisting of a simple statocyst with a short canal entering its stalk from the ring canal. The rhopalia are colourless except for a few scattered pigment cells. The bases of the adjacent marginal lappets join to form a roof over the rhopalium which is itself directed upwards (Text-fig. 4).

The colour of the young medusae is brownish-red, and this coloration extends right through the mesogloea, as in the adult, and is due to numerous spherical cells containing pigment granules. As in the adult also the opaque whitish epithelium of the gastro-vascular system shows up its pattern, and there is also an opaque white line along the axis of each mouth arm.

Reproduction

The four brood chambers protruding into the stomach cavity are covered on the gastric side in this preserved specimen by an epithelium which is folded into narrow ridges. This epithelium consists of columnar cells with nematocysts scattered among them. Around the lower periphery of the brood chamber is a raised convoluted frill along the folds of which the gastric cirri are distributed. The whole forms a band about 20 mm high.

A little above this band, running along the side walls of the brood chamber, is a stripe of modified epithelium which may be called the germinal line (Pl. II, below), as it is from its tissue that the remarkable reproductive bodies develop. In our specimen a whole range of developmental stages can be found.

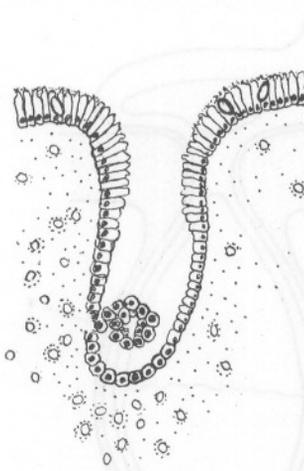
The germinal line forms a shallow groove whose epithelial cells differ from those of the surrounding columnar epithelium in being more cubical and having large rounded nuclei. The cells in the mesogloea beneath are also more numerous than elsewhere. In many places along the line there are small pits in which the cells often show an irregular arrangement. The multiplication of the epithelial cells in some of these pits produces deeper invaginations which are evidently the first stage of the processes leading to the development of the future young medusa. Text-fig. 5 shows a section of such an invagination in which there is a small clump of cells forming a vesicle, presumably the first formation of a cyst. No sexual cells could be found.

The cyst grows into an oval body with a more pointed end on the sub-umbrellar side. As this increases in size it pushes out the wall of the brood chamber so that it projects into the cavity of the chamber. At the same time at the opposite end of the cyst two outgrowths develop which run horizontally in opposite directions so that the cyst now appears T-shaped (Text-fig. 7B). At the stage when the cyst is 8-11 mm in length the tubular outgrowths run along the gastric surface of the chamber wall for 8-10 mm; the outgrowths are 2.0-2.5 mm in width.

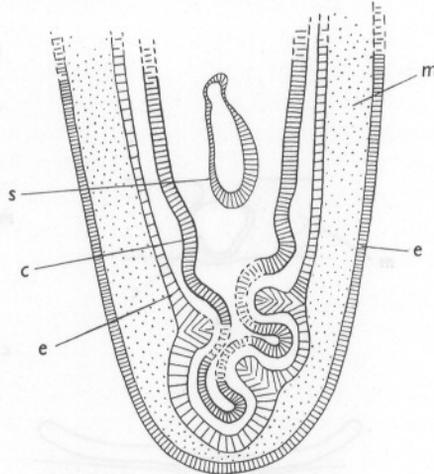
The cyst, continuing to increase in size and protruding farther into the cavity of the brood chamber, carries with it the enveloping brood chamber wall, which becomes more and more attenuated until it forms a thin membrane or capsule surrounding the cyst. At the same time the tubular outgrowths at its base grow away from the gastric wall of the chamber so that they project freely into the stomach (Text-fig. 7C).

At an early stage another body is developing within the cyst. This body we call the scyphistoma and from it a single medusa develops. From this stage onwards the cyst wall can be regarded as a chorion.

The capsule and its contents, from the outside inwards, thus consist of (a) an outer wall which is the modified wall of the brood chamber, consisting of two epithelial layers, ectodermal and endodermal in origin, with a thin mesogloea between them; (b) the cyst or chorion which consists of a single layer of tall columnar cells with an inner underlying basal membrane; these cells, presumably absorptive and secretory in function, have projections on



Text-fig. 5



Text-fig. 6

Text-fig. 5. *S. fabulosa*: section through depression on germinal line containing developing cyst. (Del. F.S.R.)

Text-fig. 6. *S. fabulosa*: diagram of longitudinal section of distal end of small capsule 8 mm long. Note the pocketed area and the young scyphistoma lying free in the cavity of the cyst. *c*, cyst; *e*, parent epithelium; *m*, mesogloea; *s*, scyphistoma. (Del. W.J.R.)

their free margins and contain very numerous granules; and (*c*) the wall of the scyphistoma which in later stages consists of two layers of epithelium with a thin layer (? mesogloea) between them.

Measurements of some of the smaller and medium-sized capsules are given in Table 1.

TABLE 1. SIZE OF CAPSULES

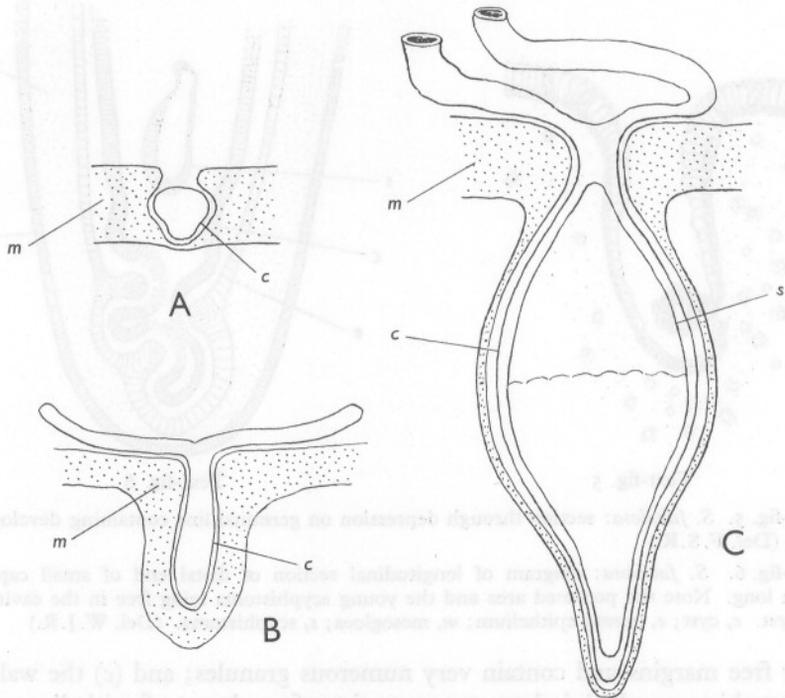
Dimensions of smaller and medium-sized capsules, projecting from the subumbrellar wall of the chamber illustrated on Pl. II (below). The measurements do not include parts embedded in the subumbrellar wall or projecting into the stomach.

	Measurements in mm							
	8.0	8.4	8.6	10.3	31.5	37.6	38.6	45.4
Total length of sub-umbrellar surface of chamber	8.0	8.4	8.6	10.3	31.5	37.6	38.6	45.4
Maximum diameter	3.0	3.0	2.4	4.0	12.0	17.6	17.8	21.3

The larger capsules over 10 mm in length are pinkish-white in colour and become oval in shape with their distal ends narrowing rather suddenly; they are thus somewhat teat-shaped, and their tips are often brown in colour.

The size of a cyst just before it begins to push out the chamber wall is 2.6 mm long and 2.0-2.3 mm in diameter.

The basal outgrowths of the cysts are hollow tubes, closed at their distal ends. They may reach a length of 20 cm, and lengths of 12-17 cm were common. Only the smaller outgrowths up to 3 cm in length are still attached and complete in our specimen. All the others were broken off near the chamber



Text-fig. 7. *S. fabulosa*. Diagrams of various stages of development of capsules. A, cyst about 2 mm long; B, showing early development of tubular outgrowths at base of cyst; C, fully formed capsule (the ends of the tubular outgrowths are shown as cut off). c, cyst or chorion; m, mesogloea; s, scyphistoma. (Del. F.S.R.)

wall and found floating loose in the fluid surrounding the medusa in its container.

These tubes have an outer layer of high columnar epithelium the cells of which have numerous granules and projections on their free margins, similar to those of the part of the chorion within the capsule. This is yellowish to orange in colour in the newly captured medusa, and in many instances the epithelium had become stripped from its basal membrane.

Inside some of the small tubes were seen many free, scattered, rounded cells some of which were in process of division. In larger tubes there were, lying free, rounded masses of cells resembling morulae, blastulae and planulae.

In the capsular portion of the chorion differentiation and formation of the scyphistoma begins at an early stage. At a capsule length of 8 mm sections revealed that the inner epithelium of the capsule wall, namely parent tissue, was much developed and pocketed in the distal tip of the capsule and that the chorion tissue was continuous in the pockets and followed their contours (Text-fig. 6). Preservation of the tissue for histological examination was, however, not at all good. Within the chorion sac, lying free in the cavity, there was a young scyphistoma 0.35 mm long. As the scyphistoma increases in size it takes the general shape of the capsule, the distal narrowed end being the developing mouth arms. Although in many of the larger capsules preservation was poor, it was possible to see the umbrella margin and the indications of a gastrovascular canal system in process of formation; but on dissection many of these disintegrated. The most developed capsule, 6.5 cm long and 4.3 cm wide, contained an almost fully developed medusa (Pl. II) complete with gastrovascular system, and mouth arms and the reddish purple coloration typical of the adult.

Some of the capsules had subsidiary capsules developing at their bases (Pl. IV, above).

In some of the capsules differentiation appears to have been abnormal and budding abortive. This feature may be linked with the four abnormal young medusae found (Russell, 1959). In these the medusa had the normal pigmentation but was flattened and pancake-shaped (Pl. IV, below). There were no mouth arms and no stomach, the digestive system being represented by a series of reticulate canals converging on a central point where the mouth should have been.

There remains the question, how does the young medusa escape from the brood chamber? Although the circular subumbrellar aperture connecting the chamber with the exterior is small (15 mm in diameter), it is possible that the young medusa, which is very plastic, might squeeze through. It should, however, be remarked that the only capsule with a very well-developed young medusa in it, although still attached to the subumbrellar wall of the brood chamber, is sticking through an opening in the wall into the gastric cavity so that the young medusa could escape through the mouth. As a few other smaller capsules had also passed through obvious tears in the wall this may not have been natural.

The excised brood chamber shown in Pl. II (below) has ten or so capsules visible to the naked eye. One cannot say how many more very small developing cysts are present. But it is evident that production of medusae is a continuous process and that the number produced by one parent medusa must be at least 50 and may be 100 or more.

Systematic position

In its structural characters *Stygiomedusa* is obviously quite a typical semaeostome scyphomedusa. In its general form and the arrangement of its gastrovascular canal system it agrees with the Ulmaridae, and it differs structurally from them only in the absence of marginal tentacles. We think that the family characters of the Ulmaridae should be enlarged to include species without marginal tentacles and that within the family there should be a new sub-family, the Stygiomedusinae of which *Stygiomedusa* would be the type genus.

DISCUSSION

Stygiomedusa fabulosa is the largest deep-water medusa known; its reddish purple colour and its viviparity are characteristics shared with many other animals living in very deep water. However, viviparity in which a few large medusae with adult characters are produced was hitherto quite unknown in the Scyphomedusae and the brood-caring mechanism by which it is achieved is unique in the history of the Cnidaria.

The brood-caring habit in its various forms is found in many benthic and bathypelagic forms and has been noted for many groups including crinoids (John, 1938), the pelagic octopod *Vitreledonella* (Joubin, 1929, p. 18) and in many gastropods (Thorson, 1950). In many species this is accomplished by the inclusion of many eggs within the single capsule and the successful ones emerge as miniature adults at the expense of the remaining eggs which are usually termed nurse cells.

In *Stygiomedusa* there are no nurse cells, nor have any sexual cells been seen; the uniqueness of its viviparity when compared with the usual methods of brood-caring will be appreciated when it is noted that it is the result of the telescoping of the metagenesis which we find in many Cnidaria and its adaptation for nursing the young medusa.

When we consider the life cycle of a common coastal Ulmarid medusa we find that it has the type of life cycle known to us in the common jellyfish *Aurelia aurita* L. Here the fertilized eggs develop into free-swimming planulae and then into polyps or scyphistomae anchored to suitable substrata in the sublittoral zone; these in turn may reproduce themselves asexually by budding or by the formation of podocysts before transforming themselves into strobilae budding off a large number of ephyrae or larval medusae. These feed on other planktonic organisms and finally acquire the characteristics of the adult. Encystment of the planula also takes place in some scyphomedusae (Rees, 1957a, p. 483), although this fact is seldom mentioned in text-books: the encysted stage, which is of variable duration, gives rise to a young scyphistoma.

In a scyphomedusa which has acquired a deep-water habit, continuation of this type of life cycle involving a benthic polyp stage is beset with difficulties.

Even if a suitable substratum could be found, food would probably be scarce both for strobilation and for the growth of the young medusa. The pelagic surface jellyfish *Pelagia perla* (Slabber) has solved this difficulty by having a more direct development in which a single egg gives rise to a single adult and it seems probable that this is what happens also in the bathypelagic medusae *Atolla* and *Periphylla*.

The hydromedusa *Bougainvillia platygaster* Haeckel is in process of becoming an oceanic species and has partly solved the difficulty of finding a suitable substratum by asexual propagation of the life cycle (Kramp, 1957; Rees, 1957*b*). In this species, the immature germinal tissue gives rise directly to stolons or polyps, which, in turn, bud off medusae. Similar phenomena, although differing in detail, have been noted in *Proboscidactyla ornata* and *Phialidium mccradyi*. Thus the familiar pattern of alternation of polyp and medusa may result either from sexual or (more rarely) asexual reproduction of the polyp phase.

Bearing this in mind, we have to consider whether *Stygiomedusa* has acquired an entirely new method of reproduction or whether the familiar Ulmarid type of life cycle has been highly modified to suit the needs of a brood-caring deep-sea species.

The cyst is produced, as has been noted, by asexual budding of parent germinal tissue and this process was hitherto not known to take place in Scyphomedusae. Apart from this, however, the life cycle is clearly a telescoped and much modified Ulmarid pattern. The germinal tissue as already noted forms a stripe of modified epithelium, and it is not possible to decide, from the single medusa available to us, whether this tissue is rudimentary or regressed, or even whether sexual reproduction also may or may not take place at some stage in the life of the medusa. In *Bougainvillia platygaster*, where a parallel case of asexual propagation is known, Kramp (1957) emphasized that 'all the specimens were immature'.

The asexually produced cysts lie in endodermal pockets in the roof of the brood chamber and are analogous with the podocysts of *Chrysaora* and *Cyanea* that may arise either from fertilized eggs or asexually from the bases of scyphistomae. In podocysts of *Chrysaora* and *Cyanea* the contents become organized within the cyst to form ectoderm and endoderm separated by mesogloea so that when the polyp emerges it quickly assumes the form of a scyphistoma. It appears likely that this preliminary differentiation into tissues also takes place in *Stygiomedusa*, but so far as we are aware no obvious primary polyp is formed.

The body within the cyst or chorion sac, which we regard as an atentacular scyphistoma and which is present when the capsule is less than 8 mm in length, results in the budding of a single medusa. This type of monodisk strobilation is also found in the rhizostome medusa *Cotylorhiza tuberculata* (Claus, 1892). The young medusae retain their connexion with the central

lumen of their scyphistomae until almost fully formed, and those with a hole in the top of the umbrella found floating freely in the container (see p. 307) had obviously been torn out of their capsules before they were quite ready for liberation.

It is considered that the abnormal medusae found in this species represent some accident or failure in the normal course of development.

Some shallow-water Scyphomedusae protect their young until the planula stage; in *Aurelia* the fertilized eggs are 'retained in small pouches near margins of the free edges of mouth-arms and finally set free in the planula stage' (Mayer, 1910, p. 625). *Cyanea* behaves similarly but nothing more elaborate than this was known, so that *Stygiomedusa* is unique in the complexity of its brood-caring mechanism.

Many deep-water organisms are thought to have been evolved by migration from shallow or surface water, and *Stygiomedusa* is probably no exception. Encystment of the larvae, such as frequently occurs in *Chrysaora* and *Cyanea*, was probably a major factor in enabling the life cycle to take place in the parent medusa. In this way the jellyfish became independent of a substratum for its polypoid phase.

To sum up, the uniqueness of the reproduction of *Stygiomedusa* will be appreciated from the fact that the cyst wall acts as a chorion for the scyphistoma and draws its nourishment directly from the lumen of the parent by means of its tube-like projections.

Our grateful thanks are due especially to Dr J. S. Alexandrowicz who has prepared many sections and helped us considerably in the interpretation of the process of development of the young medusa. We would like also to thank Mrs E. A. Peace for the photographs in Pls. I, II and III, Mr P. J. Green for those in Pl. IV, and Lt.-Cdr. C. A. Hoodless and the crew of R.V. 'Sarsia' for their care in bringing the medusa safely to Plymouth.

SUMMARY

A description is given of the deep-sea scyphomedusa *Stygiomedusa fabulosa* Russell. In general structure this is a typical semaeostome medusa except that it has no marginal tentacles. It is 50 cm in diameter and has the deep reddish colour typical of a deep-sea medusa, due to a melanin.

The medusa is remarkable in that it has an unusual method of asexual reproduction and is viviparous. The young medusae are developed in capsules projecting into the cavities of four brood chambers which protrude into the stomach.

Special cells along a germinal line of the endodermal epithelium of the brood pouch give rise to cysts which have tubular outgrowths into the stomach cavity. Each cyst produces a simple sac lying within it which may be

regarded as a scyphistoma giving rise to a single medusa. The cyst then acts as a chorion passing nourishment to the developing medusa.

The significance of this method of reproduction is discussed.

REFERENCES

- AGASSIZ, A. & MAYER, A. G., 1898. Studies from the Newport Marine Laboratory. No. XLI. On *Dactylometra*. *Bull. Mus. comp. zool., Harv.*, Vol. 32, pp. 1-11, pl. I-XIII.
- CLAUS, C., 1892. Über die Entwicklung des Scyphostoma von *Cotylorhiza*, *Aurelia* und *Chrysaora*, sowie über die systematische Stellung der Scyphomedusen. II. *Arb. zool. Inst. Univ. Wien*, Bd. 10, pp. 1-70, Taf. I-III.
- JOHN, D. D., 1938. Crinoidea. 'Discovery' *Rep.*, Vol. 18, pp. 121-222, pls. III-IV; 24 text-figs.
- JOUBIN, L., 1929. Notes préliminaires sur les céphalopodes des croisières du Dana (1921-22). Deuxième Partie. Octopodes. *Ann. Inst. océanogr. Paris*, Tome VI, Fasc. 1, pp. 1-24, 21 text-figs.
- KRAMP, P. L., 1957. Hydromedusae from the Discovery Collections. 'Discovery' *Rep.*, Vol. 29, pp. 1-128, pl. 1-7; text-figs. 1-19.
- MAYER, A. G., 1910. Medusae of the World. Vol. III. The Scyphomedusae. *Publ. Carnegie Inst.*, No. 109. Washington.
- REES, W. J., 1957*a*. Evolutionary trends in the classification of capitate hydroids and medusae. *Bull. Brit. Mus. (nat. Hist.) Zool.*, Vol. 4, pp. 453-534, Plates 12-13, 58 text-figures.
- 1957*b*. Hydromedusae from the Southern Ocean. *Nature, Lond.*, Vol. 179, pp. 618-19, 2 text-figs.
- RUSSELL, F. S., 1959. A viviparous deep-sea jellyfish. *Nature, Lond.*, Vol. 184, pp. 1527-9.
- THORSON, G., 1950. Reproduction and larval ecology of marine bottom invertebrates. *Biol. Rev.*, Vol. 25, pp. 1-45, 6 text-figs.

EXPLANATION OF PLATES I-IV

PLATE I

Stygiomedusa fabulosa. *Above*, complete specimen; there is a metre rule in front of it. *Below*, portion of umbrella margin to show pattern of gastrovascular canal system; the central section is abnormal. A bit of the brood chamber and capsular tissue is projecting through the subumbrellar aperture.

PLATE II

S. fabulosa. *Above*, the four brood chambers seen from above after removal of the exumbrellar wall of the stomach. In the right-hand top corner there is a capsule containing a nearly fully developed young medusa; this and a few other capsules are protruding into the gastric cavity through openings or tears in the wall of the brood chamber. *Below*, an excised brood chamber seen from the subumbrellar side: the capsule with the young medusa can be seen projecting beyond the centre of the lower margin. The arrow points to the germinal line.

PLATE III

S. fabulosa: two views of one of the young medusae. In the lower photograph a developing brood chamber can be seen at the base of the right-hand mouth arm. (*Ca. nat. size*).

PLATE IV

S. fabulosa. *Above*, enlarged photograph of capsule to show subsidiary capsule at its base. *Below*, abnormal young viewed by transmitted light; the specimen is torn.



(Facing p. 318)

