ON THE DEVELOPMENT OF *MUGGIAEA ATLANTICA* CUNNINGHAM

By F. S. Russell, B.A., F.R.S.

Naturalist at the Plymouth Laboratory

(Text-figs. 1–6)

In September 1937 *Muggiaea atlantica* Cunningham was very abundant off Plymouth. The presence of large numbers of eudoxids in the plankton afforded an opportunity to rear the early stages of this siphonophore. The development of *M. kochi* (Will) was worked out by Chun (1882, 1913), and he also described the eudoxid of that species. The eudoxid of *M. atlantica* has, however, never been described for certain. The allocation of eudoxids collected in the plankton to their respective species is necessarily fraught with uncertainty when more than one species is present. Throughout the whole of September 1937 *M. atlantica* was the only species of siphonophore to be found off Plymouth, and there can be no reasonable doubt that the eudoxids described below belonged to that species and that the development of the early stages from their eggs is that of *M. atlantica*.

For the terminology used in the description of the eudoxid I have followed Totton (1932), to whom I am grateful for helpful advice.

The Eudoxid

The *bract* (Fig. 2 *a*) is cone-shaped with a broad flat suture running from its apex to the base. The edges of the suture are raised into a slight flange. The right edge is continued downwards into a sweeping curve while the left edge cuts away horizontally at its lower end; the bract is thus asymmetrical. There is a slight cavity on the lower surface in which the somatocyst is centrally placed. The general form of the bract can also be seen in the different views of the whole eudoxid given in Fig. 1. The largest bract seen had an overall height of 1·9 mm.

The *gonophore* bell (Fig. 1) is cylindrical and has four longitudinal ridges running from the apex to the velar opening with a spiral twist to the right. The two ventral ridges are prolonged below the velar opening and join to form a short curved mouth-plate. The right ventral ridge is more strongly developed than any of the others (Fig. 2 *b*). Specimens with left-handed twisting, or "mirror images", are common (Fig. 2 *c*) and are presumably the second gonophores to be budded. The edges of the ridges are quite smooth, although some may show very faint traces of irregularity. The manubrium in fully developed gonophores extends more than two-thirds the length of the subumbrella cavity and has a pink tip. The radial canals follow the spiral courses of the ridges.

The height of the whole eudoxid is usually about 2–2·5 mm.; isolated gonophore bells have been found up to 2·2 mm. in height. One eudoxid was seen with twenty-one nematocyst batteries on its tentacle.

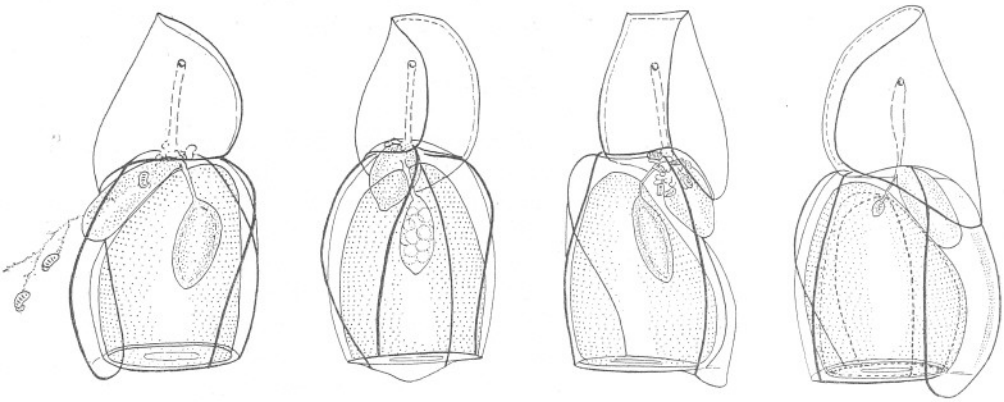
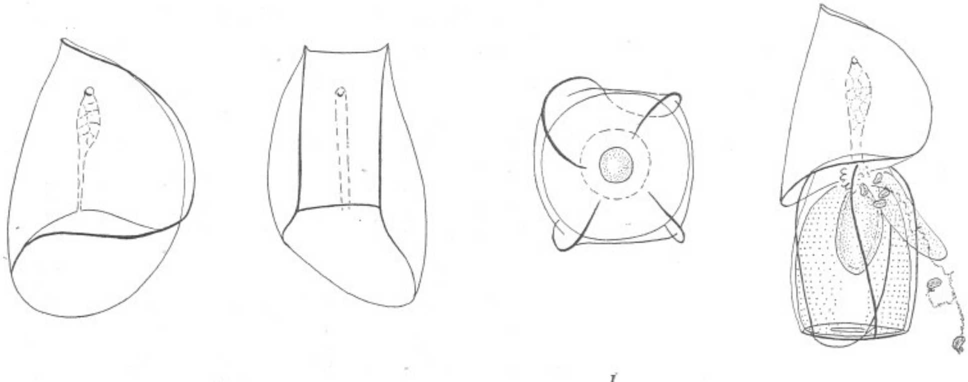


Fig. 1. Different views of eudoxids of *Muggiaea atlantica*, Plymouth, Sept. 1937. Height of original specimens from left to right 2·5, 2·5, 2·4 (bract somewhat twisted above gonophore) and 1·8 mm.



a *b* *c*

Fig. 2. Eudoxid of *Muggiaea atlantica*, Plymouth, Sept. 1937. *a*, lateral and ventral views of bract; overall height 1·7 mm.; *b*, apical view of gonophore; the ventral side is uppermost; *c*, eudoxid with "mirror image" gonophore; total height 2·2 mm.

The figures given here are drawings of living specimens; when preserved the gonophore bell appears much more angular and the ridges are more prominent owing to the contraction of the bell. In many dead or dying gonophores the apex showed the inflated condition figured by Totton (1932, fig. 33 *B*) for *Lensia subtiloides*.

No essential difference can be seen between my figures and the drawing given by Chun (1882) of the eudoxid of *Muggiaea kochi*. The only difference in Moser's (1925) account of the eudoxid of *M. kochi* is that the gonophore bell is laterally flattened; this, however, is probably an effect of preservation.

As already stated the circumstances under which my eudoxids were obtained practically remove all doubt that they belong to *M. atlantica*. Since for some years previous to 1936 *M. kochi* completely took the place of *M. atlantica* off Plymouth (Russell, 1934), I have been able to refer to previous collections. Some eudoxids were found with a sample of *M. kochi* taken on October 12 1933. When these were placed beside eudoxids of *M. atlantica* caught this year no differences could be detected, and we must conclude that the eudoxids of the two species are probably indistinguishable, at any rate in their grosser features.

The Early Development

A number of successful fertilizations from the eudoxids of *M. atlantica* were made in the Laboratory in September 1937, and the development was observed until the first appearance of the secondary nectophore.

The eggs are transparent, 0·25 mm. in diameter, and float near the surface of the water. Segmentation is regular, a spherical ciliated embryo being formed 0·27 mm. in diameter; this quickly becomes pear-shaped and within 24 hours develops into a typical elongated planula *ca.* 0·37 mm. in length. The rudiments of the primary nectophore soon appear as slight bulges on one side of the planula and proliferation of the posterior cells to form the siphon takes place. At this stage there is a pinkish tinge along that side on which development occurs. In less than 36 hr. the cavity of the primary nectophore is already formed and the somatocyst appearing (Fig. 3). Within 48 hr. the nectophore is fully formed (Fig. 3) and pulsating. The whole larva, umbrella included, is ciliated, so that when not moving by pulsation it rotates slowly by ciliary action. A cushion develops on the exumbrella on either side of the remains of the planula and a hydroecial groove is formed. By the next day all signs of the original tissue of the planula have disappeared and the primary nectophore is fully developed with somatocyst, siphon, tentacle with seven or eight nematocyst batteries and the rudiments of the secondary nectophore. Figs. 3, 4 show the course of development of specimens reared in the laboratory from the planula to the fully developed primary nectophore. The latest stage there shown is apparently abnormal, for specimens taken from the plankton at the same stage of development were larger and much higher (Fig. 5). In those from the plankton there was also an oil globule in the somatocyst showing that the animals had fed. The laboratory reared specimens were not fed and later development has probably taken place at the expense of the tissues, resulting in abnormal shape in the bell. After examination of a number of specimens from the plankton ranging between 0·9 and 1·3 mm. in height it

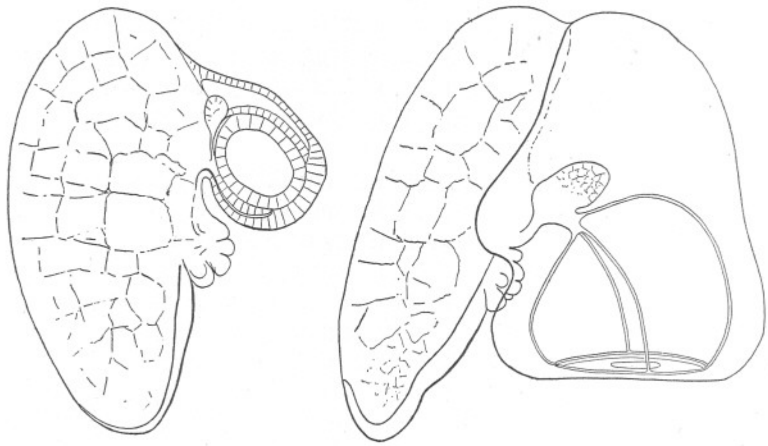


Fig. 3. Developing embryos of *Muggiaea atlantica* reared in the laboratory at Plymouth, Sept. 1937. Left, *ca*. 36 hr. old, length of planula 0·37 mm. Right, less than 48 hr. old, umbrella height 0·38 mm.

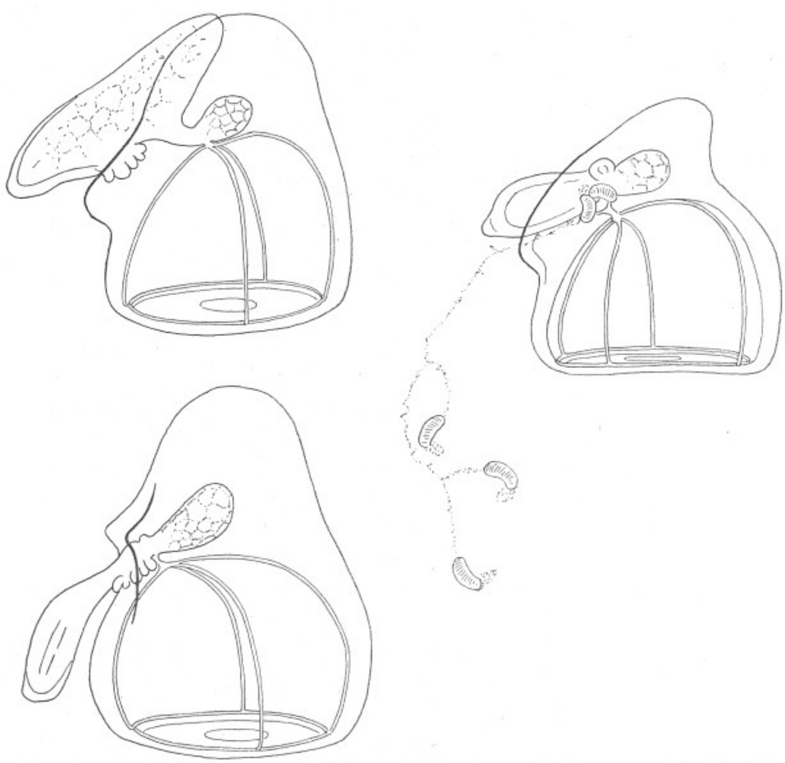


Fig. 4. Development of primary nectophore of *Muggiaea atlantica* reared in the laboratory at Plymouth, Sept. 1937. Lower left, 0·56 mm. high; right 0·5 mm. high, shape of umbrella abnormal; the developing secondary nectophore is just appearing.

appears that the normal shape is that shown in Fig. 5, though an occasional specimen more like that reared in the laboratory was found.

No specimens were seen in which the primary and fully developed secondary nectophores were both present together. But very small secondary nectophores were found with the remains of their attachment to the primary nectophore still present (Fig. 6), and many cast primary nectophores were also seen loose in the plankton. In the smallest secondary nectophore, which was

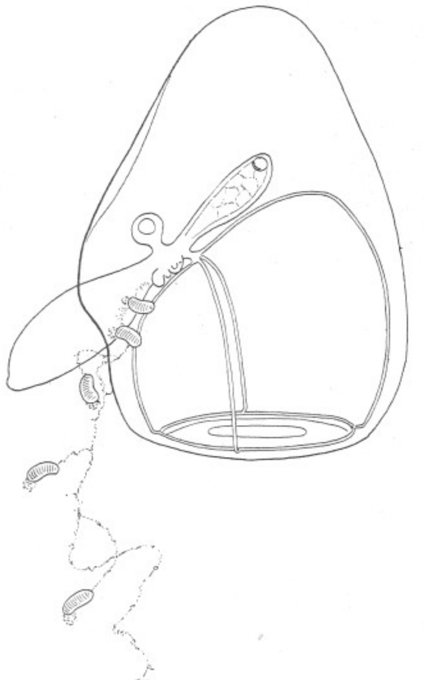


Fig. 5.

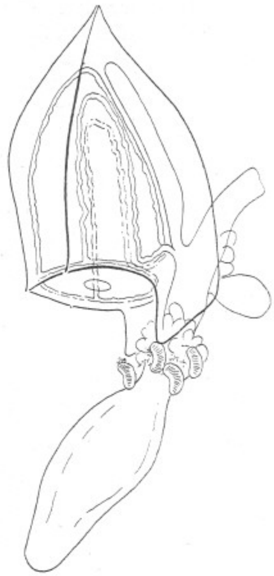


Fig. 6.

Fig. 5. Primary nectophore of *Muggiaea atlantica* 1·3 mm. high, normal shape, from plankton, Plymouth, Sept. 1937.

Fig. 6. Secondary nectophore of *Muggiaea atlantica* recently separated from primary nectophore; height from apex to velar opening 0·67 mm., from plankton, Plymouth, Sept. 1937.

0·4 mm. in height, the somatocyst already extended to the top of the subumbrella cavity and the species could thus be identified as *M. atlantica*.

The course of development here outlined agrees with that given by Chun (1882) for *M. kochi*. The normal shape of the primary bell of *M. atlantica* differs from Chun's drawing of that of *M. kochi* in that the apical process is more dome shaped. In view of the variability of this character it is not certain whether Chun's figure is that of a normal specimen and it is possible that the two species would be hardly distinguishable at this stage unless it be in the microscopic structure of the nematocyst batteries. Once the secondary nectophore is developed, however, the two species become at once recognizable by the difference in the lengths of the somatocyst, that in *M. kochi* being much the shorter.

REFERENCES

CHUN, CARL, 1882. Über die cyklische Entwickelung und die Verwandtschaftsverhältnisse der Siphonophoren. *Sitz. König. Preuss. Akad. Wiss. Berlin*, Phys.-Math. Kl., Bd. LII, pp. 1155–72.

— 1913. Über den Wechsel der Glocken bei Siphonophoren. *Ber. Verh. König. Sächs. Ges. Wiss. Leipzig*, Math.-Phys. Kl., Bd. LXV, pp. 27–41.

MOSER, F., 1925. Die Siphonophoren der Deutschen Südpolar-Expedition 1901–1903, zugleich eine neue Darstellung der ontogenetischen und phylogenetischen Entwickelung dieser Klasse. *Deutsche Südpolar-Exped.*, Bd. XVII, Zoologie, Bd. IX, pp. 1–541.

RUSSELL, F. S., 1934. On the occurrence of the siphonophores *Muggiaea atlantica* Cunningham and *Muggiaea kochi* (Will) in the English Channel. *Journ. Mar. Biol. Assoc.*, Vol. XIX, pp. 555–8.

TOTTON, A. K., 1932. Siphonophora. *Great Barrier Reef Exp.* 1928–29. *Sci. Rep.*, Vol. IV, No. 10, pp. 317–74, Brit. Mus. (Nat. Hist.).