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# PLYMOUTH:

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# On the Development of some British Echinoderms.

By

Dr. Th. Mortensen, Copenhagen.

With Figures 1-15 in the Text.

For several years I have felt the desire of going to Plymouth in order to gain practical knowledge of the excellent methods for rearing pelagic larvæ of marine animals, which have been worked out there, especially by the Director of the Marine Biological Laboratory, Dr. E. J. Allen. I was therefore very glad to receive last year an invitation from Dr. Allen to come and stay some time at his laboratory, and having got a grant for this purpose from the Carlsberg Fund and from the Danish Government, I had at length the desired opportunity.

The time I spent in Plymouth—from June 10th to July 15th this summer (1913)—was long enough for learning the methods, but, unfortunately, too short for having the full profit of my rearings, because several of the larvæ take a longer time to reach their full size and still more to pass through metamorphosis. However, the results attained are not unimportant.

No less than six different species of Echinoderms were reared to a more or less advanced stage of development, according to the date at which fertilization could be undertaken, and according to the rate of growth of the different larval forms. These six species are : Asterias glacialis, Luidia ciliaris, Ophiactis Balli, Ophiocoma nigra, Spatangus purpureus, and Holothuria nigra. Fertilization of Echinocardium flavescens was also undertaken, but unfortunately the whole culture was destroyed by an accident, and no material was got later on of the species. Some other forms, the development of which I wanted likewise to study, e.g. Echinocardium pennatifidum, Amphiura (Ophiocnida) brachiata, Ophiopsila aranea, were not ripe at that time or sufficient material could not be got.

The main purpose of these studies on the larval development of different Echinoderms—which I hope to have the opportunity of continuing during a planned voyage to the Pacific—is to find the characteristic features of the larval forms and to see if the larvæ have any bearing on the

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M.B.A. PLYMOUTH classification of the full-grown animals. The embryological development in itself is not at present the object of my researches, and in the present report, therefore, only occasionally pure embryological facts are given.

As I had, of course, not much time to study the living larvæ more closely, having so many different cultures going on at the same time, I preserved material of the different developmental stages for study later on. On examining the preserved larvæ after my return to Copenhagen I found that a very regrettable mishap had occurred. The alcohol in which the larvæ were kept had in some way or other become acid, and the skeleton of all the larvæ had been dissolved. As the specific characters are especially found in the skeleton in those larvæ which are provided with such, the value of my material had thus been considerably diminished. Fortunately I had made a preparation in Canada balsam of the larva of *Ophiactis Balli* while still in Plymouth, so that in this case nothing was lost.

After I left the laboratory my cultures were looked after for some time by the attendant, Mr. Smith, and some of the later stages were sent me. In this way I got the later stage of the *Luidia* larva; a few larvæ of *Spatangus purpureus*, with the skeleton preserved, also came to hand, but in so poor condition that only little use could be made of them. Of the other larvæ only a few of *A. glacialis* were obtained, but these were not in a more advanced stage than that reached before I left the laboratory.

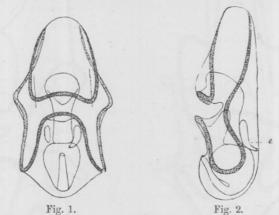
# I.-Asterias glacialis.

The development of this species has never been satisfactorily worked out, in spite of the fact that it is one of the objects commonly used in experimental embryology. A. Russo, in his paper "Contribuzione all' embriologia degli Echinodermi e sviluppo dell' Asterias glacialis O. F. Müller,"\* describes the first developmental stages, until the formation of the vibratile chord. Having reached this stage the larvæ began to degenerate. Some later stages, which were caught pelagically, were also referred by Russo to this species (his figures 22–25); it is, however, evident enough that they cannot belong to this species—the strong development of the vibratile chord at the anterior end of the frontal (or preoral) area, where the brachiolarian processes appear later on in the *Asterias* larva, is sufficient proof that they cannot belong to an *Asterias*. In my *Echinodermenlarven der Plankton Expedition* (p. 30), I have given the name *Bipinnaria Russoi* to this larva. The rearing of the more advanced stages of the *A. glacialis* larva has given the definite proof that

\* Boll. d. Soc. di Naturalisti in Navoli, Ser. I, Vol. VII (1892).

I was right then in maintaining that these later stages figured by Russo could not belong to *A. glacialis*.

The most important and interesting contribution to the development of A. glacialis has been given by Yves Delage, who has reared parthenogenetic larvæ of this species to full size and beginning metamorphosis.\* In spite of this it is still very desirable to make further studies of the normal development of this species. One can, of course, not be sure beforehand that the parthenogenetic larvæ are quite like those normally developed. Further, the figures given by Delage are partly not very satisfactory. In fact, it still remains uncertain what the specific characters of this larva are, by which it may be distinguished from other Asterias larvæ, or whether, perhaps, such characters do not exist, so



FIGS. 1-2.—Bipinnaria of Asterias glacialis, seven days old. 1, front view; 2, side view; c, enteroccel vesicle. 100/1.

that this larva could not be distinguished with certainty from other *Asterias* larvæ, for instance that of *A. rubens*.

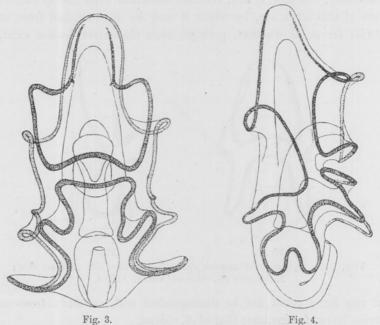
I was very glad then to have the opportunity already on the second day (the 12th June) after my arrival at the laboratory of making an artificial fertilization of *A. glacialis*. The fertilization was very successful, about 95 per cent of the eggs being fertilized. The culture went on excellently, the larvæ being fed with the diatom *Nitzschia* from Dr. Allen's cultures. However, I did not succeed in obtaining the fully developed larval form. Delage found that the rate of growth of his parthenogenetic larvæ was comparatively slow, and I had the same experience with the normal larvæ.

The differentiation of the vibratile chord began after five days, and after

\* Yves Delage, "Élevage des larves parthénogénétiques d'Asterias glacialis" (Arch. de Zool., expér. et gén. (4), II, 1904, pp. 27-46.)

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seven days (the 19th) the stage represented in Figures 1-2 was reached. For the next two weeks there was no further differentiation, and I nearly gave up the hope of getting it to proceed in its development, thinking that the diatoms were perhaps not suitable food for this larva; indeed, I found that the diatoms ejected by it had the same colour as those which had not been swallowed, so it appeared that the larvæ could not digest the diatoms. But on the 4th July I found some specimens in which the left enterocœl vesicle had begun to grow forwards, and now the development went on continually. On the 7th July the enterocœl



FIGS. 3-4.—Bipinnaria of Asterias glacialis, four weeks old. 3, front view; 4, side view, 80/1.

vesicles had united in the preoral lobe, and the long processes had begun to develop. The stage represented in Figures 3-4 was reached on the 9th July. When I left Plymouth, on the 15th, no essential advancement beyond this stage could be observed, and a few larvæ sent to me later on were not in a more advanced stage either. I am thus unable to give definite information of the specific characters of the fully developed larva.

Judging from the figures given by Delage, the larva of A. glacialis differs from the larva of A. rubens and vulgaris, the only two other species known to which it is similar, in the sucking disc at the basis of the brachiolarian processes being surrounded by a complete ring of small

papillæ, while in the two other species there are only 2-3 papillæ at each side of it (cp. text Figs. 4-6 of Delage's paper). Also the crown of the brachiolarian processes appears to afford a good specific character, there being 2-3 circles of small papillæ on a thickened ring, while in the other species there is only a single circle of papillæ at the tip and no thickened ring. If this proves to hold good for the normally developed larva of A. glacialis, it will be easily distinguishable from the other species. A number of larvæ which were taken in the Plankton at Plymouth all had only 2-3 papillæ at each side of the disc, and the crowns consisting of a single circle of papillæ; they should accordingly all belong to A. rubens, which may be possible, since also some few ripe specimens of this species were found. In any case, it is very desirable to have the A. glacialis larva reared to its full size, so that we may be able to see, with certainty, by which characters it differs from the A. rubens and A. vulgaris larvæ. As the species A. glacialis is not so very closely related to the other two species mentioned, one would expect the larvæ likewise to be distinct enough.

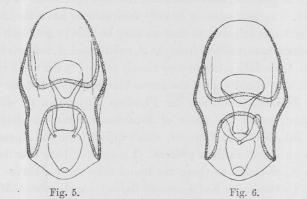
In the Echinodermenlarven der Plankton Expedition (p. 43), I have distinguished, under the name of Bipinnaria lævis, an Asterias larva found by Joh. Müller at Elsinore, which differs from the A. rubens larva in having no dorsal median process. I suggested that this larva might belong to A. glacialis, as there are found only three Asterias species in the Sound (between the Kattegat and Baltic), i.e. A. rubens, Mülleri and glacialis, the latter being, however, very rare here. The larvæ reared by Delage would seem to show that the dorsal median process is as well developed in the Bipinnaria of A. glacialis as in those of A. rubens and vulgaris, and then the B. lævis can only be an abnormal larva of A. rubens. I have never observed such specimens among the numerous larvæ of this species which I have seen.

The culture of the A. glacialis larvæ showed the interesting feature that a large number of the larvæ, about 50 per cent of them, had either two dorsal pores, one for each enterocœl vesicle, or the vesicles were united across the stomach, having one single, median pore (Figures 5–6). This feature has also been observed by Goette\* in the larva of the same species. G. W. Field, in his paper "The Larva of Asterias vulgaris" † (pp. 110–111), describes the formation of two pore canals in the young A. vulgaris larva as a normal feature, while the presence of two pore canals has otherwise been regarded as pathological. Field found the two

<sup>\*</sup> Goette, "Bemerkungen zur Entwicklungsgeschichte der Echinodermen" (Zool. Anzeiger, 1880, p. 324. Fig. 2).

<sup>+</sup> Quart. Journ. Micr. Sci., N.S., 34, 1893.

pores persisting only a short time, the right being closed again 8–12 hours after its formation. Though I have not paid attention to this on examining the living larvæ, I think I can say definitely that the formation of two pore canals is not a normal process in the larva of A. glacialis. In the larvæ which I preserved on the 16th June, at 9 p.m., the enterocœl vesicles have not been formed; in those preserved on the 17th, 10 a.m., they are formed, and the left vesicle alone has a pore. It is certainly very improbable that the pore of the right vesicle should then already have disappeared completely; this process would in that case go much faster than Field has found it in A. vulgaris. It seems to me that the



FIGS. 5-6.—*Bipinnaria* of *Asterias glacialis*, showing abnormal formation of dorsal pores. Seen from the dorsal side. 100/1.

facts here produced rather tend to show that what Field has found is an abnormality. In any case the two pores in the *A. glacialis* larva represent an abnormality. To enter on a discussion of the possible phylogenetic importance of the two dorsal pores is not the place here.

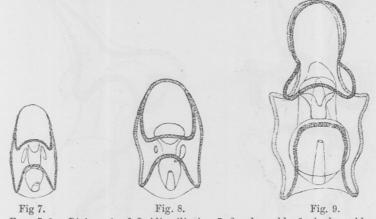
I must also mention the observation that the larvæ of this species, as well as of all the other species reared, in swimming rotate around their longitudinal axis, always turning to the left. In the *Spatangus* and *Ophiactis* larvæ this rotation ceases along with the development of the long processes; in the other larvæ it had not ceased in the most advanced stages observed.

# II.-Luidia ciliaris.

This species at first caused me a good deal of trouble. Both females and males were found with ripe genital products, but the spermatozoa did not move. Being myself not familiar with experimental work on fertilization, I asked Mr. J. Gray, who was working at the laboratory,

for advice. He suggested that we might try to raise the alkalinity of the water by adding some drops of sodium hydroxyde (NaOH). This proved excellent. The spermatozoa at once began to move, and then the fertilization succeeded completely. It was already at a rather late point of time, the 27th June, so that it could not be expected to get the complete development of this species; still a good deal was reached, and as this is the first time a *Luidia* has been reared, the observations are of some interest.

The cleavage is unequal, the relative size of the two first cleavage cells being, however, somewhat variable. The blastula has the same remarkable character as is described by Masterman for *Henricia san-quinolenta*,\* and by Gemmill for *Solaster endeca*,† the cell layer forming



FIGS. 7-9.—Bipinnaria of Luidia ciliaris. 7, five days old; 8, six days old; 9, eighteen days old. Front view. 100/1.

irregular folds. The gastrula is rather elongate and large; this stage is reached on the third day. After five days the larvæ begin to assume the shape of small Bipinnariæ (Fig. 7); the enteroccel vesicles have formed, but the vibratile chord is not yet differentiated at the anterior end. The next day, the 3rd July, the vibratile chord was complete (Fig. 8). The most advanced stage to which the larvæ reached before I left Plymouth is represented in Figure 9, from the 14th July. The processes have begun to appear, and the preoral lobe has begun to assume the characteristic elongate shape of the *Luidia* larva; the enteroccel vesicles have united in the preoral lobe.

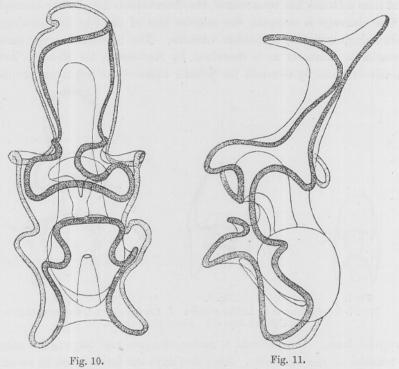
After my return to Copenhagen I had the pleasure to receive a couple

\* A. T. Masterman, "The early development of *Cribrella oculata* (Forbes), with remarks on Echinoderm development" (*Trans. R. Soc. Edinburgh*, Vol. XL, 1902). See especially Plate l, Fig. 17.

especially Plate l, Fig. 17. + James F. Gemmill, "The development of the starfish Solaster endeca (Forbes)" (Trans. Zool. Soc., London, XX, 1912).

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of larvæ from the same culture, preserved by Mr. Smith, on the 1st August, being thus a little over one month old. They are represented in Figures 10-11. Here the shape of the *Luidia* larva, so characteristic through the elongated preoral part and the long median processes, is easily recognized. The length of the larva is now 1 mm. Still the development is not sufficiently advanced for showing definitely by which characters



FIGS. 10-11.—Bipinnaria of Luidia ciliaris, five weeks old; 10, front view; 11, side view. 100/1.

this larva is distinguished from the Bipinnaria of *Luidia sarsi*. But it can now scarcely be doubted that the larva figured by Garstang, in his paper "On some Bipinnariæ from the English Channel,"\* is really the larva of *L. ciliaris*. This species is very common at Plymouth, while *L. sarsi* is rare; its breeding season is June to July, and Garstang found the larva in August. I have previously held the opinion that Garstang's larva belonged to *L. sarsi*;† I must now join Ludwig‡ in the opinion

\* Quart. Journ. Micr. Sci., N.S., 35, 1894.

+ Echinodermenlarven der Plankton Expedition (p. 40). Nordisches Plankton Echinodermenlarven (p. 11).

Echinodermenlarven (p. 11). ‡ H Ludwig, "Der Asteriden des Mittelmeeres." Fauna u. Flora d. Golfes v. Neapel, 24 Monogr., 1897 (p. 82).

that it belongs to L. ciliaris. It is, however, still very desirable that this larva should be reared to metamorphosis—and as it has now been found to be easily reared, this will probably soon be done—this large, beautiful larva must, indeed, be a magnificent object for embryological study.

In the Echinodermenlarven der Plankton Expedition (pp. 39-40), I have remarked, in connection with the suggestion made by Hensen that the young larvæ might be fixed, that this conclusion is scarcely justified, because the young larvæ have not yet been found. To this remark Hensen has added the following note (p. 40): "Meine Æusserung lautet : 'Die I. Fahrt brachte 114, die II. 11, und die III. 78 Luidien mit Stern, in Summa 203, deren Diagnose wir Hrn. Mortensen verdanken. Es müssen doch wohl die jüngeren Larven eine festsitzende Lebensweise haben, sonst könnten sie uns nicht entgangen sein.' Da Zahlen beweisen, muss ich an diesem Satz festhalten." Though I have always been quite convinced that the Luidia larva could not have a fixed stage before the free-swimming larval stage, it is quite satisfactory for me that I have now been able to give the definite proof that my opinion, founded on morphological grounds, was right, in spite of Hensen's statistics. To be sure, my observations are made on L. ciliaris, while Hensen speaks of L. sarsi: but to suppose that of two so very similar larvæ one should be fixed in its first stages, the other free-swimming, would really be too absurd.

It is very remarkable that the larvæ of L. ciliaris appear to be comparatively rare at Plymouth. Being impressed with the enormous development of the gonads in this species I have tried to make an approximate calculation of the number of eggs in a large L. ciliaris. In a specimen of 30 cm. arm length I counted the number of gonads—which are here arranged in a series along each side almost to the point of the arm instead of one large gonad at each side of the basis of the arm as is the rule in Asteroids—and found them to number 150 in each series—300 per arm. As the species is seven-rayed, a complete\* female of that size, which is nearly the average, has 2,100 ovaries; these are, however, of somewhat different size, decreasing in size towards the point of the arm. An ovary from about the middle of the arm was divided into a hundred parts of as nearly as possible equal size, and the number of eggs in one part was counted; it was ca. 3,000. This means that in one ovary there are at least ca. 300,000 eggs, probably nearer

\* The arms very easily break off, and it is quite difficult to get complete specimens, though such are often seen in the contents of the trawl, before it is hauled on deck.

half a million. Taking, however, into consideration the decreasing size of the ovaries towards the point of the arm it may be just to take as the mean number of eggs per ovary only 100,000, and for safety we may still reduce the number of ovaries to 2,000. This gives as the number of eggs in a grown female of L. ciliaris no less than 200 millions. We might expect from this that this species would be exceedingly common, the larvæ as well as the grown. But the larvæ are only rarely observed, and as for the grown specimens, one may certainly expect to get about half a dozen specimens in each haul with the trawl, and from their large size this makes the impression of a good lot—in

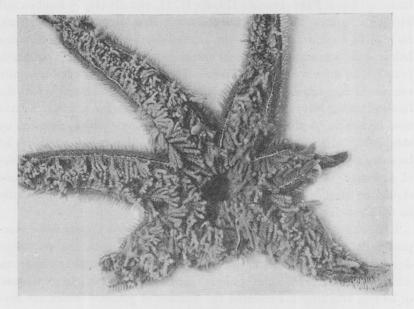


Fig. 12.

FIG. 12.—Female Luidia ciliaris, opened so as to show the genital organs. <sup>1</sup>/<sub>4</sub> of natural size. (From a photograph by Mr. F. Martin Duncan.)

reality this is a very small number, especially compared with *Ophiocoma* and *Ophiothrix*, which are generally taken by thousands in each haul. What a waste of eggs must here take place !

In Figure 12 is represented a female of L. *ciliaris* opened so as to show the gonads. It gives, however, only a slight impression of the profusion of gonads seen in such a specimen, the more conspicuous on account of the beautiful red colour of the gonads with the ripe eggs.

I may here mention that in this species a distinct sexual dimorphism may be observed, at least in the breeding season. The colour of the

female is red, that of the male brownish; the rays of the female are somewhat broader than in the male, and upon the whole the male scarcely reaches so considerable a size as the female. It is mostly quite easy to distinguish between the sexes at a glance—quite apart from the fact that generally the arms break so as to expose some of the gonads.

In the stomach of this species I have found remnants of Ophiurids (Ophiothrix).

# III.-Ophiactis Balli.

On the 17th June several specimens of this species were taken on the Eddystone grounds, especially on tubes of Chætopterus and on Ascidians. Some of these were found to contain ripe sexual products; they were placed in a large jar with only a few centimetres of water, in order to try if they would shed their eggs and sperm. Already next day I had the pleasure of finding the fertilized eggs, which had partly already reached the blastula stage; at 12 o'clock, viz. after scarcely more than eighteen hours, the first swimming blastulæ were observed. On the 19th the embryos were found swimming actively close to the surface of the water ; they were somewhat elongated, a little transparent at one end. On the 20th the first rudiments of the skeleton were formed, and the posterolateral processes had begun to appear, showing already an indication of red colour at the point. On the 21st the larvæ had already distinctly the shape of an Ophiopluteus; the antero-lateral and the postoral rods (and processes) had begun to grow out, and likewise the recurrent rod had begun to appear. On the 26th the body skeleton was completely formed, and the three pairs of processes had become somewhat longer, especially the postero-lateral. These latter processes are distinctly red at the point : also the postoral transverse chord has a reddish tint, the larva being otherwise uncoloured. It always swims near the surface, but at this stage does not any longer rotate round its longitudinal axis.

Having reached this stage the development ceased; the larvæ still remained alive for some days, but without showing further advance. Probably the diatoms were not suitable food for them. However, the stage reached is sufficiently advanced for showing the characters of the larva, so that it will be possible to recognize it also in later stages, the essential characters of the Ophioplutei lying in the body-skeleton, which had, fortunately, already reached its full development (Fig. 13).

The main features of it are the following : Recurrent rods are present, whereby two large meshes are formed in each half of the body. The cross-rods are peculiar in being slightly lobed at the end, the lobes of the two rods of each side catching into each other. The end-rods are rather

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long, straight, trifid at the point. The postero-lateral rods are provided with thorns along the inner side, and also the antero-lateral rods are slightly thorny. (These thorns will doubtless be considerably more numerous in the fully developed larva.) It must be pointed out that there is no posterior tuft of cilia; the frontal area is quite small. Otherwise there is nothing to be remarked concerning the shape of the larva,

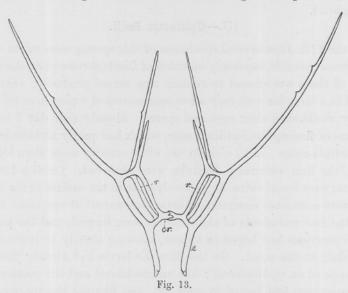


FIG. 13.—Skeleton of the Ophiopluteus of Ophiactis Balli. cr, cross-rod; e, end-rod; r, recurrent rod. 275/1.

in this stage at least; it has the typical *Ophiopluteus* shape, as appears from the shape of the skeleton.

It is very satisfactory that the larva of this species could be reared to a sufficiently advanced stage for recognition, this being the first information of the larval form of a species of the genus *Ophiactis*. (The two species *Ophiactis Kröyeri* (L.) and *O. asperula* (Phil.) appear to be viviparous.\*)

# IV.-Ophiocoma nigra.

It was not until towards the end of June that this species was found to contain ripe sexual products. On the 25th June some specimens were put in a jar in the same way as *Ophiactis*, and the next day some fertilized eggs were found. It was no large number, and I then repeated the experiment, but without success, evidently because the specimens were

\* H. Ludwig, "Brutpflege bei Echinodermen." Zool. Jahrbücher, Suppl. VII, 1904, p. 693.

not very ripe. To open the specimens and take out the eggs did not prove good either for the same reason. However, some results were obtained from the eggs got at the first experiment. The development proved to be comparatively slow. The first indication of the posterolateral processes was found on the 30th, i.e. in ca. five days old embryos. The embryos are remarkably elongate, and the oral lobe remains very large after the formation of the said processes. On the 1st July I found the first rudiments of the skeleton. On the 4th July there was seen the first indication of the postoral rod, and the postero-lateral processes had somewhat increased in length—but herewith the development apparently ceased ; the larvæ were alive and apparently healthy when I left on the 15th July, but the development was not advanced beyond the stage reached on the 4th. Probably again the food was not suitable.

The development reached a sufficiently advanced stage to show that the body skeleton is simple, without recurrent rod. The cross-rods are thorny. The body skeleton is upon the whole small, the rods short. Unfortunately I can give no figure of it, the skeleton having been dissolved in all the preserved specimens as explained above. The colour is yellow, or at the point of the postero-lateral processes, yellowish green : there is no indication of red pigment.

Though the rearing of this larva was thus not very successful, the results obtained are not without value ; from the indications given here it will doubtless be possible to recognize the Ophiocoma larva, when it is found in the plankton. The two Ophiurids, Ophiothrix fragilis and Ophiocoma nigra, are by far the most numerous Ophiurids occurring at Plymouth; they must almost cover the bottom on large areas. The larvæ of both forms must occur in large numbers in the full breeding seasons of the two species. As the larva of Ophiothrix is well known, it must be possible to find out, with the help of the indications given here, which larva belongs to Ophiocoma, and in all probability the larva is already known. In a paper on Loch Sween ("The Glasgow Naturalist," Journ. Nat. Hist. Soc. of Glasgow, IV, 1912) Professor J. Graham Kerr has figured (p. 43, Fig. 4) a very peculiar Ophiurid larva, which agrees with the Ophiocoma larva in having a simple body skeleton and a very large preoral lobe. It occurred in immense numbers at the beginning of August-the season thus being likewise in accordance with the suggestion that it is the Ophiocoma larva. In fact, Graham Kerr himself gives that suggestion, and I think it very probable that he is right. The most conspicuous peculiarity of this larva is the development of four "epaulettes," as I have previously found in a larva from the Bermudas de-

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scribed as Ophiopluteus Henseni in the Echinodermenlarven der Plankton Expedition (p. 62, Pl. VII, 2). The occurrence of a similar—though quite distinct—larva at the Bermudas is not at all against the supposition that the larva figured by Kerr belongs to O. nigra, since this genus is also represented at the Bermudas (by the species Ophiocoma echinata (Lmk.) and O. pumila (Ltk.).

This larva has also been observed at Port Erin by Dr. H. C. Chadwick, who showed me on my visit there (at the end of July) figures he had made of these and many other Echinoderm larvæ. May we hope that he will soon publish his many beautiful figures and interesting observations on the Echinoderm larvæ? They would doubtless prove of great value to students of these larvæ, which are so interesting from both a morphological and a biological point of view. Even if the larvæ can at present only partly be referred to species, they are, at least most of them, so well characterized that they can be recognized with certainty, and the observations made on the larvæ of hitherto unknown origin are by no means lost, but may be directly transferred to the species to which some such larvæ are later on proved to belong.

# V.-Spatangus purpureus.

This species is one of the very first Echinoderms of which artificial fertilization and rearing of the larvæ were undertaken. It was A. Krohn who did so in Messina in 1853 ("Über die Larve von Spatangus purpureus," Müll. Arch., 1853, p. 253, Taf. VII). He did not succeed in rearing it to metamorphosis, but still so far that he thought he was able to recognize it in free-swimming specimens. In another paper, "Beobachtungen über Echinodermenlarven" (ibid., 1854, p. 208), he gave them some further observations on the structure of this larva, from which it appears that it is characterized especially by the postoral, postero-dorsal, and posterior rods being fenestrated only in their outer part, a considerable portion at their basis remaining unfenestrated; further the postero-lateral processes ("auricularfortsätze") are "äusserst kurz, breit und abgerundet." In my Echinodermenlarven der Plankton Expedition, as well as in Nordisches Plankton I have accordingly given these characters for this larva, no later observations having been made on it. The observations of Krohn are, however, not very detailed, and especially it is an important objection that the reared larvæ did not reach a very advanced stage. There must be several other Spatangoid larvæ in the Mediterranean, and as their specific characters are not sufficiently known we have no guarantee that the pelagic larvæ which Krohn re-

ferred to Spatangus purpureus did really belong to that species. It was therefore very satisfactory to me to get the opportunity of rearing the larva of this species during my stay in Plymouth. It proved to be very easy to rear; the larvæ developed normally and reached their full size in the course of three weeks. The fertilization was made on the 23rd June; on the 14th July the larvæ had all their processes developed, and the first sign of the metamorphosis (formation of the oral disc) had appeared. Unfortunately I cannot utilize this culture for a complete description of the larval skeleton, on account of the mishap explained above. Still some notes can be given which may prove sufficient for the certain recognition of the larva.

The shape of the fully formed larva is, as shown in Figure 14, that of the typical Spatangoid larva. It is especially to be noticed that the postero-lateral processes are long and slender (and a little posteriorly directed) as in other Spatangoid larvæ, not short, broad, and rounded as stated by Krohn. If it is, upon the whole, really the S. purpureus larva which Krohn has observed, it must then have been in a stage where the postero-lateral processes are just about to appear. According to his description, "Beobachtungen über Echinod. larven," p. 209, quoted in Echinodermenlarven der Plankton Expedition, the body shape of the larva is rather complicated, with lobes and folds; in reality it is quite simple, without folds, as seen in the figure. It is, then, most probable that the larva described here by Krohn is not at all the S. purpureus larva, but the larva of another Mediterranean Spatangoid-which species cannot be ascertained at present. The only thing in the description of Krohn which agrees with the S. purpureus larva is the extraordinary length of the postoral, postero-dorsal, and, especially, the posterior processes. Very probably also the other processes will attain a greater length than shown in the figure. They are a little swollen at the point, which is conspicuously coloured with red pigment. A feature to be noticed about the larva is a groove inside the posterior transverse chord (Fig. 14); the meaning of this groove is unknown to me.

The skeleton is, as shown by Krohn, characterized by the fact that the fenestrated rods (postoral, postero-dorsal, and posterior) have no holes in their basal part; in the posterior rod it is, however, only quite a short part which is unfenestrated (Fig. 15), in the other rods the unfenestrated part may really be as long as figured by Krohn ("Über die Larve von *Spatangus purpureus*," Taf. VII, 2–3); characteristic also is the widened basal part of the antero-lateral rods (cf. Krohn, Taf. VII, 5). The most important point to settle in regard to the skeleton is the structure of the

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postero-lateral rod, which appears to be the part of the skeleton of the Spatangoid larva which affords the best specific characters. Unfortunately the only information I can give of it is that to be found in

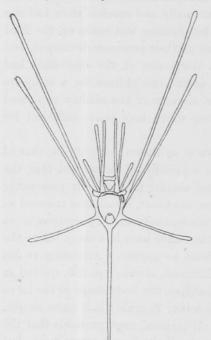


Fig. 14.

Fig. 15. FIG. 14.-Echinopluteus of Spatangus FIG. 15.-Part of the skeleton of the purpureus, three weeks old. 35/1. Echinopluteus of Spatangus purpureus. p, Posterior rod.; pl, postero-lateral

rod. 275/1.

pl

Figure 15. It is seen that its basis is not widened, and that its edges are serrated. Apparently it will be found to resemble that of the larva of Echinocardium cordatum (cp. Echinodermenlarven der Plankton Expedition, Taf. IX, 7).

The total length-processes included-is ca. 3.5 mm., not 6 mm. as

Krohn gives it (op. cit., p. 209). It may be mentioned that from the appearance of the first processes, the posterior and postoral, it ceases rotating round its longitudinal axis. The first appearance of the posterolateral processes occurred on the 7th July, viz. in the two weeks old larva; the antero-dorsal processes are the latest to appear—when the metamorphosis is beginning, in ca. three weeks old larvæ.

All processes, except the preoral, have a conspicuous red point; otherwise there are scattered red pigment cells on the body and processes, more numerous on the body and the posterior process, and at the frontal edge.

# VI.-Holothuria nigra.

The development and the larval form of this species being hitherto quite unknown, I was very anxious to try fertilizing and rearing it. Ripe specimens were found together with such as were very far from having ripe sexual products. The difficulty was with the eggs; I never found a specimen with the eggs quite ready for fertilization. The nucleus was nearly always large, and while in the other Echinoderms used by me for fertilization the eggs were found to ripen after having been some hours in sea-water (the nucleus disappearing), this was not the case in *Holothuria nigra*; even after the eggs had been twenty-four hours or more in the sea-water only in quite a small percentage of them had the nucleus disappeared. The eggs are a beautiful red, with a radiating striated membrane, as is known in other Holothurians.

On the 24th June I tried fertilization, having found a female in which more eggs than usual had no visible nucleus. (Ripe males were easy to get.) The fertilization was, contrary to my expectations, successful; on the next day I found that ca. 200 eggs were apparently in cleavage but the cleavage looked so irregular that I was nearly certain the development was not going on normally. However, these eggs were isolated, and on the 27th I found that they had developed into swimming gastrulæ. On the 1st July the vibratile chord had begun to differentiate, and on the 4th July they had developed into a typical *Auricularia, with a star-shaped spicule at the posterior end*. Beyond this stage the development had not proceeded when I left Plymouth, and as I had only very few larvæ left, I could not get material of it preserved later on. It appears from this that there will be no difficulty in rearing the larvæ of this species, contrary to Selenka's experiences with Holothuria tubulosa ("Zur Entwicklung der Holothurien. [H. tubulosa und Cucumaria

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doliolum.] Ein Beitrag zur Keimblättertheorie," Z. w. Zool. XVII, 1876). The difficulty here is to get the eggs in condition for fertilization.

The Auricularia of H. nigra very much resembles that of H. tubulosa, as figured by Selenka (op. cit., Taf. X, 9). The colour is the same as shown there, only I find it more equally distributed in the vibratile chord; also there are some patches of this colour over the body, and especially in the posterior end. Unfortunately I did not make a drawing from a living specimen; the few preserved specimens are not so well preserved that it would be worth giving a figure therefrom, and the spicule has been dissolved. Still, the information given here will be quite sufficient for recognizing the larva, especially in the waters off Plymouth, where no other Holothuria species occurs with which it could be confounded.

Judging from the larva, H. nigra must be nearly related to H. tubulosa. The suggestion made in my Echinodermenlarven der Plankton Expedition (p. 15), that the larva of H. tubulosa will prove to have a spicule at the posterior end in later stages, is very much supported by the fact that such a spicule is found in the larva of H. nigra. A similar calcareous spicule is also found in Auricularia stelligera (Joh. Müller's "Auricularia mit Kugeln"); but it has besides some pink elastic spheres, of which there is no indication in the larvæ of H. nigra and tubulosa, so that the A. stelligera would not seem to be very closely related to these larvæ.

# The Ciliary Mechanisms on the Gill and the Mode of Feeding in Amphioxus, Ascidians, and Solenomya togata.

By

J. H. Orton, A.R.C.Sc., B.Sc., Naturalist in the Plymouth Laboratory.

With Figures 1-11 in the Text,

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## INTRODUCTION.

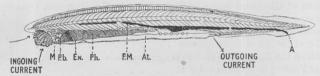
It is well known that Amphioxus obtains its food by straining off the nutritive particles contained in the current of water which is taken in continuously at the mouth and expelled at the atriopore. It is also well known that the cilia on the gill cause this continuous current, and that in some way a separation of the food-particles is effected.

The existing explanations, however, of the manner in which these two processes are effected are either very vague or only partially true and misleading. It is to clear up our ideas on this matter that the present account is written.

It is generally stated that the current through the pharynx of Amphioxus is effected by the cilia on the gill-bars, and that the food-particles are collected in the endostyle which conducts them forwards to the peripharyngeal bands (1, 2, and 3). The latter are then described as conducting the collected food to the dorsal groove, which in turn conducts it backwards to the intestine. These statements are vague and wrong and misleading, inasmuch as there are on the gill-bars at least two sets of cilia which function in quite different ways, and the endostyle does not conduct foodparticles forwards, as will be seen from the following description :—

# MODE OF FEEDING IN AMPHIOXUS.

While the animal is at rest a current of water is being taken in continuously at the mouth and expelled at the atriopore. This current serves for the nourishment of the animal, and doubtless is also a main factor in its respiration. If an Amphioxus\* be placed in water containing fine particles of carmine in suspension or in water containing diatoms and dissolved methylene blue, a mass of particles embedded in mucus very soon collects in the dorsal groove of the pharynx and is passed on into the intestine. The living animal after being fed in this manner has the appearance indicated in Fig. 1.



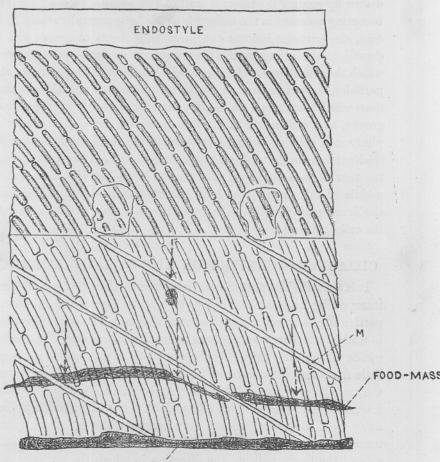
- FIG. 1.†—View of a living Amphioxus shortly after being fed with carmine particles, to show the collection of food in the dorsal groove and the intestine, and the course of the main current through the body (× about  $\frac{5}{3}$ ).
  - F.M. Food masses in the dorsal groove of the pharynx and in the intestine.
  - M. Mouth, between which and the end of the arrow indicating the ingoing current is situated the buccal cavity. The outgoing current leaves the animal at the atriopore.
  - At. The Atrium, the space between the pharynx and the body wall through which the current passes after leaving the pharynx, Ph.
  - Ph. The pharynx or branchial sac.
  - En. The endostyle.
  - P.b. The peri-pharyngeal band of the left side.
  - A. Anus.

\* The observations recorded in this paper were made on the species *Branchiostoma lanceolatum*. The general similarity in structure of the species of this genus, however, renders it highly probable that the processes here described will apply to all the group.

† I am indebted to Mrs. Orton for the drawing for this figure, and also for assistance with Figures 6, 8, and 9.

#### CILIARY MECHANISMS ON THE GILL IN AMPHIOXUS.

If the animal is examined closely by means of a microscope when feeding it is easy to make out a strong current entering at the anterior end of the animal between the buccal tentacles. Thence the current can be followed successively through the buccal cavity, the mouth, the pharynx,



# DORSAL GROOVE

- FIG. 2.—View of a portion of the body wall and pharynx of a living entire Amphioxus at about the level of the posterior two-thirds of the pharynx.\* (Drawn as seen through a microscope, × about 37.)
  - D.Gr. Dorsal groove in which becomes collected a mass of food particles embedded in mucus.
  - F.M. Cylindrical mass of mucus with embedded food-particles being transported away from the endostyle towards the dorsal groove, as is indicated by the overlying vertical arrows.
  - M. The boundary of adjacent myotomes.

\* It was found the most convenient for this examination to view the animal laid on its right side. Thus in this view the main current passes from the reader's right to the left.

and the atrium; it is finally seen to pass out of the animal at the atriopore. If now the pharynx of the living animal be examined carefully while feeding is going on the process of collection of the food-particles may be watched. As particles pass along the pharynx they may be seen to be drawn up against the internal wall of this organ. Instead, however, of becoming collected in the endostyle as has been generally stated to be the case, the particles become caught in thin sheets of mucus and travel dorsally on the internal wall of the pharynx towards the dorsal groove, into which they disappear. If the animal is taking in a large number of foodparticles, these often become worked up with mucus into a long cylindrical mass which travels as a whole away from the endostyle towards the dorsal groove, as is shown in Fig. 2. This figure is a drawing of a view of the pharynx of a living animal seen through the transparent body wall, the food-particles being visible through the gill-bars. Food-particles massed together in various shapes may also be seen-like that depicted in the middle of this figure just above the food-mass-all travelling towards the dorsal groove, which in this way becomes very quickly charged with the collected food.

# CILIARY MECHANISMS ON THE GILL OF AMPHIOXUS.

It is thus obvious that there exists some mechanism for collecting and transporting food-particles along the internal face of the gill-bars. If a portion of the living gill, such as that shown in Fig. 3, be now observed in a little water in a watch-glass under the microscope, this mechanism can be examined. The mechanism, however, is more easily made out if a little finely powdered carmine be added to the water. Very soon after the carmine grains are added they may be seen to be drawn towards the internal face of the gill-bars, along which they are hurried in a direction away from the endostyle, and may become collected into a cylindrical mass such as is shown on the right side in Fig. 3. The arrows on this side of the figure indicate the direction in which the particles and the collected mass travel. Individual particles may be seen to travel at an angle across the bars, i.e. in a ventro-dorsal direction, as is indicated also by the arrows. The mechanism which causes the movement of these particles across the gill-bars cannot be made out easily when examining the gill from this point of view, but when a single gill-bar is examined in side view, highly magnified (see Fig. 4), it is seen that on the internal face of the bar there is a row of relatively short cilia (Fig. 4, fc.) which lash rapidly along the length of the bar and thus effect the translation of such particles as are drawn against it. That the particles are drawn against the

#### CILIARY MECHANISMS ON THE GILL IN AMPHIOXUS.

bars is very easily seen even in a view like that of Fig. 3, and if the lateral, i.e. the anterior and posterior, faces of the gill-bars be focussed carefully, rows of long, rapidly moving cilia are to be seen lashing across the length of the bars. In Fig. 4 this direction is indicated by the large arrows. In a view of a portion of the pharynx, as shown in Fig. 3, these lateral cilia—as they may be called—lash in the direction shown by the arrows

## ENDOSTYLE

FIG. 3.—View of a portion of the pharynx of Amphioxus to show the cilia producing the main current (on the left) and the collection and transportation of food-particles (on the right). The portion consists of a piece of the endostyle with gill-bars attached. (Drawn from the living object, × ca. 32.)

The arrows on the reader's left indicate the direction in which the main current is drawn by the lateral cilia on the gill-bars. These cilia are shown bordering the gill-slits. The arrows on the reader's right show the direction in which the frontal or pharyngeal cilia on the gill-bars are transporting a mass of food-particles away from the endostyle towards the dorsal groove. The upper arrow on the righthand side of the figure points to the food-mass. The small arrows in the middle of the figure on the endostyle show the direction in which the outer, i.e. lateral cilia, on the endostyle transport particles out of the endostylar groove on to the gill-bars. The supporting rods of only a few of the gill-bars are shown.

on the reader's left-hand side, and thus draw water with suspended particles against the side of the gill. Water is actually lashed between the gill-bars, as is indicated by the lower arrow on the extreme left of this figure, while the suspended particles are caught in mucus on the face of the gill-bars, and, as we have already seen, are carried away from the endostyle towards the dorsal groove (see Fig. 3 again on the right). In the lateral view of a gill-bar or a gill-filament, shown in Fig. 4, scattered cilia can be seen on the atrial epithelium. These cilia appear to lash in the direction shown by the arrow on the atrial side of the bar, and by comparison with a gill-filament of a Lamellibranch, may be called ab-frontal cilia. They probably help in a small way in producing the main current and also in cleaning the atrial surface of the gill-bar.

# DIRECTION IN WHICH LATERAL CILIA LASH

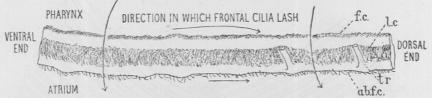


FIG. 4.\*—Side view of a single living primary gill-bar of Amphioxus, showing the ciliary mechanisms.

The direction in which the lateral cilia, l.c., lash, to produce the main current is shown by the large arrows crossing the gill-bar.

The direction in which the frontal cilia, f.c., lash is indicated by the arrow above these cilia. The true direction in which these particles transport cilia is along the face of the gill-bar and upwards towards the reader.

The ab-frontal cilia, ab.f.c., appear also to lash in a similar direction to that of the frontal cilia as is shown by the accompanying arrow.

l.c. Lateral row of cilia.

f.c.† Frontal or pharyngeal row of-cilia.

ab.f.c. Scattered cilia on the atrial or ab-frontal face of the gill-bar.

Ph. Pharyngeal side of gill-bar.

Atr. Atrial or peri-branchial side of gill-bar.

V. Ventral end of gill-bar,

tr. Connexions joining the gill-bar to others.

# CILIATION OF THE ENDOSTYLE.

There still remains for examination the ciliation on the endostyle. Under a low power in such a view as Fig. 3, particles suspended in the water may be observed to be lashed rapidly out of the endostyle on to the face of the gill-bars in the direction denoted by the small arrows in the middle of the figure (i.e. on the endostyle). Examination of the endostyle under a high power brings out the presence of three main sets of cilia, two outer or lateral sets and one median. The cilia on these lateral rows are short and lash rapidly across the length of the endostyle. These are the cilia which throw particles out of the endostyle on to the gill-bars. The median cilia on the endostyle are long and appear only to shake with

\* I am indebted to Mr. L. R. Crawshay for the lettering in this figure, and also for that in Figures 2, 3, and 5.

<sup>†</sup> The short cilia figured by Benham (15, Plate 6) have not yet been seen in the living filament, although they have been carefully looked for. Further observations, however, will be made on this point.

# CILIARY MECHANISMS ON THE GILL IN AMPHIOXUS.

a wave-like motion which begins at the attached end. Particles may indeed be observed to rest on these cilia for some time, but such particles are eventually worked towards the lateral sets of cilia, which soon transport them to the gill-bars. In the passage of the particles from the median to the lateral cilia on the endostyle one can often make out that the particles have become embedded in mucus. It is therefore doubtless the function of the median cilia on the endostyle to pass on mucus secreted by the endostyle to the lateral endostyle cilia and thence to the gill-bars. This mucus, along with that doubtless secreted also by the pharyngeal epithelium of the gill-bars, serves to entrap food-particles and render the transportation of these easier.

Between the median and lateral sets of cilia on the endostyle a narrow ciliated groove can be made out on either side (see Fig. 3). Particles are frequently caught in these grooves, but they can be seen to be passed quickly on to the lateral endostyle cilia and generally on to those portions of the endostyle overlying a primary bar, and thence to the gill-bars.

Before passing on to a recapitulation of the ciliary mechanisms and their function in Amphioxus, it will be convenient to examine the ciliary arrangements so well known in the anterior end of the animal, namely those in the buccal cavity, the wheel organ, and Hatchek's pit, and the peri-pharyngeal bands.

# THE FUNCTION OF THE WHEEL ORGAN, AND THE PERI-PHARYNGEAL BANDS IN AMPHIOXUS.\*

The action of these organs can be made out by examining the anterior end of the living animal through a microscope while it is feeding. During the act of feeding the buccal tentacles are kept folded over one another. In this way these tentacles act as a sieve, allowing only the finer suspended particles to pass on into the buccal cavity. The efficiency of the buccal tentacles in straining, when held in this manner, is increased by the presence along the sides of the tentacles of conical papillæ which subdivide the spaces between the tentacles, as is shown in Fig. 5. In this manner the larger particles carried along in the ingoing current become arrested on the buccal tentacles, only the finer particles being allowed to pass onwards. A selection of the finer food-particles is thus effected.

From the buccal tentacles the main current with the suspended particles passes through the buccal cavity, the mouth and onwards into the pharynx.

In the buccal cavity, however, some particles fall out of the main stream as a result of the occurrence of slack waters in the periphery of

\* See Appendix on page 45 for an account of Andrew's work on feeding in Amphioxus.

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this region, and become drawn against the wall of this cavity by the sets of cilia which are known collectively as the wheel organ. These sets of cilia are shown on the wall of the buccal cavity in Fig. 5. They are really ciliated grooves running antero-posteriorly in the posterior part of the buccal cavity. Around the mouth these paths are connected together by a circular ciliated path, which is stated by V. Wijhe (4) to be

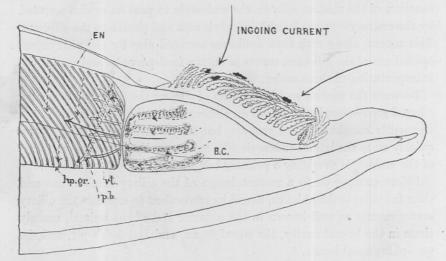


FIG. 5.—View of the anterior end of a living Amphioxus (drawn as seen through a microscope,  $\times$  ca. 27), after keeping the animal in a dilute solution of methylene blue in water. This view shows the action of the buccal tentacles in sieving off the coarser food-particles at the entrance to the buccal cavity, the action of the ciliated grooves (the Wheel Organ) in the wall of the buccal cavity, and the collection of food-particles from this region of the body into the peri-pharyngeal bands.

b.c. Buccal cavity.

hp. gr. Dorsal or hyperpharyngeal groove.

p.b. Peri-pharyngeal band.

v.t. Velar tentacles.

EN. Region of the endostyle.

The arrows in the buccal cavity lie alongside the ciliated grooves, along which food-particles are lashed towards the mouth in the direction indicated by the arrows. The large arrow passing through the mouth from the buccal cavity into the pharynx indicates the course of the main stream.

sometimes complete and sometimes incomplete. These ciliated paths have been said to be "an organ for creating currents in the mouth back to the pharynx." There can be little doubt about their function, however, if they are watched while the animal is feeding. As particles drop out of the main current in the buccal cavity they very quickly become caught in the anterior end of one or other of these ciliated paths and rapidly whirled along the groove towards the mouth, becoming rolled into a

# CILIARY MECHANISMS ON THE GILL IN AMPHIOXUS.

mass with mucus on the way. A large number of these minor food-masses. however, are swept into the main stream as they approach the oral aperture and pass onwards into the pharynx. Some particles, however, appear to pass between and sometimes along the velar tentacles on to the internal surface of the pharynx, whence they are passed on to the peripharyngeal grooves. It is well known that there are no gill openings anterior to the peri-pharyngeal grooves. Thus the part of the pharynx anterior to the peri-pharyngeal grooves serves as a collecting ground for the food-particles which have been caught in the buccal cavity. Most of the particles, however, appear to pass around the ventral part of the mouth to the peri-pharyngeal groove; while others appear to pass dorsally straight into the dorsal groove. There is also, however, a steady dribble of particles into the peri-pharyngeal groove from a position immediately ventral to it. These particles are probably collected from the extreme anterior portion of the endostyle, by which they are ejected in the same way as we have seen at other parts. Doubtless these minor streams have been the cause of the erroneous views which are current on the mode of feeding in Amphioxus. If a little methylene blue is added to the water from which an Amphioxus is feeding the edges of the ciliated paths in the buccal cavity stain blue, which doubtless indicates the presence of mucus glands at these points (see Fig. 5). The anterior end of each ciliated groove can now be easily seen to form a pit-like depression around which the cilia are lashing vigorously. As particles are caught by the cilia they are seen to be passed along in the middle of the groove towards the mouth, as has been described above.\*

# RECAPITULATION OF THE ACCOUNT OF THE FOOD AND RESPIRATORY CURRENTS IN AMPHIOXUS.

The main food and respiratory current in Amphioxus is produced by the lashing of the lateral rows of cilia on the gill-bars or gill-filaments (see Fig. 4, l.c., Fig. 3, and Fig. 6). These lateral cilia lash across the length of the filament from the cavity of the pharynx to that of the atrium. In the adult Amphioxus there are about 180 gill-filaments on each side of the body (Willey, 1. p. 17). Each of these carries two long rows of lateral cilia, hence in all there are about 720 rows of long cilia acting like oars lashing water through the body of the animal. These are indeed powerful enough to produce the strong current that is to be observed.

\* If a stronger solution of methylene blue is used the whole of the wheel organ as well as the pharynx stains a deep blue, and a surprising amount of detail can be made out over the whole of the body.

The main cilia which collect and transport the food-particles are those on the pharyngeal surface of the gill-filaments, namely, the frontal cilia-(see Figs. 4 and 6, f.c., and Fig. 3). These cilia lash in a direction which is chiefly along the length of the bars, but actually at an angle to the bars in a ventro-dorsal direction (see the arrows on the right side of Fig. 3). The gill-bars, it is to be remembered, run in the living animal in an anterodorsal to postero-ventral-course, as is shown in Figs. 1, 2, and 3. Foodcollection is effected in the following manner. Mucus is secreted by the endostyle and passed on to the gill-bars in a thin sheet by the cilia on the lateral portions of the endostyle. Probably mucus is secreted also by the pharyngeal epithelium of the gill-bars. Food-particles are drawn against the gill-filaments by the lateral cilia on those filaments, as we have already seen; the particles become entangled in the mucus in which they are hurried along the face of the gill-bars into the dorsal groove by the frontal or pharyngeal cilia. The actions of these different mechanisms are depicted in the accompanying diagram, Fig. 6.

It is thus evident that feeding in Amphioxus occurs automatically as in the Lamellibranchs. Amphioxus, however, has an advantage overmost Lamellibranchs in being able to swim away from a region where the water is laden with innutritious or undesirable particles. And, indeed, the occurrence of Amphioxus mainly on shelly or gravelly grounds may be due largely to the desire of the animal to seek outgrounds where the water is relatively free from undesirable, i.e. innutritious particles.

A food-collection of minor importance is also effected, as we have seen, in the buccal cavity. Food-particles are collected into the ciliated grooves on the wall of this cavity and transported in mucus through the mouth to the peri-pharyngeal bands, often, however, these particles are drawn into the pharynx in the main stream at the oral aperture.

These ciliated grooves in the buccal cavity doubtless lend some small aid to the lateral cilia of the gill-filaments in producing the main current, as probably also do the ab-frontal cilia of the filaments. Short cilia have also been observed on the atrial epithelium overlying the gonads. These cilia lash ventrally, and thus help somewhat in producing the main current.

# THE FUNCTION OF THE PHARYNX IN AMPHIOXUS.

It is generally stated that the gill of Amphioxus functions mainly as a respiratory and only secondarily as a feeding organ. In the light of the present researches, however, it would appear that the pharynx functions

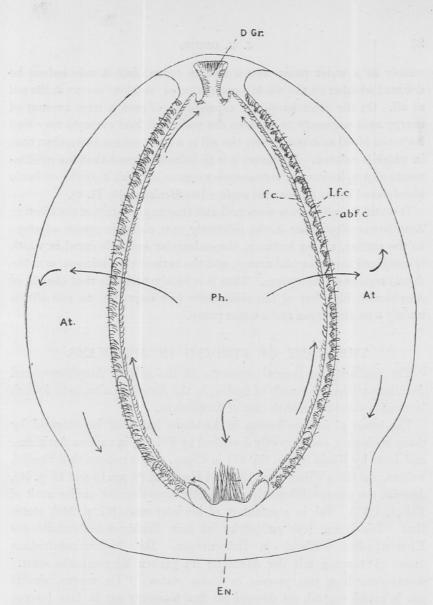


FIG. 6.—Diagram of a transverse section of the pharynx and atrium of Amphioxus to show the ciliary mechanisms on the gill, which produce the main current and collect and transport food-particles. (This diagram serves equally well also for Ascidians.)

Ph. Pharynx, in the walls of which are shown several gill-bars.

At. Atrium.

En. Endostyle, the lateral cilia of which pass on mucus and food-particles from the median cilia to the gill-bars.

D.Gr. Dorsal groove of pharynx.

l.f.c. Lateral cilia on the gill-bars.

These produce the main current which passes across the gill from the pharynx to the atrium in the direction indicated by the large arrows which cross the gill-bars about the middle of the figure. (These cilia should have been denoted in the figure by the letters l.c.)

f.c. Frontal or pharyngeal cilia. These cilia are the chief collectors and transporters of food-particles, which become caught in the mucus passed on to the gill from the endostyle. The captured food-particles are transported towards and into the dorsal groove, as indicated by the arrows along the inside of the gill-bars.

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mainly as a water pump and a feeding organ, and it may indeed be doubted whether on the whole oxygenation of the blood occurs in the gill at all. On the other hand, the expenditure of such a large amount of energy as is necessary to produce the main and food currents may well leave the blood as it issues from the gill in a less pure condition than that in which it entered. Moreover, it is to be remembered that the gill-filaments of Amphioxus are very compact organs in which only the coelomic blood-vessel lies at all near the surface (see Benham, 15, Pl. 6).

It would therefore seem more probable that oxygenation of the blood in Amphioxus takes place in the relatively vast coelomic spaces adjacent to the atrium, as, for instance, the endostylar coelomic canal in which is contained the branchial artery, and the various coelomic spaces in the dorsal regions of the atrium. Thus it is highly probable that the gill of Amphioxus, like that of Lamellibranchs (see later, pp. 44 and 45), is mainly a feeding organ and a water pump.

# THE MODE OF FEEDING IN ASCIDIANS.

The similarity in general structure in the gills of Amphioxus and Ascidians renders the mode of feeding in the Ascidians a matter of much interest in comparison with that of Amphioxus.

The mode of food-collection in Ascidians has been investigated by many zoologists, and correctly described by Fol (17) in various Ascidians, and later by Roule (8, pp. 66, 67) in Ciona. It is curious that English writers, including Willey (1, p. 185) and Herdman (9, pp. 15 and 16, p. 46), describe the process differently, apparently accepting the earlier work of Fol (4, 1872). Fol, in a summary of his later work (17, p. 240), states that "Die Rinne (the endostyle) ist kein Ernährungs-abschnitt des Kiemenkorbes sondern ein Drüsenorgan. Die Nahrungsaufnahme findet gleichzeitig mit der Athmung im ganzen Kiemenkorbe statt." Roule describing this process in Ciona states : "Un mucus, sécrété par le raphé ventral, est déversé en fins filaments sur la face interne de la paroi branchiale ; là, ces filaments agglutinent tous les petits corpuscules, amenés par l'eau, qui passent à leur portée ; puis, entraînés par les mouvements des cils vibratiles des papilles, ils se dirigent obliquement en haut et en arrière, de telle sorte que les filaments les plus antérieurs se rassemblent en une seule masse qui suit le raphé dorsal pour pénétrer dans la bouche œsophagienne, tandis que les postérieurs y parviennent directement." On the other hand, English writers describe food-collection as occurring in the endostyle and peri-pharyngeal grooves; the former groove conducting mucus with contained particles forwards to the latter,

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which in turn carries the food-mass upwards into the dorsal groove, and at the same time assists in capturing food-particles. Delage and Herouard (3, p. 144) point out the differences in the descriptions of this process, and cautiously give only a general account.

# FOOD-COLLECTION IN VARIOUS ASCIDIANS.

Observations have been made on a number of Ascidians, namely, Ascidiella aspersa, Phallusia mamillata, Ascidia mentula and virginea, Ciona intestinalis, Clavellina lepadiformis, Leptoclinum (Diplosoma) gelatinosum and a species of Morchellium, with the result that the process of food-collection has been found to be the same in all these animals as that described by Fol and Roule.

When carmine particles are added to the water in which one of these animals is living, for example, Ascidia mentula, the particles may be observed with a hand lens to be drawn into the branchial cavity and against the wall of the gill. Particles approaching the endostyle, however, are seen to be immediately lashed out of this groove on to the wall of the pharynx, just as is the case in Amphioxus. These particles become rolled into a mass with mucus, and are transported across the branchial sac to the dorsal lamina. All the particles entering the endostyle are washed out on to the pharynx in this way, and no mass of collected food has ever been seen-in any of the animals examined-to be passed forwards. along the endostyle. An examination of the endostyle through a microscope shows further that the lateral rows of cilia on this organ lash in a direction across the endostyle, and from the endostyle on to the pharynx, and no transference of food-particles along the endostyle is seen. The food-particles drawn against the pharynx become caught in mucus and gradually transferred across the wall of the pharynx to the dorsal lamina, becoming rolled into cylindrical masses with mucus on the way. This process of food-collection and transportation is very well seen in the Compound Ascidian Leptoclinum (Diplosoma) gelatinosum, as shown in Fig. 7, which is a drawing of one living zooid in the act of feeding. In such a small animal as this one is able to keep the whole animal in the field of a microscope, and so to follow the course of even small foodparticles in the pharynx. The particles entering the branchial cavity sometimes fall on to the pharyngeal wall close to the peri-pharyngeal grooves, but in none of the animals examined have the particles posterior to the grooves been observed to be drawn into these grooves. On the contrary, in Ascidiella aspersa especially these food-particles become collected in masses some distance posterior to the peri-pharyngeal groove

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as though the cilia in this region were lashing away from the groove. The particles falling on to the region between the buccal tentacles and the peri-pharyngeal grooves, however, are washed into these grooves by cilia in a manner somewhat similar to that observed in Amphioxus.

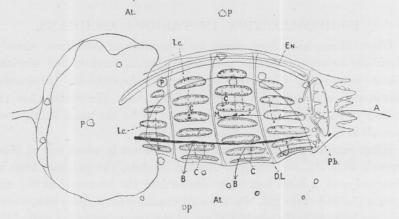


FIG. 7.—View of one entire zooid of the compound Ascidian, *Leptoclinum gelatinosum*, to show the currents produced by the ciliary mechanism on the gill and the mode of food-collection.

(Drawn from the living animal seen through the microscope,  $\times$  about 60.) The large arrows indicate the direction of the main current, and the dotted ones the course of food-particles which have been captured and are being transported to the dorsal lamina. Only the gill slits on the upper surface are shown.

- A. Arrow indicating the direction of the inhalent current produced by the lateral cilia, l.c.
- I.c. Lateral eilia on the sides of the gill slits : these produce the main current by lashing from the pharynx towards the atrium.
- B. Arrows indicating the current passing through the gill slits into the atrium.
- C. Dotted arrows indicating the paths of the food-particles, as at M, captured in mucus and travelling away from the endostyle towards the dorsal lamina, DL.
- DL. Dorsal lamina filled with collected food-particles seen through the wall of the transparent pharynx.

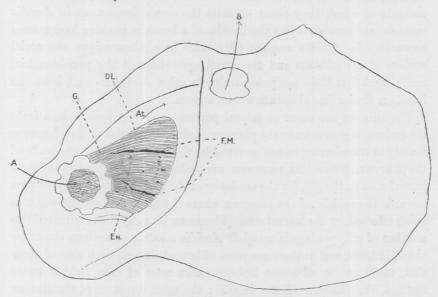
En. Endostyle.

- M. Food-particles embedded in mucus being transported by the frontal cilia on the gill towards the dorsal lamina.
- P. Pigment spots scattered about the surface of the colony.
- At. Common atrium of the colony.
- P.b. Peri-pharyngeal band.

When Leptoclinum (Diplosoma) is fed with a large amount of carmine particles the process of feeding occurs extremely rapidly. Within a few seconds from adding particles to the water the dorsal lamina becomes full of the particles embedded in mucus ready to be passed into the œsophagus. Clavellina can be observed through the microscope to feed in the same way, and almost as rapidly as Leptoclinum. Ascidiella and Ciona feed

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more quickly than the other simple forms, which feed relatively slowly. The process of food-collection at the anterior end of the pharynx in *Ascidia mentula* is shown in Fig. 8. At the posterior end of the pharynx in this animal the cilia in the dorsal groove lash food-particles *forwards* to the œsophageal opening. This process can be easily observed by cutting from the test a window, through which the processes can be followed distinctly.



- FIG. 8.—A view of the anterior end of *Ascidia mentula* to show the mode of feeding. Drawn from the living animal, as seen through a hand-lens. A part of the pharynx is drawn as though the test were transparent. ( $\times$  ca.  $\frac{4}{3}$ .)
  - A. Arrow indicating the direction of the inhalent current.
  - B. Arrow indicating the direction of the exhalent current.
  - At. Arrow in the atrium showing the direction of the main current after passing through the gill slits.
  - En. Endostyle.
  - D.L. Locus of the dorsal lamina.
  - F.M. Food-particles collected into a cylindrical mass with mucus being transported across the gill-bars and away from the endostyle towards the dorsal lamina, as indicated by the dotted arrows alongside.
  - G. One of the longitudinal bars of the gill.

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The main current through the branchial cavity of all the Ascidians examined is produced by the lashings of the cilia on the sides of the gillbars, as has been observed by Herdman for *Ascidia mentula* (10, p. 47). Food-collection is effected by the cilia on the pharyngeal surface of the

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gill-bars and the cilia on the papillæ on the bars. These cilia lash across the length of the pharynx from the endostyle towards the dorsal lamina, but are not specially active nor specially powerful in the simple Ascidians, and food-collection is accelerated by the waving of the longitudinal bars in a transverse direction. In this way the food masses are pushed on as well as lashed onwards towards the dorsal groove. The papillæ of the gill-bars thus assist in food-collection, and in those animals in which they point towards the dorsal lamina, as in *Ascidia mentula*, act somewhat like the bristles of a brush in pushing food masses onwards. In *Ascidia mentula* cilia have been observed on the atrial surface of the gill-bars and the atrial epithelium of the peri-branchial wall; doubtless these are present also in other Ascidians, and have the function of cleaning the walls of the atrium.

The cilia on the outer or lateral portions of the endostyle lash from the endostyle groove on to the pharynx, and in this way doubtless function mainly in transferring mucus secreted by the endostyle on to the walls of the pharynx. These cilia, moreover, are probably seldom required to throw particles on to the gill, for the tendency of the main stream will be to pass towards the middle of the pharynx where the main pull on the water is being effected by the lateral cilia. Herdman (9, p. 17) has estimated the number of gill openings in an adult Ascidia mentula of medium size to be about 192,000, and as there are rows of lateral cilia on each side of these slits, there are in all about 384,000 short rows of cilia lashing water through the pharynx of the animal; the main direction of the current thus produced (see Figs. 7 and 8) is away from the endostyle. It is therefore curious that this groove can ever have been regarded as an important food-collecting organ. On the outer edge of the endostyle of Ciona there are definite short transverse grooves in which the cilia are specially powerful, and lash from the endostylar groove on to the pharynx.

The median ciliated tract of the endostyle bears cilia up to two millimetres in length. Roule (8) describes the cilia as having a very slow movement directed along the length of the groove and consisting of a series of undulations beginning at the base of the cilia. I have not yet been able to detect any movement in these cilia, and am therefore in some little doubt as to their function. Since, however, food-particles are not transported in the endostylar groove, these cilia do not appear to have any transporting function. This view is further supported by the fact that transporting cilia in Gastropods, Lamellibranchs (see 5, *passim*), and Amphioxus are always relatively very short and vibrate

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rapidly. Perhaps the function of these cilia may be detected by examining their action through a microscope in the whole living and feeding animal, and an attempt will be made to find an animal in which this is possible. It is probable that they assist in passing mucus on to the walls of the pharynx, as has been suggested for the similar cilia in Amphioxus.

Examination of the peri-pharyngeal bands through a microscope shows that the cilia in these grooves lash from the endostyle towards the dorsal lamina. These grooves serve to collect and transport to the dorsal lamina such particles as fall out of the main stream at the entrance to the pharynx.

# COMPARISON OF THE MODE OF FEEDING IN AMPHIOXUS AND ASCIDIANS.

From the foregoing description it will be seen that there is an exact correspondence in the mode of feeding in Amphioxus and Ascidians. In these animals the lateral cilia on the gill-bars are the main factors in producing the main current; mucus is passed on to the gill-bars by the outer tracts of cilia on the endostyle, and food-particles are collected and transported to the dorsal region of the gill by the pharyngeal or frontal cilia on the gill-bars. The food collected in the dorsal wall of the pharynx is transported backwards, to be passed into the digestive tract. Thus the diagram of the ciliary mechanism on the gill of Amphioxus (see Fig. 6) will serve equally well for Ascidians in general. The cilia in the peripharyngeal bands in both of these groups of animals lash from the endostyle towards the dorsal groove, and collect and transport to the dorsal groove those particles which fall out of the main stream at the entrance to the pharynx. The process of feeding in both Amphioxus and Ascidians is automatic, but at the same time these animals are able to select from the food-stream the finer food-particles by means of their buccal tentacles. Ascidians, moreover, have been observed to reject food after it has been collected in masses on the gill by suddenly contracting the walls of the pharynx and expelling the whole mass. It is also not improbable that the pharyngocloacal slits observed by Garstang in Ascidians (18, p. 132), may be exits from the pharynx used for relieving that organ when overburdened with undesirable matter. On the other hand Amphioxus is obliged to ingest all that passes beyond the oral aperture.

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# THE FUNCTION OF THE GLAND AND ITS CILIATED TRACT IN THE BRANCHIAL OPENINGS OF AMPHIOXUS AND ASCIDIANS.

In the anterior region of these animals there are also similar organs which have doubtless a similar function, and a function in connexion with the mode of feeding. These organs are a gland, and a ciliated tract connecting the gland with the pharynx, namely, the sensory pit or Hatchek's pit, and the Wheel Organ in Amphioxus, and the neural gland and the dorsal tubercle in Ascidians. It has been suggested by V. Wijhe (7, p. 121) and Andrews (14, p. 227) for Amphioxus, and by Herdman (10, p. 52), Hartmeyer (11, p. 303), and Seeliger and Neumann (12, p. 61) for Ascidians, that this gland may have the function of secreting mucus which is passed on to the pharvnx by the ciliated tract. The observations here made on these groups of animals support these views. The gland probably merely secretes mucus which is passed on to the food-grooves by the ciliated tract to serve for entrapping or embedding food-particles and rendering the transportation of these easier than it otherwise would be. Thus it is not improbable that the great variations observed in the openings of the dorsal tubercle of Ascidians may be a means of distributing mucus in various ways to the pharynx in correlation with minor differences of food-collection on the pharynx; such differences as may be due to the well-known differences in structure of the pharynx.

From the occurrence of sensory cells in Hatchek's pit in Amphioxus it would seem that this organ is also in some way sensory, as V. Wijhe (7, p. 120) has pointed out. In the light of the present researches it is suggested that possibly this sensory pit may govern in some way the supply of mucus from the gland itself and the endostyle, for the capture of food-particles depends to a great extent on the amount of mucus passing over the pharynx. Thus when a large amount of food-particles is passing into the pharynx-as might be first appreciated by the sensory cells in Hatchek's pit-a large amount of mucus would be required to capture the food-particles. It is therefore not improbable that the supply of mucus may be regulated by means of this sensory pit. Whether any similar function is exercised by the neural gland in Ascidians is perhaps more doubtful, but both Herdman (10, p. 52-3) and Seeliger and Hartmeyer (11, p. 303) suggest that the dorsal tubercle in these animals may have a sensory function. It may also be pointed out here that if the neural gland in Ascidians is an organ for secreting mucus which is passed on to the pharynx by the cilia in the dorsal tubercle.

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then this mucus must be passed straight into the dorsal groove. The cilia on the dorsal tubercle of Ciona when examined under a microscope appear to lash away from the body-wall towards the lumen of the branchial opening. Thus in the whole animal it is not improbable that thin sheets of mucus are constantly passing from the dorsal tubercle into the dorsal groove. These sheets would serve to entrap food-particles in the same way as the ciliated tracts do in Amphioxus. It is hoped, however, to complete these observations on a suitable animal and to obtain more definite information on this subject.

## THE MAINTENANCE OF THE PHARYNGEAL SPACES IN ASCIDIANS AND AMPHIOXUS.

The maintenance of a current of water through the body of these animals is dependent upon the maintenance of a continuous open passage through the animal as well as upon the action of the gill as a water pump. In Ascidians doubtless the main function of the test is to maintain a cavity for the branchial sac. The body wall in Ascidians is maintained in close contact with the test by organic connexions, so that the branchial sac lies free in a cavity-the peri-branchial cavity-which the expanded pharynx does not quite fill. Thus a cavity in communication with the pharynx and the exterior is maintained outside the pharynx. The pharynx in Ascidians is kept open by the intercrossing of longitudinal and transverse bars of a sufficiently rigid consistency. In Amphioxus the pharyngeal bars are supported, as is well known, by definite skeletal rods. The peri-branchial cavity in Amphioxus, however, is maintained by dorsolateral sheaths of connective tissue arising from the notochordal sheath (see Lankester, 16, Plate 36) held in position above the pharynx and connected to the lateral surface of the notochord and dorsal skeletal system by the myotomes. A glance at a pharyngeal section of this animal indicates at once how the attachment of the myotomes to the dorsal region of the body and the dorso-lateral sheaths in the wall of the peribranchial cavity maintains this cavity. Indeed, the shape of the myotomes in Amphioxus may have been directly influenced by their function of assisting in maintaining a cavity in the ventral region of the body.

## THE CILIATION OF THE GILL OF BALANOGLOSSUS.

Up to the present it has been possible to examine only sections of the gill of this animal, but it is hoped that observations may be made on the living animal later. Examination of sections of the gill-bars of Balano-

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glossus (a species of Ptychodera) shows the presence of well-marked lateral cilia and smaller frontal or pharyngeal cilia. From the foregoing observations it is a fair deduction that these lateral cilia produce the main current of water through the body of the animal, and that the frontal cilia are concerned in some way in food-collection. It is also highly probable that observations on this group of animals may now demonstrate the function of the mucus, which is doubtless secreted by the dorsal diverticulum, the gland in this group of animals corresponding to Hatchek's pit in Amphioxus and the neural gland in Ascidians.

## OBSERVATIONS ON THE AMMOCOETE OF *PETROMYZON FLUVIATILIS.*

Some observations have also been made on rather late stages of the Ammocoete of *Petromyzon fluviatilis*. It is well known that this larva closely resembles Amphioxus in some respects. I have also learnt from fishermen that these larvæ will live in captivity for even a year by merely changing regularly the water in which they are kept. It was therefore thought probable that they might feed on Plankton in the same way as Amphioxus. Two specimens were fed on carmine particles and then preserved in 90% alcohol. On opening the branchial portion of the alimentary canal it was found that the carmine particles had become entrapped in mucus and were collected along the gill-bars and roof of the pharynx. No particles, however, were found in the intestine. Nevertheless sufficient evidence was obtained to indicate that further observations on the mode of feeding in younger forms might be highly interesting, and an effort will be made to make such observations.

## THE MODE OF FEEDING IN SOLENOMYA TOGATA.

In view of the observations formerly made on the mode of feeding in Nucula (see 5, pp. 467–70), similar observations undertaken upon any other Protobranch promised to be interesting. Acting upon a happy suggestion made by Sir E. Ray Lankester, I obtained living specimens of *Solenomya togata* from Naples at the second attempt, and made the following observations. An examination of this delicate little animal through a microscope in water containing carmine particles readily showed that as in Nucula the mantle cavity is divided into two chambers when the animal is feeding. The food-current is drawn into the mantle cavity at the antero-dorsal end and expelled posteriorly (see Fig. 7). During the process of feeding the gills are extended so that their posterior

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ends touch the mantle postero-ventrally (see Fig. 7), and the lower portions of the gill on each side also meet ventrally, while the tips of the upper lamellæ complete the partition of the mantle cavity by forming a junction with the mantle dorsally. Thus a large anterior inhalent chamber and a smaller posterior exhalent one are formed (as shown in Fig. 9), in the same way as in *Anomia aculeata* and the higher Lamellibranchs. This subdivision of the mantle cavity is of some importance, as it has been regarded by some authors (for example, Sedgwick, p. 345) as occurring only in the higher Lamellibranchiata. It will thus be seen that the whole of the gills of Solenomya resemble generally one lamella of the gill of a mussel for example.

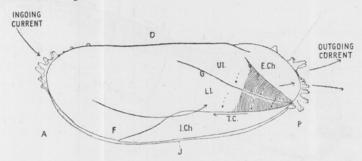


FIG. 9.—View of a living specimen of *Solenomya togata* to show the relations of the gill and the inhalent and exhalent chambers.  $(\times \text{ ca. } 10.)$ 

- G. Left gill.
- I.Ch. Inhalent chamber.
- E.Ch. Exhalent chamber.
- A. Anterior end.
- P. Posterior end.
- D. Dorsal surface.
- U.l. Upper lamellæ of gill.
- L.l. Lower lamellæ of gill.
- J. Anterior end of the fused portion of the mantle.

T.C. Region where collected food is transported forwards as shown by the arrow.

The gill of Solenomya, it will be remembered, has the outer and inner leaflets of the same side placed vertically, the one over the other, so that both appear to form one leaflet with a shallow groove along the median lateral line (see Fig. 9). These leaflets are arranged on an axis on each side at the posterior end of body with only the thin edges of the leaflets showing in a side view. The shape of a pair of leaflets may be seen in Fig. 10.

On feeding the animal with carmine grains it was observed that the food-particles collected on the outer faces of the gills were transported quickly to the ventral edges—even from the upper leaflets—and thence carried forwards towards the mouth to be eaten. The collection and

transportation of food-particles are effected by means of sets of cilia, but in order to make out the actions of these different sets it is necessary to examine separate living leaflets.

## THE CILIATION OF THE GILL OF SOLENOMYA.

When two of the living leaflets (comprising a single pair) of Solenomya are examined microscopically they are seen to resemble in general characters those of Nucula (see Figs. 10 and 11). As in Nucula the main current through the mantle cavity is produced by the

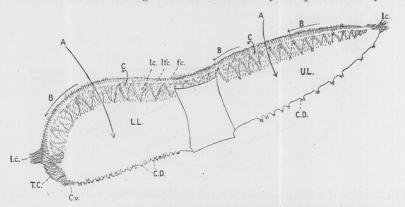


FIG. 10.—View of a pair of living leaflets of *Solenomya togata* taken from about the middle of the gill, to show the directions in which the different sets of cilia lash. ( $\times$  ca. 60.)

The arrows marked A indicate the direction in which the lateral cilia lash to produce the main current; those marked C indicate the direction of lashing of the latero-frontal cilia which act as food-strainers; while those marked B show the direction in which food-particles are lashed by the frontal cilia.

U.L. Upper lamella.

L.L. Lower lamella.

l.c. Lateral cilia forming a broad band on the side of the gill.

l.f.c. Latero-frontal cilia.

f.c. Frontal cilia.

C.D. Ciliated knobs.

- I.c. Cilia interlocking with the mantle.
- T.C. Cilia which transport food along the ventral edge of the gill towards the mouth.
- C.v. Cilia interlocking with similar ones on the adjacent leaflet.

lashings of the large lateral cilia on the anterior and posterior faces of the leaflets (see Fig. 10, l.c. and the arrows marked A). Food-particles are collected by the latero-frontal cilia (the presence of which in this species has recently been doubted, see Ridewood, p. 193) and frontal cilia, but transported solely by the latter (see Fig. 10, l.f.c. and f.c.). The latero-frontal cilia lash in a direction across the length of the edges of the leaflets, i.e. away from the spaces between the leaflets

#### CILIARY MECHANISMS ON THE GILL IN AMPHIOXUS.

(see the arrows marked C in Fig. 10). They catch the food-particles which tend to be drawn between the leaflets in the main current and pass them on to the frontal cilia. The latter lash in a ventral direction, and thus send particles along the edges of the leaflets to the ventral surface (see Fig. 10, f.c. and the arrows marked B). Here a group of cilia now lash the food-particles anteriorly towards the mouth to be eaten. As the foodparticles are lashed along the face of the gill they become embedded in mucus, which is doubtless secreted by the epithelium of the gill. The

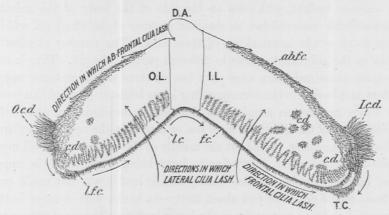


FIG. 11.—Anterior view of a living pair of leaflets of the right gill of Nucula. (× about 65.) The leaflets anterior to the pair depicted were cut away.

ab.f.c. Ab-frontal cilia.

c.d. Patches of cilia on the inner and outer leaflets.

- D.A. Dorsal surface of gill about the 30th pair of leaflets from the posterior end of gill.
- f.c. Frontal cilia.
- I.c.d. Cilia effecting a junction with similar cilia on the left gill.
- I.L. Inner leaflet of gill.
- l.c. Lateral cilia.
- l.f.c. Latero-frontal cilia.

O.L. Outer leaflet of gill.

O.c.d. Cilia effecting a junction with the mantle.

T.C. Cilia which transport collected food forwards.

secretion of mucus on the Lamellibranch gill is indeed a matter of considerable importance in the feeding process, and it is hoped to investigate the matter more fully later.

The examination of single living leaflets reveals a feature of much interest in the ciliation of the gill. On the inner edges of the leaflets, that is, on the ab-frontal surfaces, there occur numerous ciliated knobs (see Fig. 10, c.d.). These ciliated knobs have cilia whose motion is like that of the ciliated discs on the gill-filaments of the Filibranchia (for example see the Fig. of Mussel, Orton, 5, p. 465). This motion may be compared to that of the bristles of two brushes when the brushes are rubbed together slowly in a rotary manner with the bristles interlocking. To get the proper effect one brush should be started rotating before the other, and the bristles should be regarded as vibrating at the same time with a slow wave-like motion which begins at the attached end.

The function of these ciliated knobs is doubtless the same as that of the ciliated discs of the Filibranchia, namely, to interlock with similar discs on the leaflets of the gill on the other side of the body; or, in the case of the anterior leaflets, with cilia on the side of the body of the animal. When suitable material can be obtained sections of the whole gill will be made to show the interlocking of these cilia. The number of ciliated knobs on the gill-leaflets varies in different parts of the gill. Thus in one specimen examined there were only two or three on the anterior upper leaflets and twelve in the corresponding lower leaflets. Behind this point the knobs increase in number, so that at the beginning of about the middle third of the gill there were ten or eleven in the upper and thirty to forty in the lower. In about the middle of the gill there are still more knobs on both leaflets, thirty-five to forty being counted on the upper ones, but the number on the corresponding leaflet was not made out. In front of the posterior end about thirty-six knobs were counted in the upper and eighteen to twenty in the lower leaflets. There are thus more knobs in the middle of the gill and fewer at the anterior and posterior ends, and more in the lower leaflets in the anterior end than in the upper ones in this position, but more in the upper than in the lower at the posterior end. These differences are doubtless explained by the facts that at the anterior ends of the gills the upper leaflets appear to lie against the body, while the lower ones meet below, and thus require a better interlocking arrangement, while at the posterior end of the gill the upper leaflets are longer than the lower ones.

Besides these ciliated knobs there are also other interlocking cilia at the tips of the upper and at the ventro-lateral edges of the lower leaflets (see Fig. 10, I.c.). These cilia doubtless effect a junction with the mantle, and an attempt will be made to obtain sections of the gills and mantle to show these connexions.

On the anterior and posterior faces of the ventral edges of the lower leaflets there are patches of cilia which also have the rotary motion characteristic of interlocking cilia. These probably serve—like the similar patches on the gill leaflets of Nucula (see Fig. 11, c.d.)—to hold the tips of the leaflets together. Thus the living gill of Solenomya is a very compact organ, which, however, like that of Pecten, can be contracted

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into a small compass so as to leave the inhalent and exhalent chambers continuous.

The characters of a transverse section of a gill-leaflet of Solenomya can now be recognized. Ridewood (p. 193) in describing the ciliation of the gill remarks, "Cilia are confined to the thickened edge, and appear to form a continuous investment of it, not differentiated into frontal and lateral tracts. The material available is not sufficiently well preserved to allow of a definite statement upon this point, but it is worthy of remark that no gap between the frontal and lateral cilia is shown in the figures (of the transverse sections) given by Pelseneer, Kellogg, and Stempell. The cilia extend as far as the level of the outer edge of the thickened chitin bands, and the shortest are those on the frontal surface. Pelseneer shows large latero-frontal cilia, but this is possibly an error."

The foregoing examination of the living leaflets shows that Pelseneer's depiction of large lateral cilia (the latero-frontal cilia) is correct, and that all figures err in depicting a continuous covering of cilia at the tip of the gill (see Fig. 10), thus justifying Ridewood's cautious remarks in this respect. A transverse section may or may not show cilia on the ab-frontal face according as the section passed through a ciliated knob or not. An attempt will be made to make preparations from well-preserved gills and to figure a transverse section.

## RESEMBLANCE OF THE CILIATION OF THE GILL IN SOLENOMYA AND NUCULA.

From the above description of the ciliation of the gill of Solenomya it will be seen that there is a close resemblance to that obtaining in Nucula (see Fig. 11). If the frontal surfaces of these gills be compared a complete resemblance in this part is seen; frontal, latero-frontal, and lateral cilia occurring in both and having the same function in both. The ab-frontal cilia of the gill of Nucula, however, are absent from that of Solenomya, and are replaced by ciliated knobs. The small patch of interlocking cilia on the lateral faces of the leaflets of Nucula have not been seen in Solenomya, but a patch of interlocking cilia is present on the ventro-lateral portion of the inner leaflets of both gills (see Figs. 11, c.d., and 10, c.v.). Cilia interlocking with the mantle are present in both forms at the tips of both leaflets; those in Solenomya are, however, nearer to the frontal surface than in Nucula in correlation with the difference in position of the gill in the former. On the whole, therefore, the ciliation of the gill of Solenomya bears a very close resemblance to that of Nucula.

#### J. H. ORTON.

## SUMMARY OF THE ACCOUNT OF THE CILIARY CURRENTS IN SOLENOMYA.

The main current through the mantle cavity is effected by means of the lashings of the lateral cilia on the gill-leaflets. This current is drawn in at the antero-dorsal region of the shell and expelled in the posteriorregion. The food-particles brought to the gill in this current are arrested on the gill by the latero-frontal and frontal cilia, the former passing on particles to the latter. The frontal cilia transport the food-particles. along with mucus, which is doubtless secreted by the epithelium of the gill, on to the ventral edges of the lower leaflets, whence a special groupof cilia transport the collected particles and mucus towards the mouth to be eaten.\* Ciliated knobs occur on the ab-frontal edges of the leaflets. which serve to interlock with similar knobs on the fellow-leaflets on the other side of the body. Long interlocking cilia also occur at the dorsal ends of the upper leaflets and the ventro-lateral edges of the lower ones. These cilia serve to effect a junction of the gills with the mantle during feeding, and so divide the mantle cavity into an inhalent and an exhalent chamber.

On the whole, therefore, it is seen that the gill of Solenomya, like that of Nucula, is essentially similar to that of the higher Lamellibranchs. Indeed the presence of numerous ciliated knobs must rank this gill as a more highly specialized one than, for instance, that of *Anomia aculeata*, which has only interlocking arrangements at the tips. Apart from the narrowness of the filaments in *A. aculeata*, there is almost an exact resemblance between the gills of this species and those of Nucula and *Solenomya togata*. Thus the gross structure and the function of the gills in the Protobranchia and the Filibranchia have been shown to be essentially similar, and there can be very little doubt from the published accounts of the gills of other Protobranchia that these may be regarded as essentially similar to those of Solenomya and Nucula.

## THE FUNCTION OF THE GILL IN LAMELLIBRANCHS.

The gill in all groups of Lamellibranchs has now been shown to be a feeding organ. Generally, however, this organ is regarded as being chiefly a respiratory and only secondarily a feeding organ. In the light

\* Since this account was sent to the printer, a paper by E. S. Morse on Solenomya in the current number of the *Biological Bulletin*, Woods Hole, has come to hand. This paper gives an account of observations on living *Solenomya velum* and *S. borealis*. Morse has observed the palps being used for transferring food from the gill to the mouth, which fact, added to those given above, completes our knowledge of the mode of feeding in Solenomya. of recent researches on the function of the gill, however, it would appear that the order of importance in which these functions have been regarded must be at least reversed. The expenditure in the gill of the relatively large amount of energy necessary to produce the main current and food currents must enormously outbalance the aerating effect of these currents on the gill. For it is to be remembered that in the gill-filaments of Lamellibranchs the blood is not contained in a capillary plexus, but usually in a blood vessel sunk well below the epidermis. This conclusion with regard to the function of the Lamellibranch gill has indeed already been arrived at, from a morphological point of view, by Dakin (6, pp. 52-3), who states that in the genus Pecten "It seems certain, from the development of vessels in the mantle, that the great function of the gills is to produce currents of water for aeration, nutrition, and the carrying away of waste products, and the only parts of the gills performing any really important duty in respiration are the branchial expansions of the principal filaments." There is little doubt that this statement might now be made similarly of the whole of the higher Lamellibranchs. It is of interest, however, that there is one important difference in this respect in the gills of the Protobranchia. In this group the gill-filaments are broad and lamellate, and contain an extensive space between the two surfaces (see Ridewood, p. 193) over which we have seen the current passes. Doubtless with this type of gill a much greater proportion of the whole respiration is effected in the gill than is the case in the forms with narrow compact filaments. But even here it may be doubted whether respiration is effected to the same degree in the gill as in the mantle. It would be highly interesting in these respects if a ready means could be found of detecting the relative amounts of waste products in any particular part of the body at any particular instant. Such an experiment may perhaps not be an impossibility, as some of these animals can be observed living through a microscope.

## APPENDIX.

Some of the observations made in the section on the function of the Wheel Organ and Peri-pharyngeal bands in Amphioxus (p. 25) have already been noticed by Andrews in the Bahamas Amphioxus, as will be seen from the following quotation. It was unfortunately not possible to refer to Andrews' work in the general text, as some difficulty was experienced in obtaining his paper, which only became available after the text had gone to the printer.

Andrews (4) obtained living specimens of the Bahamas Amphioxus

(Asymmetron lucayanum) about which he observes: "As the animal is small and translucent, the course of food and carmine granules may be traced through most of the digestive tract. The strong current of water setting into the pre-oral chamber seems to be controlled by the longitudinal, ciliated ridges of Müller's 'Räderorgan' which pass forward from the velum on the inside of each lateral wall of the pre-oral chamber. Thus the carmine granules pass rapidly along these ridges towards the velum, where they are turned inward towards the aperture, mouth, at the centre of the velum. The granules pass along in strings as if held together by a thin mucus; once through the mouth they do not pass out through the pharyngeal slits, but continue along the median dorsal pharyngeal groove, the hyper-pharyngeal groove, still adhering to one another in strings. In actual longitudinal and cross sections these strings of granules may still be recognized in the ciliated hyper-pharyngeal groove.

"This groove leads into what may be called the stomach, within which the current of granules, or the granule containing mucous strand, turns abruptly downwards and forwards as indicated in the above diagram, yet does not enter the diverticulum, but, still under the control of the active cilia lining the digestive tract, passes back again through the centre of the stomach. It is now revolving rapidly in a constant direction from right to left, and continues to do so throughout the next division of the digestive tract, the first or larger section of the intestine. In this part of the intestine the granules, diatomes, etc., collect into clumps separated by the clear part of the continuous mucus-like strand. In this region the intestinal epithelium is especially modified in a zone that became very prominent when staining reagents are used.

"The second, final and smaller part of the intestine, contains pellets of detritus that become successively larger towards the anus, where they have the form of elongated, not spherical, masses that are discharged from the anus as the anal sphincter relaxes from time to time. The mucous strand is here broken, the granular aggregates becoming isolated from one another. These balls or pellets move along but slowly, and give up the revolving motion seen in the first part of the intestine and in the stomach.

"The time elapsing from the addition of carmine to the water to the discharge of carmine containing pellets may be much less than one hour."

It will thus be seen that Andrews has described some of the processes in the subsidiary method of feeding in the Bahamas Amphioxus which

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is doubtless the same as in the Plymouth Amphioxus. He gives the impression, however, that this is the main method of feeding, but such is not the case, as will have been seen from the foregoing description.

## SUMMARY.

The mode of feeding in Amphioxus is effected by-

- (1) The maintenance of a stream of water through the pharynx by rows of lateral cilia on the gill-bars.
- (2) The throwing out of mucus from the endostyle on to the gill-bars to serve for entrapping food-particles.
- (3) The collection of food-particles by rows of cilia on the pharyngeal surface of the gill-bars; these cilia work up the foodparticles with mucus into cylindrical masses and transport such masses dorsally into the dorsal groove which carries the collected masses backwards into the digestive tract.

Thus the ciliary mechanisms on a gill-bar of Amphioxus are exactly the same as those on the gill-filaments of some Lamellibranchs, as Pecten, and some Gastropods, as Crepidula.

A subsidiary mode of food-collection is effected in the buccal cavity of Amphioxus by the ciliated tract known as the wheel organ, and Hatchek's pit, which supplies mucus for entrapping food-particles. These particles are passed on to the peri-pharyngeal bands which conduct them in turn into the dorsal groove.

The gill of Amphioxus functions mainly as a feeding organ and a water pump, and probably not at all as an organ for aerating the blood.

The mode of feeding in Ascidians is almost exactly the same as that described above for Amphioxus. Food-collection, however, in Ascidians is effected by cilia on the papillæ and similar outgrowths on the gill, and is also helped in some forms by transverse waving of the longitudinal bars, by which process the food is pushed as well as lashed towards the dorsal region of the pharynx.

The observations here made lend support to the view that the neural gland in Ascidians is an organ for secreting mucus, which aids in the capture and transportation of food-particles, and that the dorsal tubercle of Ascidians is an organ for passing mucus on to the pharynx; the corresponding structures in Amphioxus, namely, Hatchek's pit and the wheel organ, are here shown to effect food-collection in the buccal cavity.

The cavity in the body of Ascidians through which the food stream

can pass is maintained by the test, and in Amphioxus by the expansion of stout connective sheaths over the dorsal region of the pharynx held in place by muscular attachments to the dorsal region of the body.

The ciliation of the gill-bars of Balanoglossus is essentially the same as that of Amphioxus. Hence the current of water through the body of the animal is doubtless effected by the lateral cilia and a mode of foodcollection effected by the frontal cilia.

Observations on late Ammocoete larvæ indicate food-collection on the gill-bars and the roof of the pharynx, as occurs in Amphioxus. An attempt will be made to complete these observations.

The mantle cavity of *Solenomya togata* is divided into inhalent and exhalent chambers by the gill in the same way as in other Lamellibranchs, namely, Anomia and Pecten.

The ciliation of the gill of Solenomya closely resembles that of Nucula : the lateral cilia produce the main current, the latero-frontal and the frontal cilia collect food-particles, and the latter transport them to the ventral surface of the gill, whence they are conducted forwards by special transporting cilia towards the mouth to be eaten.

Numerous small ciliated knobs occur on the ab-frontal face of the gilllamellæ and serve to interlock with their fellows on opposite leaflets.

These ciliated knobs correspond to the ciliated discs of the gill-filaments of other Lamellibranchs, for example, the Mussel.

Interlocking cilia occur on the edges of the upper and lower leaflets of the gill and serve to lock the gill to the inner wall of the mantle, and thus to partition the mantle cavity.

The function of the Lamellibranch gill is probably mainly that of a food collector and a water pump, and except in the Protobranchs is probably not an organ in which aeration of the blood occurs.

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# The Electrical Conductivity of Fertilized and Unfertilized Eggs.

By

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THE following is a preliminary account of some experiments carried out this summer at Plymouth. They were undertaken with a view to the investigation of the changes, both physical and chemical, which are induced in the egg by the entrance of a spermatozoon.

No attempt is made to discuss the results in the light of current theories regarding the phenomena of fertilization, as it is hoped that further work will make such discussions more profitable than would be the case at present.

## APPARATUS.

In order to determine the electrical conductivity of the eggs, a conductivity cell was used such as would fit the holder of a small hand centrifuge. The tube was about 10 cm. long and 1 cm. in diameter. The electrodes were two square platinum plates each possessing two equal surfaces of 25 sq. mm. These were fixed about 25 mm. apart and were carried by two silver wires which passed through glass tubes, and which were fixed through the stopper of the tube.

In some of the earlier experiments the volume of the eggs in the tube was determined by marking their level with a fine pointed grease pencil, but in all the later experiments the tube was graduated.

This form of conductivity cell has two advantages—it fits into the holder of an ordinary centrifuge, and the volume of eggs required is small. The latter point is of great importance, quite apart from the difficulty in obtaining large quantities of ripe *Echinus* eggs. If too many eggs are enclosed within a tube, it is not only impossible to ensure a good percentage of fertilizations by adding a small quantity of sperm, but the overcrowding of the eggs interferes very considerably with the development of the eggs subsequent to fertilization, i.e. the rate of division differs very considerably from that of similar eggs in a large bulk of water; in extreme

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cases the development ceases at an early stage. In all my experiments, except where specially mentioned to the contrary, the eggs developed normally, although in some cases more slowly than the controls.

The temperature at which the experiments were made never differed much from room temperature, so that it was found possible to keep the temperature of the eggs constant to within  $\frac{1}{10}^{\circ}$  centigrade by means of a simple thermostat. The whole apparatus stood in a large earthenware bowl containing water at room temperature.

The alternating current was obtained from a 2-volt accumulator connected to a small induction coil of high frequency. The resistance was measured by means of a Kohlrausch bridge (half a metre in length), and a telephone. The electrodes were platinized in the usual way by means of platinic chloride with a trace of lead acetate. The induction coil was placed outside the room in which the experiments were made, and by keeping the electrodes well platinized it was possible to obtain quite distinct minimal points with an ordinary telephone.

#### METHODS.

The procedure adopted during the whole of the experiments was as follows: The ovaries of a perfectly ripe female were shaken in one or more finger-bowls containing "outside" water. The ovaries were removed after five or ten minutes, and the sea-water containing the eggs filtered through a suitable piece of bolting silk. In this way any loose pieces of ovarian tissue were removed from the eggs. The latter were now allowed to settle to the bottom of the bowl. The ripe eggs settled somewhat slowly, but after a short time sufficient eggs for one experiment could be drawn off in a clean pipette; thence they were transferred to the conductivity tube. The requisite amount of eggs having been so obtained, the tube was filled up with clean sea-water, corked and allowed to stand in a bowl of sea-water until the eggs had again settled sufficiently for the bulk of the sea-water to be removed. This having been done, the eggs were again washed in clean sea-water. After two or three such washings all the small fragments of tissue smaller than the eggs were removed, and the tube contained nothing but ripe eggs in clean seawater. After washing in this way the eggs settled somewhat more readily than when removed from the ovary, owing to the removal of the gelatinous ovarian membranes. The conductivity tube containing the eggs was then transferred to the thermostat and left until the eggs had settled to a definite volume which could be estimated without any difficulty. Great care was used to ensure that the eggs settled uniformly

in the tube; if this precaution is not observed it will be found that repeated estimations of the resistance of the same eggs occupying the same volume give very variable results. It was found possible, however, to collect the eggs in such a way as to obtain uniform readings from repeated observations. To ensure an equal distribution of the eggs is a matter of great difficulty in the case of experiments dealing with resistances below 20 ohms; above this, however, the difficulty can be overcome by patience and repeated washings of the eggs.

The volume of the eggs having been accurately determined by means of the graduation on the tube, some of the sea-water was removed from the tube and the electrodes placed in position and the resistance of the eggs determined.

The electrodes were then removed and the tube filled with fresh seawater (care being taken not to remove any eggs with the electrodes).\* One or two drops of a dilute emulsion of sperm were then added and the tube inverted so as to distribute the eggs equally through the sea-water.

After a minute the tube was allowed to stand in the water of the thermostat, until the eggs had again settled to the bottom of the tube. It was usually found that the fertilized eggs occupied a larger volume than the same eggs unfertilized; in such cases the tube was transferred to a hand centrifuge and very gently centrifuged to the required volume. The excess of sea-water was again drawn off and the electrodes placed in position and the resistance of the egg determined. The use of the centrifuge was avoided as far as possible for fear of injuring the eggs; it was found, however, that gentle use of the machine had no effect on the resistance of unfertilized eggs, or upon the subsequent development of fertilized eggs. If, however, the unfertilized eggs were so compacted as to require rather vigorous use of the centrifuge, the experiment was discontinued after the estimation of the resistance of the fertilized eggs. Such eggs were usually found to be crushed although not broken, and when returned to abundant sea-water the large majority developed normally.†

After each estimation of the resistance of the eggs, the conductivity tube was filled with fresh sea-water and immersed horizontally in seawater whose temperature never differed from that of the thermostat by more than  $1^{\circ}$  C.

Objections may be raised against the conclusion that the observed differences in resistance of eggs at different stages of development are

\* When not actually in use the electrodes were kept immersed in clean sea-water.

+ These remarks apply to eggs which gave a resistance of 70 ohms and upwards.

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due to the direct effects of fertilization. The following alternative suggestions might be offered :---

1. That the changes are due to the injurious effect of the current upon the eggs. For this, however, evidence is entirely unavailable. Eggs upon which definite and prolonged experiments had been made on June 18th were transferred to a bowl of clean sea-water, all the eggs divided normally, and all gave healthy larvæ. Some of these early plutei were placed in a sterilized jar and fed with a pure diatom culture; on July 11th the plutei were large and healthy. They had developed at a normal rate, and a definite *Echinus* rudiment was visible. Several such observations of the development of eggs whose resistance had been measured were kept, and in each case the development was perfectly healthy and normal.\* It is therefore, I think, safe to conclude that the eggs were unaffected by the passage of the current used in these experiments.

2. That the changes are due to experimental error in returning the eggs to the same volume. To determine the degree of error due to such a source, I made successive determinations on the resistance of the same lot of unfertilized eggs. I found that the variation of the readings never exceeded 2% of the total resistance (in many cases successive readings were identical). Now such a difference might perhaps explain experiments in which the total resistance is below 20 ohms, but is quite inadequate for the much larger differences which were regularly observed for eggs compacted to give higher resistances.

3. That the decrease in resistance of the eggs subsequent to fertilization is due to the presence of the fertilization membrane and not to the substance of the egg itself. It cannot, however, be suggested that the spaces between the egg are enlarged by the membrane, for the unfertilized eggs are not crushed during the experiments, and any crushing undergone by the fertilized eggs is at the expense of the *membrane* and not of the egg. If the eggs are closely compacted after fertilization it is almost invariably found that either the membranes are much wrinkled or are removed entirely from the egg on the addition of fresh sea-water. Again, during the course of the experiments it was found that the fertilization membranes in some batches of eggs were never pushed far out from the egg, but

\* In the case of *Echinus miliaris* plutei, which according to Shearer, De Morgan and Fuchs fail to develop their green pigment if unhealthy, my cultures invariably possessed this character and were, in the opinion of Dr. Shearer, perfectly healthy. (Most of the cultures were discarded as soon as the Echinus rudiment had reached considerable size, but in two cultures which were preserved the larvæ underwent perfectly typical metamorphosis—a little more than a month after fertilization, which is in agreement with the rate of development of the egg under normal conditions.) remained rather closely applied to the egg-surface; in such cases the resistance of the fertilized eggs was, as in other cases, markedly lower than that of the unfertilized eggs. It was also found that eggs from which the fertilization membrane had been forcibly removed developed quite normally. Now Loeb has shown that the fertilization membrane is permeable to electrolytes, and I therefore conclude from the above facts that the presence of a membrane round the eggs is equivalent to a similar quantity of sea-water, and that when the eggs are reduced to the same volume as before fertilization, the distance between the eggs is identical.

The fact that after the initial fall in resistance of the eggs after fertilization there is a definite and well-marked *rise* in resistance, eliminates the suggestion that the changes observed are due to the presence of a fertilization membrane. Again, in a few cases (i.e. in experiments dealing with high resistances) a considerable number of the membranes are removed from the egg whilst determining the resistance of the fertilized eggs, so that when sea-water is added the membranes are found floating in it. If the eggs are not allowed to settle *at once* they are found still to have a resistance equal to the value obtained by the first determination after fertilization.

4. That the observed differences are due to the existence of free spermatozoa between the eggs. This is not the case, because (1) the addition of as much sperm as was used in any of these experiments does not alter the conductivity of a bulk of water equal to that of the eggs; (2) the conductivity of a concentrated emulsion of sperm is considerably *lower* than that of pure sea-water.

(Note.—McClendon states that by repeatedly washing the unfertilized eggs of *Arbacia* he was able to prevent the formation of a fertilization membrane when the sperm entered the egg. I have never observed this in the eggs of *Echinus*, but prolonged washing tends to prevent the membranes being pushed out to their normal extent.)

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## TABLE I.

	Resistar	nce in Ohm	s	Minutes aft addition o	of	
	Unfertilized Eggs (R <sub>v</sub> )	of l Ferti Eggs		sperm that determination of $R_F$ was made	on	$\frac{(R_v - R_F) 100}{R_v}$
1.	17.3		3.3	6	1.0	5.8
2.	22.5	21	.5	10	1.0	4.4
3.	30.0	28	3.5	10	1.5	5.0
4.	30.5	27	.8	12	2.7	8.8
5.	36.5	34	ŀ0	15	2.5	6.8
6.	38.0	29	9.7	6	8.3	21.8
7.	39.7	36	3.5	10	3.2	8.0
8.	40.5	37	.5	7	3.0	7.4
9.	40.6	37	.5	9	3.1	7.6
10.	41.0	38	3.0	8	3.0	$7.3^{\circ}$
11.	41.5	38	3.5	3	3.0	7.2
12.	42.8	4(	).8	11	2.0	3.7
13.	43.0	39	0.0	10	4.0	9.3
14.	44.0	39	0.0	15	5.0	11.3
15.	<b>44</b> ·0	33	3.0	2	11.0	25.0
16.	44.0	43	3.5	13	•5	1.1
17.	45.0	- 41	0.	6	4.0	8.9
18.	45.0	41	0.1	9	4.0	8.9
19.	45.0	36	5.5	7	8.5	18.9
20.	<b>46</b> ·0	41	0	15	5.0	10.9
21.	47.3	40	).5	14	6.8	14.3
22.	49.0	48	5.0	4	4.0	8.1
23.	49.0	48	3.0	15	1.0	2.0
24.	50.0	44	F•0	11	6.0	12.0
25.	50.8	40	3.0	5	4.8	9.4
26.	51.0	41	1.5	11	9.5	18.6
27.	51.0	40	)•0	7	11.0	21.6
28.	54.0	47	7.0	6	7.0	12.9
29.	54.5	48	3.7	13	5.8	10.6
30.	66.0	48	3.7	20	17.3	26.2
31.	72.0	59	9.5	9	12.5	17.3
32.	75.5	65	3.0	10	12.5	16.5
33.	80.0	68	3.5	5	11.5	14.6
34.	85.0	78	5.0	15	10.0	11.7
35.	87.0	78	8.0	10	9.0	10.3
36.	100.0	89	)·0	15	11.0	11.0

## EXPERIMENTS WITH Echinus acutus.

Average value of  $\frac{(R_{\scriptscriptstyle U}\!\!-\!\!R_{\scriptscriptstyle F})\,100}{R_{\scriptscriptstyle U}}\!=\!11\!\cdot\!2$ 

# TABLE II.

EXPERIMENTS WITH Echinus miliaris

	Resistances in Ohms	An antipalité			
	Unfertilized Eggs (R <sub>v</sub> )	Fertilized Eggs (R <sub>F</sub> )	Mins. after Fertilization	R <sub>v</sub> -R <sub>F</sub>	$\frac{\left(R_{\upsilon}R_{\textrm{F}}\right)\text{100}}{R_{\upsilon}}$
1.	16.0	15.4	15	0.6	3.7
2.	16.4	15.5	15	0.9	5.5
3.	19.1	17.0	8	$2 \cdot 1$	11.0
4.	26.5	25.5	5	1.0	3.8
5.	30.0	29.0	8	1.0	3.3
6.	32.5	29.5	18	3.0	9.2
7.	32.5	31.0	12	1.5	4.6
8.	42.0	39.5	10	2.5	5.9
9.	45.5	41.0	20	4.5	9.9
10.	47.0	40.3	15	3.3	7.0
11.	49.5	45.5	10	4.0	8.1
12.	56.5	41.0	21	15.5	28.0
13.	60.0	56.0	10	4.0	6.7
14.	61.0	51.0	7	10.0	16.4
15.	65.0	50.5	10 -	15.5	23.8
16.	65.0	55.0	15	10.0	19.4
17.	76.0	61.0	13	15.0	19.7
		1	R	1	

Average value of  $\frac{(R_v - R_F) 100}{P} = 10.9$  $R_{\sigma}$ 

### TABLE III.

EXPERIMENTS WITH Echinus esculentus.

 $R_{\sigma}$ 

18.2

7.5

Resistances in Ohms of  $(R_v - R_F) 100$ 72 10 16.0 1. 88.0

37

## TABLE IV.

6

3.0

EXPERIMENTS WITH Asterias glacialis.

	of Unfertilized	Fertilized	Mins. after		$(R_v - R_F) 100$
	Eggs $(R_v)$	Eggs $(R_F)$	Fertilization	$R_v - R_F$	R <sub>v</sub>
1.	29.0	27.5	12	1.5	5.2
2.	33.0	29.0	15	4.0	12.1
3.	35.5	33.0	10	2.5	7.0
4.	37.5	34.5	15	3.0	8.0
5.	41.5	39.5	8	2.0	4.8
			$(R_{o} - R_{F}) 100$	) 7.4	

Average value of -=7.4  $R_{\upsilon}$ 

2.

40.0

Resistances in Ohms

ELECTRICAL CONDUCTIVITY OF FERTILIZED AND UNFERTILIZED EGGS. 57

			Resistance of Unfertilized Eggs	Resistance of Within 15 mins. of Fertilization	Fertilized Eggs 15–44 mins. after Fertilization
1.	Echinus	acutus	30.0	28.5(10)	29.5 (32)
2.	"	"	43.0	39.0 (10)	43.0 (38)
3.	,,	,,	46.0	41.0 (15)	43.5 (30)
4.	,,	,,	38.0	29.7 (6)	31.0 (27)
5.	,,	,,	45.5	36.5 (7)	37.3 (28)
6.	,,	,,	51.0	40.0 (7)	41.5 (27)
7.	,,	,,	45.0	41.0 (9)	42 (26)
8.	,,	,,	50.8	46.0 (5)	51 (20)
9.	,,	,,	49.0	45.0 (4)	50.5 (15)
10.	,,	,,	80.0	68.5(5)	80 (16)
11.	,,	,,	54.0	47.0 (6)	54 (27)
12.	,,	,,	72.0	59.5 (9)	64.0 (27)
13.	,,	,,	42.8	40.8 (11)	42.8 (38)
14.	,,	,,	41.5	38.5(3)	40.0 (17)
15.	,,	,,	54.5	48.7 (13)	48.7 (30)
16.	Echinus	miliaris	32.5	29.5(18)	32.0 (38)
17.	,,	,,	<b>42.</b> 0	39.5 (10)	41.0 (44)
18.	,,	,,	65.0	50.5 (10)	52.5(28)
19.	Asterias		37.5	34.5(15)	35.5(27)
20.	,,	,;	33.0	29.0 (15)	30.5 (31)

#### TABLE V.

The figures in brackets in columns 2 and 3 indicate the actual number of minutes after the addition of sperm to the eggs.

#### CONCLUSIONS.

From these experiments I draw the following conclusions :---

- 1. That the entrance of the sperm into the egg causes an increase in electrical conductivity of the egg. This condition usually attains its maximum within ten minutes of adding sperm to ripe eggs.
- 2. That this increase in conductivity is followed by a process which returns the conductivity of the egg to or towards that of the unfertilized egg.

The chief limitation of the method lies in the fact that in order to get a measurable change in resistance between the electrodes after fertilization, the eggs must be concentrated to give an initial resistance of about 30-40 ohms. In order to cover the electrodes with the eggs, at least  $\frac{1}{2}$  c.c. of eggs is required. The volume of sea-water which the conductivity cell can hold is about 10 c.c.; the effect of these conditions is that when the eggs are shaken in sea-water after the determination of their resistance they

are so crowded that they develop at a rate different from that of control eggs kept in abundance of water. The change in rate of development varies with different batches of eggs and with their degree of concentration. Hence it is impossible by this method to determine the conductivity of normal eggs (i.e. eggs developing at a normal rate) at any stated moment. As, however, the development of the eggs in the conductivity tube is only abnormal in respect to time (i.e. the cleavage divisions are quite normal but occur at a varying time after those in a control), it may be concluded that the sequence of events in the two cases is the same.

A more important limitation lies in the fact that the resistance can only be determined by concentration of the eggs. We may conclude that when the eggs are concentrated at the bottom of the tube, their development very quickly becomes delayed until the return of normal conditions; hence it is not possible to take a large number of readings during one experiment.

These two factors would account for the variation found in curves obtained from the individual experiments. For example, most of them show the same maximum and minimum points during the first hour of development, but corresponding points on different curves do not agree in point of *time*. Again, it is almost certain that the primary rise in conductivity due to the entrance of the sperm, lasts only for some fifteen minutes or less; if therefore it is found impossible (for technical reasons) to determine the resistance of the fertilized eggs during this period, the pronounced minimal point which exists during the first ten minutes of development is entirely lost, and the curve differs radically in appearance from the normal. Owing to the rapid rate in the rise and fall of the conductivity at the commencement of development the exact time at which the resistance is determined is of considerable importance. For example, one experiment gave the following data :—

The resistance of eggs 3 mins. after fertilization was 10.5 ohms less than that of the unfertilized eggs.

					entern en		vaac e	TTYP OF OF	marca .
,,	,,	,,	9	,,	after fei	. was	12.5	ohms	less
,,	,,	,,	13	,,	,,	,,	3	,,	,,
,,	"	,,	25	,,	,,	,,	8	,,	.,,

In other words, the conductivity of the eggs has undergone profound changes within 13 minutes. It is therefore necessary to discover the position of the maximum and minimum points with considerable accuracy before any quantitative value can be ascribed to the changes in conductivity which take place during the development of the normal egg.

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Without wishing to dogmatize in any way as to the explanation of these preliminary experiments, it may be pointed out that they may possibly be due to either purely physical or purely chemical changes in the egg or to a combination of such causes. The egg in the unfertilized state is remarkably impermeable to electrolytes, and can almost certainly be regarded as being enclosed within a semi-permeable membrane. In its unstimulated condition, this surface must necessarily be polarized. If now this polarization be destroyed, the membrane must become more permeable to ions than before. On this view the entrance of the sperm effects the depolarization of the plasma-membrane. After about fifteen minutes this membrane must become polarized again, but the mechanism whereby this is effected is not at present clear.

On the other hand, if the sperm carries an enzyme into the egg, which acts on some constituent of the egg-cytoplasm, then a rise in conductivity may occur as the result of the liberations of ions from unionized substances; while a reversal of this reaction will have an opposite effect.

It is hoped that further work will produce sufficient evidence to show which of these two possibilities is the more probable explanation of the experimental data, and a discussion of the results obtained by other workers is therefore postponed.

The expenses of this work have been partly defrayed by a grant from the Government Grant Committee of the Royal Society.

# Some Rare and Interesting Sea Anemones from Plymouth.

By

Chas. L. Walton and Olwen M. Rees, B.Sc., University College of Wales, Aberystwyth. With Figures 1 and 2 in the Text.

THE anemones described in the following pages were collected by Mr. J. H. Orton, and forwarded for examination.

## I. Edwardsia timida, Quatrefages.

Quatrefages obtained his specimens at Chausey, Manche, N. France, and his descriptions of E. timida and E. harassi as new species appeared in 1842 ("Ann. des Sci. Nat." (2), XVIII). G. Y. Dixon obtained eight specimens at Malahide, Co. Dublin, and these he carefully described in 1886 ("Proc. Roy. Dublin Soc."). He also united Quatrefages' two species as E. timida. In 1889 A. C. Haddon supported Dixon's opinions and identification, gave a good figure of the mesenterial muscle characters, and contrasted these with three other British species ("Proc. Roy. Dublin Soc.").

Through the kindness of Dr. E. J. Allen and Mr. J. H. Orton, B.Sc., we have been able to examine and identify a specimen from Plymouth Sound, obtained May 22nd, 1912. This specimen was examined when alive, when killed expanded, and also anatomically by means of transverse sections.

Size.—Measurements during life were difficult to obtain as the Anemone was very timid and remained buried in sand, only expanding the tentacular crown at the surface. The latter was 12 mm. in diameter. When killed in an expanded condition, the total length was 41 mm.; length of capitulum 9 mm., diameter 3.5; diameter of scapus 4 mm.

Form.—Physa not large, and when partially invected showed eightwell-marked divisions; no attached sand grains. Scapus elongate, cylindrical, tapering below and somewhat inflated at the summit, covered by a thin coat of mucus and a number of attached sand grains; body-wall slightly wrinkled transversely and divided into eight regions

## SOME RARE AND INTERESTING SEA ANEMONES FROM PLYMOUTH. 61

by the grooves along the insertion of the mesenteries; there is a tendency to folding, and suckers are present on the upper portion. The capitulum, arising from the scapus by a gentle slope, was retractile, delicate, and smooth. Disk concave; mouth raised on a cone. Tentacles 16 in number, of fair length and somewhat obtuse; at first sight there appeared to be 17 tentacles, but this was due to the fact that one was bifurcate near the summit.

Colour.—Investing coat yellowish ; during distension, the mesenteries showed through the integuments as white longitudinal lines. Disk light brown, freckled with yellowish white spots, the eight radii yellowish white with a dark central line ; lips of a darker shade of brown than the disk and with a circle of eight reddish brown spots. Tentacles pellucid, freckled, and indistinctly and irregularly barred and blotched with white, and with a few distinct madder-brown or chocolate spots, which tended to become bars near the tip : at the base of one of the tentacles was a white spot. The colouration of the disk and tentacles harmonized so exactly with that of the sand amidst which the Anemone was living as to render it by no means easy of detection, even when fully expanded.

Anatomy.—Transverse sections showed muscle characters practically identical with those figured by Haddon. The ectoderm is thin, and broken in many places; the mesogloea is fairly thick, not very dense, and contains here and there lenticular spaces of no great size; these stain deeply. The endoderm is of about the same thickness as the mesogloea, and both broaden in the regions between the insertion of the mesenteries.

The specimen was a female, and the mesenteries were all gonophoric. In the basal muscle the mesogloea shows eight to ten folds on either side, many of them branched; the longitudinal muscles large and with from eighteen to twenty folds, a number of which are more or less branched; all are fringed, giving them much the aspect of fern fronds. The ova occurred as more or less compact masses.

## II. Edwardsia claparedi, Panceri, 1869.

Haddon (1889) suggested that the *Edwardsia* which Kingsley found washed up at Torquay in 1854, and which was described by Gosse (1860, p. 262) as "? *Edwardsia beautempsii* (Quatref.)," may have been *E. claparedi*. After stating his belief that *E. callimorpha*, Gosse, is identical with *E. beautempsii*, Quatrefages, Haddon enumerates the points of difference between that species and the specimen in question as given by Gosse, and concludes : "In the above particulars this *Edwardsia*  agrees so well with the description and beautiful figures of *E. claparedi* (Panceri) given by Professor Andres (*Le Attinie*, p. 90, pl. xi.) that we may with justice, for the present, allocate it to that species."

After examination and comparison of both external and anatomical characters, we are able to identify as  $E. \ claparedi$  two specimens from Plymouth; and the species can thus be added to the British Fauna with certainty.

Of the two specimens just mentioned, one (A) was kept alive for a considerable time at Plymouth, was safely sent to us at Aberystwyth, and remained in a healthy condition, living buried in sand in a shallow dish. When first received it was very timid and remained buried for twenty-four hours, expanding at first only by night, and closing rapidly at the least vibration. Later it would remain expanded during daylight and for much longer periods, and it also became much less sensitive to movements in its vicinity. Both specimens were obtained from Jenny-cliff Bay, Plymouth Sound.

Size.—It was impossible to obtain complete measurements of (A) during life, as it remained buried, and if uncovered retracted and at once commenced to bury itself by the use of the physa. When partially anæsthetized the total length was 50 mm.; greatest diameter of scapus 7.5 mm.; of capitulum 4 mm.; the physa was 4 to 5 mm. in length and breadth; and the expanse of the tentacular crown 12 to 13 mm. The physa was rounded, delicate in texture, and almost transparent. Scapus cylindrical, fairly stout, tapering downwards to just above the physa, ringed and folded during partial retraction ; grooved by the insertion of the mesenteries, with the intervening ridges warted. Scapus covered by a thin cuticle which is thickest on the ridges and about the warts; these latter occur in a linear row on each ridge and are seldom contiguous ; the upper third of the scapus is bare of cuticle and the warts are fewer and finally disappear. The capitulum and upper portion of the scapus can be retracted within the remainder of the scapus, and this movement can be very rapidly effected. The tentacles are sixteen in number, slender, tapering, about twice as long as the diameter of the disk; held in a most irregular manner as a rule, some extended, others flexed, others bent in a contorted manner across the disk; occasionally all are regularly extended, the tips bent inward (as shown in Fig. 1).

Colour.—Physa almost transparent. Cuticle rust-red, but darker where thickest (as around the warts). On the summit of the warts the cuticle is frequently missing and they then appear as pale spots. Capitulum dull opaque flesh colour, near the summit is an indistinct white

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ring, and above this an indistinct circle of purple. Disk fawn, with some orange mottlings about the mouth region; an indefinite white area runs from the base of the two opposite "gonidial" tentacles toward the lips, and from the bases of the remaining six tentacles of the primary cycle run similar indistinct black bars, these radial markings divide the rest of the disk into eight more or less irregular fawn-coloured, triangular areas; the mesenteries also show as pellucid white lines. Mouth usually

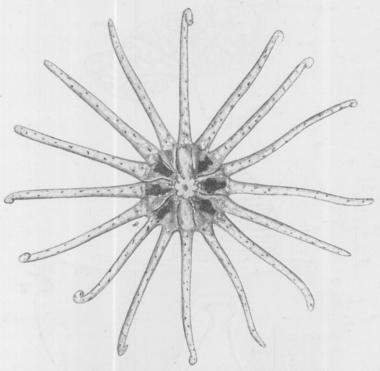


FIG. 1.-Edwardsia claparedi. Oral disk (greatly enlarged).

elevated, lips pale. Tentacles translucent, blotched with opaque-white and speckled with small red dots, the tips white : the white mottlings appear mainly on the front face.

Specimen (B).—A preserved example, obtained from mud, Jennycliff Bay, April 12th, 1912. It was strongly contracted, and somewhat damaged. Cuticle thin and brownish in colour, the mesenteries showed here and there through the body-wall in an indistinct manner; capitulum and physa invected; eight warted ridges were present, but not so strongly developed as in the last example. Length 28 mm., breadth about 8 mm. We have compared these Plymouth examples with preserved specimens of E. claparedi obtained from the Naples Marine Biological Station, and find both external and internal characters in agreement. The following is a short description of the external characters of one of the best of the Italian specimens:

Length (somewhat contracted) 45 mm., greatest diameter 5 mm. Physa small, being slightly contracted, about 1.5 mm. in length. Scapus

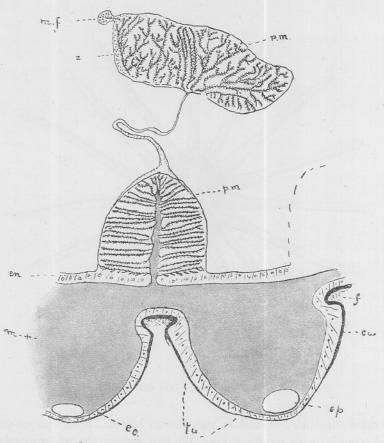


FIG. 2.—*Edwardsia claparedi*. Part of transverse section through the scapus regio showing tubercles, body wall, and mesentery (slightly diagrammatic). *Index to lettering: cu*, cuticle; *ec*, ectoderm; *en*, endoderm; *m*, mesoglæa; *m.f.*, mesenterial filament; *f*, foreign incrustations on the body-wall; *sp.*, space at summit of tubercle; *p.m.*, parieta muscle; *r.m.*, longitudinal retractor muscle; *tu*, tubercle; *z*, zooxanthellae.

cylindrical, tapering at either extremity, coated by a wrinkled, orangecoloured epidermis, and beset with eight longitudinal rows of whitish warts, devoid of covering at their summits; they are set more closely

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together on the upper third, but scarcely ever contiguous. Disk narrow, mouth pouting. Tentacles 16, obtuse, wrinkled, contracted to a length of 3 mm.

All specimens likewise agree with the figures and description of Andres, and the plate given by Delage and Hérouard in *Zoologie Concrète*. The colouration of this species is evidently extremely variable to judge by the figures and descriptions of Andres in *L'Attinie*.

Anatomy.-Transverse sections of the two British and an Italian example revealed practically identical characters. (B) was strongly contracted and somewhat injured and gave very indifferent results when sectionized. Sections showed the cuticle and a thick but irregular ectoderm (Fig. 2); the mesoglea of the column wall is comparatively thin in the capitular region, but becomes very dense and much thicker toward the physa end; the warts consist of outgrowths of the mesoglea and are frequently hollow, being then capped by a thin layer of mesoglea and ectoderm. All eight mesenteries are fertile; the retractor muscle is large and the basal muscle comparatively small in the region bearing the gonads; lower down, the retractor becomes smaller, and the basal muscle larger, and in the region of the physa the two are of about equal size. The folds of the basal muscle are about twenty in number on each side and are often bifurcated, the proximal fold gives off numerous small branches on its outer edge; the folds are long and slender and lie practically at right angles to the central strand of mesoglea, which appears in section as a fairly stout rod, branching out at its distal end. The longitudinal retractor muscle is reniform in section, but the folds are not as stout nor have they the peculiar moss-like appearance seen in E. timida ; they are fairly slender, very much branched, and are from fifteen to twenty in number. We are indebted to Mr. F. S. Wright for a figure of this Anemone in the living condition (Fig. 1).

## III. Halcampa chrysanthellum, Peach.

Originally described by Peach and Gosse from Cornish specimens, and regarded as the only British species until Haddon discovered H. arenaria in S.-W. Ireland in 1885 and 1886. As the two species bear a considerable external resemblance it is more than likely that there has been some confusion in identification. Haddon identified specimens from the East of Ireland as H. chrysanthellum, with certain anatomical characters, but he pointed out that, until specimens from the original Cornish localities had been examined anatomically it would be unsafe

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to assume actual identity. If the Cornish form should prove to be identical with the Irish specimens considered to be H. chrysanthellum by Haddon, well and good; it is also possible that H. arenaria has a much wider range. Meanwhile many identifications can only be accepted provisionally. British records of H. chrysanthellum include: Fowey (Peach); Gwyllyn Vase, Pennance, etc. (Cocks); Salcombe (Allen and Todd); River Yealm ("Plymouth Marine Invertebrate Fauna"); Isle of Man (Herdman); East of Ireland (Haddon); Firth of Forth (Leslie and Herdman), etc.

In 1907 one of us examined some twenty living specimens of Halcampa collected in the River Yealm. Considerable variability was noted as to incrusting sand, the retractility and size of the physa, and the colouration. Lack of time unfortunately prevented any further inquiry on that occasion. Recently, however, three preserved specimens collected in the Yealm were examined and found to agree in all external features. Sections have been cut, and the anatomical characters compared with Haddon's figures of his East Irish specimens and found to be identical. It is noteworthy that both Haddon and Gosse state for this species that the physa is large and non-retractible, and this character should prove to be a useful aid to identification. The following is a description of the external characters of the specimen examined anatomically (preserved in spirit): Total length 20 mm., divided as follows: physa 3.5 mm. long and 3.5 mm. broad, scapus 13 mm.  $\times 2$  mm., capitulum 3.5: Physa globular, delicate, semitransparent, studded with small white suckers to which adhered numerous sand grains; Scapus slightly wrinkled; Disk convex, elevated, M-mark on the margin distinctly visible.

In another specimen 31 mm, in length the physa was similar in form and showed the same numerous small white suckers and attached sand grains.

## IV. Halcampa arenaria, Haddon.

This species was described by Haddon in 1886 from specimens obtained from the Kenmare River, S.W. Ireland, 38-44 fathoms (1885), and again, mouth of Bantry Bay, 38 fathoms (1886). We are indebted to Mr. J. H. Orton for a specimen from Rum Bay, Plymouth Sound, November 19th, 1910. He further provided us with some interesting sketches made while the anemone was alive. In his opinion this specimen was *H. arenaria*, and our anatomical examination has proved this to be correct. The following notes describe the specimens after preservation. Total length 38 mm., greatest diameter of scapus 4.5 mm., of

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capitulum less. Body-wall thick, tough and opaque; physa damaged, but appears to be much smaller than in H. chrysanthellum, no sand grains were attached, and no suckers were observable with a lens; the small size is well shown in Mr. Orton's sketches, as is also the fact that the physa is retractible in this species, and thus agrees with the plate and description of Haddon (Proc. Roy. Dublin Soc., 1889). The scapus tapers at either extremity, and for a length of 20 mm. is coated with sand grains attached to suckers, and within this portion the physa and capitulum can be withdrawn. The capitulum is smooth, more delicate, and somewhat constricted near the summit.

Colour, pale yellowish buff, the mesenteries showing indistinctly as paler lines. Tentacles and disk much as in H. chrysanthellum; one of Mr. Orton's sketches, comprising a tentacle and portion of disk and mouth, shows the transverse bars, M-mark and the triangular brown patches figured by Haddon; but the form of these brown marks on the disk is different. Instead of being "lenticular" the marks are triangular, with the apex directed toward the tentacle.

Haddon gave a comparison of the anatomical characters of the two species of *Halcampa*, but a re-statement of the points of difference seems advisable; and ignoring for the present the colouration of the disk and tentacles, the details are here given :—

#### H. chrysanthellum.

(1) Physa large, globular, translucent, provided with small white suckers, and not capable of being withdrawn within the scapus.

(2) Scapus smooth.

(3) Number of folds of the muscular epithelium of the longitudinal muscle of the mesenteries, as seen in transverse section, 10 to 12.

In addition to the above Haddon states that :--

(4) "The oesophagus in section is, relatively to the diameter of the body, much larger in H. chry-

#### H. arenaria.

(1) Physa smaller, probably without suckers, and retractible within the scapus.

(2) Scapus with suckers to which adhere sand fragments forming a more or less dense covering.

(3) Number of folds of longitudinal muscle about 15. santhellum than in *H. arenaria.*" This character is, however, not well marked in our sections.

(5) Also, "In *H. chrysanthellum* only 6 mesenteries bear generative products." This is the case in our specimen.

(5) "All 12 mesenteries are fertile in *H. arenaria.*"

In the specimen we have examined only 10 perfect mesenteries are fertile, those that are barren being those mesenteries of the perfect lateral pairs which are nearest to the sulcar directives (the sulcosulcar laterals of Haddon)

## V. Eloactis mazeli, Jourdan.

In 1892 Garstang described a living specimen of this interesting Anemone from the Devonshire coast (*Trans. Devon. Assoc.*). Since then, more or less mutilated specimens have been dredged by the s.s. *Oithona* from the Inner and Outer Rame-Eddystone trawling grounds; and during May, June, and July, 1912, in particular, a number of examples were brought in. Almost all were much damaged, only the summit of the scapus and oral crowns being present, and these greatly distorted and contracted. Under these conditions, the tentacles being much shortened and strongly capitate, and the colouration very pale, it was only quite recently that their true identity was recognized. Several when examined still showed signs of life. As in the case of *Edwardsia claparedi* we have compared the Plymouth examples with named material from Naples both as regards external and anatomical characters. The mutilation is evidently due to the habit of lying buried in sand, the oral crown projecting, and thus being cut off by the dredge.

The following is a description of one of the least damaged specimens : Form.—Upper portion of scapus firm and smooth, but with many fine longitudinal ridges and grooves, succeeded by a fosse. Tentacles 20, set in two cycles of 10, long and short thus alternating; they consist (in this contracted state) of a stout, transversely wrinkled stalk and a strongly adhesive rounded head. Disk very tumid and much wrinkled; mouth rather large, one strong œsophageal groove. Colour.—Flesh tint, the tentacles marked with brown near the summit; disk orange-pink with somewhat lighter rays. Diameter of disk and tentacles 4 cm. when strongly contracted. Locality,  $5\frac{1}{2}$  miles off Rame Head; 25 fathoms, fine sand; taken in fine-mesh dredge.

## SOME RARE AND INTERESTING SEA ANEMONES FROM PLYMOUTH. 69

Mr. Orton sends the following notes regarding a specimen obtained from the Outer Rame-Eddystone, July 2nd, 1912 : "The tentacles were blotched with brown at the extremity, and several had double purple internal stripes ; others appear to have only one coloured stripe ; bodywall orange . . . the tentacles were examined but no knobs were visible."

A more detailed description of this species will be found on pp. 70-80.

# On Eloactis mazeli.

By

Olwen M. Rees, B.Sc., University College of Wales, Aberystwyth.

With Figures 1-4 in the Text.

JOURDAN was the first to describe *Eloactis mazeli*. In 1880 he published *Recherches zoologiques et histologiques sur les Zoanthaires du golfe de Mar*seilles (1), and in this paper *E. mazeli* is described under the name of *Ilyanthus mazelii*. Jourdan obtained his specimen from the muddy sand of the north-eastern part of the Gulf from a depth of 60-80 metres. He compares its external characters with those of Peachia, Ilyanthus, and Halcampa; the following is a translation :—

"In form it approaches Peachia, from which it differs through the absence of gonidial tubes. In the absence of terminal pores and in the smoothness of the column it resembles Ilyanthus, while its cylindrical form recalls that of Halcampa, though it differs from this genus in that it lacks tubercles and a terminal swelling. Its buccal disc is conical, of an orange tint striped with darker lines which run from the mouth to the bases of the tentacles. These last are twenty in number and are arranged in two cycles; they are white with brown apices and the inner ones are smaller than the external ones."

"The column is cylindrical, and is orange-red with paler lines which run down from the summit in the spaces intervening between the outer tentacles. The basal region is lighter in colour and more membranous; it is non-adhesive, and the lower part of the column wall is often pushed in, giving the base the appearance of being sunk in. Longitudinal and transverse sections of the basal region show that this sunken portion has no aperture."

Jourdan could not study the structure much owing to the state of preservation of his one specimen, also he was working in the early days of the serial-section method. He was therefore unable to make out the arrangement of the mesenteries, and thus could not place the animal in its correct systematic position.

In 1884 Andres, in Le Attinie (2), gave the following description of

#### ON ELOACTIS MAZELI.

E. mazeli, placing it in the Heteractiniæ with Eloactis globosa, Ropalactis, Ragactis, Heteractis, and Stauractis.

The base, he says, is "slightly adherent, often with a rounded vesicle resembling a physa. Column long, cylindrical, sulcated by 20 invections of slight depth, often minutely rugose; membranous, delicate, scarcely adhesive. Disk small. Tentacles few, bicyclic 10:10; the length of the tentacles of the external cycle twice that of the tentacles of the internal cycle; not entirely retractile, rounded at the tips; outwardly deflexed. Peristome low, rounded, concave and grooved. Mouth often prominent. No acontia. Gonidia somewhat open. Pharynx often protruded and resembling numerous angular lobes. Size fairly large."...

Delage and Hérouard (6), in 1901, described *Eloactis mazeli* thus: Eloactis is an Actinian which appears to vary in form because of its marked contractility; the base is only slightly adherent, if at all; the column is smooth or rugose according to the state of contraction; it is deeply grooved longitudinally; the tentacles are few in number and arranged in two cycles; they terminate in a rounded swelling rich in nematoblasts; there is no sphincter.

Delage and Hérouard also place it in the Heteractidæ (Andres) Heteractinæ, 11th family; but they say that the family is probably highly artificial, uniting provisionally several Actinians, concerning the anatomy of which very little is known. They all have a smooth and striated but not verrucose column, and tentacles arranged in various ways, but not branched, and armed by swellings rich in nematoblasts.

In 1892, Garstang described a living specimen of this interesting anemone from the Devonshire coast (*Trans. Devon. Assoc.*). Since then several specimens have been dredged from the neighbourhood of the Eddystone and the South Devon coast (cf. p. 68). Almost all were damaged, only the summit of the scapus and oral crown being present, and even these were greatly distorted and contracted. Under these conditions the tentacles were much shortened and strongly capitate; the coloration of these specimens was usually of little intensity. Some of the specimens still showed signs of life.

The present paper embodies the results of an investigation of specimens dredged off South Devonshire, and of one perfect specimen from the Mediterranean. It is sought—

(1) To establish the identification of the British specimens as specimens of *E. mazeli* (Jourdan).

(2) To demonstrate the affinities of Eloactis with certain other Actinian types.

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# External Characters of E. mazeli (Jourdan).

The following description of the external characters of E. mazeli (Jourdan) is based on an examination of a preserved specimen from Naples. Length of scapus, 47 mm.; it tapers gradually downwards. Diameter at summit of scapus, 11 mm.; diameter at base, 7 mm. The base, which is slightly enlarged, is very similar to that of Peachia, being invected somewhat in the centre to a depth of several mm. Upper margin well demarcated, surface of scapus without tubercles, but very much folded and wrinkled and thrown into numerous complex ridges. Tentacles, 20 in two alternating cycles of 10 each, the outer the longer. In this specimen they are contracted, rather stout, tapering slightly upwards and then expanding into a globular or ovate head. Length of outer tentacles 10 mm., inner 4 or 5 mm. Colour, greenish white (in spirit). The tentacles are mottled with dark purplish brown blotches. These become larger and confluent higher up, and in the contracted tentacles appear as slightly raised vesicles or blisters. On the head of the tentacle these marks are of a paler brown suggestive of a less degree of contractility. The disk is narrow and concave; the mouth pointed and prominent.

# Internal Structure of the Italian Specimen of E. mazeli.

The mesenteries are twenty in number, and are all perfect and fully developed. Their arrangement is very simple, the mesenteries arising in pairs and two of these pairs are directives (Fig. 1). The longitudinal muscles of each pair are on the faces which look towards the intramesenterial spaces, except in the case of the four directive mesenteries whose longitudinal muscles are on the faces which are turned towards the adjacent intermesenterial spaces. There is only one siphonoglyphe, and this is deep and well defined. The surface of the stomatodæum possesses numerous ridges which increase the digestive area. The body wall consists of ectoderm, mesoderm, and endoderm in almost equal proportions. The ectoderm has a corrugated appearance on its outer surface owing to the body wall being slightly contracted. The mesoglæa is fibrillar, especially towards the inner surface, as in Halcurias.

Jourdan, in his description of the internal characters of Eloactis, also shows the fibrillar nature of the mesoderm : "Sur les coupes transversales le picrocarmin colore vivement le mesoderme et permet d'y distinguer deux zones, l'externe composée de tissu conjonctif lache, l'interne formée de tissus lamineux" ("In transverse sections, the mesoglœa is deeply stained

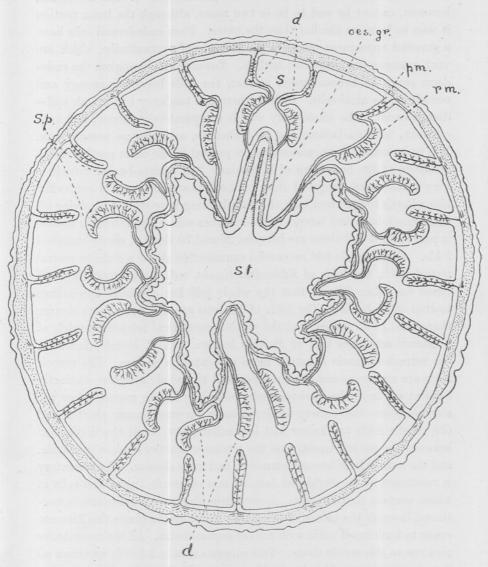


FIG. 1.—Transverse section through the column, showing stomatodæum with œsophageal groove, and septostomes in all the mesenteries except in the sulcar directive and in two sulco-lateral mesenteries: *d.* directive mesenteries, *æs.gr.* œsophageal groove or siphonoglyphe, *p.m.* parietal muscle, *r.m.* retractor muscle, *s.* sulcus, *s.p.* septostomes, *st.* stomatodæum.

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by picrocarmine showing two zones, the outer composed of loose conjunctive tissue, and the internal zone of laminated tissue"). The mesogleea, however, cannot be said to be in two zones, although the inner portion is seen to be more fibrillar than the outer. Then endodermal cells have a granular appearance owing to the presence of zooxanthellæ, which are very numerous near the free surface. Towards the mesoglea the endoderm seems to become much weaker, the cells becoming spongy and containing no algal cells. In fact, there is a tendency to form an endodermal canal. The whole body wall is comparatively narrow, and very compact, with no lacunæ and no inclusions, and also no nematocysts. It is to be noted that nematocysts are present in the outer portion of the ectoderm of the body wall of Halcurias. The parieto-basilar muscle is very much more elongated than in the Edwardsidæ, and is somewhat like a hart's tongue fern leaf, the midrib being very stout and giving off short much-branched lateral veins on either side. The retractor muscle is pear-shaped and there are between 26 and 30 slender, much-branched folds. Each muscle fold on careful examination shows a definite central strand, as in the folds of Edwardsia timida, with an irregular layer of tissue on either side, so that the whole fold has a similar appearance. to that of E. timida. The folds of Eloactis are, however, more slender than those of E. timida, and the whole longitudinal retractor muscle of E. mazeli resembles that of Peachia hastata. In P. hastata, however, the retractor muscle is rather more elongated in section. The muscle folds are numerous and more slender, and the whole is not so distinctly marked off from the parieto-basilar muscle. In the region below the stomatodæum the parieto-basilar muscle becomes much shorter and the muscle folds are longer and less arborescent, while the distinction between the parieto-basilar and the retractor muscles is more indefinite, and the muscle folds become numerous and more slender. The mesentery is continued at its distal end into a mass of sterile tissue, the cells of which contain zooxanthellæ. A very thin filament of mesogleea is continued through the centre of the sterile mass, and in places this filament opens to form small bulbs with cells of zooxanthellæ. All the mesenteries give rise to this sterile tissue. This suggests that in a fertile specimen all the mesenteries would behave alike and would thus give rise to twenty gonads. In Halcurias also all twenty mesenteries are fertile. There is one œsophageal groove as in Halcurias, but in Eloactis mazeli the groove is deep and well defined; whereas in Halcurias the siphonoglyphe is said to be neither very deep nor well defined. In E. mazeli the ectoderm of the siphonoglyphe consists of large elongated columnar cells containing

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# ON ELOACTIS MAZELI,

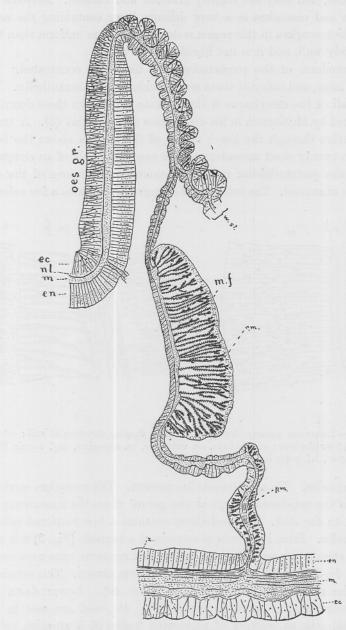
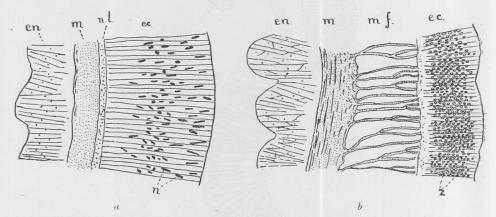


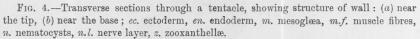
FIG. 2.—Transverse section through a mesentery, showing the muscles, also the structure of the wall of the stomatodæum and of the wall of the æsophageal groove: *ec.* ectoderm, *en.* endoderm, *m.* mesoglea, *m.f.* muscle fibres, æs.gr. æsophageal groove or siphonoglyphe, *p.m.* parietal muscle, *r.m.* retractor muscle, *n.l.* nerve layer, *z.* zooxanthellæ, *w.st.* wall of stomatodæum.

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large nuclei, and they are slightly granular and ciliated. Between the ectoderm and mesoglœa is a very delicate layer containing the nerve cells. The mesoglœa in this region is denser and more uniform than that of the body wall, and it is not fibrillar.

The ectoderm of the stomatodæum is distinctly corrugated. The cells are large, and many of them contain colonies of zooxanthellæ. The whole wall of the œsophagus is thrown into ridges like those described and figured by McMurrich in his description of Halcurias (3). A transverse section through the lower region of the column shows the body wall with twenty short mesenteries, each consisting only of an elongated form of the parieto-basilar muscle. Longitudinal sections of the oral disk were examined. The ectoderm is spongy and contains a few colonies





of zooxanthellæ. No nematocysts are present. The mesoglæa sends up folds into the ectoderm, except at the points where the mesenteries are attached to the disk. The endoderm contains a few scattered cells of zooxanthellæ. From longitudinal sections of a tentacle (Fig. 3) it is seen that the ectoderm is very thick at the tip, and contains numerous nematocysts. In this region zooxanthellæ are almost absent. This ectoderm causes the swollen tip of the tentacle (Fig. 4*a*). Lower down the zooxanthellæ become more numerous (Fig. 4*b*), and are seen in the ectodermal cells as colonies of pigmented bodies of a greenish yellow colour. The presence of these algal colonies accounts for the blotches described on the exterior of the tentacles. Near the base the ectoderm is less thick, and in places contains neither nematocysts nor

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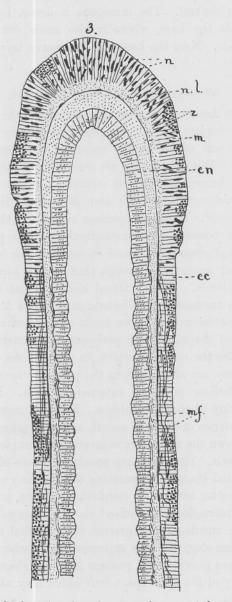


FIG. 3.—Longitudinal section through a tentacle: ec. ectoderm, en. endoderm, m mesogleca, m.f. muscle fibres, n. nematocysts, n.l. nerve layer, z. zooxnathellæ.

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zooxanthellæ. There is a definite nerve layer at the base of the ectoderm in the region around the tip where there are numerous nematocysts to control. The mesoglœa is dense, but becomes more fibrillar towards the base, where it also sends out branches which very often divide. Near the base also the nerve layer becomes much thinner.

# Septostomes or Mesenterial Stomata.

"In the genus Actinia these stomata are found in the uppermost inner angles of the complete mesenteries close beneath the mouth, and are probably the result of incomplete union of the mesentery with the stomatodæum." This is how they are described by Professor Bourne in (5). They are known as internal stomata. In some other Actiniæ, e.g. Tealia coriacea (crassicornis) and Metridium dianthus, external stomata are present. These are openings situated in the upper third of each mesentery between the longitudinal and the parietal muscles. In Metridium septostomes are found on many of the imperfect as well as on the perfect mesenteries, though there are no septostomes on the directive mesenteries. Both internal and external septostomes are present in some anemones, e.g. Hertwig says of the Actinian which he named Dysactis crassicornis, "Two kinds of stomata are found on the muscular part of the septa-the peristomial or external stomata are very large, whilst the marginal which lie close to the wall are small." These septostomes are also found in the primitive anemones, e.g. Halcampa chrysanthellum possesses external stomata. No septostomes were found in any of the Edwardsidæ. External stomata are present in all the mesenteries of *Eloactis mazeli*, and each takes the form of an elongated slit down the mesentery separating the retractor muscle from the parietal muscle. These stomata provide a means of communication between the radial chambers separating the mesenteries, and probably thus ensure a better method of circulation. Again, undoubtedly they facilitate rapid retraction, for without the septostomes there would be a danger of the mucilage, etc., present in the radial chambers of the cœlenteron getting clogged in the uppermost parts, whereas the presence of the septostomes provides free passage from one chamber to another, not only by way of the axial space into which they all open, but also via these stomata.

# Systematic Position of Eloactis mazeli.

Delage and Hérouard (6) have temporarily placed this anemone in

the 11th family of the Heteractinæ with several other anemones whose internal structure is unknown.

The elongated form of the body, the absence of a definite sphincter muscle, and the presence of a small number of mesenteries, are characters of Eloactis which show that it is related to the primitive, rather than to the more advanced anemones : the latter do not possess an elongated body, but are characterized by the presence of a definite sphincter muscle and a large number of mesenteries. The Edwardsidæ and the Halcampidæ are two of the most primitive families whose members have an elongated body form, no definite sphincter muscle, and a small number of mesenteries. The Edwardsidæ have eight mesenteries, whereas in E. mazeli there are twenty; therefore Eloactis cannot be placed with Edwardsia, the sole genus of that family.

The family Halcampidæ has been defined by McMurrich in the paper already referred to (2), as "Actiniæ with a small number of mesenteries, six, ten, or twelve pairs being all present; longitudinal muscle pennons narrow, but strong; no special sphincter muscle; conchula present or absent; base usually rounded and vesicular." In this family, therefore, McMurrich places Halcurias and Peachia as well as the genus Halcampa. Eloactis, with a small number of mesenteries and no sphincter, may be placed in the Halcampidæ. It may be closely compared with *Hal*curias pilatus, as described by McMurrich, and both are found to possess the following characters :—

Column cylindrical; ten pairs of mesenteries, all of which are perfect. There is no special sphincter muscle, and the tentacles are not covered after contraction.

There is one siphonoglyphe, and on the surface of the stomatodæum are numerous ridges.

All the mesenteries bear reproductive organs.

The mesogloea is fibrillar, especially towards the inner surface.

Halcurias has an adherent base, whereas the members of the Halcampidæ have a rounded and vesicular base. *Eloactis mazeli* and *Eloactis producta* have indications of a slightly adherent base; but in these three forms this character is outweighed by the small number of the mesenteries and the structure of their muscles.

The structure of E. mazeli shows that this form is slightly more highly specialized than *Halcurias pilatus*. In the latter, the four pairs of mesenteries situated in the sulco-lateral and lateral intermesenterial spaces are less extensively developed than the other six, and the siphonoglyphe is neither deep nor well defined. On the other hand, E. mazeli has

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all its mesenteries fully developed and has a deep and well-defined siphonoglyphe; also the distribution of nematocysts is different in the two forms. Eloactis possesses twenty highly specialized tentacles, all well armed with nematocysts, and these are present only on the tentacles, especially on their ovate heads. *H. pilatus* does not possess such highly specialized tentacles; they are more numerous, and nematocysts are present on the disk and body wall as well as on the tentacles. Thus the tentacles are not so well adapted as feeding and defensive organs, and the division of labour is not so complete as in *E. mazeli*.

Peachia is probably still more advanced :---

It has a single deep siphonoglyphe like E. mazeli, but the longitudinal retractors of the perfect mesenteries of Peachia are more elongated (in section), and there is a better developed system of musculature than in E. mazeli.

*Eloactis mazeli* is therefore an elongated anemone, with twenty highly specialized tentacles, ten pairs of perfect and fully-developed mesenteries, and a deep and well-defined siphonoglyphe, and is probably intermediate in position between Halcurias and Peachia.

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# Calliobdella lophii, Van Beneden and Hesse.

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#### By

# W. Harold Leigh-Sharpe.

ON May 12th, 1913, four specimens of the marine leech (*Calliobdella lophii*) were taken by myself whilst working at the Marine Biological Association Laboratory, Plymouth. The leeches were parasitic on the skin of a large angler (*Lophius piscatorius*), just behind the gill covers and in front of the pelvic fins, two on each side. The angler was caught in Jennycliff Bay within a few hundred yards of the shore, about 3.15 p.m., half-ebb, and was taken in a small trawl only just large enough to contain it; shrimps were present in the same catch, but no fish.

Calliobdella was previously unknown at Plymouth. The leech was named by van Beneden and Hesse in 1863 from five specimens found in March by Hesse at Brest.\* Some of the external characters alone were described by them. They omit to mention, however, that the genus is characterised by its having six annuli to each body segment, a point which it shares in common with Ichthyobdella and Pontobdella, but which separates it from other genera. They describe so accurately the beautiful appearance of this leech that their own words suffice :—

"An animal carrying a sucker at each extremity of the body, the posterior very large and simple. The body divided into two distinct regions, a neck region bare, and a region of the body properly so called, this latter carrying laterally rounded tubercles on the segments or cutaneous folds."

"This species attains a length of five or six centimetres." (Two of those captured at Plymouth were seven or eight without extreme extension.) "It lives on the angler (fishing-frog), *Lophius piscatorius*. The body is elongated, slightly convex above, flattened below. The skin is tough, with tubercles on the side, and divided into twenty-four segments, of which ten or a dozen belong to the region of the neck, the others to the body properly so called. The neck and the posterior sucker are paler than the rest of the body; the segments of the neck are covered

\* "Recherches sur les Bdellodes ou Hirudinées, 1863." NEW SERIES.-VOL. X. NO. 1. NOVEMBER, 1913.

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with minute black dots; the body is of a clear brownish green, ornamented above with broken, parallel black lines. The body is paler underneath, showing rose-pink markings in the form of a V. It is very noticeable also that the last segment but one of the neck is ornamented with an orange band which encircles it. The movements of this leech are very lively."

They were very lively in captivity, clinging firmly with the posterior sucker to the jar containing them, and seeking eagerly for some fresh host with the anterior end.

They moved occasionally with the usual loop-like movements of a leech, taking great care to place the posterior sucker as exactly as possible in the position previously occupied by the anterior.

Calliobdella is sharply divided by a constriction into a neck and a body. Blanchard,\* who mentions this leech as occurring in the Mediterranean, states that the segments of the body are formed of three to six annuli according as the three primordial rings are more or less divided by chorisis. All those in my possession have six annuli to the segment. The same author suggests that the animal is flattened when young and rounded when old. Further, he alters the name for orthographical reasons to Callobdella.

On the body, but not on the neck, are lateral protuberances, eleven pairs of hemispherical projections on each side of the animal, "rising and falling as if by respiration," as Dalyell' said of a leech he described as "Hirudo vittata," and which possibly was the same. These are rudimentary branchiæ, corresponding to the large external branchiæ of Branchellion, and similar to those of the North American and European marine and fresh-water form, Cystibranchus.

According to Quatrefages; these appendages do not receive the blood contained in the vessels, but only the lymph which becomes diffused, and which makes the respiration truly lymphatic.

Ichthyobdella is without these tubercles, and Pontobdella, which is further distinguished by its warty appearance also. Owing to the six annuli of the segment being formed by chorisis from three, the first respiratory vesicle is on the first double ring, the second on the fourth double ring, and so on. The anterior half of each double ring carrying the vesicle is spotted.

There are no eyes.

The extreme size of the posterior sucker in C. lophii, it being

- \* "Hirudinées de l'Italie, Boll. Mus. Zool. Torino," Vol. IX, 1894, No. 192.
  + "Powers of the Creator." Dalyell. Vol. II, p. 9, 1858.
- ‡ Ann. Sc. Nat., Vol. XVIII, p. 322, 1852.

# CALLIOBDELLA LOPHII, VAN BENEDEN AND HESSE.

more than twice the maximum breadth of the body, distinguishes this species from the other (or others). Ludwig Johannson,\* who describes this leech as rare, admits that he has never seen one alive, and states that the one in the museum at Stockholm was taken at Bergen in 1879, also that it occurs on the coast of Norway, and the two specimens he dissected were sent by a fisherman from Helsö in S. Bohuslän. He, adopting the altered name Callobdella, characterizes the genus by its possessing a large copulatory organ with a bursa and two seminal vesicles, while in other genera the copulatory organ is without the latter.

\* Johannson. "Die Icthyobdelliden in Zool. Reichmuseum in Stockholm, 1896."

# Habit and Habitat in the Galatheidea: a study in adaptation.

By

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With Figure 1 and Plates 1-4 in the Text.

THE heterogeneous assembly of Decapod Crustacean types classed as "Anomura" is well known to present a wide range of variation in structural features; in fact, the most apparent bond of union between its highly dissimilar sub-groups consists in the still greater disparity which exists between these and members of either "Macrura" or "Brachyura" proper. The Anomura may best be compared with that other heterogeneous group, the Amphibia : each, apparently of aquatic ancestry, has suffered in the unequal contest with a highly specialized offset from the parent-stock (Brachyura-Reptilia); the survivors of both the ill-fated groups, Anomura and Amphibia, are few in number, varied in type, and probably not closely related among themselves.

Among the Anomura, the sub-group Galatheidea present a fairly connected natural assemblage of types. Study of this sub-group reveals the presence of two distinct and widely divergent lines of specialization on the one hand, for life on shore (near or above low-tide mark), and, on the other, for life in deeper waters. Thus the group comprises, together with more or less intermediate forms, three well-marked types :

# A. The Galathea squamifera TYPE.

The characteristic species frequents the fairly open seas which surround our coasts, and is rarely found near low-tide mark except for a short time in spring; the form of body is almost Macrurous, and the abdomen, though usually flexed, is relatively large, and of no little importance in swimming.

## B. THE Porcellana platycheles TYPE.

The characteristic species lives well up in the muddler portion of the intertidal zone, and is common about midway between high and low

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#### HABIT AND HABITAT IN THE GALATHEIDEA.

tide marks. The form of body presents many peculiarities, both superficial and in detail, comparable with those which are regarded as characteristic of the Brachyura, furnishing an excellent example of "convergence."... The abdomen is greatly reduced in size, the length of the carapace scarcely exceeds its breadth, and the habit of clinging to stones is developed to a marked degree.

## C. THE Munida rugosa TYPE.

Characteristic of fairly deep waters (found at depths varying from 10 to 600 fathoms). The general form of body closely resembles that of type A, but obvious specializations for deep-sea life exist.

Thus, within the group Galatheidea, a few species (those of group C) have been driven by stress of competition in the shallower waters to seek shelter in the deeper and more sparsely populated regions of the sea; but the main line of specialization in the group is in the direction A to B —towards adaptation for life higher up the shore. It is the aim of this memoir, by describing details of the structure of the branchial and other organs of the Galatheidea, to show what peculiarities have arisen in connection with the need for special precautions :

(a) For ensuring steadiness of balance when the animal is in progression or at rest within the wave-washed region of the shore;
(b) For guarding against the choking of the branchial cavity and clogging of the branchial organs by the mud of the low shore.

In doing this, an endeavour is made to arrange these details in logical and progressive order, as indicating for the more crab-like members of the group "the base degrees whereby they did ascend."

# I. MODIFICATIONS WHICH PROMOTE EFFICIENCY IN RESISTANCE TO WAVE-WASH AND IN PROGRESSION ON THE SHORE.

It is convenient to use the type-species A (Galathea squamifera) as a starting-point from which to trace various lines of specialization within the group, this species being probably among the nearest to the Macrurous ancestor. We find throughout the genus Galathea few specializations of a definitely Anomurous character : the long, rather narrow carapace and powerful abdominal swimming "tail" with broad tail-fan obviously mark the active swimmer. In those members of the group which frequent the higher coast-zones—notably the Porcellanids—and which thus assume the creeping rather than the swimming habit, we note a reduction in importance of the Macrurous characters—a diminution

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in size of the abdomen, accompanied by a broadening of the carapace and strengthening of the ambulatory thoracic appendages. The reduction of the abdomen is well marked in Porcellana platycheles, which, as a general rule, does not swim, but moves from place to place in a crablike sidling fashion. The abdomen, which is habitually carried tucked-up beneath the thorax, is relatively very weak, and narrowly triangular in outline, and the tail-fan, though still present, is reduced in size. The abdomen is rarely unfolded except under special circumstances, as when the animal is upset on to its back. In this case, the abdomen is flapped vigorously, so as to raise the animal in the water and alter the inclination of the body, allowing it to fall back into the natural position, while the chelæ are extended to catch at any means of support to which it may be possible to cling. A similar action of the abdomen has been observed in Cancer and Carcinus individuals, when subjected to similar conditions, but in these two Brachyuran genera the absence of the tailfan renders the flapping less effective ; this deficiency, however, is not of much consequence, as their superiority in weight and strength gives Cancer and Carcinus a greater stability than is possessed by Porcellana.

Decapoda which frequent the shore have the carapace much broader and flatter than in Macrura, and this has led to the sharp lateral folding of the carapace, giving protection to the branchial organs ; this broadening is also of importance in connection with the above-mentioned habit of sideway progression, as we generally find the long axis of any body is turned in the direction of habitual movement. This method of advance in another than the forward direction is peculiarly suited to animals endowed with the Decapod Crustacean's type of sense-organs and frequenting obstructed places, and also to those whose walking limbs are spread in the almost radial fashion characteristic of the Porcellanids. The efficient clinging mechanism so afforded is based on the principle which determines the radial spreading of tent-pegs with their ropes, and of the several hooks of a grapnel, and has doubtless been developed in connection with the habit (already marked in Galathea, and most pronounced in Porcellana platycheles) of clinging to the under-surfaces of stones, and thus resisting the force of wave-wash as well as that of enemies. The radial arrangement of the limbs also endows the animal with facility of movement in an oblique, as well as in the directly transverse, direction-a valuable asset to a dweller in the intertidal zone of shifting pebbles.

In connection with the strengthening of the thoracic limbs of *Porcel*lana platycheles, we note in this species the greatest concentration of the thoracic nerve-ganglia observed in any of the Galatheidea, the condition almost approaching that which characterizes the Brachyura (see Plate 1, Figs. A, B, C, D, E). The last thoracic leg (appendage XIII), which in the Galatheidea is modified into a slender cleaning-organ, of course does not participate in the clinging action or in locomotion, and it is noticeable that, even in *Porcellana platycheles*, the ganglion of the 13th segment remains semi-isolated from the central mass formed by the fusion of most of the other thoracic ganglia.

The marked clinging-habit of Porcellana platycheles should be connected not only with the resistance to dislodging forces, but also with the general protective "melting into the background." The body is flattened, and when at rest is pressed closely against the rock-the chelæ are flattened and expanded in the horizontal plane, and are notched so as to fit accurately against the front edge of the carapace-and the whole dorsal body surface is coated with shaggy, grey, insensitive hairs, nearly matching in colour the rock to which the animal clings (see Plate 2, D). In this connection we remark also the absence of those transverse ridges of the carapace which are so conspicuous in more active members of the group. These carapace ridges in Galathea are fringed with hairs of a fairly simple, once-pinnate type (Plate 2, A, and Plate 4, B), whose continual agitation by the motion of the surrounding water probably prevents the settlement of such unwelcome guests as Hydrozoa, Polyzoa, etc., likely to retard the swimmer by increasing the frictionsurface. A sedentary form like Porcellana platycheles has no such interest in avoiding encrustation-and in it we find no trace of ridges or of waving hairs, the shaggy hairs of the dorsal surface being too close and coarse to be easily agitated by movement of the water. Again, the ridges, if present, would inevitably detract from the general protective resemblance to surroundings, and from this standpoint it seems likely that the presence of encrusting organisms may be of positive advantage to the crab. At all events, Spirorbis is quite commonly found attached especially to the chelæ of P. platycheles-a position likely to ensure commensalism (Plate 2, D).

## II. MODIFICATIONS WHICH TEND TO PREVENT CHOKING BY MUD.

A Macrurous form such as we suppose the Galatheid ancestor to have been, swimming in the clearer open water, required, and probably possessed, no special devices for protection of the branchial cavity from stoppage : we find in the Lobster, Penæus, etc., a notable absence of such protective devices. Here, the gills are just sufficiently well guarded

against dangers of friction, etc., by the lateral branchiostegite flap of the carapace, which loosely overhangs the cavity. The case of the Brachvura is quite otherwise. These shore-living Crustacea are constantly exposed to the dangers of life in the wave-washed zone, and protection against one of the greatest of these dangers is ensured by the enclosing of the branchial cavity by the strongly-curved branchiostegite. This leaves only the following apertures : a pair at the posterior end of the carapace, a pair at the bases of the chelæ, a pair near the mouth-and, on each side, a long chink, so narrow as to be practically inconsiderable, between carapace and thoracic leg-bases. The first two pairs of apertures (entrance channels for the breathing current) are well guarded by a straining apparatus formed by a fringe of hairs of very complex structure (Plate 4, G), while the aperture on each side of the mouth (an exit channel) can be protected by the folding of the plate-like maxillipedes against the body-wall. The fourth pair of apertures, mere chinks, are curtained by a fringe of hairs bordering the branchiostegite and by the tufts of "coxopoditic setæ."

One might expect to find in Galatheidæ a type of arrangement more or less intermediate between these two extremes—the Macrurous and the Brachyurous—and such is, in fact, revealed. Throughout the group, the closing-in of the branchial cavity is far less complete than in the Brachyura, although a curved and down-bent branchiostegite protects it laterally, and the paired inhalent aperture (posterior, near the bases of appendages XII and XIII) is guarded by a ring of hairs. Coxopoditic tufts also prevent the entrance of mud through the longitudinal crack between branchiostegite and leg-bases—which crack is far wider than in Brachyura, the whole branchial cavity being wide in the vertical rather than in the horizontal plane.

Galathea, an active swimmer, has retained some of the epipodites so characteristic of primitive Macrurous forms like Penæus. In G. squamifera (common around our coasts), there are epipodites, fringed with long and fairly simple hairs, on appendages VIII to XI (Plate 2, B, and Plate 1, F). One important function of the epipodites, as established by M. Bohn (" Des mécanismes respiratoires chez les Crustacés Décapodes," Bull. Sci. Fr. et Belg., XXXVI) is to brush the surfaces of the Arthrobranch gills and sweep them clear of particles. With so efficient a sweeping mechanism, it seems that elaborate precautions against the entrance of mud are unnecessary : we find that in this species the guardian-hairs which fringe the inhalent aperture are of the same fairly simple type as those which occur along the whole of the carapace edge (Plate 7, B).

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This absence of high specialization along this particular line should be correlated with the habitat of the species, which visits the muddiest part of the shore (just below low-tide mark) only for a very short time in spring. The allied species, Galathea strigosa, shows increased complexity of structure of the hairs which guard the inhalent aperture and fringe the branchiostegite. We connect the advance in specialization with the fact, noted by M. Bohn (op. cit.), that "in G. strigosa, considerable movements of the carapace supplement the action of the scaphognathite." This carapace-flapping would doubtless expose any epipodites present on appendages IX to XI to the danger of being bruised and torn-at all events, the epipodites of these segments are wanting. This reduction of sweeping mechanism within doubles the need for a guard at the entrance portals, which need is satisfied by the increased complexity of straining-hairs described above. Thus, in G. strigosa, feebleness of the scaphognathite has induced flapping of the carapace-this being in its turn connected with reduction in the number of epipodites and correlated complexity of straining hairs (see Plate 2, B, and Plate 4, F). It is interesting to note that in this species the epipodite of appendage VIII has alone survived, and this perhaps owing to its position opposite the blunt angle of the branchiostegite, where in all probability friction is not great.

Galathea intermedia, like G. strigosa, has suffered reduction in the number of its epipodites (though we are as yet unable to guess at the biological significance of this reduction); here, only epipodites VIII and IX remain, and here again correlated specialization of the straining-hairs is observed (Plate 4, E).

Two deep-water species of Galatheidea—G. nexa (to 70 fathoms) and Munida subrugosa (to 600 fathoms)—while resembling G. squamifera in their possession of the full number of epipodites (series VIII to XI), yet afford a parallel with the case of G. strigosa and G. intermedia in the relatively complex structure of the straining-hairs. This apparent anomaly seems to point to a need for special precaution against choking of the branchial passage in these two deep-water species; this is one item of a lengthy list of peculiarities which characterize the branchial apparatus of deep-sea members of widely dissociated groups (compare the peculiarities of the branchial organs of the Lepetidæ among Prosobranch Gasteropods, etc. etc.).

A striking feature of such shore-living types as Porcellana is the complete loss of the epipodites of appendages VIII to XI. This reduction should perhaps be correlated with the marked development of the clinging habit and the radial working of the legs, which entail movements likely to endanger organs occupying the position of epipodites. We should probably connect with this habit of spreading the legs radially (a habit which prevails throughout the Galatheidea, though it is most marked in Porcellana) the peculiarities of the general gill-formula of the group, which is characterized by the absence of podobranchs and importance of the pleurobranchs. Some of the leg movements involved would seem to be a source of danger to gills in the position of podobranchs (near the outer edge of the branchial chamber), exposing them to a risk of friction against one another and against the edge of the branchiostegite. Reduction of the organs exposed to this danger is accompanied by increased importance of the gills of the two inner series (arthrobranchs and pleurobranchs). (See Plate 1, F and G.)

In connection with the ascent of the shore by Porcellanidæ, the alteration in shape of the branchial cavity is noticeable, the shape of the cavity being practically of a type intermediate between those found in the swimming Galathea and the established (unrelated) shore-form, Cancer.

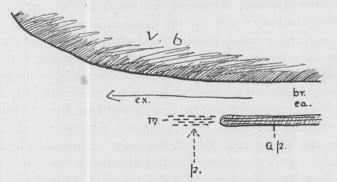
*Porcellana platycheles*, a sluggish species inhabiting the muddiest part of the mud-zone, shows a marked degree of specialization of the hairs which guard the inhalent aperture. These hairs, as well as those of the coxopoditic tufts, are of a much-branched and twice-pinnate type, and *exactly* resemble those which, in members of the Brachyura, constitute so effective a strainer, being totally dissimilar to the corresponding structures in Galathea (any species). (Plate 4, G.)

It is remarkable that *P. longicornis*, unlike *platycheles*, has none of this complicated structure : all the hairs near openings of the branchial cavity are alike of the simple type characteristic of *Galathea squamifera* (Plate 4, B).

It is necessary to bear in mind the difference in habitat of the two species, *P. platycheles* being a typical mud-dweller, whilst *longicornis* frequents such shores as those of Guernsey, where igneous rocks weather into reefs separated by steep gullies, swept perfectly clear of mud by the tidal currents.

With specializations which tend to promote efficiency of the breathing current we must class a peculiar growth of hairs found on the basal joint of the third maxillipede of all species so far examined. These hairs are short and strong, furnished with short, jagged saw-teeth, and are matted together to form a kind of felt-work across the gap between the maxillipedes of the two sides. This acts as a forward extension of the floor of the branchial cavity, and seems to guard against the entrance of water from below, which might meet and check the outgoing current (see Plate 4 and Text Figure 1).

Various members of the group show an interesting series of devices ensuring steadiness of the breathing current—such devices being particularly necessary in animals with the enclosed type of branchial cavity. Prof. Pearson, in his *Cancer* Memoir (L.M.B.C.), has pointed out the existence in that part of the carapace which floors the branchial cavity of a ridge, which by its presence helps to maintain a steady current of water past the gills. Specializations of an apparently somewhat similar function are visible in certain of the Galatheidea. The branchial cavity of Galathea and of Munida is long and narrow, with a slight spiral twist,



 $\mathbb{F}_{IG.}$  1.—Diagram-Longitudinal section through the front end of the body of one of the Galatheidea.

v.b. =ventral body-wall.

ap. = branchiostegite of one side.

br.ca. = branchial cavity of that side.

ex. = direction of ex-current stream.

p. = line of a theoretical in-current.

m. = position of matted hairs on the maxillipede bases, which prevent the entrance of the current p.

and is floored (unlike those of Brachyura) by the body-wall itself : we trace in this floor the line of a definite, though not prominent, longitudinal ridge external to a groove along which the main body of the breathing current appears to flow (Plate 3, A, i and ii).

Porcellana has a corresponding specialization more nearly of the Cancer type: the branchial cavity is partially floored (i.e. towards its front end) by a special portion of the edge of the branchiostegite, which is peculiarly twisted to produce a ridge doubtless similar in function to the rather more definite ridge of Cancer (Plate 3, B, and Plate 1, G).

Porcellana shows a remarkable respiratory habit—that of temporary suspension of the breathing activities on alternate sides of the body.

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The flagellum of one of the maxillipedes (probably of the 2nd) is obviously of use in strengthening and accelerating the ex-current stream, and its motion or stillness forms a good guide to the progress of the breathing activities on either side of the body, in addition to the indication furnished by the motion of particles in the water. It was noticed that both P. longicornis and P. platycheles, when at rest, almost invariably hold the chela of one side  $(\alpha)$  further away from the body than its fellow  $(\beta)$ : subsequent observation, many times confirmed, revealed the fact that only from the exhalent aperture of the a side did an excurrent stream proceed : apparently no respiratory stream was passing through the branchial cavity of the  $\beta$  side, and certainly the flagellum of that side was at rest. Supposing that the chela of the left side is held away from the body: only the *left* flagellum is meanwhile at work, a strong ex-current stream proceeds from the left side only, and the antennules, at their water-testing work, are constantly directed towards the right side of the animal (Plate 2, C and D). Meanwhile, on the right side of the body issues no ex-current stream, but generally the right antenna is kept in fairly constant motion, being swept from front to back, and vice versa. In other words, there is apparent suspension of the respiratory function of the right side of the body, compensated by the redoubled activity of the sensory function of the same side. In a normal captive Porcellana, the duration of this period of suspension is usually about half an hour; at the end of that time the animal becomes restless, "fidgets," and ends by reversing the functions of the two sides of the body, after a brief period of irregular movement of first one flagellum, then the other, and occasionally even of both at once. It must be noticed that in Porcellana there is no reversal of the current such as M. Bohn observes (C.R. Ac. Sci., CXXV, 1897, p. 441, "Sur le renversement du courant respiratoire chez les Décapodes ") in Carcinus, etc., and which may serve to rest the muscles of the scaphognathite or to cleanse the branchial cavity. Probably this resting of the muscles is at least as well ensured by the alternate working of the organs of the two sides. M. Bohn remarks that, in animals which have the reversal habit, the number of reversals within a given time may be increased by placing the animal in a toxic solution such as extract of Red Seaweed. Similar experiments performed on Porcellana produced no reversal of the current, but had the effect of causing the alternations in function of the two sides to become rapid and irregular. Galathea exhibits no such alternation, and on placing it in Red Seaweed extract there was detected distinct reversal of the respiratory stream, although the backward current produced was but

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feeble and irregular. The result of the experiments performed on Porcellana is surely to show that any recuperative purpose effected by the reversal of the respiratory stream in the Decapods for which such reversal has been proved is fulfilled in Porcellana by the alternate resting and working of the two sides.

Throughout the Galatheid group we note a praiseworthy striving after cleanliness on the part of its members, which must of course be referred to the habitat of these animals. Apart from the absolute necessity for keeping a clear channel through the branchial cavity, it is of distinct advantage to prevent mud particles from collecting among the hairs of the coxopoditic tufts and near the openings of the branchial cavity itself, and it is clearly the function of the curiously modified thirteenth (last thoracic) appendage to clean and brush these hairs, as well as the back of the carapace. Galathea and Munida especially have need of precaution against the settling of foreign particles in the transverse grooves of the carapace. The ultimate segment of the thirteenth appendage in Galathea, Munida, and Porcellana, bears hairs which by their structure are peculiarly well fitted for this work of cleaning out chinks and crannies (Plate 4, K), each hair being bent into a kind of sickle-shaped hook, fringed on its inner side with short, pointed teeth, and doubtless constituting a most effective scraper. In one species of Porcellana (P. platycheles, see Plate 7, K, ii), these hairs appear to have suffered degeneration from some unexplained cause (perhaps in connection with the absence of carapace ridges), growing less strongly curved and with blunt teeth. It is noticeable that members of the genus Porcellana (without epipodites) frequently thrust this appendage XIII inside the branchial cavity itself, doubtless to clean it-a course of proceeding which Galathea (furnished with epipodites) apparently does not follow.

The antennules (water-testing organs) and the antennæ (which are still important tactile organs in the Galatheidæ) must, if they are to retain their sensory function, be kept scrupulously clean, and their cleansing, which frequently takes place, is a process to delight the observer. These appendages are bent sharply downward, then the endopodites of the third maxillipedes are unfolded, and antennules and antennæ are drawn slowly upwards in such a manner as to be thoroughly well combed by the long hairs of these palps, which hairs have the form of strong double-edged saws or combs (Plate 4, I, i). These endopodites of the third maxillipedes, by the way, exhibit an interesting series of specializations throughout the group. Their main functions are (a) to gather

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in small particles of food to the mouth by a sweeping movement; (b) to comb the hairs of antennæ and antennules; and (c) to guard, when folded, the exit channels of the branchial cavity. In Galathea and Munida, the joints of the endopodite are long and thin, and the whole maxillipede approaches in form the type of the primitive Arthropod appendage, save that the endopodite is slightly flattened, and can, when folded, form a fairly plate-like structure. P. platycheles shows greater specialization of the endopodite, the joints being very much flattened and broadened, although the span of the limb when straightened is considerable. P. longicornis is in this respect almost intermediate between the two types (Plate 6, A, B). All these species have specialized hairs of two kinds on the ultimate and penultimate segments of the endopodite. These are—(a) sweeping hairs (Plate 4, C), very long and slender, bearing two regular rows of fine branches; and (b) combing hairs (Plate 4, I, i), not so long as the former, but stouter, and bearing two rows of very stiff points like the teeth of a double comb.

Comparison with the third maxillipede of Cancer and allied Brachyura is instructive. In Cancer, the broadening and flattening of the proximal portion of the endopodite and the reduction of its distal joints have proceeded far (see Plate 3, D, E, F). The function of the endopodite here is perhaps exclusively to protect the exit channel, and it is converted into an organ primarily plate-like and protective, and destitute of sweeping hairs. In connection with the life high up the shore, antennæ and antennules are reduced in size and importance (experiments prove the former to be practically insensitive to touch), so that this double reduction renders the combing of antennæ and antennules by the hairs of VIII impracticable. The combing hairs, having lost their function, are obviously degenerate : though they retain their two rows of lateral branches, these branches are so much thickened as to be almost fused in rows, and quite disqualified as combing teeth. The fact that Algal growth has been found attached to the antennæ of practically every specimen of Cancer pagurus examined appears to prove conclusively the absence of combing device and sensitivity. Carcinus (a more active Brachyuran than Cancer, and one proved by experiment to have greater power of antennal perception), has the third maxillipede just long enough to clean the antenna tip, and it is noticed that in members of this genus the combing hairs have persisted without degeneration-also Algal growth is less commonly present on the antenna, and never present near the tip. On the other hand, P. platycheles presents, in this matter of the combing hairs, a condition markedly analogous with that of Cancer. This must be connected with the general

crab-like habit and sluggish nature of the species (compare the settlement of Spirorbis, etc., on the carapace and chelæ).

In this last instance, then, P. platycheles exhibits a type of specialization markedly analogous with that of the true crabs, and the species once more asserts its right to be placed among the upper branches of our tree of Galatheid ascent.

# EXPLANATION OF PLATES.

#### Plate 1

A.-E: Thoracic nervous systems of Decapod Crustaceans.

A. Of Astacus fluviatilis (after Huxley).

Of Galathea squamifera Β. Of Munida rugosa

members of the Galatheidea.

D. Of Porcellana platycheles

E. Of Cancer pagurus.

C.

Gn. 1.	=supra-œsophageal mass.
C. æ.	=circum-œsophageal ring.
S. œ.	=sub-œsophageal ganglion.
S. n.	=gap for sternal artery.
Gn. 4, 5-8.	=last 5 thoracic ganglia.
Gn. 8.	=ganglion of segment XIII.
Vn.	=ventral nerve-mass.

F and G. Branchial cavity of right side, showing bases of thoracic legs.

A. Of G. squamifera.

B. Of P. platycheles.

Pl. X to XIII=Pleurobranchia.

Ep. VIII to XI=Epipodites.

#### Plate 2.

A. Side view of carapace of Galathea strigosa.

> Ep. VIII=epipodite of the 3rd maxillipede (usually turned into the branchial cavity).

- Β. An epipodite of G. squamifera, showing sweeping hairs. Ms:=muscle.
- P. platycheles, dorsal view. The flagellum of the left side is at work. D. (N.B.-In this specimen, the chela of the right side is the larger. The illustration by no means does justice to the general shagginess of the species.)

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C. Enlarged view (diagrammatic) of a portion of the above.

a. =antennules,

m. =plate-like endopodite of VIII.

fl. =flagellum at work.

ex. =ex-current stream.

S. = Spirorbis tube on chela.

# Plate 3.

A. Side view of branchial cavity of G. squamifera, gills removed (diagrammatic).

c. =cut edge of body-wall, etc.

In. = inhalent aperture.

Ex. =exhalent aperture.

Gr. = position of groove.

r. = line of a not prominent ridge.

A ii, B i and ii, and C i=diagrams of various branchial cavities in T.S.

A ii. Of G. squamifera.

B. Of P. platycheles (i, near front end; ii, further back).

Ci. Of C. pagurus.

B iii. = Branchiostegite of P. platycheles, inner surface.

C ii. = Branchial cavity of Cancer exposed.

r. =ridge.

br. = branchiostegite.

c. = cut edge of carapace.

D.=3rd maxillipede of G. squamifera (right side).

E = ,, ,, P. platycheles

F.= ,, ,, ,, *C. pagurus* 

en. = endopodite.

ex.=exopodite.

G. = Antenna of C. pagurus, with Algal growth.

#### Plate 4.

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Drawings of single hairs (much enlarged).

- A. Simple hair, e.g. "shaggy hairs" of P. platycheles.
- B. Once-pinnate hair, on carapace ridges of Galathea, also fringing the branchiostegite in *G. squamifera*.
- C. In-sweeping hair, on last two joints of endopodite of 3rd maxillipede in Galatheidea.
- D. Epipodite hair.
- E. Filter hair, fringing branchiostegite, etc., in G. intermedia, G. nexa, and Munida subrugosa.

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- F. Strigosa hair, fringing branchiostegite, etc., in G. strigosa.
- G. Tree-like filter hairs, fringing branchial apertures of *P. platycheles* and Cancer, etc.
  - i. Cluster, with collected mud.
  - ii. Tip of one hair, more highly magnified.
- H. Matted hairs, inner side of basal joint of 3rd maxillipede in Galatheidea.
- I i. Combing hair, last two joints of VIII in Galathea, Munida, P. longicornis, and Carcinus mænas.
  - ii. Degenerate combing hair, P. platycheles and C. pagurus.
- Ki. Sickle hair, ultimate joint of XIII in Galatheidea (except *P. platy-cheles*).
  - ii. Degenerate sickle hair (P. platycheles).

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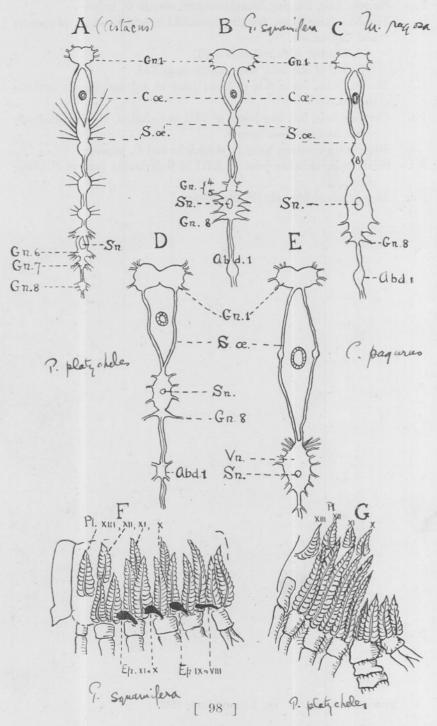
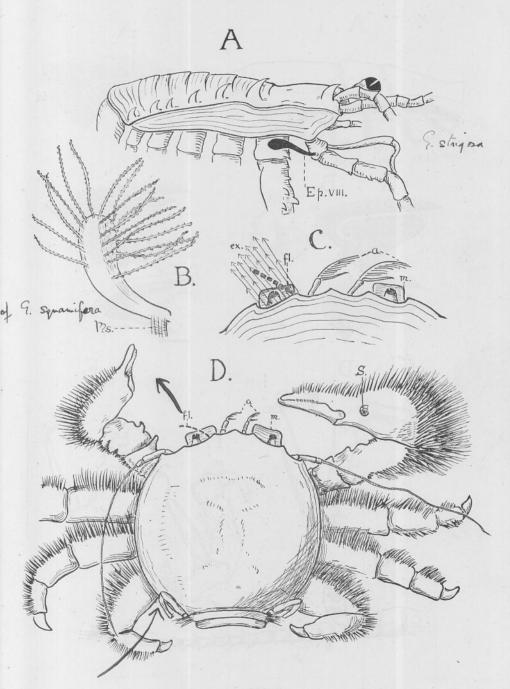


PLATE I

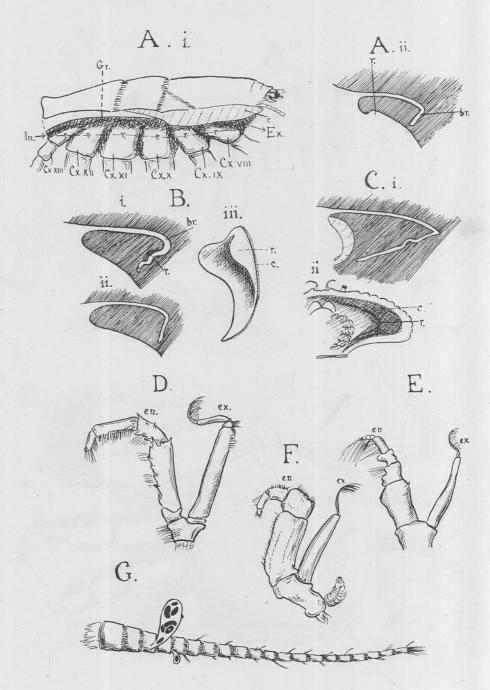
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PLATE III

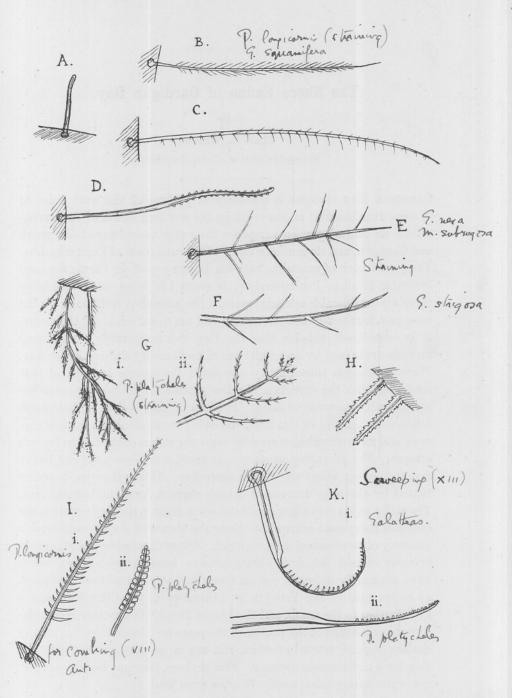
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PLATE IV



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# The Shore Fauna of Cardigan Bay.

By

Chas. L. Walton, University College of Wales, Aberystwyth.

CARDIGAN BAY occupies a considerable portion of the west coast of Wales. It is bounded on the north by the southern shores of Carnarvonshire; its central portion comprises the entire coast-lines of Merioneth and Cardigan, and its southern limit is the north coast of Pembrokeshire. The total length of coast-line between Braich-y-pwll in Carnarvon, and Strumble Head in Pembrokeshire, is about 140 miles, and in addition there are considerable estuarine areas. The entire Bay is shallow; for the most part four to ten fathoms inshore, and ten to sixteen about the centre. It is considered probable that the Bay was temporarily transformed into low-lying land by accumulations of boulder clay during the Ice Age. Wave action has subsequently completed the erosive removal of that land area, with the exception of a few patches on the present coast-line and certain causeways or sarns. Portions of the sea-floor probably still retain some remains of this drift, and owing to the shallowness, tidal currents and wave disturbance speedily cause the waters of the Bay to become opaque. The prevailing winds are, as usual, south-westerly, and heavy surf is frequent about the central shore-line. This surf action is accentuated by the large amount of shingle derived from the boulder clay. The action of the prevailing winds and set of drifts in the Bay results in the constant movement northwards along the shores of a very considerable quantity of this residual drift material. Where checked by shore contour or river current this drift accumulates to form storm-beaches, which have eventually deflected certain rivers and streams to the northward, as in the case of the Ystwyth at Aberystwyth, the Clarach stream a little further to the north, and the Leri at Borth. Other large accumulations have assisted in the raising of the sams or "causeways," extensive shallow regions, several of which run out in its northern half into the Bay for a considerable distance. One of these, the Sarn Badrig, dries at low-water spring-tides, nearly 14 miles from land.

#### THE SHORE FAUNA OF CARDIGAN BAY.

Large amounts of muddy fresh water are poured into Cardigan Bay by the numerous torrential rivers and streams which flow from the mountain regions where the rainfall is heavy. Some of these (from N. to S.) are the Soch, Rhyd-hir, Erch, Wen, Glaslyn, Dwyryd, Artro, Mawddach, Dysynni, Dyfi (with subsidiary streams Einon, Clettwr and Leri), Rheidol, Ystwyth, Wyre, Aeron, Teifi, and Nevern. Of these, the Glaslyn and Dwyryd, the Mawddach, the Dyfi and subsidiaries, and the Teifi, form estuaries of considerable extent. After heavy rain, the inshore waters of the Bay are discoloured for some distance from the rivermouths. This discolouration is chiefly to the northward of the river mouths, owing to the surface waters being driven in that direction by the prevailing rain winds. The junction between the surface of the muddy fresh water (floating over sea water) and the clear sea is frequently plainly visible. The Bay is bounded for the most part by high land, but the continuity is broken by the deep clefts and estuaries of numerous rivers. The coast-line comprises an alternating series of (1) steep, rocky cliffs, consisting of Cambrian Ordovician and Silurian grits and shales, though there are some exposures of igneous rock, (2) drift cliffs of lower elevation, and (3) estuaries. In each of these the characteristics of the tidal area are different. In the first it is chiefly reef and hard erosion plane, with great variability in local conditions according to the strike and dip of the rock, the amount of exposure, and the quantity of detritus which washes to and fro in the gullies between the rock-ridges. If the strike of the rocks is fairly parallel with the coast, the dip of the rocks becomes an important factor as regards the Fauna. If it is low, the whole surface is exposed to wave action and the rocks are barren; if it is high with a landward dip, they are also barren; but if high and seaward, there may be a fairly good Fauna on the more sheltered landward slope. Outlying reefs may provide shelter, even if submerged, because they break the force of a ground swell and lessen the amount of wave-borne detritus. The shingle derived from boulder clay and carried along the coast is often largely augmented by detritus from the grit cliffs of the locality.

(2) Where drift cliffs prevail, much of the foreshore consists of shingle with large stretches, or low reefs of boulders, and local patches of coarse sand.

(3) In the estuaries, and often for some distance on either side, the tidal area is sandy or muddy and the foreshore is dune-capped. More recently there appears to have been a considerable influx of finer sand (presumably from deeper water) along the greater part of the shore-line,

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resulting in appreciable local modifications of some of the elements of the Fauna.

The portion of the Bay in which the above-mentioned conditions are most typically developed lies between Portmadoc to the north and Cardigan to the south. Aberystwyth lies practically in the centre, and as the faunistic work has been carried out from that point, and since time, distance, and accessibility have, as usual, played their parts, the coast in the vicinity of Aberystwyth has been much more thoroughly examined than the rest. Practically no records have been made south of the Teifi, and but few above Portmadoc. It is fortunate that the region most readily accessible includes all the types of coast. It will be seen that there are three principal types of shore, and that these are subject in a marked degree to several important factors. (1) Wave disturbance (surf action). (2) Erosion by detritus and shingle. (3) Muddy fresh water.

These adverse conditions are reflected in the comparative poverty of the Fauna. In connection with the above factors, peculiarities have been observed in the distribution of certain groups, notably some of the Mollusca, and these are dealt with separately. It is hoped, later, to study the Fauna of the Bay below low-water mark and a number of records are already available : the comparison should prove of interest. It follows from what has been said above, that the shore Fauna will consist chiefly of the more hardy species, supplemented by some others that may survive in the more sheltered spots. The nomenclature adopted is mainly that of the "Plymouth Marine Invertebrate Fauna," 1904.

It will be observed that the Echinoderms and Ascidians are very poorly represented. The Crustacea and fishes have been limited as far as possible to shore forms, but a hard-and-fast line cannot be drawn. The worms have not been at all adequately examined and require the attention of a specialist. The following abbreviations are used to denote the observers responsible for the various records :---

H. J. F. = Prof. H. J. Fleure, D.Sc.
F. S. W. = F. S. Wright.
C. L. W. = C. L. Walton.

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#### THE SHORE FAUNA OF CARDIGAN BAY.

### LIST OF LITTORAL ALGÆ.

A-Aberystwyth; C-Clarach and north; S-Allt Wen and south.

CHLOROPHYCEAE. Enteromorpha compressa, Grev.; A, C, S.

Enteromorpha linza, J. Ag.; C.

Enteromorpha intestinalis, J. Ag.; A, C, S. Ulva latissima, J. Ag.; A, C, S. Chaetomorpha melagonium, Kütz.;

A, S. Chaetomorpha tortuosa, Kütz.; A. Cladophora pellucida, Kütz.; A. Cladophora albida, Kütz.; A, C. Cladophora sericea, Reinb. Bryopsis plumosa, C. Ag.; A, C.

# Phaeophyceae.

Desmarestia aculeata, Lamx.; A, C. Dictyosiphon faniculaceus, Grev.; A. Punctaria latifolia, Grev.; A, C. Myriotrichia clavæformis, Harv. var. filiformis, Farl.; A. Asperococcus echinatus, Grev.; A. Streblonema faciculatum, Thur.; A. Ectocarpus confervoides, Le Jol.; A, C. var. siliculosa, Kjell. E. tomentosus, Lyngb.; A, S. Elachista fucicola, Fries.; A. Sphacelaria cirrhosa, C. Ag.; A. Sphacelaria plumigera, Holm.; A. Cladostephus spongiosus, C. Ag.; A, C, S. Cladostephus verticillatus, C. Ag.; A,C. Stypocaulon scoparium, Kütz.; C, S. Ralfsia verrucosa, Aresch.; A. Stilophora rhizodes, J. Ag.; S. Chordaria flagelliformis, C. Ag.; A. S. Mesoglæa vermiculata, Le Jol.; S. Castagnea virescens, Thur.; A, S. Castagnea griffithsiana, J. Ag.; A. Leathesia difformis, Aresch.; A, C, S. Phyllitis fascia, Kütz.; A. Chorda filum, Stackh.; A.

Laminaria saccharina, Lamx.; A, C, S. Laminaria digitata, Edm.; A, C, S. Fucus cerenoides, Linn.; A. Fucus vesiculosus, Linn.; A, C, S. Fucus serratus, Linn.; A, C, S. Ascophyllum nodosum, Le Jol.; A, C, S. Pelvetia canaliculata, Dene eb, Thur. Halidrys siliquosa, Lyngb.; A, C, S. Dictyota dichotoma, Lamx.; S.

#### Rhodophyceae.

Bangia fuscopurpurea, Lyngb.; C. Porphyra linearis, Grev.; A. Chantransia virgatula, Thur. Chondrus crispus, Stackh.; A, S. Gigartina teedii, Lamx.; A. Phyllophora membranifolia, J. Ag.; A. Ahnfeldtia plicata, Fries.; A. Catanella spuntia. Rhodymenia palmata, Grev.; A. Lomentaria articulata, Lyngb.; A. Laurencia hybrida, Lenorm.; S. Polysiphonia urceolata, Grev.; A. var. patens, J. Ag. Polysiphonia elongata, Grev.; S. Polysiphonia violacea, Wyatt; A. Polysiphonia nigrescens, Grev.; A. Callithamnion hookeri, C. Ag. Plumaria elegans, Bonnem.; S. Ceramium strictum, Harv. var. divaricata, Holm. & Batt. A. C. diaphanum, Roth.; A. C. rubrum, C. Ag.; A. var. proliferum, J. Ag. C. acanthonotum, Carm.; A. C. ciliatum, Ducluz; A. Furcellaria fastigiata, Lamx.; S. Polyides rotundus, Grev.; A. Hildenbrandtia prototypus, Nard. var. rosea, Kütz.; A, C, S. Lithothamnion polymorphum, Aresch.; A, S.

Corallina officinalis, Linn.; A, C, S.

#### CHAS. L. WALTON.

The region between Ystwyth and Dyfi appears to be hostile to certain Alga, notably Stilophora rhizoides, Mesoglae vermiculata, Dictyota dichotoma and Laurencia hybrida, which are absent from it, and Chondrus crispus and Castagnea virescens, which become more common outside it.

## LIST OF SHORE FAUNA.

## PORIFERA.

Sycon compressum, Fleming. Low-water mark, in sheltered spots, upon Algæ, etc. (H. J. F.; C. L. W.)

S. coronatum, Ellis and Sol. Same as last. (C. L. W.)

Halisarca dujardini, Johnston. Under surface of stones. (C. L. W.)

Halichondria panicea, Pallas. Common in sheltered spots almost everywhere. (C. L. W.)

Hymeniacidon sanguineum, Grant. Aberystwyth. (C. L. W.)

#### CŒLENTERATA.

Podocoryne carnea, M. Sars. Aberystwyth. (C. L. W.)

Coryne vaginata, Hincks. On Algæ in rock-pools or reefs south of Borth. (C. L. W.)

Zanclea implexa, Alder. One colony, collected by Dr. Salter, 1907. (C. L. W.)

Obelia dichotoma. On piles of Railway Wharf, Aberdovey, and rockpools Gwbert-on-Sea. (C. L. W.)

O. geniculata, Linnæus. Generally distributed. (H. J. F.; C. L. W.)

Sertularia pumila, Linnæus. Generally distributed; often abundant on *Fucus*. (C. L. W.)

Plumularia echinulata, Lamarck. Aberystwyth. (C. L. W.)

P. pinnata, Linnæus. General in sheltered pools. (C. L. W.)

P. similis, Hincks. (H. J. F.)

Actinia equina, Linnæus. Generally distributed and locally common. Aberystwyth, Y-Gamlas, Mochras, etc. (C. L. W.) See Journal Marine Biological Association, October, 1911. pp. 228–230.

Anemonia sulcata, Penn. Generally only a few. Aberystwyth and for a few miles to the south. Tonfunau, etc. (C. L. W.)

Sagartia miniata, Gosse. One specimen. Aberystwyth. (C. L. W.)

S. undata, O. F. Müller. Observed at Clarach, a little bay to the north of Aberystwyth. Small specimens occur under stones which have become fixed in grooves, on an otherwise very barren erosion plane. Individuals, when kept in captivity, very averse to light. One large specimen on reef below the College. (C. L. W.)

2. g. H.D.

#### THE SHORE FAUNA OF CARDIGAN BAY.

- S. ornata, Holdsworth. This rare Actinian has occurred in pools at extreme low water, on reefs below the University. (C. L. W.) See Journal Marine Biological Association, October, 1911. pp. 236-237.
- Tealia coriacea, Cuvier. Not common, but occurs in favourable situations as in pools at Clarach, which are sheltered by large shelving rocks; there specimens of large size may be seen. One individual observed among Mussels at Mochras. (C. L. W.)

#### ECHINODERMATA.

- Henricia sanguinolenta, O. F. Müller. One specimen. Aberystwyth; extreme low water, February, 1913. (C. L. W.)
- Asterias rubens, Linnæus. Has been common 1898 and 1904-5, but now scarce, Aberystwyth. (H. J. F.) Sometimes occurs on the seaward Mussel beds, Aberdovey. (C. L. W.)

Amphiura sp. Not uncommon under stones. (C. L. W.)

Ophiothrix fragilis, O. F. Müller. A number were observed under stones among Laminaria during the abnormally low tides of February, 1913. (C. L. W.)

# TURBELLARIA.

Fovia affinis, Stimpson. Under stones, near Harbour, Aberystwyth. (C. L. W.)

Leptoplana tremellaris, O. F. Müller. Common. (C. L. W.)

## NEMERTINI.

Amphiporus lactifloreus, Johnston. Aberystwyth. (C. L. W.) Lineus longissimus, Gunn. Abervstwyth. (H. J. F.) Tetrastemma sp. Aberystwyth. (C. L. W.) Dinophilus tæniatus, Harmer. Aberystwyth. (H. J. F.)

### POLYCHÆTA.

Lagisca floccosa, Savigny. Aberystwyth. (C. L. W.) Harmothoe imbricata, Linnæus. Gwbert-on-Sea, two specimens.

(C. L. W.) Central dorsal area dark, margins pale. Eulalia viridis, Müller. Frequent on reefs and with Sabellaria. (C. L. W.) Psamathe fusca, Johnston. Aberystwyth. (C. L. W.) Castalia punctata, Müller. Clarach, with ova, June 9th, 1910. (C. L. W.) Nereis pelagica, Linnæus. Aberystwyth. (C. L. W.) Lysidice sp. Aberystwyth. (C. L. W.)

Terebella sp. Fairly common. Aberystwyth. (C. L. W.)

Lanice conchilega, Pallas. Local. (C. L. W.)

Arenicola marina, Linnæus. Abundant on Cockle beds in estuaries. (C. L. W.)

Cirratulus cirratus, O. F. Müller. Aberystwyth. (H. J. F.)

Pomatoceros triqueter, Linnæus. Not uncommon under stones. (C. L. W.) Spirorbis borealis, Daudin. General on *Fucus*, etc. (C. L. W.)

Sabellaria alveolata, Linnæus. Locally very abundant near sandy areas, and has then a considerable influence in binding together boulders and loose stones. It is almost invariably accompanied by *Eulalia viridis* and *Ulva*, but precludes many other species by filling up the crevices and bases of rocks and stones which otherwise afford them shelter. (C. L. W.)

# GEPHYREA.

Sipunculus nudus, Linnæus. One specimen, Aberystwyth. (H. J. F.)

### POLYZOA.

Scrupocellaria reptans, Linnæus. Aberystwyth. (C. L. W.)

Membranipora pilosa, Linnæus. Aberystwyth, etc. (C. L. W.)

M. membranacea, Linnæus. Aberystwyth. (C. L. W.)

Crisia cornuta, Linnæus. Under stones, Aberystwyth. (C. L. W.)

C. denticulata, Lamarck. Aberystwyth. (C. L. W.)

Alcyonidium hirsutum, Fleming. Upon *Algæ*, Aberystwyth, Borth, etc. (C. L. W.)

Amathia lendigera, Linnæus. Upon old Mussels, Aberdovey. (C. L. W.) Bowerbankia imbricata, Adams. With above. (C. L. W.)

Pedicellina cernua, Pallas. With A. hirsutum, Clarach. (C. L. W.)

# MOLLUSCA.

Acanthochites fascicularis, Linnæus. Aberystwyth, etc. (C. L. W.)

Trachydermon cinereus, Linnæus. Aberystwyth. (H. J. F.) Morva, Clarach. (C. L. W.)

- Patella vulgata, Linnæus. Abundant; mainly on the sheltered landward side of shelving rocks, and then often of very large size. (C. L. W.)
- Helcion pellucida, Linnæus. Aberystwyth, above extreme low tides rather rare. (H. J. F.) Fairly common on Laminaria when tides are unusually low. (C. L. W.) Coves, Gwbert-on-Sea, fairly common. (C. L. W.) One specimen was discovered near Aberystwyth at high-water mark attached to a stone, evidently due to Laminaria cast up after storms.

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# THE SHORE FAUNA OF CARDIGAN BAY.

Fissurella græca, Linnæus. One specimen, Aberystwyth. (H. J. F.) Acmæa virginea, Müller. Llanina, near New Quay, one specimen.

(C. L. W.) Shells are fairly frequent. (H. J. F.)

Gibbula magus, Linnæus. Y-Gamlas, near Pwllheli. (C. L. W.)

- G. cineraria, Linnæus. Rare. Two living specimens south of Llanrhystyd and two at Gwbert-on-Sea. (C. L. W.)
- G. umbilicata, Montagu. Very abundant in certain areas. (H. J. F.; C. L. W.) New Quay, Llanrhystyd, north of Towyn, Mochras, near Pwllheli, etc. Considerable differences in form and colouration are observable. The general shell form varies from a dorso-ventrally flattened or "Tam-o'-Shanter," to a clumsy rounded turban shape. In the latter the summit is generally eroded and the penultimate whorl often imbricate and inflated. These differences appear to be due to age. The umbilicus varies between large, open, and deep, and narrow, slit-like, and shallow. These differences appear equally in local examples and in specimens sent from Plymouth, and do not depend entirely upon age and size; as in several instances the umbilicus was wider and deeper as size increased. The narrowing appears to be due to growth of the adjacent edge of the inner lip, which takes place in some individuals, but not in others. The colour bands may be few and obvious, or numerous and obscure.
- Monodonta crassa, Montfort. Distribution more restricted than the last; often very abundant and large. (C. L. W.)
- Calliostoma zizyphinus, Linnæus. One small specimen, Aberystwyth. (C. L. W.)
- Phasianella pullus, Linnæus. One specimen, on *Laminaria*, extreme low water, Aberystwyth. (C. L. W.)

Lacuna divaricata, Fabricius. On Algæ, not uncommon. (C. L. W.)

- L. puteolus, Turton. Aberystwyth, one specimen living among *Balanus* perforatus. (C. L. W.)
- Littorina littorea, Linnæus. Common almost everywhere. Strongly ribbed when young, ribbings becoming either faint or obsolete after a height of 20 mm. has been attained. (C. L. W.)
- L. neritoides, Linnæus. Seldom common, but widely distributed. (C. L. W.)
- L. obtusata, Linnæus. Abundant everywhere, on *Fucus*. (H. J. F.; C. L. W.)
- L. rudis, Maton. Abundant almost everywhere. The largest shell so far found in the Bay is from Aberdovey. Total length, 19 mm.;

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greatest diameter, 13 mm.; aperture of mouth, 11 mm. long, 8 mm. broad. Shell thick, apex acute.

Paludestrina stagnalis, Baster (Hydrobia ulvæ). Exceedingly abundant on sands, Ynys Lâs, Dyfi estuary; and on stones and muddy sand at

Borth-y-Gest, Glaslyn estuary. (C. L. W.)

Trivia europea, Montagu. Rare, Aberystwyth. (H. J. F.)

Purpura lapillus, Linnæus. Abundant. (H. J. F.; C. L. W.)

Nassa reticulata, Linnæus. Aberystwyth, not common. (H. J. F.)

Æolidia papillosa, Linnæus. Aberystwyth, etc., not uncommon. (H. J. F.; C. L. W.)

Aeolidiella augulata, Alder and Hancock. One specimen under a stone very low water, Aberystwyth, February 22nd, 1913. (C. L. W.)

Æ. glauca, Alder and Hancock. Rocks below College.

Facelina drummondi, Thompson. Aberystwyth. (H. J. F.)

F. coronata, Forbes and Goodsir. Not uncommon, Aberystwyth. (C. L. W.)

Doto coronata, Gmelin. Aberystwyth. (H. J. F.)

Archidoris tuberculata, Alder and Hancock. Gwbert, near New Quay, Aberystwyth, Clarach, etc. (H. J. F.; C. L. W.)

Jorunna johnstoni, Alder and Hancock, Aberystwyth. (C. L. W.)

Polycera lessoni, D'Orbigny. Rare, Aberystwyth. (C. L. W.)

Acanthodoris pilosa, Müller. Aberystwyth, rare. (C. L. W.)

- Lamellidoris bilamellata, Linnæus. Aberystwyth, Llannia, Gwbert, etc. (C. L. W.)
- Goniodoris castanea, Alder and Hancock. One specimen, Aberystwyth, on *Botryllus violaceus* coating *Halidrys*. (C. L. W.)
- G. nodosa, Montagu. Not uncommon,. Aberystwyth, Clarach, etc. (C. L. W.)

Ancula cristata, Alder. Aberystwyth. (C. L. W.)

Anomia ephippium, Linnæus. Fairly common under stones. (H. J. F.)

Mytilus edulis, Linnæus. Locally very abundant on shores and in estuaries. Small where marine conditions prevail; large and of considerable commercial importance in the estuaries of Portmadoc, Barmouth, and Aberdovey. (C. L. W.)

- Volsella barbata, Linnæus. Two specimens among Sabellaria, Clarach, 1906. One, Aberystwyth, 1913. (C. L. W.)
- Scrobicularia plana, da Costa. In mud on the Cockle beds of the various estuaries. (C. L. W.)
- Tellina tenuis, da Costa. One living specimen among Cockles, Ynys Lâs, Dyfi estuary. (C. L. W.)

Macoma balthica, Linnæus. Abundant on Cockle beds. (C. L. W.) Donax vittatus, da Costa. Borth. (C. L. W.)

Tapes decussatus, Linnæus. Aberystwyth. (H. J. F.; F. S. W.) Occasionally; Aberdovey, not uncommon; Monk's Cave (south of Aberystwyth). (C. L. W.)

T. virgineus, Linnæus. Borth, etc. (C. L. W.)

- Cardium edule, Linnæus. Very abundant in the various estuaries (C. L. W.)
- Saxicava rugosa, Linnæus. Aberystwyth, Clarach, etc. Often with Sabellaria. (H. J. F.; C. L. W.)

# CRUSTACEA.

[I am indebted to Mr. F. S. Wright for this list, and the records are his unless otherwise indicated.]

Canthocamptus palustris, Brady. Aberystwyth, Clarach, etc. (H. J. F.) Balanus balanoides, Linnæus. Aberystwyth. (H. J. F.)

B. perforatus, Bruguière. Aberystwyth, etc. (C. L. W.)

Chthamalus stellatus, Poli. Aberystwyth, etc. (C. L. W.)

Verruca stræmia, O. F. Müller. Aberystwyth, etc. (C. L. W.)

Sacculina carcini, Thompson. Aberystwyth, etc. On Carcinus. (H. J. F.; C. L. W.)

Dexamine spinosa, Montagu. Aberystwyth. Common.

Amathilla homari, Fabricius. Two specimens in stony pools, very low water, Aberystwyth. (C. L. W.)

Gammarus pulex, de Geer. Aberystwyth, etc., common.

G. locusta, Linnæus. Aberystwyth, etc., common.

Caprella linearis, Linnæus. At low water, Aberystwyth.

Calliopius læviusculus, Kroyer. Aberystwyth and Clarach.

Idotea baltica, Pallas, Aberystwyth.

I. marina, Linnæus. Aberystwyth.

Sphæroma serratum, Fabricius. Aberystwyth, common.

- Jæra marina, Fabricius. Aberystwyth, common under stones. (C. L. W. F. S. W.)
- Gnathia edwardii, Spence Bate. A female was discovered under a fixed stone in a deep pool. It occupied a burrow within a colony of *Halichondria panicea*, and within the burrow were found a number of small yellow ova, June 24th, 1910.

Ligia oceanica, Linnæus. Common.

Leander serratus, Pennant. Aberystwyth, common.

Crangon vulgaris, Linnæus. Common.

# CHAS. L. WALTON.

Hippolyte varians, Leach. Aberystwyth. (C. L. W.; H. J. F.) Athanas nitescens, Leach. Occasional, Aberystwyth.

- Axius stirhynchus, Leach. One specimen, March 24th, 1909, at extreme low water, Aberystwyth, in a handful of gravelly sand. Kept in confinement in a glass vessel with a little sand, it kept the water turbid by constant movement of the swimmerets. The identification was confirmed by Canon A. M. Norman.
- Homarus vulgaris, Milne-Edwards. Sometimes found at low-tide mark on rocky shores. (C. L. W.)
- Galathea squamifera, Leach. Aberystwyth. In sheltered areas not subject to severe wave action. Generally in early summer, but appearance very erratic; sometimes abundant, at others rare or absent. (H. J. F.) A number occurred during the very low tide of February 21st-22nd, 1913. (C. L. W.) One specimen, October, 1912, Gwbert. (C. L. W.)

Porcellana platycheles, Pennant. Abundant under stones.

- P. longicornis, Linnæus. Extreme low water, Aberystwyth. Appearance very uncertain. (H. J. F.)
- Dromia vulgaris, Milne-Edwards. One small specimen, Aberystwyth. (H. J. F.)

Eupagurus bernhardus, Linnæus. Common.

Portunus puber, Linnæus. Not uncommon, Aberystwyth, etc.

Carcinus mænas, Pennant. Common.

Cancer pagurus, Linnæus. Common.

Pilumnus hirtellus, Linnæus. Rare.

Pinnotheres pisum, Linnæus. Appears to be abundant with *Mytilus* edulis, Aberdovey, etc. (C. L. W.)

# PYCNOGONIDA.

Pycnogonum littorale, Stræm. Aberystwyth. (H. J. F.) Nymphon gracile, Leach. Upon *Plumularia pinnata*. (F. S. W.)

# TUNICATA.

Styelopsis grossularia, van Beneden. One specimen, Aberystwyth. (C. L. W.)

Botryllus violaceus, M.-Edwards. Common under stones, Aberystwyth, etc. (H. J. F.; C. L. W.)

Botrylloides sp. Aberystwyth.

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### PISCES.

- Blennius pholis, Linnæus. Common and often very large. (F. S. W.; H. J. F.)
- B. gattorugine, Bloch. Aberystwyth, occasionally. (F. S. W.)
- Cottus bubalis, Euphrasen. Fairly common and large, in rock-pools. (F. S. W.; H. J. F.)
- Centronotus gunnellus, Bloch. Fairly common. (F. S. W.)
- Onos (Motella) mustelus, Linnæus. Common, often high in tidal zone. (H. J. F.; F. S. W.)
- O. (Motella) tricirratus, Bloch. One specimen, Aberystwyth, February 22nd, 1913. (C. L. W.)

Lepadogaster decandolii, Risso. One specimen found at Aberystwyth during a low spring tide, March, 1909. (F. S. W.)

- Liparis montagui, Donovan. Specimens have occurred occasionally in tide-pools below the University. (F. S. W.)
- L. vulgaris, Fleming. Occasional young specimens, Aberystwyth. (F. S. W.)

Nerophis lumbriciformis, Willoughby. Scarce; two specimens in halftide pools, Aberystwyth. (F. S. W.)

Gasterosteus spinachia, Linnæus. Rare, Aberystwyth. (H. J. F.)

Crenilabrus melops, Cuvier. Two young specimens, Aberystwyth. (F. S. W.) One, February, 1913. (C. L. W.) Summer, 1910.

Ctenolabrus rupestris, Linnæus. Fairly common. (H. J. F.; F. S. W.) Cyclopterus lumpus, Linnæus. Fairly common. (H. J. F.; F. S. W.) Trachinus draco, Linnæus. Rare, Aberdovey. (H. J. F.)

Zeugopterus punctatus, Bloch. Occasional. (H. J. F.; C. L. W.) One specimen was obtained clinging to the under surface of a stone by means of the margins of the body. I have since seen this species adhere to the sides of a tank in Plymouth Aquarium, in a similar manner. (C. L. W.)

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# The Distribution of some Littoral Trochidæ and Littorinidæ in Cardigan Bay.

By

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THE physical characteristics of the Bay having been set out in the preceding paper, it will not be necessary to repeat that description here, since only special local features will be dealt with, as occasion arises. Peculiarities of distribution had been noted for the Trochidæ and Littorinidæ, and it was with a view to obtaining further information as to the operation of local littoral conditions and their effects upon the fauna that these groups were more particularly examined. These notes detail some of the peculiarities, and outline what are believed to be the controlling causes, at any rate for the central area of the Bay. It would be of great interest to know whether similar peculiarities have been, or can be, observed for other areas of coast. The region discussed lies between Gwbert-on-Sea at the mouth of the Teifi, to the south ; and a point a few miles beyond Pwllheli to the north. The portion more closely examined extends from near Llanrhystyd, some eight miles south of Aberystwyth, to Mochras, a few miles south of Harlech. Some observations were also made about Portmadoc, Borth-y-Gest, and Pwllheli in the northern part of the Bay; and about New Quay, and the mouth of the Teifi to the south, the most southerly being some miles below Cemm æs. Head.

Much of the coast is difficult of access, and the investigation has been going on for a number of years.

The following species have been observed living within tide marks :----

# TROCHIDÆ.

- (1) Gibbula cineraria (Linnæus).
- (2) G. umbilicata (Montagu).
- (3) G. magus (Linnæus).
- (4) Monodonta crassa (Montfort).
- (5) Calliostoma zizyphinus (Linnæus).

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# LITTORINIDÆ.

(6) Littorina littorea (Linnæus).

(7) L. neritoides (Linnæus).

(8) L. obtusata (Linnæus).

(9) L. rudis (Maton).

# GENERAL DISTRIBUTION.

(1) G. cineraria.—This species is rare throughout the whole of the region examined. Two large living specimens were obtained after careful search, in the coves at Gwbert; these coves are situated seaward of the bar, and their general fauna is rich (for Cardigan Bay). Two small specimens were also found, under stones about eight miles south of Aberystwyth. Dead shells are not infrequent, so that this species may be more abundant below tide marks.

(2) G. umbilicata is, in certain districts, exceedingly abundant; but at Gwbert, in the coves above mentioned, I found but two. In New Quay Bay it abounds, also locally from Llanrhystyd (and probably between there and New Quay) to within some two miles of the River Ystwyth, where it gradually dies out. Further north it reappears near Towyn to the north of the Dysynni. It is abundant about Mochras, and occurs at Y-Gamlas on the Zostera beds beyond Pwllheli. There it is accompanied by (3) G. magus, the only locality for this fine species that has so far been noted in the Bay.

(4) M. crassa has very much the same distribution as G. umbilicata, but its range is more restricted, and always lies within the area occupied by that species. Both are often exceedingly abundant for considerable distances.

(5) C. zizyphinus.—So far only one small living specimen has been recorded, and that at Aberystwyth, where no other species of the Trochidæ exist. It probably occurs in deeper water.

(6) *Littorina littorea* has a wide distribution, but is more especially abundant and much larger in certain places.

(7) L. neritoides is, as elsewhere, very local. Its distribution around the Bay appears to be quite normal and to be governed by its usual requirements; a rocky foreshore, affording crevices just above highwater mark, and not exposed to the midday sun and the resulting desiccation. Given these conditions, it often will occur in very restricted areas. South of Aberystwyth, the foreshore for considerable distances is chiefly smooth rock, with a steep seaward inclination. One or two large squared masses of fallen cliff are situated just about high-water

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mark, and their stratified wall-like sides afford crevices, inhabited by this species and *L. rudis. L. neritoides*, however, only occurs on the upper portions, and on the N. and E. faces. A few may be observed on the S.E. also, but this is exceptional. I have seen practically the same thing in similar positions on the Devon coast. On the sea walls of the promenade at Aberystwyth, this species occurs, chiefly where the rays of the summer sun will not strike about midday.

(8) L. obtusata occurs throughout the littoral region examined wherever Fucus grows, and hence is the most thoroughly persistent form.

(9) L. rudis.—This also is generally present, and frequently exceedingly abundant. It usually accompanies L. littorea in its distribution, though at a somewhat different level. These two frequently appear and disappear simultaneously, but one or other may be locally dominant.

# VERTICAL DISTRIBUTION.

The distribution of the species may also be considered vertically, that is, in zones. These zones, of course, overlap considerably and are seldom all well developed, or even present in any given locality. By contrasting varying localities a general succession appears. This is not by any means arbitrary, as some of these zones may occur intermixed at times, particularly in the case of M. crassa, L. littorea, and L. obtusata. L. neritoides is constant when conditions permit, and L. obtusata is dependent on the presence of Fucoid Algæ. C. zizyphinus has occurred once, but in its normal position.

Allowing for local differentiation and overlap, the succession is, more or less, as follows :---

L. neritoides. L. rudis. M. crassa. L. obtusata. L. littorea. G. umbilicata. G. magus. G. cineraria. C. zizyphinus.

The succession of the Littorinidæ can be best followed in the Aberystwyth district, where the Trochidæ are absent.

On the sea wall of the promenade below the University the following succession can be observed :---

(a) Barren stonework.

(b) Zone of L. neritoides.

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(c) Zone of small green Algæ and many L. rudis.

(d) ,, ,, few scattered Fucoids and a few L. rudis.

(e) ,, ,, thick coating of Fucus and a few L. obtusata.

(f) Base of wall, with pools at foot, with *Enteromorpha*, *Ulva*, etc., and *L. littorea*.

M. crassa is local in Cardigan Bay, but often extremely abundant; and in the area south of Aberystwyth exhibits a striking peculiarity in that it there breaks zone by following fresh-water influence, sometimes as far as the low-water mark of spring-tide ; it is then often of remarkable size. Proceeding southwards from Aberystwyth, the mouths of the Rheidol and Ystwyth and a storm beach are passed, and a high slaty cliff with eroded rocky foreshore is reached. About halfway around this headland (Allt Wen), i.e. two miles from Aberystwyth, G. umbilicatus puts in an appearance, at first only sporadically, two or three small individuals here and there. As it becomes more numerous, M. crassa also appears, and both increase rapidly to the south of the headland, where the cliffs are composed of glacial drift. A number of springs flow down, and in one or two localities fresh water percolates through a shingle bank on the foreshore, and affects more or less the whole of the lower rocky and stony portions of the tidal region, which is there mainly composed of boulders covered to some extent by Algæ. Where there is fresh-water influence, M. crassa follows it. Streamlets often follow a kind of channel or gutter, where the boulders lie less thickly, and the shore level is somewhat lower. In these channels, M. crassa swarms upon the nearly bare boulders, and extends almost to low water. G. umbilicata is seldom to be observed within the freshwater influence, although abundant close by. Where a section of the shore is affected by fresh water, M. crassa tends to become abundant throughout. It appears to feed upon minute Algæ, and I am indebted to Dr. Fleure for a recent attempt to determine the food of this species : all that could be made out, however, was that "the contents of the gut consisted of finely triturated vegetable matter, too fragmentary for identification." H. J. Fleure and M. M. Gettings state (Q.J.M.S., 1907), "T. crassus [M. crassa] is found to some extent with the previous species [G. umbilicata], but it lives, for the most part, near high-tide level, so much so that specimens may remain for a considerable time in corners washed only by high spring-tides. It crawls over the rocks chiefly at halftide level, but is more lethargic than T. obliquatus [G. umbilicata], and less inclined to browse on the larger Algæ. During stormy periods, especially in winter, numbers may be found huddled in sheltered nooks,

often with a number of *Littorina littorea* as companions. As is well known, the spire of T. obliquatus is much lower than that of T. crassus, and this is probably correlated with the greater activity of the former in the shore zone, where a high spire would give too much purchase to a side blow from a wave." Recent observations lead to the same conclusions : the animals crowd the tops of the boulders in calm summer weather, and in winter tend to occupy the sides and angles of boulders and reef-pools.

It is evident that in this region Trochus is extending its range northward. Quite recently Mr. W. Whitehouse informed me that he had seen specimens on the Aberystwyth side of Allt Wen. This I found to be the case, as I found a colony of *G. umbilicata* and one specimen of *G. cineraria* about the spot indicated. This is well to the north of any other record, but is close to an isolated patch of boulder clay. I have examined this spot at intervals ever since 1906, and Prof. Fleure knew it well for some years before that, and no Trochi have ever been seen there.

A remarkable influence of fresh water in larger volume upon the littoral Mollusca has been noted, about the mouths of several of the smaller rivers. It is particularly noticeable for some half-mile or so on either side of the mouth of the Afon Wyre, near Llanrhystyd. The cliffs thereabouts are very low, and composed of glacial drift, with the usual result that the foreshore consists of shingle, while the lower portion of the tidal region is occupied by boulders of medium size. These extend to low-water mark, but pass into sand and shingle both to the N. and to the S.; and this boulder area is fairly well covered with Algal growth. The river debouches upon a shingle bed, and spreads out in a fan-like manner over the boulders; and, to judge by the distribution of mussels, would appear, as usual, to trend up-coast, at least during some states of the tide. To the south of the river where the boulder area commences (and, indeed, throughout the area) the zones of L. neritoides and the upper portion of that of L. rudis are absent owing to the presence of shingle. The boulders are at first considerably incrusted with Sabellaria, and no Mollusca are present except a few specimens of Patella, probably owing to the proximity of much sand and shingle. As the boulder area widens G. umbilicata appears, and rapidly becomes abundant. That lack of shelter and attrition are the excluding factors is borne out by the fact that, where Gibbula first appears, the shells of many are much worn and eroded, and in several cases actually broken. I examined certainly 1000 Gibbulas, and only discovered two specimens of cineraria.

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Both were small, flattened, and occurred beneath stones. L. obtusata accompanies Fucus, and is the most persistent species throughout. L. littorea appears about the same time as G. umbilicata, but does not become abundant until fresh-water influence is an appreciable factor; it then increases in number and size. G. umbilicata is dominant for a considerable distance, but as the river is approached, M. crassa appears, here one and there one, amidst the crowds of Gibbula. Those first noticed are rather small, but there is a gradual increase in size and abundance until it equals G. umbilicata in numbers. That species then dies out as fresh water is approached, and is replaced by a rather squat, solid, smooth form of L. rudis, which in its turn rapidly becomes larger and more numerous, while M. crassa, after being a dominant species for a while, dies out in its turn. Then for a space, L. rudis and L. littorea alone occupy the ground; but both are absent from the actual flow of the stream. On the northern side of the river, mussels are abundant in the crevices of the stones for some distance along the shore, and are accompanied by L. rudis and L. littorea. Then, as the mussels disappear, M. crassa reappears, and in company with the Littorinas becomes very abundant. G. umbilicata recommences by degrees, increases in numbers, and with M. crassa continues until the boulder area once more gives place to shingle.

This lateral distribution or zoning may be expressed thus (the order in each instance is that of abundance) :---

1.	2.	3.	4.
G. umbilicata.	G. umbilicata.	G. umbilicata.	G. umbilicata.
	L. littorea.	L. littorea.	M. crassa.
	G. cineraria.	M. crassa.	L. littorea.
		G. cineraria.	
	Littorina obtusat	a	
5.	6.	7.	8.
M. crassa.	L. rudis.	L. rudis.	L. rudis-littorea.
L. littorea.	L. littorea.	L. littorea.	
G. umbilicata.	M. crassa.	M. crassa.	
L. rudis.	G. umbilicata.		
Littorina ob	tusata.		

 1.
 2.
 3.
 4.

 River.
 L. littorearudis.
 L. rudis-littorea. M.crassa.
 M. crassa.
 L. littorearudis.

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# THE LITTORINIDÆ.

It may be mentioned that the shells of L. obtusata often bear a striking resemblance in both form and colour to the vesicles and conceptacles of the species of *Fucus* upon which they live; so much so, in fact, that when collecting this species, I have more than once mistaken the vesicles of the Alqa for the shell of the Mollusc.

The conceptacles of all the species of Fucus are of shades varying from white to bright yellow, and, indeed, the whole of the parts of the plant exposed to sunlight are frequently much lighter in hue than the more sheltered portions, which are usually dark brown or olive. One would expect that the lighter coloured forms of L. obtusata would tend to occur upon the surface, and the darker among the masses of the plant. I have made a considerable number of observations in the district with the object of testing this idea. What I have found is, that the darkest varieties are seldom found upon the surface of the Algal masses, and that the majority of varieties are found in abundance crawling on the exterior, but are often in harmony with their surroundings. It may be mentioned that many shells which appear out of harmony, are not so in reality, the change of colour being due to drying of the shell during low water. The greatest resemblance is between the light brown and yellow-shelled varieties and the vesicles of F. vesiculosus and between the colour of the frond and the ordinary brown and olive shells. Bright yellow Littorinas may be found at times upon the dark stems of the Algæ, and are then very conspicuous. I do not find the yellow variety to be really common in the district.

The Littorinidæ persist in the areas devoid of Trochidæ; and, as has already been stated, *L. obtusata* appears to be less affected by the adverse conditions than the other species; this is in all probability largely due to the protection afforded it by the food plant, and its shell-characters. *L. rudis* and *L. littorea*, are neither so large, so numerous, nor so evenly distributed as in the areas where Trochidæ are abundant. Several varieties of *L. rudis* occur in Cardigan Bay, and of these *tenebrosa*, Montagu, has so far only been found under stones some three miles south of Aberystwyth on a portion of the shore influenced by fresh water. This influence was sufficiently strong to attract a number of eels which were also hiding under the stones. Tryon describes the variety as "thin, whorls rounded, with elevated spire, brownish or yellowish, usually tessellated with white." In the Aberystwyth specimens the ribbings of the shell are not very strong, and the colour olive-green to greyish. The chequered appearance is due to the presence of a series of short white streaks dis-

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posed in a spiral sequence; these white marks, alternating in each turn of the spiral produce a chequered appearance. The usual forms, *similis* and *lævis* of Jeffreys, were both present in the same locality. The variety *patula*, Thorpe, is sometimes abundant on steep rocks at the foot of cliffs, somewhat influenced by fresh-water springs, and may be yellow, olivegreen, pale greenish white, black and white in bands, or pinkish; *compressa*, Jeffreys, occurs a little to the south of Aberystwyth.

The complete sequence of species of Littorina may be interrupted, and a barren area may occur between the cliff rocks and the lower tidal reefs, owing to a belt of shingle. The result of this truncation of zone is that the upper portion of the *rudis* zone may be absent except here and there where conditions allow; while below the break, *rudis* and *littorea* may be found together in quantity, giving the impression that the latter is above its usual horizon.

Dr. Fleure considers that L. rudis spawns largely in the shelter afforded by the interior of dead Balanus, and I have found many of the young of both rudis and littoralis so small as to be just recognizable clustered within the angles of empty Balanus. The absence of Balanus from the rudis zone may also have a limiting effect, locally, on the distribution of the species. A curious and interesting form of Molluscan association is common on some parts of the cockle beds of the Dyfi estuary, and usually on the more muddy areas. Scattered over from one to several acres in such places, are clusters, or groups, composed primarily of one or more mussels, attached to either various dead shells which lie upon the surface, or to one or more living cockles of varying sizes. The latter occupy their usual positions in the sand, thus anchoring the mussels. Upon the cockles grow trailing tufts of various green Alga, and clinging to the mass are generally several individuals of L. littorea and L. rudis, more often the former. Within the mass, amongst the byssal threads of the mussels, one or more specimens of Macoma balthica are frequently to be found. There are often a dozen individuals, belonging to five species of Mollusca. involved in these clusters.

# FACTORS GOVERNING DISTRIBUTION.

The facts concerning distribution, association, etc., are matters of observation, record, and comparison; the causes of distribution are problems of a much more difficult nature, and require careful consideration following wide investigation. With regard to the distribution of the Trochidæ in Cardigan Bay, it is not yet possible to state that the problem has been completely elucidated. It would appear, however,

that there is a correlation between such distribution and shore drainage. The barren area receives most of its shore drainage from lime-free slates and grits, while the "Trochus" areas receive water from boulder clay in the southern, and the same, and igneous rocks, in the northern portions of the Bay. The streamlets followed by M. crassa drain from boulder clay. An attempt was made to obtain additional data by a comparison of the Algae from various portions of the Aberystwyth district. Certain differences were discovered (see list of Alga), but none of them appear to have any direct connection with the Mollusca under consideration; and the evidence afforded is thus more cumulative than decisive. The boulder clays of different districts appear to have different lime contents. The water of the New Quay district is "hard," fruit trees grow well there and the drifts probably contain lime, whereas the boulder clay from the region drained by the Ystwyth has been analysed by Dr. T. C. James, and found to be quite devoid of lime. The northerly drift along the coast has been mentioned already; and it is noteworthy that drainage from the areas containing lime would tend to influence the coast some distance northward on that account. The limeless drainage of the Ystwyth, moreover, coincides with an area of slate and shale rocks; and this is the most barren as regards Trochidæ. The reappearance of the Trochidæ to the north again coincides with the reappearance of boulder clay, and river drainage from districts containing volcanic rock, etc.

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# Marine Biological Association of the United Kingdom.

# Report of the Council, 1912.

# The Council and Officers.

The Council have to record with regret the death of the Duke of Abercorn, who had been a Vice-President since the foundation of the Association, of Professor Adam Sedgwick, F.R.S., for many years a member of the Council, and of Mr. G. H. Drew, who became a member of Council in June last.

The thanks of the Council are due to the President and Council of the Royal Society for the use of the rooms in which their meetings have been held.

# The Plymouth Laboratory.

The work done during the spring of 1912 to the front walls and roof of the building has proved efficient in keeping out the damp, and as regards the structure everything appears now to be in good order. The machinery and apparatus both of the Aquarium and the Laboratory have been maintained in an efficient state.

# The Boats.

Owing to the state of the finances the steamer *Oithona* was laid up somewhat earlier than usual. The collecting work has since been done by the sailing boat *Anton Dohrn* and the small motor-boat which was presented to the Laboratory by Colonel G. M. Giles.

It has been decided to sell the *Anton Dohrn*, which has done good service during the last ten years, and to replace her by a new sailing boat of similar type.

### The Staff.

The staff at work at the Laboratory has consisted of the Director, Dr. E. J. Allen; Hydrographer, Mr. D. J. Matthews, and three

### REPORT OF THE COUNCIL.

Naturalists, Messrs. L. R. Crawshay, J. H. Orton and R. S. Clark. The latter has recently been appointed to make investigations on the biology of marketable fishes.

# Occupation of Tables.

The following Naturalists have occupied tables at the Plymouth Laboratory since the last report was presented to the Association :----

Prof. CHAS. CHILTON, D.SC., New Zealand (Amphipoda). J. CLARK, D.SC., Kilmarnock (Crustacea). W. DE MORGAN, Plymouth (Protozoa). G. H. DREW, B.A., Plymouth (Tissue Growth). F. MARTIN DUNCAN, Oxted (Photography of Marine Animals). H. M. FUCHS, Cambridge (Echinoderm Development). J. GRAY, Cambridge (Echinoderm Development). H. HENRY, M.D., Sheffield (Parasitic Protozoa). G. J. HILL, London (General Zoology). H. B. JOHNSTON, Oundle (General Zoology). S. P. KRAMER, M.D., New York (Elasmobranchs). Miss D. JORDAN LLOYD, Cambridge (Echinoderm Development). Mrs. MATTHEWS, Plymouth (Development of Alcvonium). C. A. NEWMAN, Oundle (General Zoology). GUY DE PITARD, Berne (Anemones). C. SHEARER, M.A., Cambridge (Dinophilus and Echinoderm Development). GEOFFREY SMITH, M.A., Oxford (Blood of Carcinus). C. L. WALTON, Aberystwyth (Anemones).

# General Work at the Plymouth Laboratory.

During the six months covered by the present report the staff have for the most part been employed in a continuation of the researches then described. The Director's experiments on the conditions of growth of plankton diatoms have made considerable progress and results of great scientific interest are promised. Mr. Matthews's investigations on the chemistry of sea-water have to some extent been interrupted by the preparation of a report on the hydrographical work of the Irish Fishery Department, by whom Mr. Matthews is in part employed.

Mr. L. R. Crawshay's report on the fauna of the deeper portion of the English Channel to the south-west of the Eddystone has been published in the Journal of the Association. This report, in conjunction with the previous papers by Mr. Crawshay and Mr. Worth on the bottom-deposits of this region, forms a valuable addition to our knowledge of the English Channel both from the biological and geological points of view. Mr. Crawshay has since the completion of this work been engaged with considerable success in experimental work on rearing copepods and other plankton animals in the Laboratory, with a view to working out the details of their life-histories, a subject upon which very much remains to be done.

In addition to extending the general faunistic records of the Plymouth neighbourhood Mr. J. H. Orton has been specially studying the rate of growth of invertebrates. A large collection of material and of data has been brought together, and an important contribution to our knowledge of this comparatively unworked subject is anticipated when the work is reported upon.

Mr. R. S. Clark is continuing the investigations on the mackerel fisheries off the Cornish coast which were commenced some years ago by the Director and Mr. Bullen. There seems reason to hope that a thorough investigation of the causes which induce the migrations of this fish may make it possible to assist the fishermen in finding the shoals.

The work of Messrs. Shearer, De Morgan and Fuchs, who have been further assisted by Messrs. J. Gray and L. Doncaster and Miss D. Jordan Lloyd, on the hybridization of Echinoids and the rearing of parthenogenetic echinoderm larvæ, has been published in a number of papers in the Quarterly Journal of Microscopical Science, which have attracted considerable attention.

Mrs. Matthews has been investigating the development of *Alcyonium* and has been able to obtain all stages from the fertilized egg to the fixed polyp in considerable numbers.

Mrs. Sexton and Mrs. Matthews have been studying a species of brackish-water *Gammarus* with a view to determining the nature of the variations in structure or appearance which are brought about by changes in the conditions under which the animals live. They have succeeded in rearing five generations in about six months, and they now have the animals living and breeding both in entirely fresh water and in sea-water of normal salinity.

# Published Memoirs.

The following papers, either wholly or in part the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association :—

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WIJNHOFF, G. Die Systematik der Nemertinen. Zoologischen Anzeiger, Bd. 40, October, 1912.

# The Library.

The thanks of the Association are due for the following books and current numbers of periodicals presented to the Library during the period June 1st to Dec. 31st, 1912:—

Académie Imp. des Sciences de St. Pétersbourg. Bulletin.

American Museum of Natural History. Annual Report.

American Microscopical Society. Transactions.

American Philosophical Society. Proceedings.

Armstrong College. Calendar.

Arendals Fiskeriselskab Beretning.

Australian Museum. Records.

Bergens Museum. Aarbok.

----- Skrifter.

Bernice Pauahi Bishop Museum, Honolulu. Occasional Papers.

Board of Agriculture and Fisheries. Annual Report of Proceedings under Acts relating to Sea Fisheries.

---- Monthly Return of Sea Fisheries, England and Wales.

----- Report of Proceedings of Annual Meeting.

---- Report upon the Epidemic amongst Salmonidæ in the summer of 1911.

---- Statistical Tables.

--- Memorandum on German Eel Culture.

Boston Society of Natural History. Proceedings.

#### REPORT OF THE COUNCIL.

British Museum. Catalogue of the Chætopoda in the British Museum (Natural History). Arenicolidæ.

- National Antarctic Expedition, 1901-4. Zoology and Botany.

Bulletin Scientifique de la France et de la Belgique.

Bureau of Science, Philippine Islands. Journal of Science.

California Academy of Sciences. Proceedings.

Club Montanyenc, Barcelona. Butlletí.

College of Science, Tokyo. Journal.

Colombo Museum. Spolia Zeylanica.

R. Comitato Talassografico Italiano. Bollettino.

—— Memoria.

----- Bollettino delle Crociere Periodiche.

Comité du Laboratoire de Carlsberg. Comptes Rendus.

Conchological Society of Great Britain and Ireland. Journal of Conchology.

Connecticut Academy of Arts and Sciences. Transactions.

Conseil perm. internat. pour l'Exploration de la Mer. Bulletin Hydrographique.

—— Bulletin Planktonique.

----- Bulletin Statistique.

— Publications de Circonstance.

----- Rapports et Procès-Verbaux des Réunions.

Cornwall Sea Fisheries Committee. Reports.

Cuerpo de Ingenieros de Minas del Peru. Boletin.

Dept. of Agriculture, etc., Ireland. Report.

Dept. of Commerce and Labor, Bureau of Fisheries, U.S.A. Bulletin.

--- Pamphlets.

Dept. of Marine and Fisheries, Canada. Annual Report.

Dept. of Trade and Customs, Melbourne. Zoological Results of the Fishing Experiments carried out by the F.I.S. Endeavour 1909-10.

Deutschen Fischerei-Vereins. Zeitschrift für Fischerei.

Deutscher Seefischerei-Verein. Mitteilungen.

Dove Marine Laboratory. Report.

Falmouth Observatory. Meteorological and Magnetic Reports.

La Feuille des Jeunes Naturalistes.

Field Museum of Natural History. Publications.

Finnländische Hydrographisch-Biologische Untersuchungen. Abhandlungen. — Tidvattnen i Östersjon och Finska viken. By R. Witting.

Fisheries Society of Japan. Journal.

The Fisherman's Nautical Almanac. By O. T. Olsen.

Fishery Board of Scotland. Annual Report.

---- Scientific Investigations.

---- Fisheries and Marine Motor Exhibition, Copenhagen, 1912. Report on Fishing Boat Motor Engines exhibited, etc. By Capt. J. R. M'Ewan.

Fiskeri-Beretning.

Control March Market

Government Museum, Madras. Report.

Guernsey Society of Natural Science. Report and Transactions.

Illinois State Laboratory of Natural History. Bulletin.

Imperial Bureau of Fisheries, Japan. Report.

Imperial Fisheries Institute, Japan. Journal.

--- Report.

### REPORT OF THE COUNCIL.

Indian Museum. An Account of the Deep-Sea Asteroidea collected by the R.I.M.S.S. *Investigator*. By R. Koehler.

-- An Account of the Shallow Water Asteroidea. By R. Koehler.

---- An Account of the Littoral Holothurioidea. By R. Koehler and C. Vaney.

---- Catalogue of the Indian Decapod Crustacea. By A. Alcock.

- ---- The Alcyonarians of the Deep Sea. By J. A. Thomson and W. D. Henderson.
- --- The Alcyonarians of the Littoral Area. By J. A. Thomson- and J. J. Simpson.

Institut für Meereskunde, Berlin. Veröffentlichungen.

Institut Océanographique. Annales.

Institut de Zoologie, Montpellier. Travaux.

R. Irish Academy. Proceedings.

Kommission zur wissenschaftlichen Untersuchung der Deutschen Meere, etc. Wissenschaftliche Meeresuntersuchungen.

Kommissionen für Havundersögelser, Copenhagen. Meddelelser.

K. Bayerischen Akademie der Wissenschaften, München. Abhandlungen. — Sitzungsberichte.

Kgl. Danske Videnskabernes Selskab. Oversigt.

Laboratoire Biologique de St. Pétersbourg. Bulletin.

Laguna Marine Laboratory. Report.

Lancashire Sea Fisheries Laboratory. Report.

Lancashire and Western Sea Fisheries. Superintendent's Report.

Linnean Society. Transactions.

Linnean Society of New South Wales. Proceedings.

Liverpool Biological Society. Proceedings and Transactions.

Los Angeles Zoological Society. Proceedings.

Marine Biological Association of the West of Scotland. Report.

Marine Biological Laboratory, Woods Hole. Biological Bulletin.

Marine Biological Station, Port Erin. Report.

Mark Anniversary Volume.

Mededeelingen over Visscherij.

Meteorological Office. Barometer Manual.

---- Geophysical Manual.

---- Monthly Pilot Charts.

—— Annual Report of the Committee.

R. Microscopical Society. Journal.

Ministère de l'Instruction publique, France. Deuxième Expédition Antarctique Française (1908–1910).

Musée Océanographique de Monaco. Bulletin.

Museo Nacional, Buenos Aires. Anales.

Museo Zoologico, Napoli. Annuario.

Museum of Comparative Zoology, Harvard College. Bulletin.

- Memoirs.

----- Report.

Muséum National d'Histoire Naturelle, Paris. Bulletin.

The Museums Journal.

Nederlandsche Dierkundige Vereeniging. Tijdschrift. —— Verslag.

New York Academy of Sciences. Annals.

New York Zoological Society. Bulletin.

- Report. \_\_\_\_ Zoologica.

New Zealand Institute. Transactions and Proceedings.

Norges Fiskeristvrelse. Aarsberetning vedkommende Norges Fiskerier.

La Nuova Notarisia.

Oberlin College. The Wilson Bulletin.

Owens College, Manchester. The Dorsal Vibrate Fin of the Rockling (Motella). By J. S. Thomson.

- Observations on living Gorgonias (Gorgonia vertucosa) occurring in the English Channel. By J. S. Thomson.

- Observations on some Alcyonaria from Singapore. By E. W. Shann.

- The Presence of Maxillulæ in Larvæ of Dytiscidæ. By J. Mangan.

----- Structure of the Alimentary Canal of the Stick-Insect, Bacillus rosii Fabr. By A. E. Cameron.

Physiographiske Forening, Christiania. Nyt Magazin for Naturvidenskaberne.

Quarterly Journal of Microscopical Science. (Presented by Sir E. Ray Lankester, K.C.B., F.R.S.)

Rijksinstituut voor het Onderzoek der Zee. Helder. Jaarboek.

Royal Society of Edinburgh. Proceedings.

- Transactions.

Royal Society of London. Philosophical Transactions.

- Proceedings.

Royal Society of Victoria. Proceedings.

Scottish Microscopical Society. Proceedings.

Selskabet for de Norske Fiskeriers Fremme. Norsk Fiskeritidende.

Smithsonian Institution. New Diptera from Panama. By J. R. Malloch.

A Study of the Salinity of the Surface Water in the North Pacific Ocean and in the adjacent enclosed Seas. By A. H. Clark.

Societas pro Fauna et Flora Fennica. Acta.

Société Belge de Géologie, etc. Bulletin.

Société Centrale d'Aquiculture et de Pêche. Bulletin.

Société l'Enseignement des Pêches Maritimes. Bulletin Trimestriel.

Société Imp. Russe de Pisciculture et de Pêche. Vyestnīk R'ibopom'shlennostī.

Société Zoologique de France. Bulletin.

South African Museum. Annals.

Kgl. Svenska Vetenskaps-Akademien. Arkiv för Botanik.

----- Arkiv för Zoologie. ----- Handlingar.

Tôhoku Imperial University, Japan. Science Reports.

Torquay Natural History Society. Journal.

Transvaal Museum. Annals.

Tufts College. Studies.

United States National Herbarium. Contributions.

- United States National Museum. Bulletin.

--- Proceedings.

R. Università di Napoli. Lavori fatti nell' Istituto di Anatomia comparata. Apparati Reticolari Sarcolemma nella fibra muscolare cardiaca. By M. Fedele.

NEW SERIES .- VOL. X. NO. 1. NOVEMBER, 1913.

Т

# REPORT OF THE COUNCIL.

R. Università di Napoli. La morfologia della cromatina dal punto di vista fisico. By P. Della Valle.

University of California. Publications. Zoology, Physiology, Botany.

University College Library, London. Catalogue.

University of Toronto. Studies.

Kgl. Vetenskaps Societeten, Upsala. Nova Acta.

Visscherij-Station, Batavia. Mededeelingen.

Zoological Museum, Copenhagen. The Danish Ingolf-Expedition.

Zoological Society of Japan. Annotationes Zoologicæ Japonenses.

Zoological Society of London. Proceedings.

—— Transactions.

Zoologische Sammlung des Bayerischen Staates. Beiträge zur Naturgeschichte Ostasiens.

Zoologisches Museum, Berlin. Bericht.

---- Mitteilungen.

Dr. H. R. Mill. Symons's Meteorological Magazine.

Mrs. Hill. A number of works from the library of her brother, the late W. I. Beaumont.

To the authors of the Memoirs mentioned below the thanks of the Association are due for separate copies of their works presented to the Library :---

Barroso, M. G. Briozoos de la Estación de Biología Marítima de Santander.

Billard, A. Hydroïdes de Roscoff.

Breitfuss, L. L. Wissenschaftlich-praktische Murman-Expedition. Bericht über die Tätigkeit pro 1905.

Buchanan, J. Y. Experimental Researches on the Specific Gravity and the Displacement of some Saline Solutions.

Burrows, M. T. A Method of Furnishing a Continuous Supply of New Medium to a Tissue Culture in Vitro.

— Rhythmische Kontraktionen der isolieren Herzmuskelzelle ausserhalb des Organismus.

- The Growth of Tissues of the Chick Embryo outside the Animal Body, with Special Reference to the Nervous System.

Carrel, A., and Burrows, M. T. Cultivation of Tissues in Vitro and its Technique.

---- Cultivation in Vitro of the Thyroid Gland.

----- Cultivation in Vitro of Malignant Tumors.

Caullery, M. Présence de Physalies et de Vélelles dans le Pas-de-Calais au début d'Avril, 1912.

Clark, J. An Annotated List of Cornish Fishes.

---- Notes on Cornish Crustacea. I. Brachyura and Macrura.

Cotton, A. D. Clare Island Survey. Marine Algæ.

Crossland, C. Supplement to the "Physical Description of Khor Dongonab, Red Sea."

Dakin, W. J. Aquatic animals and their environment. The Constitution of the external medium and its effect upon the blood.

Davenport, C. B. Light thrown by the Experimental Study of Heredity upon the Factors and Methods of Evolution. Donnison, H. Report on Crab Investigations.

Drew, G. H. An Experimental Investigation of the Cytological Changes produced in Epithelial Cells by long-continued Irritation.

Fabre-Domergue. Épuration bactérienne des Huîtres par la stabulation en eau de mer artificielle filtrée.

---- Nouvelles expériences sur l'épuration bactériologique des huîtres en eau filtrée.

---- Instructions pour l'établissement et l'emploi de bassins de stabulation destinés à l'épuration des Huîtres et autres Mollesques comestibles.

Farran, G. P. Plankton from Christmas Island, Indian Ocean. I. On Copepoda of the Family Corveæidæ.

- Clare Island Survey. Decapoda.

Fauvel, P. Sur quelques Néréidiens (Perinereis Marionii Aud. Edw. P. macropus Clap. Neanthes succinea Leuck.).

Freund, L. Krankheiten der Fische.

Gemmill, J. F. Laboratory Aquarium Notes.

— Aerator suitable for Laboratory Aquaria.

- ---- Notes on the Adult Anatomy of Solaster endeca (Forbes).
- The Locomotor Function of the Lantern in Echinus, with Observations on other Allied Lantern Activities.

— The Development of the Starfish, Solaster endeca (Forbes).

Goodrich, E. S. Nerilla an Archiannelid.

---- Observations on the Nephridia of the Alciopinæ.

Hartmeyer, R. Revision von Heller's Ascidien aus der Adria.

- Helland-Hansen, B., and Nansen, F. The Sea West of Spitsbergen. The Oceanographic Observations of the Isachsen Spitsbergen Expedition in 1910.
- Heron-Allen, E., and Earland, A. On some Foraminifera from the North Sea, etc., dredged by the Fisheries Cruiser *Goldseeker* (International North Sea Investigations—Scotland). I. On some New Astrorhizidæ and their Shell Structure.

Hornell, J. New Cestodes from Indian Fishes.

Hoyle, W. E. The Cephalopoda of the Scottish National Antarctic Expedition.

Ikeda, I. Studies on some Sporozoan parasites of Sipunculoids. I. The Life-History of a new Actinomyxidian, *Tetractinomyxon intermedium g. et* sp. nov.

Issel, R. Biologica neritica mediterranea. Il bentos animale delle foglie di Posidonia studiato dal punto di vista bionomico.

— Biologica neritica mediterranea, Richerche di etologia sull' Isopodo tubicolo. Zenobiana prismatica (Risso).

Kofoid, C. A. Protozoa.

Korotneff, A. A. Dié Planarien des Baikal-Sees (Tricladen).

Lee, A. B. L'étape strepsinématique des auxocytes mâles de l'Escargot.

Lohmann, H. Die Probleme der modernen Planktonforschung.

M'Intosh, W. C. Notes from Gatty Marine Laboratory.

- Man, J. G. de. Sur quelques "Palæmonidæ" et sur une espèce de "Penaeus" de l'Afrique occidentale avec des observations sur le "Palæmon (Eupalæmon) acanthurus" Wiegm. de l'Amérique du Sud.
- Odontopharynx longicaudata n. g. n. sp. Eine neue Form von Anguilluliden.

#### REPORT OF THE COUNCIL.

Mines, G. R. An accessory time signal for use in experiments where the recording apparatus is not run continuously.

- Functional Analysis by the action of electrolytes.

----- Some observations on electrocardiograms of cold blooded animals.

----- Some observations on Electrograms of the Frog's Heart.

----- Calcium Salts in Relation to Neuromuscular Mechanisms.

Nicoll, W. On two new Trematode Parasites from British Food-Fishes.

Nilsson, D. Beiträge zur Kenntnis des Nerven-systems der Polychaeten.

Orton, J. H. An Account of the Natural History of the Slipper Limpet. Pax, F. Hypertrophie bei Actinienlarven.

---- La paléontologie et la distribution géographique des Actinies.

---- Aktinienstudien.

---- Vorarbeiten zu einer Revision der Familie Actiniidæ.

----- Studien an Westindischen Actinien.

----- Aktinien der Aru-Inseln.

---- Die Aktinien der Ostafrikanischen Inseln.

---- Die Steinkorallen der Deutsche Südpolar-Expedition, 1901-1903.

---- Anthozoa. Die Aktinien-fauna Westafrikas.

Popta, C. M. L. Fortsetzung der Beschreibung von neuen Fischarten der Sunda-Expedition.

---- Die geographische Verbreitung der Süsswasserfische zwischen Asien und Australien.

Reinke, E. A Preliminary Account of the Development of the Apyrene Spermatozoa in *Strombus* and of the Nurse-cells in *Littorina*.

- Schaxel, J. Zur Analysis des Spiraltypus der Annelidenfurchung bei normalen und abnormen Verlauf.
- ---- Weitere Untersuchungen über die Eibildung der Meduse Pelagia.
- Schmidt, J. Contributions to the biology of some North Atlantic species of Eels.

Sexton, E. W. Some Brackish-Water Amphipoda from the Mouths of the Weser and the Elbe, and from the Baltic.

Shearer, C. The Problem of Sex Determination in *Dinophilus gyrociliatus*. Pt. I. The Sexual Cycle.

Tattersall, W. M. Clare Island Survey. Cumacea, Schizopoda, etc.

Van Name, W. G. Simple Ascidians of the Coasts of New England and Neighbouring British Provinces.

Viguier, C. Nouvelles études sur le Plankton de la Baie d'Alger.

## Donations and Receipts.

The receipts for the seven months ending December 31st, 1912, include the grants from His Majesty's Treasury ( $\pounds$ 1000) and the Board of Agriculture and Fisheries, Development Fund ( $\pounds$ 500), Special Donations ( $\pounds$ 26), Annual Subscriptions ( $\pounds$ 71), Rent of Tables in the Laboratory ( $\pounds$ 86), Sale of Specimens ( $\pounds$ 299), Admission to Tank Room ( $\pounds$ 81).

# Vice-Presidents, Officers, and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1913-14:---

#### President.

#### Sir E. RAY LANKESTER, K.C.B., LL.D., F.R.S.

#### Vice-Presidents.

The Duke of BEDFORD, K.G. The Earl of Ducie, F.R.S. The Earl of Stradbroke, C.V.O., C.B. Lord AVEBURY, F.R.S. Lord Walsingham, F.R.S. The Right Hon. A. J. Balfour, M.P., F.R.S. The Right Hon. JOSEPH CHAMBER-

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The Right Hon. AUSTEN CHAMBER-LAIN, M.P.
W. ASTOR, Esq., M.P.
G. A. BOULENGER, Esq., F.R.S.
A. C. L. GÜNTHER, Esq., F.R.S.
A. R. STEEL-MAITLAND, Esq., M.P.
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Rev. Canon NORMAN, D.C.L., F.R.S.
EDWIN WATERHOUSE, Esq.

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E. T. BROWNE, Esq.
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H. G. Maurice, Esq.
Edgar Schuster, Esq., D.Sc.
Geoffrey W. Smith, Esq.
Prof. D'Arcy W. Thompson, C.B.

Chairman of Council. A. E. SHIPLEY, Esq., D.Sc., F.R.S.

Hon. Treasurer.

J. A. TRAVERS, Esq., Tortington, Arundel.

#### Hon. Secretary.

E. J. ALLEN, Esq., D.Sc., The Laboratory, Citadel Hill, Plymouth.

The following Governors are also members of the Council:-

G. P. BIDDER, Esq., M.A. The Earl of PORTSMOUTH (Prime Warden of the Fishmongers' Company).

Sir RICHARD MARTIN, Bart. (Fishmongers' Company). The Hon. NATHANIEL CHARLES ROTHS-CHILD (Fishmongers' Company).

- Prof. G. C. BOURNE, D.Sc., F.R.S. (Oxford University).
- A. E. SHIPLEY, Esq., D.Sc., F.R.S. (Cambridge University).

Prof. W. A. HERDMAN, D.Sc., F.R.S. (British Association).

# Statement of Receipts and Payments for

To Current Income :	£	s.	d.	£ s.	d;
H.M. Treasury for year ending 31st March, 1913 Annual Subscriptions Rent of Tables, including £50 from the University	1,000 71		0 0		
of London, on account of 1911, 1912, and 1913	86	0	0	1,157 8	0
,, Extraordinary Receipts :					
Donations-					
Dr. C. Shearer (part payment as Founder)         24         1         3           Dr. S. P. Kramer         1         10         0           C. A. Newman         0         19         0	26	10	3		
Board of Agriculture and Fisheries, Grant from Development Fund, for year ending 31st March, 1913	500	0	0	526 10	3
			_		
The Balance is apportioned as follows :					
Repairs and Renewals	200	0	0		
Less General Account overdrawn	54	2	4		
	£145	17	8		

Examined and found correct.

(Signed) N. E. WATERHOUSE, F.C.A. L. W. BYRNE, EUSTACE GURNEY, W. T. CALMAN,

3 FREDERICK'S PLACE, OLD JEWRY, E.C. 6th February, 1913.

Dr.

# the Seven Months ending 31st December, 1912.

By Balance from Last Year :	£	<i>s</i> .	d.	£	s.	d.
Loan from Bank	400	õ	0			
Overdraft at Bank	63	1	0			
	463	1	0			
Less Cash at Bank 120 10 8	100	+	0			
Cash in hand 0 1 2	120	11	10	342	9	2
" Current Expenditure : Salaries and Wages						
Director (Half Year)	100	0	0			
Hydrographer		10	0			
Naturalist (Five Months)	104	3	4			
Additional Naturalist	98	4	0			
Assistant Naturalist	101	0	0			
Salaries, Wages, and Compensation paid	353	12	9			
	844	10	0 1			
Less Compensation recovered from Employers' Lia-						
bility Corporation	24	3	0	820	7	1
Travelling Expenses				90	10	
Travelling Expenses				-30	19	4
Library	46	4	8			
Less Duplicates sold	0	2	6	46	2	2
Journal	80	1	3			
Less Sales	4	8	10	75	12	5
Buildings and Public Tank Room-						
Gas, Water, and Coal	44	3	2			
Stocking Tanks and Feeding	30	7	4			
Maintenance and Renewals	184	2	1			
Rent, Rates, Taxes, and Insurance	33	15	2			
	292	7	9			
Less Admission to Tank Room	80	14	2	211	13	7
Laboratory, Boats, and Sundry Expenses-						
Glass, Apparatus, and Chemicals	104	15	10			
Less Sales	49	14	8			
	55	1	2			
Purchase of Specimens Maintenance and Renewal of Boats, Nets,	51	0	1			
Gear, etc 139 5 10						
Less Sales, etc	43	7	2			
Hire of Boats	22	2	2			
Insurance of s.y. Oithona	24	-	4			
Less Rebate	18	17	7			
Coal and Water for Steamer		15	9			
Stationery, Office Expenses, Carriage, Printing, etc.		10	5			
,,	302					
Less Sale of Specimens	299			3	13	6
"Bank Interest				7	3	4
"Balance :						
Cash at Bankers	135	11	10			
Cash in hand	10	5	10	145	17	8
and a second and the		-		£1,683	18	3
The amount of the manufacture of the second se					10	

Cr.

# Marine Biological Association of the United Kingdom.

# LIST

OF

# Gobernors, Founders, and Members.

# 1st OCTOBER, 1913.

\* Member of Council. + Vice-President. ‡ President.

Ann. signifies that the Member is liable to an Annual Subscription of One Guinea. C. signifies that he has paid a Composition Fee of Fifteen Guineas in lieu of Annual

Subscription.

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The British Association for the Advancement of Science, Burlington	
House, W.	£500
The University of Oxford	£500
The University of Cambridge	£500
The Worshipful Company of Clothworkers, 41, Mincing Lane, E.C.	£500
The Worshipful Company of Fishmongers, London Bridge, E.C £1	0,705
Bayly, Robert (the late)	
Bayly, John (the late)	£600
Thomasson, J. P. (the late)	£970
G. P. Bidder, Esq., Cavendish Corner, Cambridge	£1500

# II.-Founders.

1884	The Corporation of the City of London	£210
1884	The Worshipful Company of Mercers, Mercers' Hall, Cheapside£3	41 58.
1884	The Worshipful Company of Goldsmiths, Goldsmiths' Hall, E.C	£100
1884	The Royal Microscopical Society, 20, Hanover Square, W	£100
1884	The Royal Society, Burlington House, Piccadilly, W	£350
1884	The Zoological Society, Regent's Park, London, N.W	£100
1884	Bulteel, Thos. (the late)	£100
1884	Burdett-Coutts, W. L. A. Bartlett, 1, Stratton Street, Piccadilly, W	£100
1884	Crisp, Sir Frank, Bart., Treas. Linn. Soc., 17, Throgmorton Avenue, E.C.	£100
1884	Daubeny, Captain Giles A.	£100
1884	Eddy, J. Ray, The Grange, Carleton, Skipton	£100
1884	Gassiott, John P. (the late)	£100

<b>‡1884</b>	Lankester, Sir E. Ray, K.C.B., F.R.S., 29, Thurloe Place, South	
	Kensington, S.W	£100
1884	The Rt. Hon. Lord Masham (the late)	£100
1884	Moseley, Prof. H. N., F.R.S. (the late)	$\pm 100$
1884	The Rt. Hon. Lord Avebury, F.R.S. (the late)	£100
1884	Poulton, Prof. Edward B., M.A., F.R.S., Wykeham House, Oxford	£100
1884	Romanes, G. J., LL.D., F.R.S. (the late)	£100
1884	Worthington, James (the late)	£100
1885	Derby, the late Earl of	£100
1887	Weldon, Prof. W. F. R., F.R.S. (the late)	£100
1888	Bury, Henry, M.A., Mayfield House, Farnham, Surrey	£100
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1889	The Worshipful Company of Grocers, Poultry, E.C	£120
1889	Thompson, Sir Henry, Bart. (the late)	£110
1889	Revelstoke, The late Lord	£100
1890	Riches, T. H., B.A., Kitwells, Shenley, Herts	$\pounds 230$
1902	Gurney, Robert, Ingham Old Hall, Stalham, Norfolk	$\pounds105$
1909	Harding, Colonel W., The Hall, Madingley, Cambridge	£100
†1910	Murray, Sir John, K.C.B., F.R.S., Challenger Lodge, Wardie, Edinburgh	£100
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1913	Shearer, Dr. Cresswell, 30, Thompson's Lane, Cambridge	£100

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1913	Adams, Alfred, M.B., B.Ch., Oxon., Looe, Cornwall	Ann.
1897	Adams, W. R., Howfield, 111, Denmark Hill, Camberwell, London, S.E.	Ann.
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	Allen, E. J., D.Sc., The Laboratory, Plymouth	
	Alward, G. L., Enfield Villa, Humberstone Avenue, Waltham, Grimsby	
1910	Ashworth, J. H., D.Sc., The University, Edinburgh	Ann.
1892	Assheton, R., M.A., Riversdale, Grantchester, Cambridge	£20
+1911	Astor, W., M.P., 4, St. James's Square, London, W.	С.
1910	Atkinson, G. T., 43, Parliament Street, London, S.W.	Ann.
	Baker, R. J., 3, Ash Villas, Collings Park, Mannamead, Plymouth	
	Balfour, Prof. Bayley, F.R.S., Royal Botanic Gardens, Edinburgh	
	Ballard, Edward, Zomba, Nyasaland, E. Africa	
1884	Bayliss, Prof. W. Maddock, D.Sc., F.R.S., St. Cuthberts, West Heath	
	Road, Hampstead	
1884	Bayly, Miss, Seven Trees, Plymouth	£50
	Bayly, Miss Anna, Seven Trees, Plymouth	
1885	Beck, Conrad, 68, Cornhill, E.C.	С.
1884	Beddington, Alfred H., 8, Cornwall Terrace, Regent's Park, N.W	С.
+1907	Bedford, His Grace the Duke of, K.G., Endsleigh, TavistockC. & Ann. £1	010s.
1903	Bidder, Capt. H. F., Ravensbury Manor, Mitcham	Ann.
1910	Bidder, Mrs. M. G., Cavendish Corner, Cambridge	Ann.
1912	Bles, E. J., Elterholm, Madingley Road, Cambridge	Ann.
1910	Bloomer, H. H., 40, Bennett's Hill, Birmingham	Ann.
1910	Borley, J. O., M.A., 43, Parliament Street, London, S.W.	Ann.
*1884	Bourne, Prof. Gilbert C., M.A., F.R.S., Savile House, Mansfield Road,	
	Oxford	Ann.

1910	Bowkett, Sidney, 40, Old Bond Street, London	Ann.
	Bowles, Col. Henry, Forty Hall, Enfield	
	Bradford, Sir J. Rose, K.C.M.G., M.D., D.Sc., F.R.S., 8, Manchester	
	Square, London, W.	
1910	Bridgman, F. J., Zoological Department, University College, London	
	Brighton Public Library (Henry D. Roberts, Chief Librarian)	
	Brooksbank, Mrs. M., Leigh Place, Godstone, Surrey	
	Brown, Arthur W. W., 62, Carlisle Mansions, Carlisle Place, London, S.W.	
	Browne, Edward T., B.A., Anglefield, Berkhamsted	
	Browne, Mrs. E. T., Anglefield, Berkhamsted	
	Byrne, L. W., B.A., 7, New Square, Lincoln's Inn, London, W.C	
*1908	Calman, Dr. W. T., British Museum (Natural History), Cromwell	
	Road, S.W	
1912	Cavers, Dr. F., Goldsmith's College, New Cross, London, S.E.	Ann.
	Chamberlain, Rt. Hon. J., M.P., 40, Prince's Gardens, S.W.	
	Childs, Christopher, M.D., Boscarne, Looe	
1911	Chilton, Prof. C., Canterbury College, Christchurch, New Zealand	Ann.
1884	Christy, Thomas Howard	<i>C</i> .
1911	Clark, Dr. J., Technical School, Kilmarnock, N.B.	Ann.
	Clarke, G. S. R. Kitson, Meanwoodside, Leeds	
1887	Clarke, Rt. Hon. Sir E., K.C., 5, Essex Court, Temple, E.C	£25
	Coates and Co., Southside Street, Plymouth	
1885	Collier Bros., George Street, Plymouth	<i>C</i> .
1900	Cooper, W. F., B.A., Ashlyns Hall, Berkhamsted	Ann.
1909	Crawshay, L. R., M.A., The Laboratory, Plymouth	Ann.
1910	Darbishire, A. D., M.A., The Zoological Department, The University,	
	Edinburgh	
	Darwin, Sir Francis, F.R.S., 10, Madingley Road, Cambridge	
	Darwin, W. E., Ridgemount Bassett, Southampton	
1911	Davies, Humphreys, 6, Southwick Place, London, W.	Ann.
	De Morgan, W. C., c/o National Provincial Bank, Plymouth	
	Dendy, Prof. A., F.R.S., Dale Lodge, Hampstead Heath, N.W.	
	Devonport Education Authority	
	Dewick, Rev. E. S., M.A., F.G.S., 26, Oxford Square, Hyde Park, W	
	Dixey, F. A., M.A. Oxon., Wadham College, Oxford£26 5s. and	
1910	Dobell, C. C., M.A., Imperial College of Science and Technology, South Kensington, S.W.	
1000	Driesch, Hans, Ph.D., Philosophenweg 5, Heidelberg, Germany	
	Ducie, The Rt. Hon. the Earl of, F.R.S., Tortworth Court, Falfield, R.S.O. £	
	Duncan, F. Martin, The Cottage, The Avenue, St. Margaret's, Twickenham	
	Dunning, J. W., 4, Talbot Square, London, W	
	Durining, 5. W., 4, Tattor Square, London, W.	
1004	Gloucester	
1906	Elliott, Sir Thomas H., K.C.B., The Royal Mint, Tower Hill	
	London, E.	

1908 Elwes, Maj. Ernest V., Glendower, St. Albans Road, Babbacombe ....... Ann. 1913 Evans, Lewis, 16, Hornton Court, Kensington, London, W. ...... C.

	Evans, Thomas Adam, 16, Hornton Court, Kensington, London, W Ewart, Prof. J. Cossar, M.D., University; Edinburgh	Ann. £25
1000	Brait, 1101. 0. Cossai, M.D., Cheversey, Bachoargh	0220
	Ferrier, Sir David, M.A., M.D., F.R.S., 34, Cavendish Square, W	
1884	Fison, Sir Frederick W., Bart., Boarzell, Hurst Green, Sussex	С.
*1913	Fleure, Prof. H. J., D.Sc., University College of Wales, Aberystwyth	Ann.
1897	Foster, Richard, Windsworth, Looe, R.S.O	Ann.
1885	Fowler, G. Herbert, B.A., Ph.D., The Old House, Aspley Guise, Bedfordshire	Ann.
1884	Fry, George, F.L.S., Carlin Brae, Berwick-on-Tweed	£21
	Fuchs, H. M. de F., Zoological Department, Imperial College of Science and Technology, South Kensington, S.W	
*1007	Gamble, Prof. F. W., D.Sc., F.R.S., 38, Frederick Road, Edgbaston,	
-1907		Ann.
1906	Gardiner, Prof. J. Stanley, M.A., F.R.S., Caius College, Cambridge	Ann.
1907	Garstang, Prof. W., D.Sc., 2, Ridge Mount, Cliff Road, Headingley, Leeds	Ann
1885	Gaskell, W. H., F.R.S., The Uplands, Shelford, Cambridge	<i>C</i> .
1901	Giles, Col. G. M.	<i>C</i> .
1910	Gooding, H. C., Ipswich Street, Stowmarket	Ann.
1910	Goodrich, E. S., F.R.S., Merton College, Oxford	Ann.
1885	Gordon, Rev. J. M., St. John's Vicarage, Redhill, Surrey	Ann.
1912	Gray, J., King's College, Cambridge	Ann.
	Guinness, Hon. Rupert, Elveden, Thetford£3	
+1884	Günther, Dr. Albert, F.R.S., 2, Lichfield Road, Kew Gardens	Ann.
*1900	Gurney, Sir Eustace, Sprowston Hall, Norwich	Ann.
1884	Halliburton, Prof. W. D., M.D., F.R.S., Church Cottage, 17, Marylebone Road, London, W.	
1909	Hamilton, Dr. G. C.	Ann.
1884	Hannah, Robert, 82, Addison Road, Kensington, W	С.
	Harmer, S. F., D.Sc., F.R.S., British Museum (Natural History), Crom- well Road, S.W.	
1912	Hart, E. Tulk, M.D., Totteridge, Dyke Road, Hove	Ann.
	Harvey, T. H., Cattedown, Plymouth	
1888	Haselwood, J. E., 3, Richmond Terrace, Brighton	С.
	Haslam, Miss E. Rosa, Ravenswood, Bolton	
		Ann.
1884	Heape, Walter, F.R.S., 10, King's Bench Walk, Temple, London, E.C.	С.
	Hefford, A. E., B.Sc., 43, Parliament Street, London, S.W	
	Hepworth, Commander M. W. Campbell, C.B., R.N.R., Meteorological Office, South Kensington, London, S.W.	Ann.
	Herdman, Prof. W. A., F.R.S., The Zoology Department, The University, Liverpool.	Ann.
1913	Heron-Allen, E., F.L.S., F.R.M.S., F.G.S., 33, Hamilton Terrace, London, N.W.	Ann.
1884	Herschel, Col. J., R.E., F.R.S., Observatory House, Slough, Berks	С.
	Hicks, F., Zoological Laboratory, King's College, London, W.C	
	Hickson, Prof. Sydney J., M.A., D.Sc., F.R.S., Ellesmere House, Wilenslow Road, Withington, Manchester	
1910	Hill, Dr. Alex., Royston, Herts	Ann.

*1907	Hill, Prof. J. P., F.R.S., The Zoological Laboratory, University College, London. W.C.	Ann
1897	Hodgson, T. V., 54, Kingsley Road, Plymouth	Ann
*1905	Holt, E. W. L, Department of Agriculture and Technical Instruction for	AIIII.
1000	Ireland (Fisherics Branch), Dublin	Ann
1913	Howell, G. C. L., I.C.S., Director of Fisheries, Punjab	Ann.
	Hoyle, W. E., M.A., D.Sc., National Museum of Wales, City Hall, Cardiff	
	Huxley, J. S., Balliol College, Oxford	
1012	Harley, J. S., Danior Control, Owford	Ann.
1888	Inskip, Capt. G. H., R.N., 22, Torrington Place, Plymouth	Ann.
	TA WENT A MARKED OF DIT OF DE THE A	
1885	Jackson, W. Hatchett, M.A., D.Sc., F.L.S., Pen Wartha, Weston-super- Mare	Ann.
1910	Jenkinson, J. W., D.Sc., 27, Polstead Road, Oxford	Ann.
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1911	Kirkpatrick, R., British Museum (Natural History), Cromwell Road, S.W.	Ann.
1897	Lanchester, W. F., B.A., 19, Fernshaw Road, Chelsea, London, S.W	C.
	Langley, Prof. J. N., F.R.S., Trinity College, Cambridge	
	Lister, J. J., M.A., F.R.S., St. John's College, Cambridge	
	Liversidge, Prof. A., F.R.S., Fieldhead, George Road, Coombe Warren,	
1010	Kingston, Surrey	
1010	Lucas, Keith, M.A., Trinity College, Cambridge	Ann.
1010	Hillers, Kellin, M.H., Frankry Concept, Cantorrage	Ann.
1005	Macalister, Prof. A., F.R.S., St. John's College, Cambridge	1
	MacAndrew, James J., Lukesland, Ivybridge, South Devon MacBride, Prof. E. W., M.A., D.Sc., F.R.S., Royal College of Science,	
~1910	South Kensington, S.W.	
1000	Macfie, J. W. Scott, Rowton Hall, Chester	C Ann.
	Major, Surgeon H. G. T., 24, Beech House Road, Croydon	
	Makovski, Stanislaus, Saffrons Corner, Eastbourne	
1000	Marr, J. E., M.A., F.R.S., St. John's College, Cambridge	<i>C</i> .
	Martin, C. H., The Hill, Abergavenny	Ann.
1906	Masterman, A. T., D.Sc., Board of Agriculture and Fisheries (Fisheries	
1010	Division), 43, Parliament Street, London, S.W.	
	Matthews, D. J., The Laboratory, Plymouth	
	Matthews, Mrs. D. J., The Laboratory, Plymouth	Ann.
*1912	Maurice, H. G., Board of Agriculture and Fisheries, 43, Parliament	
	Street, S.W.	
	McClean, W. N., 63, Evelyn Gardens, South Kensington, S.W	
	McIntosh, Prof. W. C., F.R.S., Nevay Park, Meigle, N.B	
	Michael, Albert D., The Warren, Studland, nr. Wareham, Dorset	
	Midgley, J. H., Birstwith, Torquay	
	Mill, H. R., D.Sc., 62, Camden Square, London, N.W.	
1899	Minchin, Prof. E. A., 4, Tennyson Mansions, Cheyne Row, Chelsea, S.W.	Ann.
1905	Mitchell, P. Chalmers, D.Sc., F.R.S., Secretary Zoological Society,	
	Regent's Park, London, N.W.	
	Morford, Rev. Augustin, The Friary, Saltash, Cornwall	
1910	Müller, Prof. Hugo, F.R.S., 13, Park Square East, Regent's Park,	
	London, N.W.	
+1896	Murray Sir John KCB, FBS, Challenger Lodge Wardie Edinburgh	Ann

LIST	OF	GOVERNORS.	FOUNDERS.	AND	MEMBERS.

	Newman, C. A., Bramston House, Oundle	Ann.
	Herts	Ann.
1911	Oldham, Chas., Kelvin, Boxwell Road, Berkhamsted, Herts	Ann.
 1910	Orton, J. H., B.Sc., The Laboratory, Plymouth	Ann.
	Pennell, Lieut. H., Awliscombe, Honiton, Devon	
	Plymouth Corporation (Museum Committee)	
	Plymouth Education Authority	
	Port of Plymouth Incorporated Chamber of Commerce	
1910	Porter, Horatio, 16, Russell Square, London, W.C.	Ann.
	Potts, F. A., M.A., Trinity Hall, Cambridge	
	Preston, H. B., F.Z.S., 53, West Cromwell Road, London, S.W Purves, Miss, 5, Holyrood Place, Plymouth	
	Pye-Smith, P. H., M.D., 48, Brook Street, W.	
1001	1 jo Smith, 1, 11., 11.D., 40, Drook Street, W	0.
1893	Quintin, St. W. H., Scampstone Hall, Rillington, Yorks	Ann.
	Raymond, Major G., 35, Connaught Avenue, Mutley, Plymouth	
1892	Rüffer, M. A., M.D., Conseil Sanitaire, Maritime et Quarentenaire, Alexan-	
	dria, Egypt	Ann.
1911	Saunders, J. T., B.A., Christ's College, Cambridge	Ann
	Scharff, Robert F., Ph.D., Science and Art Museum, Dublin	
	Schiller, F. W., Butterhill, Stafford	
	Schuster, Edgar, D.Sc., 110, Banbury Road, Oxford	
	Sclater, W. L., Odiham Priory, Winchfield, Hants	
	Scott, D. H., M.A., Ph.D., F.R.S., East Oakley House, Oakley, Hants	
	Scott, S. D., Boyne House, Cheltenham	
	Serpell, E. W., Loughtonhurst, West Cliff Gardens, Bournemouth	
	Sexton, L. E., 3, Queen Anne Terrace, Plymouth	
	Shaw, Joseph, K.C., Bryanston Square, London, W.	
	Sheldon, Miss Lilian, High Park, Bideford	
*1884	Shipley, Arthur E., M.A., F.R.S., Christ's College, CambridgeC. and An	ın., £5
	Sinclair, F. G., Friday Hill, Chingford, Essex Sinclair, William F., 102, Cheyne Walk, Chelsea, S.W	
	Skinners, the Worshipful Company of, Skinners' Hall, E.C.	
	Slade, Rear-Admiral Sir E. J. W., K.C.I.E., K.C.V.O., 128, Church	,
	Street, Campden Hill, London, W	С.
	Smith, Geoffrey W., New College, Oxford	
1888	Spencer, Prof. W. Baldwin, M.A., F.R.S., University of Victoria, Melbourne	Ann.
1907	Sprague, Thomas Bond, M.A., LL.D., 29, Buckingham Terrace, Edinburgh	Ann.
1097	Straker, J., LL.M., F.Z.S., Oxford and Cambridge Club, S.W.	<i>C</i> .
*1899	Thompson, Prof. D'Arcy W., C.B., University College, Dundee	Ann
1890	Thompson, Sir H. F., Bart., 9, Kensington Park Gardens, London, W.	Ann.
	Thornycroft, Sir John I., F.R.S., Eyot Villa, Chiswick Mall	
1906	F Tims, H. W. Marett, M.D., Bedford College, Regent's Park, London, N.W.	Ann.
1903	B Torquay Natural History Society, Torquay	Ann.

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*1897	Travers, J. A., Tortington House, Arundel	Ann.
1910	Travers, Miss R. C., Tortington House, Arundel	Ann.
1891	Vaughan, Henry	С.
1884	Walker, Alfred, O., Ulcombe Place, Maidstone	Ann.
1884	Walker, P. F., 36, Prince's Gardens, S.W.	Ann.
1910	Wallace, W., D.Sc., 43, Parliament Street, London, S.W.	Ann.
†1884	Walsingham, The Rt. Hon. Lord, F.R.S., Merton Hall, Thetford	£20
1912	Ward, Dr. Francis, 20, Park Road, Ipswich	Ann.
1906	Waterhouse, N. E., 3, Fredericks Place, Old Jewry, London, E.C	Ann.
1909	Waters, Arthur W., F.L.S., Alderley, McKinley Road, Bournemouth	Ann,
1909	Watson, A. T., Southwold, Tapton Crescent Road, Sheffield	Ann.
	Weldon, Mrs., Merton Lea, Oxford	
1910	Willes, W. A., Elmwood, Cranborne Road, Bournemouth	Ann.
1900	Willey, A., D.Sc., F.R.S., McGill University, Montreal, Canada	Ann.
1908	Williamson, Lieut. H. A., R.N., The Central Flying School, Upavon	Ann.
1884	Wilson, Scott, B., Heather Bank, Weybridge Heath	С.
1913	Wise, W. H., 34, George Street, Plymouth	
1900	Wolfenden, R. N., M.D.	Ann.
1905	Woolf, M. Yeatman, Wimpole House, Wimpole Street, London, W	Ann.
1893	Worth, R. H., 42, George Street, Plymouth	Ann.

# IV.-Associate Members.

1889 Caux, J. W. de, Great Yarmouth.

1904 Donnison, F., Deep Sea Fishing Co., Boston.

1904 Edwards, W. C., Mercantile Marine Office, St. Andrew's Dock, Hull.

- 1904 Freeth, A. J., Fish Quay, North Shields.
- 1904 Hurrell, H. E., 25, Regent Street, Yarmouth.
- 1904 Inskip, H. E., Capt., R.N., Harbour Master's Office, Ramsgate.
- 1904 Johnson, A., Fishmongers' Company, Billingsgate Market, London, E.C.

1889 Olsen, O. T., F.L.S., F.R.G.S., Fish Dock Road, Great Grimsby.

- 1904 Patterson, Arthur, Ibis House, Great Yarmouth.
- 1889 Ridge, B. J., Newlyn, Penzance.
- 1901 Sanders, W. J., Rockvall, Brixham.
- 1889 Sinel, Joseph, 8, Springfield Cottages, Springfield Road, Jersey, C.I.
- 1890 Spencer, R. L., L. and N.W. Depôt, Guernsey.
- 1890 Wells, W., The Aquarium, Brighton.

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List of Publications Recording the Results of Researches carried out under the Auspices of the Marine Biological Association of the United Kingdom in their Laboratory at Plymouth or on the North Sea Coast from 1886–1913.

THE following list has been classified, so far as practicable, according to subjects, in order that it may be useful for purposes of reference. The list does not include publications recording the results of observations made on material supplied by the Association to workers in different parts of the country, of which a considerable amount is sent out each year.

In attempting to distinguish between economic and more purely scientific publications considerable difficulty has been experienced; indeed such a distinction is in reality impossible, since all researches bearing on the distribution and habits of marine life of any kind have a more or less direct bearing on fishery problems. All papers dealing with the distribution, habits, and young stages of fishes have been included in the economic division, whether the fishes are themselves marketable or not.

September, 1913.

# Economic Publications.

### FISHES.

# 1. GENERAL.

The Natural History of the Marketable Marine Fishes of the British Islands. Prepared by order of the Council of the Marine Biological Association especially for the use of those interested in the Sea-Fishing Industries. By J. T. Cunningham, M.A. With a preface by E. Ray Lankester, M.A., LL.D., F.R.S. London: Macmillan and Co., Ltd., 1896.

### Eggs and Larvæ.

- The Ovaries of Fishes. By J. T. Cunningham, M.A. Journ. M.B.A. N.S. iii. 1893-95, p. 154.
- On the Histology of the Ovary and of the Ovarian Ova in certain Marine Fishes. By J. T. Cunningham, M.A. Quart. Journ. Micr. Sci. XL. 1897, p. 101.
- A Contribution to the Knowledge of the Ovary and Intra-ovarian Egg in Teleosteans (with Plates XI. and XII.). By W. L. Calderwood. Journ. M.B.A. N.S. ii. 1891–92, p. 298.
- Observations on Ovarian Ova and Follicles in certain Teleostean and Elasmobranch Fishes. By W. Wallace, M.A. Quart. Journ. Micr. Sci., vol. xlvii. p. 161.
- A Record of the Teleostean Eggs and Larvæ observed at Plymouth in 1897. By E. W. L. Holt and S. D. Scott, B.A. Journ. M.B.A. N.S. v. 1897-99, p. 156.
- Studies on the Reproduction and Development of Teleostean Fishes occurring in the neighbourhood of Plymouth (with Plates I.-VI.). By J. T. Cunningham, M.A. Journ. M.B.A. N.S. i. 1889-90, p. 10.
- On Some Larval Stages of Fishes (with Plates III. and IV.). By J. T. Cunningham, M.A. Journ. M.B.A. N.S. ii. 1891–92, p. 68.
- On Some Disputed Points in Teleostean Embryology. By J. T. Cunningham, M.A. Ann. and Mag. Nat. Hist. 1891.
- Recherches sur la Reproduction des Poissons osseux. Par E. W. L. Holt. Ann. Mus. Hist. Nat. Marseille, v., 1899.
- Preliminary notes on the Reproduction of Teleostean Fishes in the South-Western District. By E. W. L. Holt. Journ. M.B.A. N.S. v. 1897-99, p. 41.
- Notes on the Reproduction of Teleostean Fishes in the South-Western District. By E. W. L. Holt and L. W. Byrne, B.A. Journ. M.B.A. N.S. v. 1897-99, p. 333.
- Report on the Eggs and Larvæ of Teleostean Fishes observed at Plymouth in the Spring of 1902. By F. Balfour Browne, M.A. Journ. M.B.A. vi. 1903, p. 598.
- Notes on the Reproduction of Teleostean Fishes in the South-Western District. By E. W. L. Holt. Journ. M.B.A. N.S. v. 1897–99, p. 107.
- Report on a Collection of Very Young Fishes obtained by Dr. G. H. Fowler in the Faeroë Channel. By E. W. L. Holt. Proceed. Zool. Soc., London. 1898, p. 550.
- Report on the Results of the Fish-Egg Cruise made by the s.s. *Huxley* in June, 1909. By H. J. Buchanan Wollaston. Internat. Fish. Investigations. Mar. Biol. Assoc. Report III. 1906–08 (Cd. 5546). 1911, p. 207.

Notes on Teleostean Ova and Larvæ observed at Plymouth in Spring and Summer, 1909. By A. E. Hefford, B.sc. Journ. M.B.A. N.S. ix. 1910-13, p. 1.

## Age, Growth, and Maturity.

- The Rate of Growth of some Sea Fishes and their Distribution at Different Ages. By J. T. Cunningham, M.A. Journ. M.B.A. N.S. ii. 1891-92, p. 95.
- On the rate of Growth of some Sea Fishes and the Age and Size at which they begin to breed. By J. T. Cunningham, M.A. Journ. M.B.A. N.S. ii. 1891-92, p. 222.
- Report on the Probable Ages of Young Fish collected by Mr. Holt in the North Sea. By J. T. Cunningham, M.A. Journ. M.B.A. N.S. ii. 1891–92, p. 344.
- On the Relation of Size to Sexual Maturity in Pleuronectids. (North Sea Investigations.) By E. W. L. Holt. Journ. M.B.A. N.S. ii. 1891–92, p. 363.
- On the Relation of Size to Sexual Maturity in Round-fish. (North Sea Investigations.) By E. W. L. Holt. Journ. M.B.A. N.S. iii. 1893–95, p. 78.
- On the Relations of the Generative Organs and of the Sexes in some Fishes. (North Sea Investigations.) By J. T. Cunningham, M.A. Journ. M.B.A. N.S. iv. 1895-97, p. 28.
- Hybridism in Marine Fishes. By H. M. Kyle, D.sc. Journ. M.B.A. vi. 1903, p. 623.

## Destruction of Immature Fish.

- An Examination of the Present State of the Grimsby Trawl Fishery, with especial reference to the Destruction of Immature Fish. By E. W. L. Holt. Journ. M.B.A. N.S. iii. 1893–95, p. 339. (Cf. N.S. iv. 1895–97, p. 410.) Also issued as a separate publication.
- Destruction of Immature Fish. By G. C. Bourne, M.A. Journ. M.B.A. N.S. i. 1889-90, p. 153.
- On the Destruction of Immature Fish in the North Sea. Remedial Measures. (North Sea Investigations.) By E. W. L. Holt. Journ. M.B.A. N.S. ii. 1891–92, pp. 380, 388.
- The Immature Fish Question. By J. T. Cunningham, M.A. Journ. M.B.A. N.S. iii. 1893-95, p. 54.
- Growth and Distribution of Young Food-Fishes. By J. T. Cunningham, M.A. Journ. M.B.A. N.S. iii. 1893-95, p. 272.
- On the Destruction of Immature Fish in the North Sea. (North Sea Investigations.) By E. W. L. Holt. Journ. M.B.A. N.S. iii. 1893–95, pp. 81, 123, 169, 288.

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NEW SERIES,-VOL. X. NO. 1. NOVEMBER, 1913.

Statistics of Small Fish landed at Grimsby. (North Sea Investigations.) By J. T. Cunningham, M.A. Journ. M.B.A. N.S. iv. 1895-97, p. 10.

## Fish and Fishing Grounds.

- The Impoverishment of the Sea. By W. Garstang, M.A. Journ. M.B.A. N.S. vi. 1900, p. 1.
- Notes on the Fishing Industry of Plymouth. By Walter Heape, M.A. Journ. M.B.A. Old Series. No. 1. 1887, p. 45.
- Monthly Reports on the Fishing in the neighbourhood of Plymouth (with 8 charts). By W. L. Calderwood. Journ. M.B.A. N.S. ii. 1891-92, p. 277 and p. 394. N.S. iii. 1893-95, p. 107.
- Preliminary Note on Trawling Experiments in certain Bays on the South Coast of Devon. By F. B. Stead, B.A. Journ. M.B.A. N.S. iv. 1895–97, p. 90.
- Report on Trawling in Bays on the South Coast of Devon. By E. W. L. Holt. Journ. M.B.A. N.S. v. 1897-99, p. 296.
- Report on Trawling and other Investigations carried out in the Bays on the South-east Coast of Devon during 1901 and 1902. Prepared for the information of the Devon Sea Fisheries Committee by Walter Garstang, M.A. Journ. M.B.A. N.S. vi. 1903, p. 435.
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