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Luter

Studies on the Obelia medusa with special reference to its reactions to light.

The thesis gives a brief review of the literature dealing with the reactions to light of various Hydro-medusae and proceeds to a study of the controversy surrounding the subject of the "ocelli" of the Leptomedusan Obelia and to a statement of the results of an investigation into the cytology of the basal bulbs of the tentacles of this medusa.

The main body of the thesis is devoted to the ~~experiments~~ ~~which were carried out~~ in order to determine the reactions of the Obelia medusa to light under varying conditions in the laboratory, with the results of the experiments, and with their interpretation leading to the conclusion that light acts as a constant stimulus to Obelia which exhibits negative phototaxis. The reactions of Obelia have been compared with those of the Anthomedusan Leuckartiara throughout.

A discussion of the rudimentary condition of the velum in Obelia precedes the summary which concludes the paper.

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## 1. INTRODUCTION

The importance of light in the environment of the smaller marine animals is one of the most conspicuous facts of field ecology.

The study of the behaviour of plankton involves the study of the behaviour of populations, which result from the behaviour of the individuals which make up the population; hence the value of the study of the reactions of the individuals.

By far the greater number of previous researches have been carried out on bilaterally symmetrical animals, most of whose reactions to light can be placed in the category of response to unequal stimulation of symmetrically placed sensory areas. Hence the interest of the study of the reactions to light of a radially symmetrical animal, such as Obelia.

The study of tropisms in medusae was initiated by Romanes (1885) who performed simple experiments on Sarsia. He passed a beam of light through a bell-jar containing a number of specimens, and found that they collected in the beam and were most numerous in that part of it which was nearest the source. If the so-called "marginal bodies" were removed the medusae were no longer able to respond to luminous stimulation of any kind or degree.

Romanes found that a sudden transition from darkness

to light acted as a stimulus upon Sarsia but that there was no response to sudden darkening, from which he concluded that, "it is the light per se and not the sudden nature of the transition from darkness to light which in the former case acted as the stimulus". If the light be cut off during the occurrence of a swimming bout the quiescent stage frequently sets in immediately, and, in general, Sarsia is more active in the light than in the dark, the quiescent stages being shorter in the former case, from which Romanes concluded that "light appears to act towards these animals as a constant stimulus". The response of Sarsia to luminous stimulation is apparently instantaneous, i.e., there is no appreciable latent period.

The next important contribution to the study of the phototropic reactions of medusae was made by Yerkes (1902) who from his experiments on Gonionemus murbachii found that it, like Sarsia, was more active in the light than in the dark, and that a flash of light sometimes caused two or three contractions, but the action was only predictable if the light was very strong. He noticed temporary aggregations of the medusae near the illuminated side of the vessel, followed by collection of the animals in the darker region. He concludes that, "in ordinary daylight, when swimming, they are positively phototactic, in very weak light on the contrary, they are not directed by the stimulus to any

appreciable degree, and therefore appear to be indifferent. They come to rest in an intensity of light which is below that necessary to direct their movements to any important extent, and are therefore negatively photopathic .... they are positively phototactic to intensities of light to which they normally negatively photopathic .... intense light directs their movements causing them to go towards the source of the stimulus; but they come to rest in relatively dark regions only. He assumes that the light directs the animals' movements by unequal stimulation of symmetrical points.

Later, in conjunction with Ayer (1903), in continuing the work on Gonionemus, he discovered that if the animals were placed in a field half of which was illuminated by direct sunlight, whilst the other half was left in shadow, after a few minutes the majority of the animals were to be found in the shaded region owing to the following phenomena, "when an individual, in swimming, chances to cross from the sunlit region into shadow it very quickly ceases swimming and sinks to the bottom. If, later, in swimming about, it chances to cross from the shaded region into the sunlight it in most cases ceases swimming, turns over and sinks passively to the bottom; but, in this case, it does not move indifferently in any direction as it does when in the shadow; instead it usually turns in such a way as to move back into the shaded region".

If, after being in the dark, the medusae were placed in a field of weak light intensity they were merely stimulated to activity, but if the light was of a medium or greater intensity they at first moved towards the source, but later tended to avoid it, i.e., they confirmed Yerkes' previous result that they tend to form temporary aggregations in the more strongly illuminated parts of the vessel. The above authors continue, "Thus far we have learned that Gonionemus is either positively or negatively phototactic according to the intensity of the stimulus; that its activity is inhibited by strong light, and that light and not the heat accompanying it is responsible for the reactions described, and that the direction of the movements is definitely determined by light as well as by other localised or unequally applied stimuli".

Yerkes and Ayer conclude that, "under experimental conditions Gonionema moves towards the source of light, i.e. is positively phototactic. It comes to rest in the darkest portion of the vessel, and is therefore negatively photopathic to ordinary intensities of light".

Morse (1906) repeated Yerkes' experiments on Gonionema and concluded that in no case was there a collection of the medusae in the lighted portion of the dish. He could find no inhibition of movements in passing from light to darkness, the effect being the same whether the border from light to shadow was vertical, horizontal or



oblique. Morse failed to find that the medusae swam more often towards the shadow than away from it, as Yerkes had found for medusae that had previously been in the shadow, but found that the medusae swam in all directions so that they sooner or later entered the shadow and were trapped, as, owing to the absence of the stimulating effect of light the movements ultimately ceased.

Morse's conclusions caused Yerkes to carry out further experiments on the behaviour of Gonionemus when he obtained results that supported his original conclusion that there is often a temporary gathering in the illuminated portion of the vessel. He found that when the beam of light was slightly oblique, if, on sinking the animals were entirely in the sunlight they moved away from the region of shadow as often as towards it, but that if parts of the body were in shadow they turned back towards the shaded region in about 70% of the cases, but with the light perpendicular to the bottom of the vessel he obtained the same results as Morse, finding no evidence of the directive influence of light.

Murbach (1909) from his experiments, also on Gonionema, was led to the belief that the movements of this medusa were not so definitely directed as had hitherto been supposed, and that quantitative differences near the optimum intensity for the medusa constituted the natural light stimulus.

Yerkes had previously pointed out that, "it is

impossible because of the form of the medusa and its method of locomotion that the direction of its movements be as accurately determined by light stimulation as are those of other animals whose structure permits of a more accurate orientation in reference to the source of light". Murbach contends that this statement is not wholly true, pointing out that Gonionema can swim in nearly straight lines when coming to the surface in the "surface reaction", he admits, however, that the only stimulus to which it seems to respond in nearly straight lines is that of gravity. He further declares that Yerkes' statement, "that the direction of its (Gonionema's) movement is definitely determined by light" is based on analogy, not on experiment.

Murbach agrees with Morse that the medusae do not turn directly towards the shadow, or swim into it more often than away from it, but he favours Yerkes' view that strong light turns the animal immediately, when they have been in weak light, but says further, that turning by strong light does not cause the animals to move parallel to the direction of the light rays, therefore this turning cannot be considered as true orientation, and would not lead to swimming directly away from the source of light.

Morse performed an experiment in which medusae were placed at one end of a tank through which sunlight was reflected horizontally; the medusae swam to the surface in characteristic fashion, each time bending their

upward course a little further from the vertical and away from the source of light. Thus, ultimately, they passed to the further side of the tank into a region of lower light intensity. The promising feature of this explanation is that it is based on the peculiar habit of the animal, swimming to the surface when disturbed. The majority of the medusae reached the less illuminated end by swimming about at random resting longer each time they had progressed further from the source of light, and a shorter time between bouts that took them towards the light source again.

Murbach concludes that "the medusae do not usually direct their movements to favourable locations but continue swimming at random until they come into an optimum environment when they settle down ..... relative intensity in the field not ray direction determines the place of rest".

Russell (1931) observed, in his study of the migrations of the marine plankton, no consistent marked movement towards the surface at night in any medusa except Leuckartiara octona.

The investigations carried out at Plymouth of the reactions to light of Obelia medusae were suggested to me by Professor C. L. Boulenger, to whom my thanks are due for his advice and interest throughout the preparation of this paper. I am also indebted to Dr. Allen and his staff at the Plymouth Laboratory, and in particular to Mr. G. M. Spooner for his valuable advice on the experimental aspect of the problem.

## 2. THE SO-CALLED OCELLI OF OBELIA.

In most animals reactions to light are, at least in part, of the nature of responses to stimulation of sensory organs, and before any experimental work could be profitably carried out it was necessary to investigate the light sensitivity and its probable localisation in these medusae.

Obelia is a common 'laboratory type' described in most elementary treatises on zoology and it is therefore surprising to find an extraordinary lack of uniformity in the descriptions given by various authors of the sens-organs of the medusoid stage. Obelia is classified among the Leptomedusae, characterised typically by the absence of ocelli in the umbrella margin, the characteristic sense organs in this group being statocysts, although exceptionally in a few forms, e.g. *Tiaropsis*, both types of sensory structures occur.

Most of the older text-books, e.g. Parker and Haswell (1910) describe the Obelia medusa as a typical Leptomedusan in respect of its sense organs. Obelia is also described as non-ocellate by Delage and Herouard (1901) and by Mayer (1910) in his monograph on the medusae of the world. Bourne (1922) however, described and figured ocelli in Obelia geniculata as occurring on the subumbrella side of all the tentacle bases, and in this respect he is apparently followed by Woodger (1924) and O'Donoghue (1931).

Ocelli are similarly described and figured in the seventh edition (1911) of Marshall and Hurst's text-book. In later editions mention of these is omitted in the text- although the figure showing the eye spots remains.

Dakin (1927) described a typical jellyfish ocellus and illustrated his description with a diagram of a portion of the umbrella margin of Obelia, adding that the complete Obelia possesses approximately 24 ocelli.

Examination of living Obelia medusae from the plankton showed no well developed ocelli such as occur in the Anthomedusae and whereas the majority exhibited no trace of pigment in the marginal region of the umbrella others showed definite aggregations of pigment granules in the interstitial cells of certain of the tentacle bulbs. The pigment granules invariably occurred in the basal bulbs of the perradial, adradial and subradial tentacles.

Thus there are at least two kinds of Obelia medusae, those which possess pigment in the umbrella margin and those which do not.

This fact had been noticed by Browne (1902) who succeeded in hatching medusae from O. dichotoma and geniculata, and rearing them to full size. He was unable to distinguish between them, and in neither case was there any trace of pigment in the tentacle bulbs, from which he concluded that Obelia nigra must be the medusoid stage of the remaining common hydroid, O. Longissima, a conclusion in

which he is supported by Kramp. According to Browne the peculiarities of O.nigra do not manifest themselves until an advanced stage of development is reached so that when young the various species of Obelia medusae are indistinguishable.

I was able to examine a few specimens of O.nigra; the pigment, where it occurs in this species, is in the form of granules in the interstitial cells of the tentacle bulbs. Its colour varies from yellowish-brown to dark brown, but in no case was I able to observe any of the almost black pigment which is so characteristic of the ocelli of such forms as Sarsia and other Anthomedusae.

Vital staining by McConnell's modification of the methylene blue method showed that the nerve cells in the tentacle bulbs are smaller and more numerous than those occurring elsewhere on the body. There is, however, no apparent intimate relationship between the nerve cells and the pigment containing cells in O. nigra.

Examination of numerous sections of the tentacle bulbs failed to reveal any sign of a structure which might possibly function as a light perceiving organ.

The basal bulbs of Obelia consist of irregularly shaped interstitial cells surrounding the origin of the tentacle, the cells being most numerous on the subumbrella side of the tentacle; it is these cells which contain the granules of pigment in Obelia nigra. Numerous small multipolar nerve cells are intercalated between the interstitial cells.

Thus, from the microscopical study of the medusae, there is apparently not only no evidence of the possession of visual organs by Obelia, but also a complete lack of pigment which might possibly have a visual function, except in the adult O.nigra.

The confusion in the literature on this subject is probably mainly due to failure to recognise the true function of the bulbous swellings at the bases of the tentacles, which in the past have sometimes been referred to as 'ocellar bulbs' because in the Anthomedusae the ocelli occur in this situation. These bulbs, so characteristic of both Leptomedusae and Anthomedusae were shown by Boulenger (1910) and Hadzi (1911) to be due to the accumulation in this position of masses of interstitial cells, and to be of the nature of "factories" and storage places for the nematocysts used in such large numbers on the tentacles. The tissue is usually thickest on the inner (subumbrella) side of the tentacle bases, hence the 'ocelli' described by Bourne and others in this position in O.geniculata. Dakin's ocelli are the enlarged pigmented bulbs which occur in O.nigra only, from which his figure must have been taken. There seems to be no evidence that this pigment is visual, indeed, as described above it appears quite different from the pigment in the ocelli of the Anthomedusae.



### 3. EXPERIMENTAL. THE REACTIONS OF THE MEDUSA TO LIGHT.

From what has been said above it can be taken that O. geniculata and O. dichotoma the two forms of Obelia common at Plymouth are not only without ocelli but also without any pigment in the umbrella margin which might possibly have a visual function.

The investigation of the reaction to light, if any, of such medusae presents a particularly interesting problem and in addition a comparison between such reactions in Obelia and those in a medusa, Leuckartiara an ocellate form belonging to the Anthomedusae was attempted.

Owing to the difficulty of rearing the medusae from the hydroid to the adult condition the animals experimented upon, unless otherwise stated, were taken from the plankton. They were captured in tow-nets in the coastal waters off Plymouth, those most frequently used, being in the healthiest condition, were those taken in the "medium" and "coarse" tow-nets.

The Leuckartiara experimented on were obtained in the same way.

Although Obelia is supposedly very common, in the spring and early summer of 1935 it proved very difficult to obtain, occurring in small numbers and frequently being absent from the tow-nets for days at a time.

The medusae were removed from the "tows" as soon as possible, and placed in fresh "outside" sea water.

If placed in diffuse daylight or darkness they remained alive for approximately two days, their viability being slightly greater if the water was changed at frequent intervals.

Obelia nigra was never present in the tows in appreciable numbers, and the animals used in the experiments were those of the other common species, probably chiefly O. geniculata.

The experiments were carried out in a specially darkened room. The sources of light used in the experiments were always adequately screened. Precautions were taken to eliminate the effect of the light which diffused from the beams themselves, and that which is reflected from the sides and corners of the experimental dishes. The source of light in all cases was placed at such a distance from the experimental dish that the temperature of the water in the latter remained constant.

The water used in the experimental dishes was always pure "outside" sea water that had reached room temperature.

(1) Obelia and Leuckartiara were observed in darkness and in diffuse daylight.

(2) The animals were placed in a rectangular glass dish covered with black paper except at one end, which was exposed to the light.

(3) The animals were scattered irregularly in so that they occurred in approximately equal numbers in the two halves of the dish, one of which was exposed to the light,

the other being in shadow.

(4) A divergent beam, i.e., one in which intensity diminishes with distance from the source, was passed through a dish containing Obelia and Leuckartiara, scattered irregularly, placed at the end nearest the source, or at the opposite end of the dish.

(5) A parallel beam of light was passed through a dish in which the animals were scattered irregularly, and in this way the animals were subjected to the effects of ray direction but not to changes of intensity, the latter remaining approximately constant throughout the length of the beam.

The side of the dish through which the beam passed to the animals was selected for its lack of flaws. A convergent lens was inserted in the beam in order to counteract any loss of intensity which might otherwise occur owing to absorption.

(6) A convergent beam was passed through the experimental dish, the convergent lens used in (5) being replaced by a much stronger convergent lens, so that a beam was produced in which there was a marked decrease of intensity as the source was approached.

(7) The animals were placed in a light gradient, i.e., in light in which the line of increasing intensity was perpendicular to the direction of the light rays. This was obtained by placing a triangular dish filled with an absorbing fluid horizontally between the light source and the experimental dish. A screen was fitted round the filter in such a way that

no direct light reached the experimental dish other than that which passed through the filter.

The absorbing medium used in the filter was a gel of a solution of Indian ink of 1 in 7, 200, a concentration which gave an appreciable amount of illumination over one third of the dish. The Indian ink particles caused differential scattering of the components of the radiation so that the light which came through the filter became increasingly red towards the darker end, where only the red outline of the filament was visible.

#### 4. Results of the Experiments.

(1) After being left in the dark for some time the Obelia were found to be scattered irregularly, the majority lying on the bottom of the dish sub-umbrella surface uppermost, contracting at infrequent intervals; a few were floating near the surface, occasionally contracting against the surface film.

The Leuckartiara were also scattered irregularly after being left in the dark, most being at rest on the bottom, rising to the surface by rapid contractions at intervals to sink slowly to the bottom again.

In general, both Obelia and Leuckartiara were more active in the light than in the dark.

Sudden illumination stimulated the medusae to violent contractions, a few being induced to start a swimming bout, but the effect of sudden light is transient. Obelia has a short latent period, approximately five seconds, between stimulation and response. The response of Leuckartiara is approximately instantaneous. In neither is sudden darkening effective in causing a response.

(2) One-sided light had no marked effect on a dult Obelia from the plankton, but the young medusae, less than three days after hatching from the hydroid formed aggregations at the more strongly illuminated side of the vessel.

Leuckartiara showed a tendency to form temporary aggregations at the more strongly illuminated side of the

vessel; later its distribution was random.

(3) In the case of Obelia, after 15 minutes 63.41% of the animals were to be found in the shaded half of the dish.

Leuckartiara showed a similar preference for the dark half of the dish.

(4) When the Obelia were scattered irregularly in the dish, after 15 minutes 25% were at the side nearest the source of light, the remaining 75% being at the end farthest from the source.

When the animals were placed at the end of the dish farthest from the source an occasional one travelled towards the source, but these later retraced their courses, the majority remaining quiescent or performing very restricted movements.

When the animals were placed at the side of the dish nearest the source after 15 minutes 78.26% had travelled the whole length of the dish to lie against the side farthest from the source.

Leuckartiara showed a slight tendency to move to the end of the dish nearest to the light source.

(5) The distribution of the animals at the end of an hour was noted. The Obelia take up their positions rather slowly, but these alter little on being left for periods longer than an hour.

In every case there were no Obelia in the beam

itself, a few occurred below the beam, and a few floated near the surface above the beam, but the majority of the animals were found in the corners of the dish farthest from the source.

When the Obelia were placed in the beam by means of a wide mouthed pipette they tended, after an appreciable latent period, to swim out of it as soon as possible.

	<u>No. of Specimens.</u>	<u>Towards Source.</u>	<u>From Source.</u>
Obelia .....	149	48	101
Leuckartiara ...	98	53	45

(6) Convergent beam.

	<u>No. of Specimens</u>	<u>Towards Source</u>	<u>From Source</u>
Obelia .....	47	15	32
Leuckartiara ...	68	17	16

35 specimens of Leuckartiara swam out of the beam immediately.

(7) Light gradient.

<u>No. used.</u>	<u>To Source.</u>	<u>From Source.</u>	<u>To Light.</u>	<u>To Dark.</u>
Obelia 156	62	94	85	71
Leuckartiara 71	36	35	39	32

INTERPRETATION OF THE RESULTS.

The numerical data were taken as conclusive evidence of directed movement if the observed differences exceeded twice the standard deviation. The latter was found from the formula

$$\text{standard deviation} = \frac{pqn}{n}$$

where 'p' and 'q' are the expected ratios if the movements were random, and 'n' is the total number of animals used in the experiment.

(1) The fact that sudden illumination acts as a stimulus to Obelia whereas sudden darkening does not agrees with the conclusions drawn by Romanes from his work on Sarsia, that light itself and not the sudden change of intensity acts as the stimulus. This is borne out by the greater activity of the animals in the light than in the dark. It is also true for Leuckartiara.

(2) Newly hatched Obelia medusas are more markedly influenced by light than the adults.

(3) Both Obelia and Leuckartiara show a definite preference for the dark.

(4) Obelia moves away from the source of light, but as the beam is divergent the animal may be either negatively phototactic or negatively photopathic, being influenced by the direction of the rays of light or the change of intensity along the beam.

Leuckartiara shows a slight positive movement,



much less marked than *Obelia*'s negative reaction.

(5) *Obelia* moves away from the source of light, but in this case the beam is parallel so that the intensity is approximately constant throughout the length of the beam. Therefore *Obelia* is influenced by the direction of the rays of light, i.e., it is negatively phototactic.

*Leuckartiara* shows no directed movements in a parallel beam, i.e., when under the influence of ray direction alone *Leuckartiara* performs random movements.

(6) *Obelia* tend to move away from the source of light even though this involves passing into regions of greater light intensity. This supports (5) in proving that *Obelia* is negatively phototactic. It is not influenced to any appreciable extent by the changes of intensity encountered during the course of the experiment.

The movements of *Leuckartiara* are not directed, the majority of the animals passing out of the beam, and those that remained in it passing indiscriminately towards or away from the source.

(7) *Obelia* again shows a definite movement away from the source of light, but is uninfluenced by the change of intensity experienced in its course, deviating equally towards the darker and lighter ends of the dish.

*Leuckartiara* still exhibits random movement.

## 6. THE VELUM IN OBELIA

In the early part of this paper attention was called to the lack of uniformity occurring in the accounts given by the various text-books on the subject of the sense organs of the Obelia medusa; similar discrepancies occur with regard to the velum of this jellyfish.

Obelia is one of the Craspedota, characterised, as the name of the division suggests, by the presence of a velar shelf. Such a velum is shown well developed and conspicuous in the figures given by Parker and Haswell (1910) and others. On the other hand Borradaile (1924) describes it as being reduced to a low ridge directed inwards, whilst Bourne (1922) makes no mention of it at all. Mayer (1910) states that it is absent, and this is apparently the view taken by Hadzi (1911) judging from the figures he gives of the umbrella margin.

Whilst investigating the light reactions of the medusa an attempt was made to eliminate these discrepancies, and numerous series of sections of the adult medusa were cut. In none of these could any trace of the velum be seen, and there can be no doubt that the adult medusa is a craspedote.

The researches of Goette (1907) and others have shown that the velum is a developmental necessity in the Hydromedusae, and it was thought of interest to investigate at what point during development the disappearance of this characteristic organ took place.

An attempt was made to trace the velum in the early stages of the life history by cutting thin sections through

the blastostyles of the hydroid so that the sections passed longitudinally through the developing medusoid individuals.

The medusa bud in a typical Hydromedusan begins as an evagination of the two layers of the body wall. The ectoderm at the apex thickens to form the entocodon in which a split occurs, the future sub-umbrella cavity. Later an invagination into the latter from the base forms the manubrium. The peripheral double layer of ectoderm at the apex of the bud forms the velum which becomes perforated as the umbrella cavity opens.

Goette has already shown (1907) that the early stages in the development of the medusa bud are typical in this respect, and my sections confirm his account in every detail. The medusa buds of Obelia, however, are characterised by the very precocious development of the manubrium, which arises before the subumbrella cavity is properly opened so that the latter at its first appearance is in the form of a crescentic slit.

This manubrial rudiment is extraordinarily broad and the breadth increases so rapidly that the whole bud becomes disc-shaped instead of pear-shaped as in a more normal form. The result of this is that the covering ectoderm (the velar rudiment) becomes stretched, thinned out, and eventually broken so that the umbrella cavity is open very shortly after its first appearance instead of remaining closed until a late

stage of development as in the normal forms. Remains of the velar ectoderm can be seen for a short time longer but undergo no further growth and disappear long before the medusa is liberated.

Obelia is decidedly atypical among the Hydromedusae in the absence of the velum, which is generally retained in the adult where it is probably of use in the performance of the characteristic swimming movements; it narrows the umbrella opening causing a more powerful stream of water to issue during pulsation.

In comparing the swimming of Obelia with that of Leuckartiara it was found that active specimens of the two species contract at approximately the same frequency but whereas Leuckartiara is shot through the water for some distance at each contraction, Obelia moves only a short distance, a centimetre at most.

In a similar comparison made between newly hatched Sarsia and Obelia a corresponding difference was noted; further, whereas the Sarsia moved towards their object, the source of light in a definite manner, the contractions of Obelia were less effectual in bringing about directed locomotion.

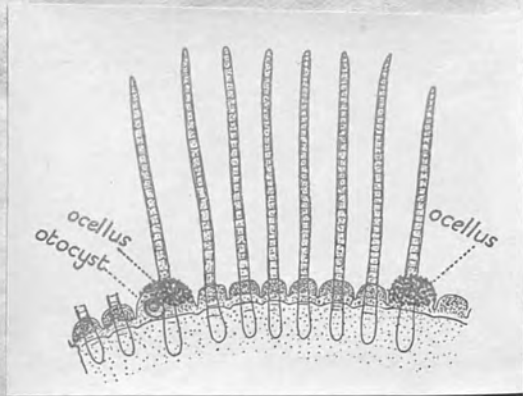
Thus by the loss of the velum Obelia has sacrificed a great deal of the effectual forward component in its locomotory movements, but this is in all probability no serious handicap in its natural habitat, since it is no doubt at the mercy of the elements.

7. SUMMARY

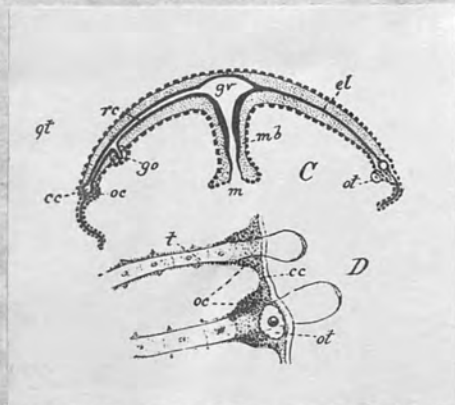
The microscopical study of the medusae yields no evidence of the existence of visual organs in Obelia. Such pigment as occurs in O. nigra appearing quite different from that which occurs in the ocelli of the Anthomedusae; further there is no evidence that the pigment in O. nigra has any visual function.

Obelia shows a definite negative phototaxis, moving away from the source of light whatever the changes of intensity encountered along its path. The ocellate form Leuckartiara shows no definitely directed movements with respect to light, but the latter acts towards it, as towards Obelia, as a constant stimulus, regulating its activity, so that a shaded region acts as a trap owing to the diminished activity of the animals in the absence of light. Neither species is photopathic to any appreciable degree.

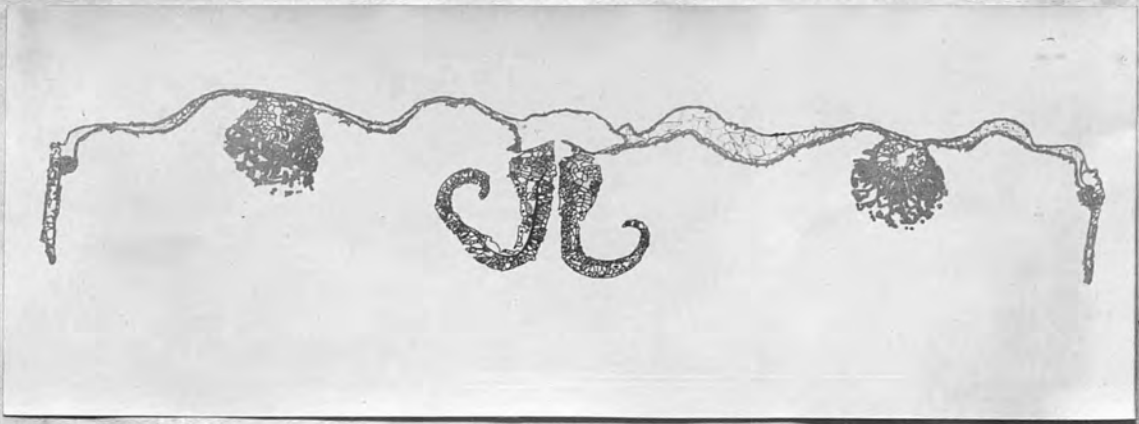
The velum of Obelia disappears early in the life history, owing to the enormous flattening of the umbrella, resulting in a considerably reduced power of locomotion in the adult compared with that of other genera of the Craspedota.



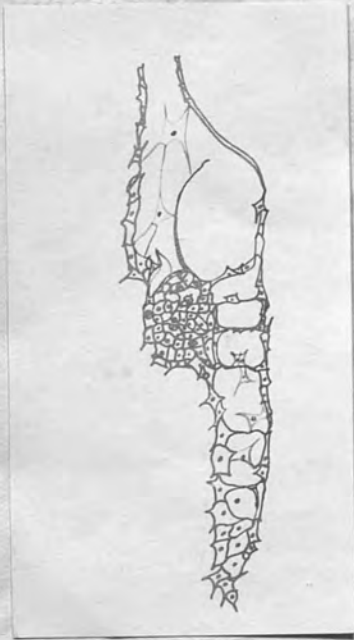
Part of margin of an Obelia medusa, showing ocelli and statocyst (otocyst in Fig.) (From Dakin's Elements of General Biology.)



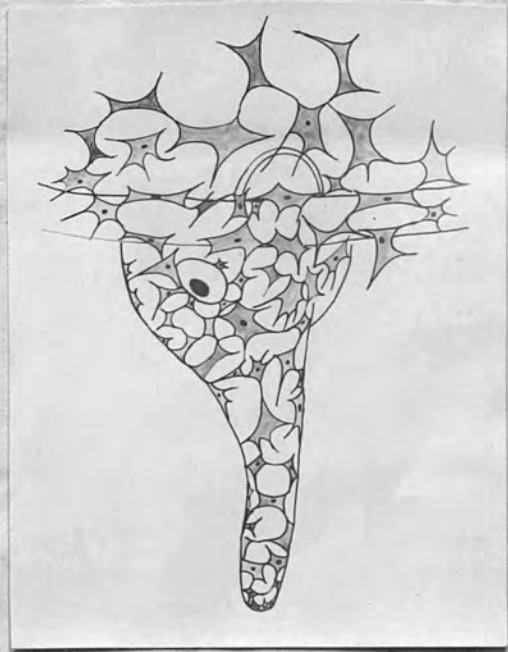
C, Diagrammatic longitudinal sections through a medusa, (O. geniculata.) oc. ocellus; ot, otocyst.  
 D, the bases of two tentacles magnified.  
 (From Bourne's Introduction to the Comparative Study of Animals. Vol. 1.)



Section through a medusa of O. geniculata.



Longitudinal section of tentacle and basal bulb of O. geniculata.



Basal bulb of tentacle of O. nigra showing nerve cells.

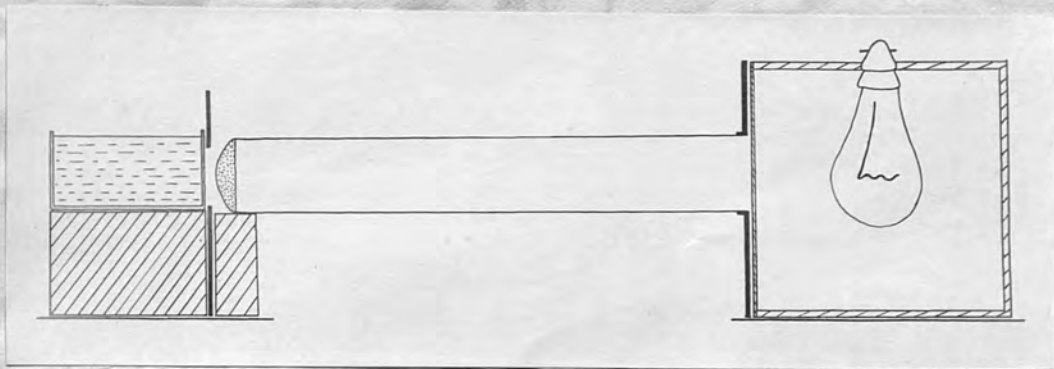


Diagram of the apparatus used for procuring a parallel beam.

- A. 100 watt daylight lamp
- B. Ground glass screen
- C. Cardboard screen
- D. Cardboard cylinder
- E. Convergent lens
- F. Experimental dish

Early stage in the  
development of *S.*  
*geniculata*.

Later stage in the  
development of *S.*  
*geniculata*.



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Developing medusa  
of Clytia. (From  
Hadzi)

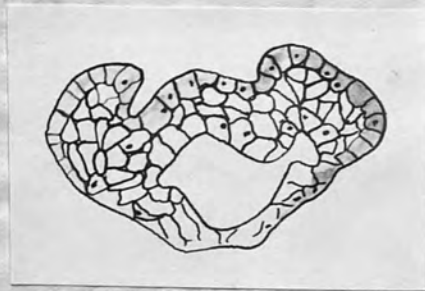
Borradaile, L.A., ...

Chalenger, C.H., ...

Cooper, C.C., ...



Early stage in the  
development of O.  
geniculata.



Later stage in the  
development of O.  
geniculata.

of the direction of movement of ...  
by light.

Delage and Hertwig, ...

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