IMAGE EVALUATION
TEST TARGET (MT-3)

150mm

6″

APPLIED IMAGE . Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989

Technical and Bibliographic Notes / Notes techniques et bibliographiques

The Institute has attempted to obtain the best original copy available for filming. Features of this copy which may be bibliographically unique, which may alter any of the images in the reproduction, or which may significantly change the usual method of filming, are checked below.

L'Institut a microfilmé le meilleur exemplaire qu'il lui a été possible de se procurer. Les détails de cet exemplaire qui sont peut-être uniques du point de vue bibliographique, qui peuvent modifier une image reproduite, ou qui peuvent exiger une modification dans la méthode normale de filmage sont indiqués ci-dessous.

- [x] Coloured covers/ Couverture de couleur
- [ ] Covers damaged/ Couverture endommagée
- [ ] Covers restored and/or laminated/ Couverture restaurée et/ou pelliculée
- [ ] Cover title missing/ Le titre de couverture manque
- [ ] Coloured maps/ Cartes géographiques en couleur
- [ ] Coloured ink (i.e. other than blue or black)/ Encre de couleur (i.e. autre que bleue ou noire)
- [x] Coloured plates and/or illustrations/ Planches et/ou illustrations en couleur
- [ ] Bound with other material/ Relié avec d'autres documents
- [ ] Tight binding may cause shadows or distortion along interior margin/ La reliure serrée peut causer de l'ombre ou de la distorsion le long de la marge intérieure
- [ ] Blank leaves added during restoration may appear within the text. Whenever possible, these have been omitted from filming/ Il se peut que certaines pages blanches ajoutées lors d'une restauration apparaissent dans le texte, mais, lorsque cela était possible, ces pages n'ont pas été filmées.

- [ ] Coloured pages/ Pages de couleur
- [ ] Pages damaged/ Pages endommagées
- [ ] Pages restored and/or laminated/ Pages restaurées et/ou pelliculées
- [x] Pages discoloured, stained or foxed/ Pages décolorées, tachetées ou piquées
- [ ] Pages detached/ Pages détachées
- [x] Showthrough/ Transparence
- [ ] Quality of print varies/ Qualité inégale de l'impression
- [ ] Continuous pagination/ Pagination continue
- [ ] Includes index(es)/ Comprend un (des) index

Title on header taken from:/ Le titre de l'en-tête provient:

- [ ] Title page of issue/ Page de titre de la livraison
- [ ] Caption of issue/ Titre de départ de la livraison
- [ ] Masthead/ Générique (périodiques) de la livraison

- [x] Additional comments:/ Commentaires supplémentaires: Pages wholly obscured by tissues have been refilmed to ensure the best possible image.

This item is filmed at the reduction ratio checked below/
Ce document est filmé au taux de réduction indiqué ci-dessous.

10X	12X	14X	16X	18X	20X	22X	24X	26X	28X	30X	32X
								✓			

The copy filmed here has been reproduced thanks to the generosity of:

National Library of Canada

The images appearing here are the best quality possible considering the condition and legibility of the original copy and in keeping with the filming contract specifications.

Original copies in printed paper covers are filmed beginning with the front cover and ending on the last page with a printed or illustrated impression, or the back cover when appropriate. All other original copies are filmed beginning on the first page with a printed or illustrated impression, and ending on the last page with a printed or illustrated impression.

The last recorded frame on each microfiche shall contain the symbol ⟶ (meaning "CONTINUED"), or the symbol ∇ (meaning "END"), whichever applies.

Maps, plates, charts, etc., may be filmed at different reduction ratios. Those too large to be entirely included in one exposure are filmed beginning in the upper left hand corner, left to right and top to bottom, as many frames as required. The following diagrams illustrate the method:

L'exemplaire filmé fut reproduit grâce à la générosité de:

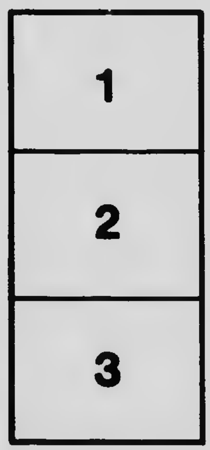
Bibliothèque nationale du Canada

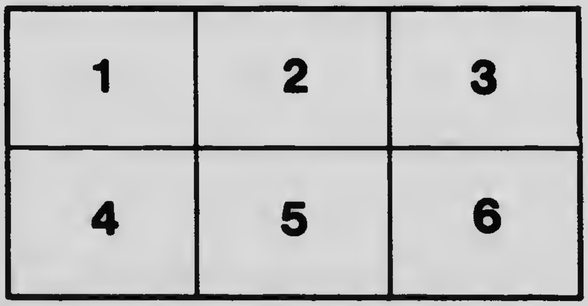
Les images suivantes ont été reproduites avec le plus grand soin, compte tenu de la condition et de la netteté de l'exemplaire filmé, et en conformité avec les conditions du contrat de filmage.

Les exemplaires originaux dont la couverture en papier est imprimée sont filmés en commençant par le premier plat et en terminant soit par la dernière page qui comporte une empreinte d'impression ou d'illustration, soit par le second plat, selon le cas. Tous les autres exemplaires originaux sont filmés en commençant par la première page qui comporte une empreinte d'impression ou d'illustration et en terminant par la dernière page qui comporte une telle empreinte.

Un des symboles suivants apparaîtra sur la dernière image de chaque microfiche, selon le cas: le symbole ⟶ signifie "A SUIVRE", le symbole ∇ signifie "FIN".

Les cartes, planches, tableaux, etc., peuvent être filmés à des taux de réduction différents. Lorsque le document est trop grand pour être reproduit en un seul cliché, il est filmé à partir de l'angle supérieur gauche, de gauche à droite, et de haut en bas, en prenant le nombre d'images nécessaire. Les diagrammes suivants illustrent la méthode.





Prof A. B. Macallum
with the respect of his former student
E. V. Cowdry.

UNIVERSITY OF TORONTO STUDIES

BIOLOGICAL SERIES

No. 10: THE COLOUR CHANGES OF *OCTOPUS VULGARIS* LMK., BY E. V. COWDRY

THE UNIVERSITY LIBRARY: PUBLISHED BY
THE LIBRARIAN, 1911

THE

COLOUR CHANGES OF OCTOPUS VULGARIS LMK.

BY

E. V. COWDRY, B.A.

TABLE OF CONTENTS

THE COLOUR CHANGES OF *OCTOPUS VULGARIS* LMK.

INTRODUCTORY NOTE

The work embodied in this paper was done at the Bermuda Biological Station for Research during the summer months of 1909 and 1910. The object was to study the colour changes of the Octopus from the standpoint of animal behaviour. The expenses of the first summer were paid by the University of Toronto. It is a great pleasure to thank Professor E. L. Mark of Harvard University, the director of the Biological Station, for very much kindness and for many extremely valuable suggestions, and also Professor F. W. Carpenter, who was the director in the summer of 1909 and under whom the work was initiated. My thanks are also due to Mr. Louis Mowbray, the director of the Aquarium, who allowed me ready access to the tanks of the Aquarium at all times and helped me in the collection of material.

I. LITERATURE

The literature on the changes in colour of the Cephalopods has been recently (1906) so very carefully reviewed, in chronological order, by Van Rynberk that it will be quite unnecessary to go over the same ground in the same way. Mention will simply be made of the condition of our knowledge of the factors operating in the colour changes. The forms in which they appear in the most marked degree and upon which the great majority of the investigations have been made, are classed among the Dibranchiate Cephalopods, chief among which are the Cuttlefish and the Squids of the order *Decapoda*, and the Octopi of the order *Octopoda*.

It has long been known that alterations in colour result from the movements of the chromatophores. These structures are large pigment-containing cells distributed in the superficial layers of the skin over the whole surface of the body. By equal dilation of these cells the pigmented surface is increased and the animal consequently becomes darker in colour; on the other hand by unequal dilation in different regions a great variety of patterns may be produced. Some of these colour changes are very striking, so much so that they have been observed and described by a series of workers extending from Aristotle to the present day. The iridocysts are light-reflecting cells of a yellowish colour distributed like the chromatophores in the dermis; they cause the peculiar iridescent shimmer which is so often observed. The chromatophores consist, first, of a spherical or oval body, which contains coloured pigment, and, secondly, of slender radially arranged processes, which connect the body to the surrounding skin musculature.

The chromatophore is generally looked upon as being developed from a single cell; but opinions still differ very widely on this point. The body is, no doubt, multinucleated, for Chun (1901), Steinach (1901), and all the later observers come to this conclusion. Small nuclei are arranged at the bases of the radial processes, about the periphery, and a large central nucleus also has been described. The fine granules of pigment in a single chromatophore are of the same colour, but different chromatophores are often coloured differently. In some species they may be of one colour only, while in others there may be chromatophores of several varieties of colour, such as purple, orange, brown, etc. The wall of the pigment cell is predominantly elastic, and a band of tissue has been observed about the equator in the plane of the radial processes. Steinach (1901a, pp. 8-9), using Hansen's modification of the Van Gieson method, finds that in a variety of forms this band and the radial processes are stained yellow: he concludes from this that they are muscular in nature. He did not use any other differential connective tissue stains. Hofmann (1907a, p. 418) states that this band is formed by the spreading out of the insertion of the radial muscles upon the surface of the chromatophore.

Chun (1901, p. 172) believes that the radial processes are formed from the developing chromatophore by the protrusion and differentiation of a number of protoplasmic extensions. Steinach found that in preparations stained with cochineal and picrofuchsin these processes exhibited a longitudinal striation, and he figures a nucleus in the wall of the chromatophore at the base of each. Hofmann (1907a, p. 390), working on *Loligo*, calls attention to the physiological significance of the abundant interlacing of the radial processes of neighbouring chromatophores.

The question of the innervation of these structures has been much debated; but it seems that the conclusions arrived at by Hofmann are final, namely, that with his methylene blue method nerve endings may be seen in the radial processes, but not in the wall of the chromatophore itself. He calls attention to the fact that a single nerve innervates a definite, limited group of chromatophores, and that such areas of innervation often overlap, so that certain regions may receive nerve twigs from more than one source. He believes, further, that there is in the skin a continuous peripheral nervous network for the propagation of impulses. It will be readily seen, therefore, that there is in the skin of Cephalopods a very elaborate mechanism well calculated to produce a great variety of colour changes, which may be sharply defined, or the individual shades may grade insensibly the one into the other.

The chief credit of showing that the radial bands are of muscular nature is due to Phisalix (1892) and Steinach (1901). Phisalix (1892, p. 222), working on *Sepia officinalis*, destroyed the central portion of the chromatophore with a fine needle point and left the periphery intact. She found that, in such cases, the movements of expansion were not interfered with; but that after the destruction of the radial processes only, no dilation was possible. Steinach, in addition to his experiments with the Van Gieson stain, brings forward the following arguments in favour of the muscular nature of the radial processes. (*a*) There is a difference in the character of the movements of the skin and of the chromatophores. (*b*) Pulsating chromatophores occur when the skin is in complete rest. (*c*) The chromatophores are often quiet when the skin is in motion. (*d*) The arms of *Eledone moschata* react to electrical stimulation fifteen hours after amputation by skin contraction and browning; but later by skin contraction only. It is, therefore, generally accepted that the dilation of the chromatophores results from the contraction of the radial processes, and that the contraction is due chiefly to the elasticity of their walls.

Now that we have dealt with the character of the fundamental processes involved in the movements of the chromatophores, it becomes necessary to consider what is known of the causation of these movements. There is no doubt that the chromatophores can move independently of any impulses from the nervous system, either central or peripheral. This is shown by experiments in which the nerves to certain areas have been cut and also in degenerations. In the first instance it can be easily demonstrated that, while section of the pallial nerve, which sends branches to the dorsal surface of the mantle of one side, results in the suppression of all reflex changes in colour of that region, still the chromatophores react to certain stimuli. In the second place, Phisalix and Steinach have called attention to the fact that an arm kept in sea water appears to have lost all reflex irritability ten to sixteen hours after amputation; but that movements of the chromatophores may be produced for about thirty-four hours later. In connection with this direct stimulation the valuable results of Hofmann and Hertel will be considered in greater detail.

Hofmann (1907b, pp. 448-450) observed that an amputated Octopus arm bleaches if it is left in sea water; but if it is exposed to the air and is not allowed to dry it becomes brown. He thought that the bleaching in sea water was due to the deficiency in oxygen and made experiments to prove it.

He took a piece of skin, spread it out on a glass plate, and covered a portion of it with a tightly fitting cover-glass. After from fifteen to twenty minutes the skin under the cover-glass was bleached, but the remainder was still dark in colour. He then covered the skin so that the oxygen could diffuse in from the sides and it remained dark. And finally he covered another piece, closely enclosing a bubble of air, beneath which the skin became dark. Hofmann obtained the same results with *Sepia* and *Eledone*, and argues that the concentration of the carbon dioxide in the skin under the bubble and in the surrounding portions is practically the same, and that the bleaching of the skin is caused by the absence of the oxygen only.

Hertel, in the same year, made some detailed observations upon the physiological effect of many varieties of light rays upon pigment cells. He experimented with dead Loligos and found that there was an elective action of the blue rays upon the yellow cells and of the yellow rays upon the violet-red cells, and concludes that different cells are adapted to receive light of different wave lengths. Further, in Loligo and Octopus application of ultraviolet rays caused a deepening in colour and movements of flight; while blue and yellow light caused only the change in colour. He argues that since movement follows slowly when ultraviolet rays are applied, particularily to regions devoid of chromatophores, and since illumination with yellow and blue light of skin possessing chromatophores in the intact animal does not cause any movement, it follows that the chromatophores do not play any part in the initiation of the movements. Hertel believes that, in this case, locomotion results from the stimulation of the cutaneous nerves directly by the ultraviolet rays, and that the reflex thus generated passes through a special reflex arc to the suckers. He therefore considers his most important conclusion to be that the nervous substance can be directly stimulated by ultraviolet rays, but by visible rays through the help of the pigment only. The irregular movements and the streaming of the individual granules of pigment are also minutely described. He used atropine to paralyze the nerves connected with the chromatophores, and concludes further that light stimulates the movements of these cells directly through the medium of the pigment.

Victor Bauer (1909, p. 183) sums up our knowledge of the centres which control the movements of the chromatophores very much as follows:—The centres for the play of the chromatophores seem to lie in the basal portions of the two last central ganglia. Stimulation of these regions either by section or by heat produces darkening (Phisalix, 1892, p. 216). The tracts for coloration pass through the posterior commissure and the subœsophageal ganglia, as has been shown by section experiments (Uexküll, pp. 603-604). Destruction of the pedal ganglion results in the paralysis of the chromatophores of the opposite side. The tracts of the chromatophore nerves apparently cross here also (Phisalix, 1892, p. 215). Phisalix postulates, further, special inhibition centres in the supraœsophageal ganglia, and contends that the bleaching reflex, which consists of a diminution in size of the chromatophores, is suppressed by destruction of this part: when only half is destroyed the reflex is retained on both sides (1892, pp. 98-99).

Hofmann (1907b, p. 420) has worked out very carefully and accurately the innervation of the chromatophores and concludes that the evidence for the existence of inhibitory nerves is quite insufficient.

Two reflexes have been described by Steinach (1901a, pp. 27-28) in Eledone and Octopus. The first is from the suckers along the centripetal nerves to the coloration centre in the brain, and thence by the efferent nerves to the chromatophore muscles. He believes that certain colour changes result from the strengthening of the peripheral tonus of the chromatophores by impulses passing through this reflex arc. The second is supposed to explain certain movements of locomotion which follow light stimulation. This reflex, he believes (1901b, [illegible]) passes from the chromatophores to the suckers by pure[illegible] muscular paths without the intervention of any nervous elements. Hertel (1906) very rightly objects to this idea.

There have been very few observations recorded on the effect of alterations in the temperature and the purity of the water upon the colour changes, and none on the results of changes in pressure and salinity. Hofmann's work, already mentioned, dealt with the effect of oxygen and carbon dioxide in the water and thus indirectly with the question of its purity. Phisalix (1894, p. 93) records an experiment in which she increased the temperature of the water, wherein she had placed a Cuttlefish, so that, in about an hour, it rose twenty-four degrees, and the animal became lighter and lighter in colour until at last it died in extreme pallor. With a dead animal she obtained quite different results, for it became darker when the temperature of the water was raised. Steinach (1901a, p. 23) applied the heated end of a hook-formed dissecting needle to the periphery of the chromatophores and caused them to pulsate. Where he let the point of the needle rest the skin became white; for the muscles were injured by the strong and continuous heating. He found also that continued milder warming paralyzed the radial bands and led to bleaching of the skin. Hofmann (1907b. p. 447) writes that in sudden temperature changes, expansion results from warming, retraction from cooling, and that the result of maintaining the same temperature is bleaching in warm water and darkening in cold.

Finally, reference must be made to the relation between these colour changes and the habits of the living animals. The idea of protective coloration originated with Aristotle. Fredericq (1878, p. 573), Klemensiewicz (1878), and many others believed that these animals changed colour to correspond to their environment. Bauer (1909, p. 187) quotes Klemensiewicz to the effect that the brightness of the background calls for a reflex coloration of the skin, and that section of the optic tract shows that the eyes are the receptors; because after this operation the chromatophores react in no way to alterations in the colour or the brightness of the bottom.

This conception of protective coloration has been accepted by many travellers who have had just fleeting glimpses of the animals in their natural environments. Charles Darwin observed the habits of some Octopi in the Cape Verde Islands, and writes in his "Voyage of a Naturalist round the World" as follows:

"They [the Octopi] seem to vary their tints according to the nature of the ground over which they pass: when in deep water their general shade was brownish purple; but when placed on the land or in shallow water this dark tint changed into one of a yellowish green."

The recent work of Steinach appears to throw some light upon these alleged changes in colour to correspond to the environment. It has already been mentioned that he records a reflex in Eledone from the suckers to the chromatophores by which their tonus is increased and colour changes result. He goes on to say that the function of this reflex mechanism is to give to the animals in their natural surroundings that coloration which renders them least noticeable. If they are attached to smooth bodies, such as the coarse gravel of the sea-bottom, or to the veined, weathered rock of the shore, they assume a flecked or marbled appearance. On the other hand if the animals are on the sand, where the suckers cannot be firmly attached, the flecked coloration is reduced or absent, on account of the reduced tonus: the skin becomes quite light-coloured, speckled, and appears tolerably well adapted in shade to the surface of the sand. These animals take on a uniform inconspicuous grayish brown coloration when the sucker apparatus is inactive, as in swimming and when, under natural conditions, they are subjected to great danger. He adds that in strong sunlight this adaptation, resulting from the changes in the consistency of the bottom, does not obtain, and that light is a second and more potent factor in the colour changes.

The question as to whether there is such a thing as warning coloration in the Cephalopods is important. I have been able to find this phenomenon recorded only once; for Steinach (1901a, p. 24) writes that Sangiovanni (1823) came to the conclusion that these animals changed their colour to frighten away their enemies. He himself ridicules the idea.

Fredericq (1878, pp. 10-12) records the observation that the changes in colour of *Octopus vulgaris* result from certain emotions, such as anger and fear. On extreme irritation, caused by the insertion of a stick in the mantle cavity, the animal becomes furious and turns dark in colour. Movement of the hand across the glass window of the aquarium in the direction of the animal causes the chromatophores about the eye to become active, especially those in the longitudinal axis of the pupil, so that a dark streak appears instantaneously at its two extremities and dilates. Phisalix (1892, p. 218) writes that on irritation these animals generally become quite black; but when they are repeatedly annoyed or under the influence of fear, the dark colour fades and the animal becomes quite pale. She goes on to say that it is only necessary to place a Sepiola in the presence of a Cuttlefish to see it bleach immediately.

Hofmann (1907a, p. 388) describes what he calls a terror reflex in Sepia; this consists of a striking local expansion of the chromatophores in a small round area on either side of the median line on the dorsal surface of the mantle, the remainder being white. He says that he has often observed this pattern when he put his hand near the animal or cast a shadow upon it. Hofmann also describes a "Zebrastreifung," characterized by alternate dark and light bands upon the dorsal surface of the animal, as occurring when two Sepias approach each other.

And finally Annie Isgrove (1909, pp. 10-12), in a memoir on Eledone, calls attention to certain colour changes which were observed in the Eledone tank of the Plymouth aquarium. She mentions that their general colour while at rest is buff with flecks of cream, and continues as follows:

"When the animal is excited the skin becomes of a very dark reddish terra-cotta tinge. When Eledone is frightened in any way the skin changes colour, and an intense pallor spreads over it, causing it to become quite ghostly in appearance. At this time the eyes stand out very prominently, because the iris remains dark orange, as does the eyelid surrounding it, and thus an orange patch marks out the eye on a whitened body. However, under normal conditions, this patch does not stand out in any way. At the same time that the pallor is seen the animal tries to escape by rapidly swimming backwards, and attempts to eject ink. Almost immediately the pallor is replaced by an intense darkening or blush of terra-cotta colour over the whole body. If allowed to come to rest now, the colour gradually lightens until the normal condition is reached."

From this brief résumé it will be readily seen how incomplete is our knowledge of the phenomena of colour changes in the Cephalopods.

II. MATERIAL AND METHODS

Octopus vulgaris, Lmk., was the only Cephalopod used in this research. It occurs in Bermuda in fairly large numbers, and its hardiness and great vitality render it a very suitable animal for experimental work. Normal adults, larvæ, and experimentally blinded animals were used, but in addition to these, animals were studied in which the nerve supply to certain regions had been cut off. The adults had an expanse of from 1 to 1.5 metres, and the larvæ were about 1 mm. in length. The general proportions of the former are shown in the illustrations. In the male the third arm on the right is hectocotylized.

The specimens have been oriented for description in the manner adopted by Hoyle (1886, p. 53). The animal is regarded as being stretched out with the arms pointing in one direction and the apex of the mantle in an opposite one. The tips of the arms are then said to be anterior and the apex of the mantle posterior; while that surface which bears the siphon and the mantle opening is ventral, and the opposite one dorsal. The side of the arms which is turned toward the mouth and is supplied with suckers is termed the inner and the opposite one the outer. The same principle is applied when the two surfaces of the interbrachial membrane or umbrella are referred to.

A number of water-colour paintings have been made from the living animals. In order to obtain the correct proportions for these, the outlines of Figs. 1 to 6, inclusive, were traced from a photograph of an anaesthetized animal. The only alteration was the addition of the siphon which did not appear in the photograph. In the case of the remaining illustrations, Figs. 7 and 8 are free-hand sketches, and Fig. 9 is a representation of the colours used in the experiments on the environment.

The observations were made, (*a*) in the natural environments, (*b*) in an Octopus car, (*c*) in the tanks of the aquarium, and (*d*) in large glass aquaria in the laboratory. The natural environments will be described in detail in the next section. The dimensions of the Octopus car were, 1.8 metres long, 1.2 metres deep, and 1.5 metres in breadth. It consisted of a strong wooden frame lined with galvanized wire of 1.2 cm. mesh. A lid was arranged opening on hinges and in the construction as little wood as possible was used. This cage was placed on a sandy bottom near the laboratory so that its bottom was covered by water to a depth of about 75 cm. at low tide, and its top to a depth of about 15 cm. at high tide. Great care was taken throughout the experiments to prevent the animal from seeing the observer, and to preclude any movement or vibration of the car, or any other means of irritation. The tanks used for the Octopi in the aquarium were 1.5 metres long, 1.3 metres broad, and 1.3 metres deep. The bottom and three walls were constructed of flat and fairly smooth plaster; while the fourth side, through which the observations were made, was of glass. The light came in from above, so that the observer was in semidarkness and practically invisible to the animals. The walls were covered with a fairly even, but rather thin coating of dark green algae. The colour of this growth is well represented by sample no. 8 of the colour chart, Fig. 9. The tanks were constantly supplied with fresh sea-water, which was forced in at the bottom. The glass aquaria used in the laboratory were cylindrical and had a capacity of about thirty litres.

III. BEHAVIOUR

This species of Octopus occurs in Bermuda among the rocks of the shore, upon the reefs, in old wrecks, and in any other sheltered places in depths varying from one to six metres. It is sometimes found in tidal pools and its presence is then detected by the water which it ejects from its siphon when disturbed. Octopi are especially numerous, however, among old pipes and tins in places where refuse is thrown into the sea; and also on reefs which rise up from a bottom covered with Eel grass (*Zostera marina*), and upon which mussels and scallops are to be found. Each animal occupies a nest which consists of a sheltered place of some description. It is often a cranny in the reef, and may be from one to two metres in extent. On the other hand, the nest may be simply the inside of an old kerosene-tin. These nests are generally rendered very conspicuous by piles of from fifty to a hundred mussel and other shells, which the animals heap up outside of them. Indeed, it may be determined by the freshness of these shells whether the nest is inhabited or not. It is not known how long one animal occupies a single nest; but it seems from the size of the heap of shells that it cannot be for longer than a few months, or at most a year. It could not be determined whether they inhabit the nests all the year around or only at certain seasons. There may be a period during which they roam about and have no settled abode. During the months of July and August two Octopi were never found associated in the same nest.

The method of locomotion of these animals is very interesting. It consists of either crawling or swimming movements. The former is brought about chiefly by the contraction of the extended arms; but in some cases the arms seem actually to push the animal along. When the motion is in a sidelong or backward direction the water ejected from the siphon seems to be of assistance. They sometimes scuttle along by using the distal portions of their arms in a very peculiar, almost graceful, tip-toe sort of way, but they may move by using only the proximal portions of their arms, the tips being elevated. The interbrachial membrane serves as a kind of parachute which enables the animal to glide easily from one place to another, or to sink slowly to the bottom. In such cases the arms are often waved in such a way as to suggest that they aid in progression. Swimming is carried out in the characteristic cephalopod manner. Water is powerfully ejected from the siphon and as a result the animal shoots along with the apex of the mantle in advance, and the arms trailing out behind. When they swim for some distance they do so in a jerky way, the accelerated periods corresponding to the times when the water is forced out. An Octopus breathing in water by expansion of the mantle is represented in Figures 7 and 8. It is a peculiar fact that the larvæ, for at least one week after hatching, can swim in either an anterior or a posterior direction. They all died about seven days after hatching so that it could not be determined just when the ability to dart in a forward direction was lost; but its loss was probably caused by the great increase in the relative size of the arms and of the interbrachial membrane.

In Bermuda, copulation takes place during the months of April and May. It was not observed in the natural environments, but I learn from Mr. Mowbray that in the tanks of the aquarium, the animals pair off, and that the members of the individual pairs do not molest one another. Furthermore, I was told that during this period, the animals maintain, more or less continuously, a uniform dark reddish brown coloration, like that represented in Fig. 3. Eggs were laid about the beginning of July and attached to the walls of the tank, in a corner, in the form of thick, white, gelatinous threads. They may also be laid in the month of October. The female attached herself to the wall, so as to cover the eggs, and from time to time kept the water in circulation about them by the contractions of her mantle. The animal very rarely moves away from the eggs until they are hatched, not even to obtain food. In one instance an Octopus so persistently annoyed one of these females that she deliberately left her nest and killed it. The colour of the animals at this time is light gray and is represented in Fig. 1. The inner surface of the arms is sometimes blotched with red. The rate of respiration is about thirty-four times per minute. When the larvæ begin to escape from the egg-capsules the female becomes very excitable, swims about the tank a good deal, and will dash at one's hand if it is placed in the water. She pulls down most of the eggs from their point of attachment and scatters them about. When the animal rests she always attaches herself to the place where the eggs were originally deposited.

The Octopus preys on many animals, but it is particularily fond of crabs and the large Bermuda crayfish. An Octopus will swim after a crab for some distance and capture it by alighting upon it from above with arms extended, or it may creep along stealthily until it comes within striking distance and then make a sudden dash at it. An Octopus was once observed to capture a crab, to see another two or three metres distant, pursue and capture it, still clinging to the first, and so on until four crabs, each about eight centimetres in diameter, had been taken, the crabs were then consumed one by one. This is always done in a definite way; the crab is quickly brought near the mouth, the legs are torn away and the flesh of the body is extracted from the ventral side, so that the carapace is left intact. This feeding reaction is seldom interrupted; when it is once begun it is almost invariably carried through to the end. The position assumed when feeding is unmistakable. It is characterized by the humping up of the mouth or head region, due to the presence of the victim and also to the fact that the suckers on the proximal portions of the arms are in action, the animal resting chiefly on the distal portions of the arms. It is, therefore, quite easy to tell from a considerable distance whether a certain animal is feeding or not. Mussels, however, are the chief article of food. The Octopus sallies out in search of them and brings them back to its nest. It may make several journeys until fifteen or twenty have been collected. The animal then settles down at the entrance to its nest and begins its feast. It could not be ascertained just how it opens the mussels which have been collected in such numbers, but this is probably accomplished by a continuous pull (through the medium of the suckers) upon the two valves of the shell until the adductor muscle relaxes and finally gives way. This idea is supported by the fact that the shells are seldom broken. The Octopus will not take dead crabs or crayfish; but if it has not had a meal for some time it will even kill and devour other Octopi; neither will it attack a resting crab which it has not, fifteen or twenty seconds previously, seen in motion. This latter statement needs perhaps a little qualification. In such cases the criteria for determining just when the Octopus first noticed the crab were: a certain movement or gathering together of the body of the Octopus; accompanied by a change in colour, characterized by the production of a brown band running longitudinally across one or both eyes (Figs. 2, 4 and 5) and the appearance of a greater or less amount of brown mottling, the whole corresponding in time to a plainly visible movement of the crab.

The very interesting question arises as to how the Octopus finds its way back to its hole. This problem seems just as difficult of solution as it is to explain how bees can find their way back to their nest over great stretches of country. It is not known how far an Octopus will venture away from its nest, but they were occasionally seen at least fifty metres distant. They certainly go out of sight of their hiding-place and still find their way back again. The question of memory in the Cephalopods is discussed by Uexküll (1905) and Polimanti (1910) both of whom worked on Eledone.

The adult Octopi have very few dangerous enemies, for they can make themselves secure from attacks in their nests and even in the open are well adapted to defend themselves. However, certain large-mouthed fish, such as the Hamlets (*Epinephelis striatus*) are said by the fishermen to attack them in the open by making sudden dashes at them. With the larvæ, which are produced in great numbers, it is different. They are at first free-swimming and it is likely therefore that they would be rapidly devoured by plankton-feeding fish.

The adults sometimes eject ink when they are being captured or pursued. They generally throw out the ink when at rest and then attempt to escape under cover of it, but it may be squirted out in several jets when the Octopus is swimming. If the animal is still pursued, after the ink has been once ejected, it may throw out a second or even a third jet. The coloration of the animal is very interesting at this time on account of the belief that both it and the ejection of ink are of use for protection. It is true that in the majority of cases both the animal which throws out the ink and any others in the immediate vicinity settle down, become quiet, and take on a dark reddish brown coloration, which certainly renders them almost invisible in the darkly tinted water. This coloration is represented in Fig. 3 and often persists for five or ten minutes. It must be stated, however, that the ejection of ink is not invariably accompanied by such a darkening in colour. It may be of interest to note that the larvæ of about 1 mm. in length, and not more than a week after their escape from the egg-capsules, often ejected ink when irritated.

Before this section is concluded brief mention will be made of the method by which the Octopi were captured. The white heap of shells is easily seen against the dark background. If the water is more than a metre deep some common salt, wrapped up loosely in a piece of paper, is placed well within the hole. The salt dissolving in the water irritates the Octopus and it comes out and is easily captured in the hands or in a landing-net. Sometimes the administration of the salt has to be repeated before the animal is dislodged. When the entrance to the nest can be reached without diving, the procedure is more simple and rapid. A small quantity of crude commercial formalin is squirted into the hole with a syringe. This invariably brings out the Octopus immediately. Most of the Octopi were taken in one of these two ways; but some were brought in by the fishermen who find them in their fish-pots.

IV. COLOUR CHANGES

It is necessary to mention the structure and the distribution of the chromatophores, and of the cirri, and to discuss the wave play and the pulsation of the chromatophores, before the description of the colour changes is entered upon.

There are two kinds of chromatophores in *Octopus vulgaris*. One is yellow and the other dark reddish brown in colour. These two types are particularly distinct in the young larvæ, for in them they are distributed quite differently. The former is found on the ventral surface of the mantle, on the dorsal and ventral surfaces of the head, and on the outer sides of the arms. There is also a band of about eight chromatophores on the anterior dorsal lip of the mantle. The latter, the dark reddish brown chromatophores, are seen only on the dorsal surfaces of the body and head, on the ventral surface of the head, and on the outer side of the arms. There are no chromatophores of any kind on the dorsal surface of the mantle.

In the adult the reddish brown chromatophores are about 0.1 mm. in diameter; and are slightly larger, more numerous, rounded, and uniform in shape than the yellow cells. The minute anatomy of these structures has already been discussed in Section I. In the living embryos, before they escape from the egg-capsule, and in the larvæ for at least one week afterwards, the radial processes and a round, clear, highly refractile body in the substance of the chromatophore can be easily distinguished. This round body is probably the nucleus. In the adult neither the radial processes nor the round body can be made out. Furthermore, it is interesting to note that, although in these larvæ the chromatophores are as large as they are in the adult, still there are only about seventy-five of them in a single animal. As the larvæ increase in size new chromatophores must be formed until the adult condition is reached.

The distribution and the abundance of the chromatophores in the several body regions of the adult Octopus are of the greatest importance. In the neighbourhood of the median line on the dorsal surface of the mantle there are, on an average, about sixty of each variety per sq. mm., although there are none in this region in the larvæ, while on the ventral aspect the number is reduced to eight or ten per sq. mm. The skin of the head, the iris, and the outer surface of the eye-ball are also richly supplied. On the siphon and at its base thirty-eight or more may be counted in a sq. mm., but there are no chromatophores inside the mantle cavity. As one passes around the margin of the mantle opening it is seen that the line where the chromatophores disappear is very definite and sharply marked. They are more numerous on the outer surfaces of the first two pairs of arms than they are in the case of the third and especially of the fourth pair. The same applies to the corresponding parts of the interbrachial membrane. The inner side of the arms and of the interbrachial membrane presents a peculiar condition, for here the chromatophores are distributed in patches. These patches vary widely in shape and size and may be separated by as much as 0.1 mm. The reddish brown chromatophores in these areas in the case of the first pair of arms average about one hundred per sq. mm., and the yellow ones only fifty. These numbers decrease continuously as one passes to the second, third, and fourth pairs of arms, and the intervening portions of the interbrachial membrane. The two most striking features in the distribution of the chromatophores are that the relative number of the yellow variety is greatly reduced on the inner surface of the arms; and that both types, in general, are distributed more thickly on the dorsal surface of the body and on the outer sides of the arms than elsewhere.

When we remember that these structures are more numerous on the dorsal than they are on the ventral arms we see that the chromatophores are distributed more thickly on those parts of the body which are exposed to the light, to the attacks of the enemy, and to the eyes of the observer.

In the living animals the skin is very loose and is thrown into a number of folds and wrinkles, which become partially straightened out when the different parts of the body are extended. This unevenness of the skin is particularly noticeable on the dorsal surface of the mantle, between the eyes, and on the outer sides of the first two pairs of arms, together with the intervening portion of the interbrachial membrane. These wrinkles appear like fine dark lines and are illustrated in Fig. 5.

The cirri are of especial interest because it has been suggested that they have a protective function, inasmuch as when elevated they make the animal indistinguishable in irregularity of surface from its surroundings. These structures have a constant and very definite distribution, which is particularly represented in Figs. 5 and 6. The largest ones are found on the dorsal surface of the mantle, between the eyes, and on the outer surfaces of the first two pairs of arms. Smaller elevations may be made out distributed thickly on the sides of the mantle and on the outer surface of the interbrachial membrane. The shape of the cirri on the mantle is peculiar, for when viewed from the side they present a fairly narrow base which expands into a fan-shaped extremity; but when seen from the front or back they look almost like spikes with a broad base and a pointed apex. When fully extended these structures may be from 1 to 1.5 cm. long. The cirri are only occasionally elevated, and when they are in the retracted condition, they are represented only by a slight puckering of the skin. They are generally coloured in the same way as the surrounding surface.

The cirri on one side of the body may be elevated independently of those on the other side. This is probably an instance of the bilateralism which is often apparent in the Octopus. There is a group of three cirri over each eye, which are arranged in longitudinal series, and are represented over the left eye in Fig. 6. One or more of these may be very much elevated over one or both eyes without being accompanied by the extension of any of the others. The causation of the raising up of the cirri is very obscure. They were not observed when the animals were in the act of swimming; neither were cirri raised in regions from which the nerve supply to the skin had been cut off; but it must be said that in this case they were not particularly looked for. Furthermore, the cirri were elevated in animals from which either one or both eyes had been removed, and it is perhaps worthy of note that the Octopus was always, at the time, of a dark reddish brown coloration. We see, therefore that it is very difficult to discover a simple reflex the excitation of which would bring about the elevation of these structures. Any reflex passing through the eye has been excluded, and the only other reflex path which seems at all possible is one which might pass from the suckers to the erector muscles of the cirri. This possibility is favoured by the fact that cirri were never elevated in an animal swimming freely, when obviously such a reflex could not be functioning. The question now arises as to whether there is any relation between the character, whether rough or smooth, of the bottom and the raising of the cirri. Unfortunately no special experiments were made to determine this point; but elevation was observed in the tanks of the aquarium, where the walls and the bottom are firm and smooth, and on the wire sides of the Octopus car, where the surface was extremely irregular and afforded a very poor opportunity for attachment. The elevation seems to be controlled by the central nervous system; for when there are several Octopi in the tank, under the same conditions, the cirri are only occasionally raised in some of them. Even if this reflex does exist, it does not bring us very much nearer an understanding of the rôle played by the central nervous system or of why individual cirri over the eye, for instance, are elevated.

Another peculiar phenomenon was observed. It consists in an indefinite, indescribable quivering or vibration of the colour pattern, which remains without any other perceptible change. This agitation is not very noticeable and cannot be observed from any distance. It does not seem to begin anywhere or to end anywhere; nor is it definitely localizable. It occurs on the dorsal surface of the head and mantle, and on the outer side of the arms and interbrachial membrane; but it was not observed on the inner surface of the arms along the peduncles of the suckers.

The changes which take place during such a vibration are obscure. Observation of the skin with a hand lens failed to show any definite changes; but the variations were probably too delicate and too rapid to be detected in this way. When a portion of the skin, out of water, was viewed in an oblique direction the light which was reflected from it did not seem to change in direction at all synchronously with the vibration. It is obvious, therefore, that we are not dealing with a tremor of the skin. Stroking the skin with the finger calls forth these changes in a very marked degree. After a consideration of the literature it seems probable that this strange quivering in the colour pattern is identical with the "Wave play" which is so often mentioned.

The pulsation of the chromatophores is evidenced by rhythmically occurring flashes of colour in fairly definitely circumscribed regions, and is especially noticeable on the inner surface of the arms, where the chromatophores, as already stated, are distributed in patches. The chromatophores in one of these patches may be pulsating very vigorously, while those in neighbouring areas may be completely at rest. The rate is about twenty-five times a minute; but it seldom lasts as long as that. It seems to be more rapid out of water. The pulsation was not very evident when the skin on the outer surface of the arms was closely examined; neither could it be made out satisfactorily on the head or mantle. That it may take place on the mantle was shown, however, in an experiment in which one of the nerves to that region was sectioned (*vide* Section V).

The causation of the pulsation of the chromatophores is likewise undetermined. It is certainly due to some peripheral stimulus; for, as already mentioned, it occurs, in an even more marked degree, when the nerve supply has been cut off. It occurs also in regions distal to the point of section of the central nerve of the arm. As in the case of the wave play, so also here stroking of the skin on the under side of the arm with the finger causes pulsation of the chromatophores in some only of the areas touched: here and on the surface of the mantle from which the nerve supply had been cut off we get pulsation resulting from mechanical stimulation. But still we are no nearer an explanation of why, in the normal animal, all the chromatophores in certain patches should pulsate; while those in neighbouring areas, under apparently the same conditions, remain at rest. It is true that the abundant interlacing of the radial processes, as emphasized by Hofmann (1907a, p. 390), may account for the fact that the chromatophores in any one of these patches always pulsate together as a whole. On the other hand the possible existence of a peripheral ganglion and of an individual nervous connection for each area might offer an explanation of the phenomena.

We shall now pass to a consideration of the colour patterns themselves. In all of them, as the result of the distribution of the chromatophores, both the outer and the inner surfaces of the dorsal arms are darker in colour than the corresponding portions of the more ventral ones. The same gradation in colour is exhibited in the interbrachial membrane. Furthermore, the dorsal surface of the mantle is always darker in colour than the ventral surface. The colours range from those at the red end of the spectrum to the orange and even border on the green; but no purples, blues, or violets are ever seen. In addition to these, shades of gray and brown are very common. The colorations often grade insensibly one into another; but for convenience of description they may be arbitrarily divided into uniform, mottled, and striped phases.

1. *Uniform phases*—Under this heading four different colorations will be described. They are represented in Figures 1, 2, 3, and 4 respectively. In general these colorations seem to be fundamentally independent of optic reflexes (see Section V), although they may almost all be initiated by them.

The first (Fig. 1) is a light shade of gray tinged with brown or even very lightly with green. It is extremely variable in this respect. The colour is often appreciably darker between the eyes and on the dorsal surface of the mantle. The siphon occasionally appears quite brown against the light gray background of the arms, and the peduncles of the suckers are darker than the remainder of the inner surface of the arms and the interbrachial membrane. This coloration is often complicated by the dilation of the chromatophores in some of the patches on the inner surfaces of the arms, resulting in an irregularly distributed red colour, or the location of the cirri may be marked out by brown blotches. This appearance generally obtains when the animals are at rest, either at the entrance to their nests, in the tanks of the aquarium or elsewhere. In the tanks of the aquarium they are often attached to the walls by the suckers on the proximal portions of their arms only. Their eyes are frequently closed and they do not seem to notice the movements of anything near them in the water. The closure of the eyes is brought about by the contraction of the pupil and the rotation of the eye-ball ventrally, accompanied by a partial closure of the eye-lids. This coloration very commonly occurs also when the vitality is reduced by disease or after operation; but it likewise obtains when the animal is swimming freely or crawling actively over the surface of the bottom.

Another uniform coloration is represented in Fig. 2. It is a shade of brownish red with a distinct tinge of green about the edges of the outer surface of the interbrachial membrane and between the eyes. The fine black lines marking the folds in the skin are particularly prominent. There is also a suggestion of a white blotching on the dorsal surface of the head and mantle and on the outer surface of the arms and interbrachial membrane. The brown band at either end of each eye-slit, which runs in a longitudinal direction, is very interesting and will be discussed subsequently. The under side of the arms and of the umbrella is lighter in colour and even shows an almost orange tint. The peduncles of the suckers are reddish brown. This phase of coloration is often very strikingly modified by a great increase in the brightness and the number of the white spots. These blotches are roughly rounded and are larger and further separated on the head and on the dorsal surface of the mantle than they are at the edges of the interbrachial membrane, where they are densely crowded together. The whole animal may therefore present a peculiar dappled appearance, which is exceedingly bright and is almost impossible to represent adequately in a painting. This spotted coloration seldom persists for more than five seconds. The original pattern, as represented in Fig. 2, occurs when the Octopus is active, crawling or swimming, or when it is touched by other Octopi, or with a stick. It is not very common.

The next coloration, illustrated in Fig. 3, is the simplest of all, for it is quite uniform. It is one of the few phases of colour mentioned in the literature; for Fredericq, Phisalix, and Annie Isgrove all refer to it (see Section I). The reddish brown colour is considerably lighter in the case of the ventral arms and of the corresponding portions of the interbrachial membrane. It is also lighter on the ventral surface of the mantle. The iris and the eye-ball share in the dark coloration. Cirri may or may not be elevated; but a few of them are represented as raised in Fig. 3. Some animals show a decided tendency toward the production of this coloration. It sometimes appears when the Octopus is continually irritated, either by being poked with a stick or when annoyed by other animals. It is of common occurrence when the Octopi are feeding. This uniform reddish colour may persist and also appear when the animal is in the act of swimming, or it may flash out for no known reason when the Octopus is at rest. It has already been mentioned that it is fairly constant and that it remains during the greater part of the period of copulation; but the most interesting fact of all is that it often appears immediately after ink has been ejected. The matter is further complicated when we remember that the other animals, in the immediate vicinity, take on the same coloration, although they have not themselves thrown out the ink. The darkening in colour of the animal, which did not eject the ink, obtains before it is enveloped in the cloud of pigment: indeed before the darkly tinted water even touches it. This points to the conclusion that it is the stimulus caused by the sight of the ink in the water and not the exertion, or the accompanying sensation of throwing it out, which causes this coloration.

The pattern represented in Fig. 4 can hardly be termed uniform, but still it may be most conveniently considered under this heading. The dark lines which mark out the peduncles of the suckers appear in striking contrast to the brilliant white of the rest of the body. The brown lines along the eye-slits are typical and fairly constant; and the siphon is often of a light brownish shade. The iris is white. The eminences formed by the eye-balls are not at all prominent. This results from the lateral rotation of the eyes and the increased distance between them. The animal sometimes seems to crouch down; but at others it arches its arms over its body and presents their inner surfaces as if to ward off an attack. Phisalix and Annie Isgrove call attention to a bleaching of this sort in Sepiola and Eledone respectively. It occurs when an Octopus first notices the approach of an enemy, such as a large fish, or it may flash out when one approaches it in the water, or touches it with the hand or anything else; and it is peculiar in that it does not obtain in totally blinded animals (Section V) whereas the darkening (Fig. 3) does. It is very transient and only obtains for a few seconds. When the Octopus is already dark in colour, it often—especially when the stimulus is not sudden—passes through the dappled phase (*vide supra*) before taking on this coloration. This colour was never seen when the Octopus was swimming, and it does not occur when the vitality of the animal is lowered for any cause.

2. *Mottled phases*—The mottled colorations are the most numerous and the most diversified of all the colour patterns exhibited by the Octopus. Some of them are so brilliant and so complicated that all attempts to reproduce them on paper are in vain. They are more dependent than are the uniform colorations upon optic reflexes. Two of the more simple are represented in Figures 5 and 6.

In the first (Fig. 5) the ground colouring is light grayish brown, and upon this a number of dark yellowish blotches are superposed. These blotches are slightly irregular in shape and may be confined to certain parts of the animal. In the coloration figured they are restricted to the right side. Their location seems to be constant: that is, they always appear in the same places. They are continuous from the outer to the inner surfaces of the arms and they are also found on the outer side of the interbrachial membrane. These patches become smaller and more closely set together as one passes from the base to the extremity of the arms. They are often wedge-shaped and are placed at right angles to the long axis of the arm. The peduncles of the suckers are of a reddish colour. The brown eye-band is shown on the right side, and the iris is white.

The occurrence of this colour pattern is an excellent instance of the bilateralism which frequently obtains in these colorations, for the mottling often appears only on the same side as the eye with which the animal observes a movement of some sort. The line of division between the coloured and the non-coloured portions is sometimes very sharp. If the exciting stimulus is repeated the coloration may spread to the opposite side and the whole animal may darken considerably, to a shade very much like that represented in the next figure. As a coloration of this sort usually lasts for only a very short time, it is exceedingly difficult to determine the exact location of the blotches; but they seem to appear time after time in exactly the same places.

In Fig. 6 the ground colouring is of the same shade, and the blotches are of approximately the same shape and distribution. They are more evident on the dorsal arms than they are in the case of the more ventral ones, and they are the same on both sides of the body. There are several irregular white lines and patches on the dorsal surface of the head and mantle, and on the outer side of the arms and the interbrachial membrane. These patches are extremely variable in their number and size, and by their increase in both may alter the whole appearance of the coloration, merging into the dappled phase already described. In these regions also a few elevated cirri may be distinguished, which stand out as brown dashes against the lighter colour of the background. The iris on both sides is white and the siphon is light brown in colour. The blotches or the dark reddish brown bands on the arms are, as in the coloration just described, continued round to their inner surfaces. In addition to this, the inner surfaces of the arms and of the interbrachial membrane present a fine mottling of brown against a light yellowish ground colour. The peduncles of the suckers are of a light steel-gray shade.

The exact conditions under which these dark blotched colorations appear are unknown. They are associated with activity, not with rest, and they seldom persist for more than five or at most ten minutes. They appear when the animal is in the act of swimming, but they are even more transient when in this condition. Moreover, these patterns are of fairly common occurrence when the Octopi are devouring their prey.

3. *Striped phases*—As the mottled patterns are the most variable, so the striped are the most constant. They are more transient than either of the other two types of coloration and are characterized by the suddenness and the abruptness with which they flash out and then disappear again. The stripes are always very definite, occur in precisely the same regions, and throughout show a marked tendency to be controlled by optic reflexes. Three main types will be described.

The first of these is the more circumscribed and perhaps the least noticeable; but it is by no means the least complicated. It is illustrated in Figures 2, 4, and 5, and consists of a principal band about 25 mm. long, by 3 to 4 mm. broad, which runs antero-posteriorly and is continuous, on either side of the eye, parallel to the long axis of the pupil: this holds only when the eye is in its usual position and is not rotated. When this area is coloured the chromatophores on the iris, at either extremity of the pupil, and occasionally those along its dorsal margin, are also dilated, so that a similar brown coloration results. It is interesting to note that Fredericq, as far back as 1878, clearly described this stripe and made some notes on its occurrence (see Section I). In addition to this principal stripe, two other smaller areas of coloration may appear, the location of which is indicated on the left side in Fig. 4. They are situated dorsad and mediad of the eye. The posterior one is the larger and the more prominent, and is often continuous with the principal stripe ventrally and laterally. It was once observed that the whole of the skin over the orbit became dark in colour; while the remainder of the animal retained its uniform light gray shade.

These bands flash out when the animal notices the approach of a fish or any other object in the water. They only appear across the eye which notices the movement. The stimulus does not pass over from one side to the other; but it was noticed that there were varying degrees of reaction. This is shown by the fact that if disturbance is slight or some distance off the coloration is only light; but if it is repeated or comes nearer, the colour deepens to a very dark brown. Indeed, it is only when the animal is strongly stimulated in this way that the accessory bands appear. The principal band may pulsate and actually vary in intensity in different parts. It may be darker in front of the eye or behind it, or either of these parts may not be coloured at all. The accessory bands never appear when the principal stripe is absent; and of the two, the posterior one is the more prominent and may flash out independently of the other. When the animal sees the object with both eyes the coloration appears on both sides of the head. These patterns appear when the Octopi are at rest, crawling about, or swimming vigorously. They apparently exhibit the phenomena of fatigue; for following repeated stimulation, after they have appeared and disappeared several times, there is a period when they do not occur. If the Octopus is now allowed to rest for ten or fifteen minutes and is again stimulated, in the same way, it reacts by coloration as it did in the beginning. These stripes do not occur in animals which are not perfectly healthy and vigorous. As one would expect they do not obtain when the animal is out of water; for the optic reflexes would necessarily be reduced to a minimum.

The next coloration, that illustrated in Fig. 7, may be regarded as a modification of the one just described. It is characterized by a dark brown stripe, extending from the distal end of the second arm over the optic prominence to the posterior end of the mantle. It may occur on one or both sides. This stripe is not always of the same extent, but its breadth is fairly constant.

This long band is one of the rarest of the colorations, and it is peculiar in that it seems to be of more frequent occurrence when the animals are swimming, although it was once observed to flash out in an Octopus which had just come to rest. Some animals show a strong tendency to exhibit this pattern. It is generally produced when an Octopus, showing the principal stripe (*vide supra*) across the eye, is pursued while swimming, and it may be regarded as an enlargement and an elongation of this stripe. There is some reason to think that there is a correspondence between the side facing the pursuer and the side upon which this great band appears; but this could not be determined with certainty. If it is true, however, as one would expect, then both bands would appear when the animal sees the enemy with both eyes, and this seems to be the case. Like the smaller stripes, they are transient and fade away in three or four seconds, after the stimulation is withdrawn or when the Octopus comes to rest. They were never observed with animals in the aquarium tanks.

The last coloration to be described is the one shown in Fig. 8; it is perhaps the most remarkable and interesting of them all. The general colour of the animal is dark reddish brown, somewhat similar to that illustrated in Fig. 3. This is strikingly modified by the presence of white stripes. The largest of these extends along the dorsal margin of the first arm on the right, takes in a portion of the interbrachial membrane, and runs along between the eyes to the posterior end of the mantle. The relative breadth is indicated, but it varies considerably in different cases. In addition, there are two lateral stripes on the dorsal margins of the second and third arms, and on the adjacent parts of the interbrachial membrane, which come to a termination before reaching the head region. It could not be seen whether there was a stripe on the fourth or most ventral arm; but its presence is highly probable. The ventral surface of the mantle presents the same shade of white. Sometimes both the median and the lateral stripes are confined to the interbrachial membrane, so that the arms participate but little in the banding.

The dark background is generally the fundamental colour and the white stripes seem to appear secondarily; but exceptions to this rule were observed. The long median white band occasionally appears when the Octopus is at rest, and is generally the precursor of movement; but the lateral bands do not appear unless the animal is in the act of swimming. The same holds in the case of the white shade of the under surface of the mantle. The lateral stripes disappear almost immediately after the Octopus comes to rest, and the ventral surface of the mantle becomes of the same shade as the rest of the animal. This disappearance may be effected by either a darkening of the areas or a bleaching of the whole Octopus.

As in the case of all the other striped colorations, so also here, they seem to result directly from the excitation of a reflex through the eye. This hypothesis is supported by the observation that the lateral bands occur only on the side of the eye by which the Octopus notices the approach of another animal. Sometimes, presumably when the stimulus affected both eyes, the two sides become simultaneously striped. In some animals these changes take place so rapidly that only five minutes' observation is sufficient to show the occurrence of the long median band, either alone, or accompanied by the lateral stripes on one or both sides. The lateral bands never appear independently of the median band. The matter is complicated by the fact that this coloration is limited to certain animals, which show it with unusual frequency. This tendency of certain individuals to produce time after time a particular colour pattern is very remarkable and seems to indicate the operation of factors of which we know nothing. It is especially liable to occur when the animal in question is disturbed by other Octopi; but it may also be elicited in various other ways. When one Octopus in the tank constantly shows this coloration, there seems to be a tendency for some of the others to exhibit it also; for they do not do so when it is removed. The males show it as well as the females; but it occurred in the most marked degree in the case of a young female. It seems to be the same as that mentioned in the literature as a "Zebrastreifung." Hofmann (1907a, p. 388) writes that in Sepia this "Zebrastreifung" is characterized by the alternate occurrence of dark and light bands of colour, and adds that it occurs when two Sepia approach each other. This is the least understood of all the colorations which the Octopus assumes.

From the preceding description of the colour changes it will be noted that they are extremely variable and complex: indeed it seems that nowhere in the animal kingdom are the colour changes so rapid and so brilliant. When one sees a dark red Octopus on a white background, or striped animals swimming in their natural environments, one cannot help thinking that colour seems almost to have gone to waste. The colour patterns were observed in males and females alike, and they all occurred in a great variety of environments. In the following pages an attempt has been made to explain the causation and the purpose of these colour changes.

V. THE RÔLE OF THE EYES AND OF THE CENTRAL NERVOUS SYSTEM

This study was carried on from the operative standpoint. The operations consisted in blindfolding or extirpating one or both eyes, and in sectioning deep and cutaneous nerves. The results are summarized at the end of the section. In all cases, the anaesthetic used was magnesium sulphate, which, although not entirely satisfactory, serves the purpose fairly well. When used it is added, in small quantities at a time, to a dish of water in which an Octopus has been placed; this is kept up until the response to mechanical stimulation ceases. To obtain this result about 500 grams to 2 litres of water are necessary; the amount varying of course with the volume of water used. The solution may be employed repeatedly until the mucus secreted by the animal renders it foul. The colour of the Octopus under this anaesthetic usually becomes light gray, and the respiration slow and shallow. The animal may be kept under the anaesthetic for ten or fifteen minutes if the water in the dish is carefully and continuously aerated. Respiration occasionally ceases entirely and reviving may then be difficult. In such cases the animal was placed in fairly cool sea water (about 25° C.) and periodically, about every two seconds, some of the water was squirted into the mantle cavity, the mantle being squeezed in the intervals, so that complete artificial respiration was kept up. The Octopi are very hardy and almost invariably recover from the operations.

Blindfolding was attempted as a means of eliminating optic stimuli. A small piece of opaque oil-cloth was tightly sewn over both eyes so that it was impossible for the animal to see anything; but it is possible that some light leaked in from the sides. When the Octopus had recovered from the anaesthetic it did not respond in any way to movements of objects in its vicinity. If it was placed in the water of a large glass aquarium in a dark room no change in colour from its original light gray coloration occurred when a bright acetylene light was flashed upon it. The Octopus responded to jarring of the aquarium by the production of a brown mottling on the arms. It was found very difficult to keep the animals permanently blindfolded in this way, and it was felt that the results obtained were indefinite and unsatisfactory, and so extirpation of the eyes was resorted to.

In the single extirpations a longitudinal incision, parallel to the long axis of the eye, and about 1.5 cm. in length, was made in the skin on the dorsal surface of the optic prominence. Some connective and muscular tissue was then cut through, and the chromatophores on the dorsal surface of the eye-ball were thus laid bare. Slight pressure was then applied to the ventral surface of the eye-ball so that it slipped through the incision on to the dorsal surface of the head. The optic muscles and the optic nerve fibres were cut through, just proximal to the retina, and the eye was removed. Finally the edges of the wound were carefully drawn together by means of one or two stitches. The advantage of this procedure is that neither the optic ganglion nor the optic gland are interfered with, indeed the former is not even seen, and there is practically no loss of blood.

Recovery from this operation is very rapid; for in the course of half an hour or so the animals appear quite normal, except of course for the direct results caused by the loss of vision on one side. Neither are there any bad after-effects, as the animals can be kept practically indefinitely in this half-blinded condition. The operation was performed on two Octopi, one of which was killed in a few days and the other kept for two weeks. At the end of this time the animal was quite active and vigorous.

The behaviour of these semi-blind animals does not seem to be modified in any particular, except that they do not react to visual stimuli on the side of the extirpation. In one of them the right eye was removed and in the other the left. The elevation of the cirri is not affected in any way. The animals swim freely, crawl about, pursue and capture crabs and crayfish, and exhibit all the reactions of normal animals.

The coloration is little modified. All the uniform colour patterns appeared as in the normal animal; but in the case of the mottled patterns the mottling seemed to appear more readily on the side of the uninjured eye. This was noticed particularly after mechanical stimulation, which, if long continued, however, always resulted in mottling of equal brilliancy on both sides. The colour of the animals while at rest is either light gray or uniformly mottled with brown. It is, however, in the case of the striped colorations that the greatest change is observed. The small brown stripes represented in Figures 2, 4, and 5, appeared only in connection with the uninjured eye. The large longitudinal brown stripes were not observed at all. Neither was the white striping, illustrated in Fig. 8, seen, although one of the animals showed it before the operation.

In the case of the double extirpations the operation was performed in two stages. When one eye had been removed, in the manner indicated above, the animal was revived and after an hour or two the second eye extirpated. No Octopi were ever lost as a result of the operation. It was performed on one male and one female only. Recovery was very rapid, as shown by the fact that the next day when a crab was placed so that the Octopus could feel it, it gathered itself together made a sudden dash at it and captured it. Three fair-sized crabs were taken and devoured in this manner in succession. Both of the Octopi took crabs in this way.

The behaviour of these blinded animals was altered comparatively little. They were generally found resting quietly on the bottom or attached to the sides of the tank, but they sometimes crawled about or swam freely. They remained alive and active, and fed whenever the opportunity offered for about three weeks, when they were killed, so that we must credit them with reacting normally to all except optic stimuli.

The examination of the colour changes in animals from which all the optic reflexes have been clearly and definitely eliminated affords very valuable results. Immediately after the operation, when the animals were stimulated by being gently poked with a rod, the colour darkened from the light uniform gray to the dark greenish brown represented in Fig. 2. This colour soon faded to the original gray. A few hours after the operation the arms of one of the two Octopi took on a brown mottled coloration, intermediate in intensity between those illustrated in Figures 5 and 6, which persisted almost continuously for two days. The body of the animal was slightly mottled also. After this time neither of the two animals exhibited any mottled or striped colorations of any description. When resting they were of the gray shade represented in Fig. 1, and when irritated they changed to the uniform dark red of Fig. 3.

The conclusion is therefore justified that reflexes through the eyes are very important factors in the causation of the striped and also to a less degree of the mottled patterns; but the uniform colorations are not entirely dependent upon them, although, as already mentioned, these uniform colorations may be initiated by visual stimuli. Furthermore, we learn from the single extirpations, that there is a fairly ready diffusion of optic stimuli from one side to the other, so that the coloration is little altered by the operation. The behaviour and the colour of both the semi-blind and the totally blind animals have been studied in different environments and will be discussed in the next section.

The nerve supply to the chromatophores on the arms was studied and for this purpose two kinds of operations were performed. In the first kind, an incision about 4 cm. in length (i.e. about one third of the circumference of the arm at this level) was made in the skin on the dorsal surface of the second arm of the right side, at right angles to its long axis and opposite the twelfth sucker. Everything was cut through down to the circular layer of muscle. The edges of the wound were then drawn together by stitches. Immediately after the

Octopus had been revived, it turned a uniform red colour, with the exception of a band of skin about 2 mm. wide on either side of the wound, which remained quite white. Subsequent observation showed that the arm distal to this point changed colour in precisely the same way as the other arms.

In the other kind of operation the large nerve running down the centre of the arm inside the various layers of muscle was sectioned. This was performed in the second arm on the right side and on the left by thrusting in a sharp thin-bladed knife in the median line on the inner surface opposite the twelfth sucker. The result was that there were no colour changes in either of the two arms distal tc the point of section, other than those caused by the pulsation of a few isolated patches of chromatophores. Whatever the coloration of the rest of the body these arms retained a bright white appearance. They hung limp and inert, responding to mechanical stimulation only by local pulsation of the chromatophores in the regions stimulated. The nature of this pulsation will be described in a subsequent case, where the nerve distributed to one side of the mantle was sectioned. The suckers distal to the point of section did not attach themselves to anything with which they were placed in contact, although those proximal to the cut did. There was both sensory and motor paralysis. Subsequent autopsy showed that the central nerve and artery in each arm had been completely cut across.

Therefore all the colorations, except those caused merely by the isolated pulsation of the chromatophores, result from impulses passing from the central nervous system to the periphery. In the case of the arms the impulses to the chromatophores must pass along the central nerves and then branch out to the skin at right angles.

The last experiment of this sort consisted in sectioning the left pallial nerve, which constitutes the nerve supply to the left half of the mantle. A transverse incision of about 3 cm. in length was made in the skin on the dorsal surface of the head, about 2 cm. behind the optic prominence. The muscular and connective tissues were cut through and separated until a large nerve running in a postero-lateral direction was laid bare. This nerve was sectioned and the edges of the wound were then drawn together by stitches.

As soon as the Octopus had recovered from the effect of the anaesthetic, it was noticed that the left side of the mantle was quite white and did not change in colour. When the Octopus was poked with a rod the characteristic red coloration appeared over the whole surface, with the exception of the left side of the mantle, which was very sharply and clearly limited at the dorsal and ventral median lines. A few hours later brownish spots, from 0.5 to 1 cm. in diameter, appeared scattered over this area. After the lapse of ten days, examination showed that this region changed colour in a very peculiar manner. When the animal was at rest and of a light gray shade, the patches pulsated and varied considerably in intensity of coloration. They pulsated in some cases at the rate of twelve times in thirty seconds, and two such spots very close together often flashed out at quite different times. If the Octopus was handled it grew darker in colour, and the spots increased in number. On the left side of the mantle the prick of a pin called forth no motor responses whatever; but when the skin just to the right of the median line was stimulated in this way violent movements of the arms resulted. The skin on the left side when scratched with a needle showed a reddish brown streak, which came and went several times in a rhythmical manner. It would be present for about twenty seconds, and then again absent for the same period, and so on. This coloration was limited precisely to the regions stimulated, so that simple patterns, such as crosses and squares, could be reproduced in colour.

This experiment confirms the previous one and also furnishes some additional data bearing on the question of the pulsation of the chromatophores, which has already been discussed in Section IV. It is to be noted that the abolition of the colour changes is always accompanied by both sensory and motor paralysis.

The most important conclusions to be drawn from these various operations may be summed up as follows.

1. Optic reflexes are very important factors in the production of the striped and also, to a less degree, of the mottled patterns; but the uniform colorations are not wholly dependent upon them.

2. All the colour changes are brought about by reflexes which pass from the central nervous system along the various nerve trunks to the chromatophores; but simple pulsation of the chromatophores may take place independently of the central nervous system.

VI. THE EFFECT OF CHANGES IN THE ENVIRONMENT

These experiments were performed with the hope of determining whether the Octopus changes its colour to correspond to that of its environment. There was little evidence of such a phenomenon when the Octopi were observed in their natural haunts, as they were repeatedly. True, they sometimes are very hard to distinguish upon certain backgrounds; but it seems that just as often they presented a coloration which in no way resembled their surroundings.

The methods used in the attempt to solve this problem were frequently altered and improved, and so it was not until the very last that anything but purely negative results were obtained. At first the animals were placed in large glass aquariums which were surrounded with differently coloured translucent paper. After a time they always assumed a uniform light gray shade. It was felt, however, that they were under very abnormal conditions and this method was therefore abandoned.

In order to experiment under conditions as nearly natural as possible, the Octopus car described in Section II was built. A long series of experiments was then carried out, in which the car with the Octopi in it was placed in different environments, the colour changes being carefully observed. These environments were as follows: (1) a smooth white sandy bottom; (2) a smooth sandy bottom covered with Eel-grass (*Zostera marina*) so that its general shade was dark greenish gray. In addition to these (3) a glossy black oil cloth and (4) some old gunny sacks were placed under the car giving a black and a dark brown background respectively. The observer was hidden from the animals and great care was always taken to prevent any jarring or movement of the car or any outside disturbance. Under each of these conditions the colour changes were noted when the animals were at rest and when irritated, when crawling about, and when swimming, when feeding on crabs or crayfish, and when they noticed the advent of an enemy, such as a large Hamlet (*Epinephelis striatus*). The Octopi exhibited practically all the colorations described in Section IV; but the results were still purely negative; for no constant relation between the changes and the colour or the brightness of the environment could be determined.

Then I read of Steinach's idea (1901a, p. 28), that the changes in colour are controlled by the evenness or the consistency of the bottom through the medium of the suckers and determined to change my method. Heretofore the animals always rested on the extremely irregular wire bottom of the cage; but in the series of experiments next tried an artificial bottom was arranged inside the cage. The observations were all made on both male and female animals put into the cage separately, both in direct sunlight and in shadow. The bottoms were as follows:—

1. Fine white sand, represented in No 1 of the colour chart, Fig. 9 (soft white bottom).
2. Large roofing slates, painted white, No. 5 (hard white bottom).
3. Finely powdered hard coal, No. 2 (soft black bottom).
4. Slates painted black, No. 4 (hard black bottom).
5. Slates painted yellow in imitation of the Brain corals (*Meandra labyrinthiformis* and *Meandra cerebrum*), which are common on the reefs, No. 9.
6. Slates painted the same shade of red as a sponge which is also of very common occurrence, No. 7.
7. The large green Alga (*Ulva latissima*), No. 3.

Octopi were left on some of these bottoms for as long as three days, and were observed almost continually during the daylight of that period. The coloration exhibited was not modified in any noticeable way by the environments. On each day they showed a great diversity of colour patterns. The brown bands across the eyes appeared when the animal noticed the movement of anything in the water near it; the uniform dark reddish brown colour, when irritated in any way or following the ejection of ink: moreover, the colour always bleached when the Octopus was touched with the hand or with the end of a stick.

It was then noticed that the Octopi always seemed to turn dark in colour when they were returned to the tanks of the aquarium. The colour of the walls of these tanks is dark green and is represented in No. 8 of the colour chart. Another series of experiments was initiated with the object of determining whether a change to correspond to the brightness of the environment takes place when the animal first enters new surroundings. For this purpose half of the bottom of the cage was covered with white slates and the other half with black slates. Slates were also leaned up against the walls. A small Octopus, of a light coloration, was then induced to move from the light environment into the dark, and it was observed that when it came on the black slates, five or ten seconds after, it turned a uniform dark reddish brown colour like that illustrated in Fig. 3. When, on the other hand, it moved over from the dark to the light bottom, it became either of a light gray coloration, Fig. 1, or of a light gray shade with a faint brown mottling. The same results were obtained on different days, in sunlight and in shadow, and with a large number of animals, including both males and females. Yellow, red, and brown No. 6, and white slates mottled with irregular brown blotches, about 4 cm. in diameter, were used; and when there was sufficient contrast between the two environments bleaching or darkening always resulted.

The change seemed to be dependent upon the brightness of the environment only, and it persisted for ten or fifteen minutes. It may take place as soon as the animal crosses the boundary, or it may be deferred until it comes to rest. The change often occurs when the animal is in the act of swimming, and consequently not in contact with the bottom. It appears simultaneously over the whole surface of the Octopus; but the coloration which results is not always uniform; for it may be either a dark or a light mottling. Furthermore, the change does not always take place. In a sickly animal or in a fatigued healthy one, there may be no adaptation at all. If a healthy and vigorous Octopus, which has adapted itself to any of the bottoms, be poked with a stick or touched with the hand it invariably takes on the light coloration illustrated in Fig. 4; but when repeatedly irritated in any manner the uniform red depicted in Fig. 3 always appears.

The same experiments were performed with semi-blind and blind animals. In the case of the former the results were particularly interesting. The change with the brightness of the bottom took place in exactly the same way as with normal animals, with the exception that the manner of the bleaching was modified. It constantly took place two or three seconds later on the side from which the eye had been removed. Indeed, at a certain time the halves of the body are very definitely demarcated from each other by their difference in shade. This difference in the rate of bleaching is evident, no matter whether the original colour was of a mottled or of a uniform character. It is a peculiar fact that no difference could be noticed in the rate of darkening on the two sides, and I am unable to formulate any explanation of this. Sudden bleaching, particularly in this case, where it is more rapid on the side possessing the most direct and potent optic reflexes, and also the instantaneous production of the ghostly white coloration of Fig. 4, seem to indicate that the contraction of the chromatophores may be an active process and may not be wholly dependent upon the elasticity of their walls. In the semi-blind animals also, this white coloration and the red phase illustrated in Fig. 3 could be brought about by alarming the animal and irritating it, if such terms may be used, at any time in any of the environments, so that we must conclude that factors such as these are most powerful. It is difficult to overestimate the importance of the influence of the physiological condition of the Octopus upon the colour changes.

In order to make these experiments complete and convincing two totally blind animals were used. They seemed quite healthy and vigorous; for they crawled about the car, occasionally swam freely, and devoured crabs with as great avidity as did normal animals. As one would expect, there was no change in colour of any description when either of the two moved from a dark environment into a light one or *vice versa*.

The conclusion is therefore justified that the Octopi do, in a general way, change their shade to correspond to the brightness of the environment. There is not as yet sufficient evidence in support of the belief that these animals become mottled or striped in imitation of the bottom on which they may be resting or over which they may be swimming. As it was impossible, on account of the difficulties of the technique, to experiment with environments of which the colour had been accurately measured and determined, and as it is not even known whether the Octopus can distinguish colours, it could not be ascertained whether the colour of the bottom plays any part in these changes. It is extremely unlikely, however, for the coloration of the habitat of the Octopus is mostly characterized by greens, bright yellows, and even blues, and we know that these are the very colours which the animal cannot exhibit; and also for other reasons. The experiments show, further, that this change in colour depends upon the excitation of a reflex arc, which passes from the retina through the optic nerve to the brain and thence by the different nerves to the chromatophores. In addition to this, the fact that the change may take place when the animal is in the act of swimming, indicates that tactile reflexes, due, for example, to the physical condition of the bottom, can have no influence in the darkening or the bleaching as the case may be. This reflex has been traced through the retina to the brain, and if proof were required that it passed by the various nerves to the chromatophores, this is supplied by the observation that the parts of the animal from which the nerve supply has been cut off do not change, like the rest of the animal, in brightness to correspond to the environment.

VII. THE EFFECT OF CHANGES IN THE WATER, AND OF LIGHT

Many experiments were performed with a view of determining the effect, if any, of changes in the temperature, the purity, and the salinity of the water upon the colour changes. With small alterations, the results obtained were almost entirely negative, and this is what is to be expected when we remember that in the natural environments, on the reefs and elsewhere, such changes practically do not occur. As, under natural conditions, the colour changes are so vivid and so sudden, the conclusion is warranted that they are in no way governed by changes of this sort. Since the object of this work is to study the colour changes under normal conditions and their relation to the behaviour of the animal, these experiments will not be described.

It seems that the effect of light upon the colour changes has been exaggerated. Steinach (1901a, p. 28) finds that when the sun shines down through the water the animals (Eledone) become uniformly darker in colour and flee into the shade. I found that when a dozen or more Octopus larvae, contained in a glass bowl, were moved from a shaded place into bright sunlight, they all became active and darker in colour. This was repeated several times; but in the experiments with adults on change in environment no constant difference could be observed in sunlight or in shadow, although they were particularily looked for. Furthermore, when sunlight was condensed by means of a lens upon normal animals, dead animals, and totally blinded animals, resting in glass aquaria and protected by 10 cm. of water, for periods as long as a minute, no darkening could be observed.

VIII. DISCUSSION

The position is a peculiar one. At the head of the Invertebrate phyla we have a class of animals, the Cephalopods, which have existed for millions of years, almost unchanged in their general structural characteristics, and are very highly specialized. We find, further, that the members of the order Octopoda of this class are remarkable in that they exhibit more vivid, complicated, and rapid colour changes than do any other members of the animal kingdom. It is not to be wondered at, therefore, that these animals, above all others, should be chosen as objects by means of which to investigate the general and also the more particular questions involved in change of colour. The following discussion will deal with the possibility of the active nature of the diminution in size of the chromatophores; and with the causation, the purpose, and the acquisition of the ability to change colour.

There is certainly no histological evidence of the existence of nerve fibres which might conduct impulses resulting in the contraction of the chromatophores and the bleaching of the animal; but careful observation of the colour changes in the gross seems to point to some such mechanism. It is hard to believe that the sudden bleaching which occurs when the animal is poked with a stick is purely passive, and results, simply, from the elasticity of the walls of the chromatophores. Similarly, the abrupt appearance of the long white stripes, the rest of the animal remaining dark, as illustrated in Fig. 8, is hard to reconcile with this view. Moreover the experiments with half-blind animals demonstrated that both the darkening and the bleaching result from optic stimuli—that is that they are both active processes. Of course the possibility remains that the bleaching may be fundamentally passive and result solely from the inhibition of the impulses passing from the central nervous system to the chromatophores; but if this is the case we should have to assume that in the normal light gray coloration of the resting animal (Fig. 1) the chromatophores are continually receiving impulses from the brain and that consequently the radial muscles are always in action, for we meet with a still lighter coloration as illustrated in Fig. 4. The difference in the shade of the body and of the outer side of the arms in the resting condition (Fig. 1) and in the frightened state, if we may use that phrase (Fig. 4), is sometimes even greater than is indicated. Furthermore, an animal which has been dead for two or three days seems also to be darker in colour than the condition represented in Fig. 4). The conclusion is therefore justified that, although the anatomical findings seem to show conclusively that the diminution in size of the chromatophores is purely passive and results from the elasticity of their walls, still close observation indicates that this may not be the case.

Steinach's conception of the causation of the colour changes has already been mentioned. He states that, in Eledone, the changes in colour are due to the excitation of a reflex which passes from the suckers along the nerves to the brain and thence by the various nerve fibres to the chromatophores. When the suckers are attached to a hard firm bottom the chromatophores are supposed to be stimulated and changes in colour to take place. When, on the other hand, the Octopus is resting on sand the suckers are not in action and no stimulation of the chromatophores results: so that, as the hard rocky bottoms are in general dark in colour and the sandy bottoms light, there would be a change in brightness to correspond to the environment.

Steinach cites two experiments in support of this hypothesis. He worked with Eledone and, in the first instance, cut off all the arms and the suckers remaining on the stumps. The result of the operation was that, in the majority of cases, the animal was highly coloured for about two days, in either a mottled or a uniform manner. Subsequently, the animal rested quietly on the bottom of the aquarium and maintained a uniform silvery white shade. In the second experiment one arm and its suckers were left intact, and the animal exhibited the various colour patterns and the spontaneous colour changes without modification. On the basis of such experiments he concludes, in addition, that the origin of the colour changes is not central but peripheral.

This hypothesis seemed at first sight to explain the phenomena observed in a very satisfactory manner, especially as it did not postulate any very high degree of intelligence on the part of the animal, and as it depended only upon the functioning of a simple reflex. It does not seem to hold, however, in the Octopus, although one would certainly expect it to do so; for the Octopus and Eledone belong to the same family and resemble each other in many ways. If the coloration, in the absence of direct sunlight, is dependent upon a mechanism of this sort, then one would not look for a modification of the colour changes when the optic reflexes are eliminated; but in both semi-blind and totally blind animals the patterns are found to be definitely altered. The most important evidence which can be brought against this hypothesis is derived from observation of the living animals under natural conditions. Thus, there are often several Octopi in the same tank under identical conditions clinging to the wall; but they all may be coloured differently. An Octopus is often seen attached to the walls of the tank by a few of its arms only, the others hanging limp in the water. In such cases, the animal is usually of a light gray shade, but some of its suckers are in action and others are not, and if Steinach's idea is correct, some at least of the chromatophores ought to be dilated; but they are not. In the open, the Octopi are very often of a dark red coloration when on a soft sandy bottom, and of a light shade when they are on hard, dark rock. When the animal is swimming out of contact with everything except water, the suckers being unquestionably quiescent, it is frequently coloured in a variety of ways, and, when in this condition, it may even change its colour.

It has been suggested that there might be a peripheral reflex mechanism which would be capable of governing the colour changes. This theory is rendered more attractive after a study of Hofmann's work (1907a), dealing with a continuous nervous network, formed by the branching of ganglion cells, running in the peripheral musculature of Cephalopods; and also when we consider that Hertel (1907) has shown that light rays of different colours have a specific action upon the chromatophores. Such a theory, however, is obviously insufficient to explain the colour changes which have been recorded above in *Octopus vulgaris*.

It has been shown that in animals generally optic reflexes are exceedingly important in the colour changes and a close parallelism may be traced between the degree of development of the eye and the rapidity and the brilliancy of these changes. In the Octopi and the Squids the eyes are very highly developed and efficient. They are even capable of accommodation, and are much superior to those of many vertebrates. The present experiments, in which one or both eyes were removed, show that there is indeed such an interdependence.

The effect of the physiological condition of the Octopus upon the colour changes has already been referred to, particularly in Sections V and VI. Thus if an Octopus is irritated or excited it will turn red, or if it is pursued by another animal or poked with a stick its colour will bleach, no matter what bottom it is on. Similarly in the case where an Octopus is pursuing a crab it will often remain of a mottled coloration until it has seized its prey when, in consequence perhaps of the excitement, it will darken to the uniform dark reddish brown coloration so often mentioned, quite irrespective of the brightness of the background. When the animals are actively engaged in feeding they often present the same coloration. It has already been stated that this colour is associated with muscular activity. When the vitality of the animal is lowered for any cause, of all the colorations this darkening and to a less extent the bleaching persist the longest. Thus a sickly animal will not change its colour with the brightness of the bottom, but it will darken when it is annoyed and bleach when it is touched. To repeat, the importance of the physiological condition of the animal is illustrated by (1) the fact that the colour changes resulting therefrom (darkening and bleaching) overpower and replace those caused simply by optic reflexes; (2) the persistence of the darkening, and also to a less degree of the bleaching, when the colour changes resulting from optic reflexes, etc., have been eliminated by lowered vitality; and (3) the uniform character of these changes, the animal as a whole reacting, not simply a portion of it.

Throughout these experiments a record of each animal was kept, and no difference was found in the coloration of the males and of the females, so it is unlikely that sex is at all an important factor in the colour changes.

When we consider the purpose of these phenomena we enter into a discussion which is almost purely speculative. It has been hinted that they are purposeless and of no use to the animal; but I find that such a conclusion is hard to accept; for, although there are many instances of organs which are apparently useless, still such structures are seldom, if ever, of so high a degree of functional activity as are the chromatophores. For this reason we may conclude that the chromatophore-system and the accompanying ability to change colour are of service to the animal, and it becomes necessary to determine, if possible, just what benefits the Octopi derive therefrom. The change with the environment seems to be of direct utility to the animal, but the effect is marred by the over-ruling of the emotions, if such a term may be applied to so lowly an animal. The ejection of ink is undoubtedly protective in that it aids the animal to escape from its foes.

It is very doubtful whether the Octopi exhibit any warning colours; but when an Octopus notices the approach or feels the bite of a small fish, it will change colour immediately and the fish will dart away. The colour assumed in such cases is variable; it may be either uniform or mottled. In two cases the colour displayed was very strange; for it consisted of an irregular network of dark brown lines and blotches upon a creamy white background. This coloration persisted for only a few seconds. The Octopus does not move in such a way as to suggest this motion as the cause of the fish's alarm, in fact in some cases it does not move at all.

The acquisition of the ability to change colours, as we know it in the Octopus, is very difficult to understand, and it seems that, in this respect, we shall remain in the dark until very much more detailed and accurate work has been done. A study of the ability to change colours and of the appearance of the various colour patterns in ontogeny might lead to some very interesting results. The question also arises as to what would be the effect of rearing Octopi in coloured and colourless environments of varying degrees of brightness, and in this connection the work of Gamble (1910), chiefly concerned with the Crustacea, should be mentioned. What is needed above all, however, is an investigation into the psychology of the Octopus. It is evident that the order Octopoda provides a field for this most facinating kind of research.

IX. SUMMARY OF CONCLUSIONS

1. All the colour changes are brought about by impulses which pass from the central nervous system along the different nerves to the chromatophores; although simple pulsation of the chromatophores may take place independently of the central nervous system (see p. 40).

2. Optic reflexes are very important factors in the production of the striped, and also, though to a less degree, of the mottled patterns, but the uniform colorations are not wholly dependent upon them (see p. 39).

3. *Octopus vulgaris* does, in a general way, change its

colour to correspond to the brightness of the bottom, particularly when it enters a new environment (see p. 44).

4. This change in colour depends solely upon the excitation of a reflex arc, which passes from the retina through the optic nerve to the brain and thence by the various nerve trunks to the chromatophores (see p. 44).

5. The physiological condition of the Octopus is the most important factor in the colour changes (see p. 49).

BIBLIOGRAPHY

Bauer, Victor.
1909. Einführung in die Physiologie der Cephalopoden, mit besonderer Berücksichtigung der im Mittelmeer häufigen Formen. Mitth. d. Zool. Stat. zu Neapel, Bd. 19, Heft 2, pp. 148-286.

Chun, Carl.
1902. Über die Natur und die Entwicklung der Chromatophoren bei den Cephalopoden. Verh. Deutsch. Zool. Ges., pp. 162-182.

Darwin, Charles.
1845. Voyage of a Naturalist round the World. London, Murray.

Fredericq, Léon.
1878. Recherches sur la physiologie du Poulpe commun (*Octopus vulgaris*). Arch. de Zool. exp. et gén., sér. 1, tom. 7, pp. 535-583.

Gamble, F. W.
1910. The Relation between Light and Pigment-formation in Crenilabrus and Hippolyte. Quart. Jour. Micr. Sci., London, New series, No. 219, pp. 541-583.

Gariaeff, W.
1909. Zur Histologie des centralen Nervensystems der Cephalopoden. 1. Subösophagealganglionmasse von *Octopus vulgaris*. Zeit. f. wiss. Zool., Bd. 92, pp. 149-187.

Girod, Paul.
1883. Recherches sur la peau des céphalopodes. Arch. de Zool. exp. et gén., sér. 2, tom. 1, pp. 225-266.

Hertel, E.
1907. Einiges über die Bedeutung des Pigmentes für die physiologische Wirkung der Lichtstrahlen. Zeit. f. Allg. Physiol., Bd. 6, pp. 43-69.

Hofmann, F. B.
1907a. Gibt es in der Musculatur der Mollusken periphere, kontinuierlich leitende Nervennetze bei Abwesenheit von Ganglionzellen? 1. Untersuchung an Cephalopoden. Arch. f. d. ges. Physiol., Bd. 118, pp. 375-412.

Hofmann, F. B.
1907b. Über einen peripheren Tonus der Cephalopoden-Chromatophoren und über ihre Beeinflussung durch Gifte. Arch. f.d. ges. Physiol., Bd. 118, pp. 413-451

Hofmann, F. B.
1907c. Histologische Untersuchungen über die Innervation der glatten und ihr verwandten Musculatur der Wirbeltiere und Mollusken. Arch. f. mikr. Anat. Bd. 70, pp. 361-413.

Hoyle, W. E.
1886. Report on the Cephalopoda collected by H.M.S. Challenger during the years 1873-1876. Challenger Reports, Vol. XVI, Part XLIV, pp. 1-245.

Isgrove, Annie.
1909. Eledone. L.M.B.C. Memoirs. (London: Williams and Norgate.)

Klemensiewicz, R.
1878. Beiträge zur Kenntniss des Farbenwechsels der Cephalopoden. Sitzungsber. Akad. Wiss. Wien, Bd. 78, math.-naturw. Kl. Abth. 3, pp. 7-50.

Phisalix, C.
1892a. Recherches physiologiques sur les chromatophores des céphalopodes. Arch. de Physiol. norm. et path., sér. 5, tom. 4, pp. 209-224.

Phisalix, C.
1892b. Structure et développement des chromatophores chez les céphalopodes. Arch. de Physiol. norm. et path., sér. 5, tom. 4, pp. 445-456.

Phisalix, C.
1894. Nouvelles recherches sur les chromatophores des céphalopodes. Centres inhibitoires du mouvement des taches pigmentaires. Arch. de Physiol. norm. et path., sér. 5, tom. 6, pp. 92-100.
Polimanti, M. Osv.
1910. Les céphalopodes ont-ils une mémoire? Arch. de Psych., tom. 10, no. 37, pp. 84-87.
Pouchet, G.
1876. Des changements de coloration sous l'influence des nerfs.. Jour. Anat. et Physiol. norm. et path. tom. 12, pp. 1-90.
Rynberk, G. van.
1906. Über den durch Chromatophoren bedingten Farbenwechsel der Tiere (sog. chromatische Hautfunktion). Ergeb. der Physiol., Bd. 5, pp. 347-571.
Sangiovanni, M.
1829. Des divers ordres de couleurs des globules cromophores chez plusieurs Mollusques 'phalopodes; *Description* de quelques espèces nouv les, et particulièrement de l'Argonaute. Ann.des Sci. Nat., sér. 1, tom. 16, pp. 315-336.
Steinach, E.
1901a. Studien über die Hautfärbung und über den Farbenwechsel der Cephalopoden. Arch. f.d. ges. Physiol., Bd. 87, pp. 1-36.
Steinach, E.
1901b. Ueber die locomotorische Function des Lichts bei Cephalopoden. Arch. f.d. ges. Physiol., Bd. 87, pp. 38-41.
Uexküll, Jacob von.
1905. Leitfaden in das Studium der experimentellen Biologie der Wassertiere. (Wiesbaden: J. F. Bergmann.)

PLATE I.*

Explanation of Figures.

1. A uniform phase of coloration which generally occurs when the animal is at rest (see text p. 25).

2. This phase is darker and is associated with muscular activity (see text p. 26).

*By an unfortunate error, discovered too late for correction, each plate is headed "Univ. of Toronto Studies Biological Series No. 8" instead of "No. 10."

PLATE I.*

EXPLANATION OF FIGURES.

1. A uniform phase of coloration which generally occurs when the animal is at rest (see text p. 25).

2. This phase is darker and is associated with muscular activity (see text p. 26).

*By an unfortunate error, discovered too late for correction, each plate is headed "Univ. of Toronto Studies Biological Series No. 9," instead of "No. 10."

1

2

E. V. C. del.

D. Meisel, lith. Boston

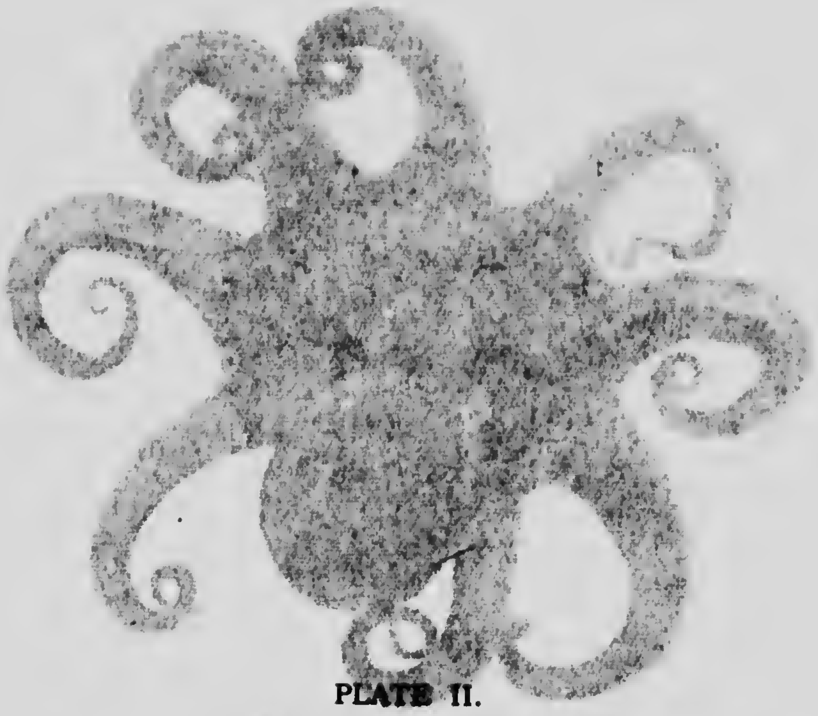


PLATE II.

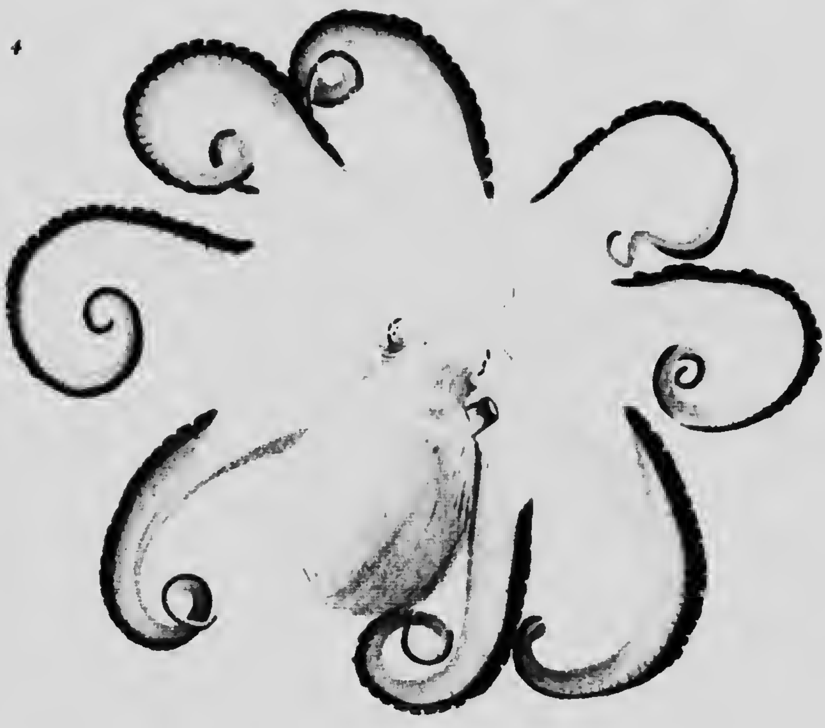
Explanation of Figures.

3. Another uniform phase of coloration which occurs when the Octopus is irritated and often follows the ejection of ink (see text p. 27).

4. This coloration occurs when the animal is frightened or pursued by an enemy or when it is poked with a stick (see text p. 28).

3

4



E.V.C. del

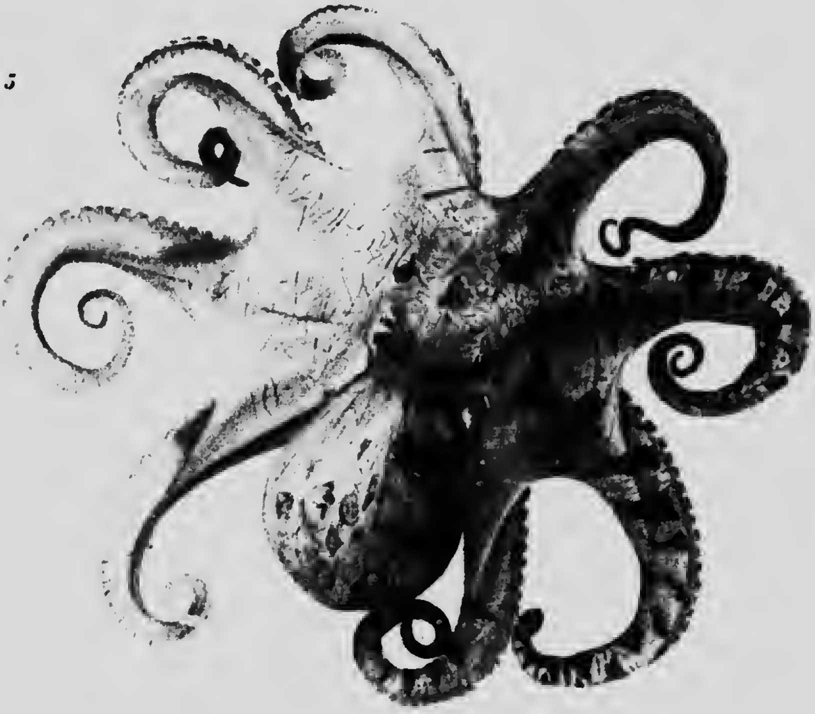
B. Meisel lith dest.

PLATE III.

Explanation of Figures.

5. One of the lighter mottled patterns (see text p. 28).
6. A darker mottled pattern (see text p. 29).

5



6

B. Meisel, lith. Boston

PLATE IV.

Explanation of Figures.

7. The rarest of all observed colorations, occuring only when the Octopus is in the act of swimming (see text p. 31).

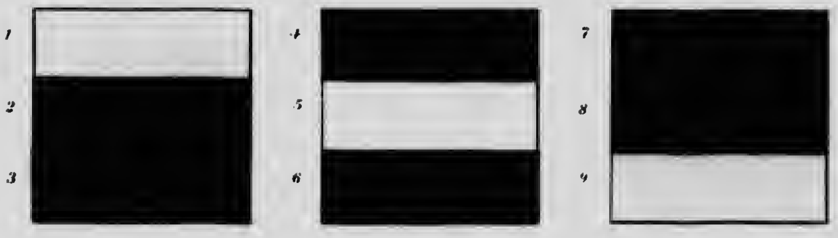
8. One of the most remarkable of the striped patterns, on account of its startling appearance and of the fact that some Octopi show it very frequently, while in others it is never seen (see text p. 32).

9. A chart indicating the colours used in the experiments on change in environment.

7

8

9



E V G del.

UNIVERSITY OF TORONTO STUDIES.

BIOLOGICAL SERIES.

No. 1:	The gametophyte of Botrychium Virginianum, by E. C. JEFFREY	o.p.
No. 2:	The anatomy of the Osmundaceae, by J. H. FAULL	o.p.
No. 3:	On the indentification of Meckelian and mylohyoid grooves in the jaws of Mesozoic and recent mammalia, by B. ARTHUR BENSLEY	o.p.
No. 4:	The megaspore-membrane of the Gymnosperms, by R. B. THOMSON	1.00
No. 5:	The homologies of the stylar cusps in the upper molars of the Didelphyidae, by B. ARTHUR BENSLEY	0.50
No. 6:	On polystely in roots of Orchidaceae, by J. H. WHITE.	0.50
No. 7:	An early Anadidymus of a chick, by R. RAMSAY WRIGHT	0.25
No. 8:	The habits and larval state of Plethrodon Erythronotus, by W. H. PIERSOL	0.50
No. 9:	Spawn and larva of Ambystoma Jeffersonianum, by W. H. PIERSOL	0.25
No. 10:	The colour changes of *octopus vulgaris* Lmk., by E. V. COWDRY	1.00