CHANGES IN SHADE, COLOR, AND PATTERN IN FISHES, AND THEIR BEARING ON THE PROBLEMS OF ADAPTATION AND BEHAVIOR, WITH ESPECIAL REFERENCE TO THE FLOUNDERS PARALICHTHYS AND ANCYLOPSETTA

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By S. O. Mast

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Contribution from the United States Fisheries Biological Station, Beaufort, N. C.,
and the Zoological Laboratory of the Johns Hopkins University

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INTRODUCTION.

Color and color patterns in plants and animals have a fascinating interest for almost every one. The layman as well as the artist, the scientist, and the philosopher shares in this. There are not only the questions as to the origin, inheritance, and philogenetic development of such phenomenal, though relatively permanent, color schemes as are found particularly prominent in many tropical birds and fishes, but also the still more interesting questions regarding the biological significance and the mechanism of changes in such surface characteristics in individuals; not only ontogenetic changes which are more or less permanent, but especially such rapid and reversible changes as are well known to occur in the chameleon and a considerable number of other widely separated species.

The literature on the subject in general is very extensive. In an excellent review covering the more important references bearing only on changes in the color in animals, Van Rynberk (1906) has collected a bibliography consisting of 402 titles, and since the publication of this review many more papers have appeared. But in spite of all the work done, it will be necessary to do much more before the more fundamental problems involved are solved.

This paper, as the title indicates, deals primarily with the reversible changes that occur in the shade, the color, and the pattern in fishes, with especial reference to their extent and biological significance and the factors involved in their production. Considerable space, however, is also devoted to problems in behavior.

That there are marked changes in the appearance of fishes has long since been known. The Romans, Van Rynberk maintains, more than 2,000 years ago were wont to entertain the ladies at dinner with exhibits in changes in the color in fishes, mostly due to injury. In more recent times records show that under various circumstances very striking changes in both pattern and color have been observed by numerous investigators in many different fishes. These changes, in accord with their supposed cause or significance, have been classified as follows: (1) Psychic, (2) sexual, (3) adaptive.

(1) Townsend (1909) and others have observed that many fishes often suddenly change in appearance, sometimes without any apparent external cause, but more often

when mechanically stimulated or when some object, as, e. g., another fish comes within the range of vision. In general, the difference in the shade of the various regions of the skin becomes, under such conditions, much more pronounced. Such changes are usually referred to as psychic. They may possibly be protective by way of warning off enemies.

(2) Many authors have observed that during the breeding season the colors in various fishes, especially the males, become much brighter and the entire surface becomes more conspicuous. These changes are generally supposed to be functional in sexual selection. Hess (1913), however, has recently offered serious objections to this view. He maintains that in some species which spawn at a depth of 60 meters the males become brilliantly colored during the breeding season, and that red and yellow predominate, although at that depth these colors do not exist, for all of the longer waves of light have been absorbed.

(3) It is held by many that fishes simulate the background, not only in shade but also in color. Stark (1830), De Vescovi (1886), Van Rynberk (1906), Frisch (1912), Šećerov (1913), and others have come to this conclusion regarding a considerable number of genera (*Blennius*, *Gobius*, *Labrus*, *Crenilabrus*, *Solea*, *Rhomboidichthys*, *Nemachilus*, *Phoxinus*, etc.). Van Rynberk (1906, p. 549) says that particularly in *Rhomboidichthys* the skin assumes a color strikingly similar to that of the background, "exquisite anpassung an den Farbenton des Bodens," and Frisch is equally positive in asserting that there is color adaptation in *Phoxinus*.

These conclusions, however, have not gone unchallenged. Schöndorff, on the basis of results obtained in experiments on trout of the same species studied by a number of the investigators referred to above, concludes that there are no adaptive color changes in fishes. He writes (1903): "Wenn früher einige Autoren wie z. B. Stark (54) die Behauptung aufstellten, die Farbe der Fische richte sich nach dem Grunde des Gefässess, in dem sie gehalten würden, so beruht dies auf einem Irrthum." Hess is even more positive in his denunciation of the idea of adaptive coloration in fishes, although his criticism is directed primarily toward the work of Frisch. He repeated and extended much of Frisch's work and found no evidence indicating production of color in the skin in harmony with that of the environment. He says (1913, p. 439): "Frisch's Angaben über die Farbenanpassung der Pfrille sind sämtlich unrichtig. Die Farbe des Grundes hat keinen Einfluss auf die Farbung der Pfrille."

Not only has it been maintained that fishes simulate the background in brightness or shade and in color, but it has also been asserted, particularly by Sumner, that the pattern in the skin changes, so as to continually harmonize with that of the background. Sumner found in experiments on some of the flatfishes, especially *Rhomboidichthys*, that the size of the figures in the skin changes to correspond to a most remarkable degree with those in the bottom on which they lie. This is illustrated in his excellent photographs (1911, p. 481–505). A careful study of these photographs shows clearly that if the light and dark areas in the background are small the figures in the skin are also small, and if the areas are large the figures are correspondingly large. But the form of the figures in the skin does not appear to depend upon that of the areas in the background. It is essentially the same in fishes on a bottom containing alternate black and white squares as it is on one containing alternate black and white stripes, or black spots on a white field, or white spots on a black field, or an irregular pattern as is found in nature on gravel bottoms. Sumner says (p. 468): "Squares, crossbands, circles, etc., were never copied in any true sense by the fishes." But he does maintain (p. 472) "that there may be very specific relations between the distribution of light and shade in the background and the pigment pattern assumed by the fish."

Pitkin, Loeb, and others, however, appear to hold that there is in the skin of these fishes an actual reproduction of the pattern in the background, especially in reference to the spacial interrelationship, form, and size of the light and dark areas. On the basis of this assumption very important conclusions have been formulated.

Pitkin (1912, p. 401) points out that since the eyes of the flatfish are so near the bottom the images on the retina are much foreshortened; that is, an area on the bottom having, e. g., a circular outline produces an image having an elliptical outline. He maintains, however, that in reproducing the pattern of the bottom the fish makes corrections for perspective distortion. He holds that the configuration of the bottom is reproduced in the skin, not as it would appear to an observer with eyes in the position of the eyes of the fish, but as it would appear to one with eyes directly above. Thus, Pitkin ascribes to this simple vertebrate most remarkable abilities.

Loeb (1912), overlooking entirely the question of foreshortening referred to above, holds that the different points stimulated in the retina bear the same spacial interrelation as the different points in the background which produce the image; and on the basis of the assumption that there is in the skin an actual reproduction of the pattern found on the bottom, he maintains that the impulses, as they travel through the nervous system, have the same spacial interrelation as have the different points stimulated in the retina. All this, he asserts, supports the theory of localization in the brain. He says (p. 81): "There exists, therefore, a definite arrangement of the images of the different luminous points of the ground on the retina and a similar arrangement of the images of the luminous points on the skin of the fishes." And from this he concludes that "vision is a kind of telephotography."

Thus the main points of contention concern the question as to the relation between the color of the environment and that of the fish, and the question as to whether or not there is in the skin of the fish an actual reproduction of the pattern of the background.

Regarding the biological significance of changes in the shade, the color, and the pattern in the skin there are various opinions. Some hold that these changes are purely accidental and have no biological value; others maintain that they function as a protection from enemies or in capturing prey; still others assert that they are primarily of value in the process of courtship and mating; a few contend that they function chiefly in regulating the temperature; and some even think they are of use in all of these ways and that they have still other functions. Townsend says (1909, p. 3): "Under natural conditions the changes of color are made chiefly for the purpose of concealment from enemies. They are also used for the capture of prey, for signaling, warning, mimicry, courtship, and other purposes." Unfortunately, however, none of these ideas are supported by experimental evidence. In no case has it ever actually been proved that changes in the appearance of the skin have any value whatsoever.

In regard to the mechanism involved in the phenomenon in question, practically all that is known is that it is largely dependent upon the distribution of pigment in certain cells found in the skin, and that the process of distribution is to a large extent regulated through the sympathetic nervous system. We shall later refer directly to the literature on this phase of the subject.

GENERAL SURVEY OF CHANGES IN SHADE, COLOR, AND PATTERN IN FISHES.

During the summers of 1913 and 1914 a considerable number of different fishes were kept in aquaria about the laboratory at Beaufort, for various purposes, by different investigators. Superficial observations were made from time to time on all of these fishes. No detailed record was kept of these observations, nor were the species recorded, although it may safely be said that there were at least 30. Changes in shade occurred in practically all of the species observed, changes in color in a relatively large number, and changes in pattern in relatively few. In some these changes were slight and insignificant, in others very striking. Some of the changes observed occurred very suddenly and were transient; others proceeded gradually and slowly, requiring hours or even days for complete adjustment. In some species most of the changes occurred without any apparent reference to the environment, the stimulus evidently being internal, and in these there was little evidence of adaptation. In others, nearly all of the changes were clearly due to alterations in the shade, configuration, or color of the background. These animals, in some instances, came to resemble their surroundings to a most remarkable degree.

In a number of the species referred to above the changes in shade, color, and pattern were somewhat more thoroughly studied by putting them successively into different boxes painted on the inside as follows: Black, white, white with black spots, yellow, red, green, and blue. The results of these observations are briefly summarized in table 1.

In judging the effect of a given background, the fishes were frequently put upon a different background [a] and compared with specimens which had been on this long enough to become fully adjusted. In most cases the changes in the skin were so marked that there was not the slightest doubt concerning them. All of those concerning which there was any doubt are indicated in the table by means of a question mark.

By referring to this table it will be seen that all of the species mentioned assumed a light shade on a light bottom and a dark shade on a dark bottom, and that a number changed in color so as to harmonize in this respect with the bottom, but that the skin assumed a pattern similar to that of the bottom in only a few species. These changes were of such a nature that I was fully convinced that whatever the significance may be, they are related to the background in such a way as to make the individuals incon-

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[a] This precaution is very important, especially in judging the effect of the background on the color, particularly in translucent forms, such as *Menidia*. Enough light passes through these creatures to make them resemble somewhat the background in color, no matter what it may be. It was found, however, in this case that when those which had been in a box of a given color were put into one of a different color, they still showed a predominance of the color of the box from which they had been taken, in spite of the interference of the color reflected from the new background. For example, an individual taken from the green box and put into the yellow box appeared very distinctly green, especially above the eyes and along the sides, while in the individual which had been in the yellow box continuously these same parts appeared yellow and not a trace of green could be seen. In the observations, the results of which are recorded in table 1, similar tests were applied in practically all cases.

spicuous. This is especially marked in *Paralichthys*[a] *dentatus* and *P. albiguttus*, and fairly prominent in *Ancylopsetta quadrocellata*. In *Paralichthys*, especially *albiguttus*, the simulation of the background, both in color and pattern, is so accurate that in many instances the animals become almost invisible, as will be shown in detail later.

TABLE I.—DEGREE OF ADAPTATION TO THE BACKGROUND IN VARIOUS FISHES.

Species.	Background.						
	Black.	White.	Spotted.	Yellow.	Red.	Blue.	Green.
Paralichthys albiguttus...	Very dark...	Very light...	Spotted.....	Yellow......	Reddish brown.	Bluish......	Greenish.
P. dentatus..............	.....do......	.....do......	.....do......	.....do......	.....do......	.....do......	Do.
Ancylopsetta quadrocellata.	.....do......	.....do......	.....do......	.....do......	.....do......	Bluish gray.	Greenish gray.
Etropus crossotus.........	.....do......	.....do......	Darker but not spotted.	.....do......	Brownish...	.....do......	Do.
Achirus faciatus..........	Slightly darker.	Somewhat lighter.	Not spotted.	(?)..........	(?)..........	(?)..........	(?)
Spheroides (puffer, several sp.).	Dark........	Very light...	.....do......	Yellow......	Brownish...	(?)..........	(?)
Menidia sp.?..............	Very dark...	.....do......	.....do......	Distinctly yellow.	Reddish.....	Dark blue(?)	Distinctly green.
Synodus fœtens (sand pike).	Dark........	Light.......	.....do......	Yellow......	Brownish...	Not tested..	Not tested.
Ceratacanthus and Monocanthus (foolfish) sp.?	.....do......	Light to very light.	.....do......	.....do	(?)..........	Purplish....	Strikingly greenish.
Fundulus, two species.	Very dark...	Very light...	.....do......	.....do......	Brown......	Bluish gray.	Greenish gray.
Mugil sp.?..............	.....do......	.....do......	.....do......	Not tested..	Not tested..	Not tested..	Not tested.
Symphurus plagiusa......	Slightly darker.	Somewhat lighter.	.....do......	.....do......	.....do......	.....do......	Do.
Dasyatis (sting ray, two sp.).	Dark........	Much lighter	.....do......	.....do......	.....do......	.....do......	Do.
Pteroplatea maclura (butterfly ray).	.....do......	Very light...	.....do......	.....do......	.....do......	.....do......	Do.
Opsanus tau (toadfish)...	.....do......	Light......	.....do......	.....do......	.....do......	.....do......	Do.

After having made these rather superficial observations I was fully convinced that, contrary to the opinion implied in the statements of Schöndorff and Hess, quoted above, adaptive color changes in fishes occur not only in a marked degree, but that they are rather widespread. Bearing on the first of these conclusions I hope to present irrefutable evidence. In general, these observations seem to indicate that adaptation in shade is almost, if not quite, universal among fishes; that adaptation in color is much more limited; and that adaptation in pattern is confined to relatively very few species. It was found only in *Paralichthys* and *Ancylopsetta*.

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[a] The two species of *Paralichthys* mentioned are very nearly alike, both in form and structure, and in the shade, the color, and the marking of the skin. They can, however, be readily distinguished in most cases by the difference in the number of dark oscillated areas present. *Albiguttus* has but three such areas, while *dentatus* has more, the two near the posterior end of the base of the fins being particularly prominent. (Pl. XXXVI, fig. 70; pl. XXXVII.)

DETAILED STUDY OF CHANGES IN SHADE, COLOR, AND PATTERN IN PARALICHTHYS AND ANCYLOPSETTA.

BEHAVIOR.

Observations were made throughout two seasons (July 17 to Sept. 1, 1913, and June 17 to Sept. 23, 1914) on flounders, especially *Paralichthys* and *Ancylopsetta*, with reference to their habitat, activities, character of food, method of feeding, modifiability in reactions, etc. In these observations two methods were followed—direct observations on specimens kept in aquaria, both in the laboratory and outside, and inquiry among fishermen.

Nearly all of the specimens kept in the aquaria were taken in seines on the sandy beaches of the marshes in the immediate neighborhood of the laboratory at Beaufort. They varied in length from about 3 to 33 cm. Most of them were kept in large, shallow, wooden aquaria containing water about 5 cm. deep. These fish are naturally very hardy, and under such conditions they thrived very well with a surprisingly small amount of change of water. This was especially true of the larger ones, 5 cm. long and larger, practically all of which lived the entire season. For a few days after they were put into the aquaria they appeared to be somewhat shy and did not feed, but after that most of them fed freely and nearly all became very tame, so that they could be handled without becoming noticeably excited. A number of individuals became so tame that, if hungry—and they appeared to be hungry nearly all of the time—they would come to the surface of the water whenever anyone came near, apparently looking for food, and if offered they would take it directly from the fingers.

In general, the specimens in the aquaria seemed to prefer living minnows or shrimp, but most of them came to take readily dead specimens either entire or cut. They were usually fed every other day, almost entirely on living menidia and dead anchovies.

In nature and in aquaria containing soil, flounders are usually found partly buried. Oftentimes only the eyes and the mouth are visible. (Fig. 5.) When they are thus buried, or bedded, as it is ordinarily called, it usually requires considerable stimulation to cause them to leave, and after they do leave they usually swim only a short distance and then suddenly bed again. This is accomplished by a series of rapid vibratory movements in different parts of the body, the fins and the tail successively, of such a nature that while the animal remains stationary strong currents of water are produced under it which carry the soil out in all directions. The fish then suddenly comes to rest on the bottom and the soil settles down on it. If it is fine the entire animal usually becomes well covered; if coarse only a portion along the edge. (Pl. XIX, XX.)

In aquaria without soil they give the bedding reaction quite as freely as in those with soil, and they continue to give it for at least several months, but there is some evidence indicating that they give it less frequently and less vigorously. This was particularly noticeable in a few specimens of *P. albiguttus* after they had been in a wooden aquarium for four months.

After completing this section some observations were made which throw considerably more light on the question of modification in behavior. On September 21, 9 a. m., four large specimens of *P. albiguttus* were taken from the aquaria in the laboratory, where they had been for over three months, and set free in a small tide pool. All four immediately came to rest on the bottom, but none of them bedded. This is very unusual. Flounders, under such conditions, ordinarily bed at once. At 10 a. m. each one was still in precisely the place where it came to rest. The tide was at this time ebbing and the water in the pool was rapidly running out. One of the flounders was stimulated with a stick and driven out of the pool. After leaving the pool it swam about 20 meters and came to rest on the sand in about 15 cm. of water, but it did not bed. Another specimen was then stimulated. It swam about 1 meter and came to rest without bedding. It was again stimulated, after which it again swam a short distance, but this time it bedded when it came to rest. The bedding reaction, however, was so feeble that only the edges of the fins became covered with sand. Thereafter this specimen bedded every time that it came to rest, but none of the other specimens gave this response. The water in the tide pool had in the meantime become so low that the remaining two specimens could no longer swim out. Both were caught and carried out. All four specimens were now lying on the sand in shallow water, one bedded and three not. Half an hour later all four were found stranded on the beach. None had moved as the tide ebbed until it was so low that they could not get away. They had so completely forgotten the ways of the sea that all would have perished had they not been rescued. They were carried out and thrown into water about 30 cm. deep and left.

At low tide another observation was made, but only one specimen was found. All of the others had evidently gone out with the tide. This one, however, the only one which had given the bedding reaction, failed to get out and was found dead under a board. It apparently had become so accustomed to stimulation in the aquarium, where it was daily stroked and handled, that it failed to respond when the board sank with the ebbing tide, until it was too late. It had obviously completely forgotten the danger of the tides. These observations show in a striking way that the responses of these animals to given stimuli can be greatly modified.

Flounders in general are relatively quiet, especially during the daytime, when they frequently lie quiet for hours at a time. One specimen, after having been in an aquarium in the laboratory for several days, was observed to remain in a given position, without the slightest noticeable change, from 8 a. m. until nearly 6 p. m. Many others were seen to remain quiet for shorter periods, both in the laboratory and outside. In aquaria which do not contain any soil they tend to huddle together and partly cover each other (pl. XXXVII).

During the night, however, they are much more active. This is true, at least, for specimens kept in captivity. After dark considerable noise usually came from the aquaria. *Ancylopsetta* particularly has a tendency to jump out of the water. On several occasions, during the night, specimens jumped out of an aquarium, the sides of which extended 8 inches above the surface of the water.

Fishermen report that flounders often take pieces of meat of various sorts, but that they usually feed on crustacea, mollusks, and minnows; that they usually lie concealed on the bottom until their prey gets within range, then suddenly spring and seize it, but that they sometimes feed on schools of small fry near the surface, pursuing and capturing them as other fish do.

These reports were confirmed by observations in the laboratory. It was ordinarily found that the latter method prevailed only in case the fish had not been fed for a few days and were presumably hungry. I am of the opinion that this method of feeding was much more common in fish that had been in the laboratory a few weeks than in those recently brought in. It was observed that flounders, especially *Ancylopsetta*, frequently stalk their prey. Specimens were repeatedly seen creeping on the bottom with their fins, toward a minnow hovering above them, just out of reach, so slowly and smoothly that their motion was scarcely perceptible and, when they got within striking distance, spring suddenly upward and forward, capturing their prey. They rarely, if ever, take dead minnows or pieces of meat lying on the bottom motionless, but do not hesitate to to take them, even when badly decayed, if they are in motion. In fact, they appear to take decayed food quite as readily as fresh. Thus it would appear that the selection of food depends very largely, if not entirely, upon vision.

After this work was completed I found a blind specimen which learned to capture minnows, showing that vision can be dispensed with in the process of feeding. This specimen lost both eyes on September 1. From this time until September 17 it ate nothing and gave no feeding reaction. On this day, however, it was seen several times to snap at minnows that chanced to come near. On September 19, 15 minnows were put into a rather small inclosure with the blind specimen. In a few minutes it captured and swallowed one of them. After this it fed regularly on living minnows, but it was impossible to make it take dead ones. I am of the opinion that the presence of the minnows was detected only by contact, although I was not able fully to establish this point.

Owing to their peculiar habits and characteristics and their hardiness, *Paralichthys* and *Ancylopsetta* are among the most favorable of fishes for experimental work, especially of the sort described in the following pages.

ADAPTIVE CHANGES IN SHADE, COLOR, AND PATTERN.

NATURAL BACKGROUND.

It is well known that *Paralichthys* and *Ancylopsetta* usually resemble somewhat the bottom on which they lie—those taken on dark bottoms are usually dark and those taken on light bottoms are usually light. Further than this, however, practically nothing is known. Little or nothing is known concerning the nature, the degree, and the function of this resemblance. In trying to solve some of the problems just referred to, observations were made under various conditions on specimens kept on three essentially different sorts of bottoms: (*a*) Natural background; (*b*) black and white background, artificial; and (*c*) colored background, artificial.

In studying the adaptive changes on natural backgrounds, some specimens were placed directly on, and others in glass dishes over, fine gray sand; fine black sand; medium, and very coarse yellowish sand, consisting largely of small shells and fragments of larger ones; broken oyster shells; coarse black cinders; and bluish-gray pebbles.

Nearly all of the specimens used in this experiment had been for some time in a white aquarium and were uniformly very light in shade with little or no color. Very soon after they were put on the different bottoms, in some cases almost immediately, the shade, the color, and the pattern in the skin began to change, and within five minutes a striking difference could be clearly seen between the individuals on the different bottoms, although there was at this time in most cases very little resemblance between the fish and the background. Gradually, however, they came to look more and more like the background until, in the course of several days, in some cases in a few hours, in others a number of weeks, it required more than casual observation to locate the animals. This was particularly true with reference to those on the different kinds of sand. But on all of the bottoms there was a most remarkable similarity between the fish and the background in color as well as in shade and configuration. Some features of this resemblance are well represented in the photographs. (Pl. XIX, XX, fig. 1–7.)

In taking these photographs, as well as all of the others, and also the autochromes,[a] referred to later, especial precautions were taken to get the illumination of the object, depth (2 to 3 cm.) and character of the water, and the exposure and treatment of the plates in all cases as nearly alike as possible. The exposures were all made in front of a large window, in strong diffused sunlight.[b] In each case, before the exposure was made, the specimen to be photographed was kept for some time in a crystallizing dish or a shallow box in the place in which it was photographed. In these retainers the fish were fed and supplied with running water. (Fig. 1, p. 186.) They were observed frequently and gently touched and stroked until they became thoroughly accustomed to their new environment. As previously stated, however, these creatures are readily tamed and many of them, in a surprisingly short time, can be pushed about the aquarium and even picked up without showing any marked effect. Moreover, the camera was often adjusted and kept in place for some time before making the exposure. In short, the animals were given a preliminary course of training.

Such precautions are of the greatest importance in work of this sort, for the appearance of the skin changes greatly if the animals are disturbed. (Fig. 21, 22.) In animals just brought into the laboratory the slightest movement about the aquarium usually induces such changes; merely directing one's eyes toward them is often sufficient.

No changes, by retouching or otherwise, were made in any of the figures. Standard Orthenon plates were used almost exclusively. Moreover, careful observations were made and recorded in each case at the time the photograph was taken, and in printing these descriptions served as a guide in attempting faithfully to reproduce the various shades and patterns assumed by the fish. Thus the inaccuracies in reproduction were reduced to such an extent that I feel certain they are of no serious consequence, especially in conclusions resting upon a comparison of the skin with the background or of the skin in individuals under different conditions.

By referring to these photographs it will be clearly seen that the light and dark areas in the skin are relatively large in the individuals on coarse-grained bottoms and relatively small in those on the fine-grained bottoms, and that the shade of the skin in general corresponds well with that of the background. But the adaptation in color,

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[a] The technical work connected with the photographs and autochromes was done by F. H. Harper, to whom I am under great obligations for apparatus as well as for expert service.

[b] Some autochromes were later taken in direct sunlight.

not shown in the photographs, was fully as striking as the adaptation in shade and pattern. In the specimens on the shells the skin was very distinctly brownish yellow; in those on the gray sand it was yellowish gray; while in those on the black sand there was no trace of yellow or brown, nothing but black and white. The adaptation in color, however, was more clearly evident in specimens kept in boxes painted on the inside. These experiments we shall consider in detail later.

Thus by changes in the shade and color, and in the pattern in the skin and by partly burying, these animals become very effectively concealed on a variety of different bottoms. But there is still another peculiarity in their reactions that serves this same purpose. When they lie on the bottom the central portion of the body is usually considerably raised in such a way as to form a channel from the lower gill to the posterior end, and while in this position they frequently breathe only through this gill, the exposed gill being closed and perfectly quiet. Thus when buried in sand the water enters the mouth, passes through the lower gill, back under the body and up on either side of the caudal fin (fig. 5), where it can be seen oozing up through the sand, moving the grains slightly. This is the only movement that can be detected, except a very slight and inconspicuous movement in the mouth. As to the function of the concealment we have all sorts of suggestions, but as yet no direct evidence. I hope, however, to deal with this matter experimentally in the near future.

BLACK AND WHITE BACKGROUND, ARTIFICIAL.

While the study of *Paralichthys* and *Ancylopsetta* on natural bottoms shows conclusively that the skin tends to assume a pattern such as to make the fish inconspicuous, it shows but little concerning the relation between the pattern assumed and that found in the background. It does not tell us precisely why the pattern in the skin resembles the bottom. It gives but little knowledge concerning the degree of accuracy with which the configurations in the bottom are reproduced. For this purpose it is essential to be able to test the effect of figures which can be varied as desired with reference to size, form, and interrelationship. This can readily be done by means of artificial backgrounds. Such backgrounds were made by painting, with india ink, various figures on bristol board.

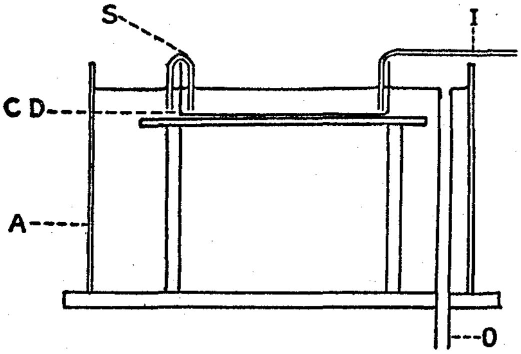

FIG. 1.—Vertical section of apparatus used in studying adaptation to artificial backgrounds. A, aquarium; CD, crystallizing dish; S, siphon; I, inlet for water; O, outlet.

The fish to be tested were in all cases put into 21 cm. glass crystallizing dishes and these, containing water about 2 cm. deep, were set in water of the same depth on the painted boards, which were always put between two thin clear glass plates so as to protect them against the action of the water. To change the background it was only necessary to remove one board and push under another with a different figure. In every case all bubbles of air were removed from under the dish. This is of the greatest importance, for if not removed there is so much refraction and reflection that the figures may appear much distorted, and if the air is sufficient to form a continuous layer many of them can not be seen at all when viewed from such a small angle of elevation as the eyes of these animals have.

The fishes were supplied with oxygen by means of a continuous stream of sea water from the storage tank. This water flowed out of the dish through a siphon so arranged as to insure in the dish a constant depth of water. This could be varied as desired by simply raising or lowering the dish. (Text fig. 1, p. 186.)

The different sorts of backgrounds used in these experiments and the general results obtained are summarized in tables II and III and in the photographs reproduced on plates XXI–XXXV.

TABLE II.—RELATION BETWEEN THE PATTERN IN THE SKIN OF THE FISH AND THE FORM, SIZE, AND ARRANGEMENT OF THE FIGURES IN THE BACKGROUND.

Form of figures.	Size.	Relation.		Pattern in skin of fish.
		In size.	In position.	
Square	2 cm	Equal	Alternate	Very coarse, large black spots.
Do	1 cm	do	do	About the same, but more black spots.
Do	5 mm	do	do	Smaller black spots more numerous.
Do	2 mm	do	do	Very fine spots much more numerous.
Rectangular	5 by 10 mm	do	do	Somewhat coarser than on 5 mm. squares.
Rotated rectangular.[a]	do	do	do	Do.
Stripes	10 mm. wide	do	do	More white than on 10 mm. squares.
Do	5 mm. wide	do	do	More white than on 5 mm. squares.
Black spots	1 square cm	Black equals white		Same as on 10 mm. squares.
White spots	do	do		Fewer spots than on 10 mm. squares.
Black spots	do	Black equals ¼ white		Much more white. Fewer black spots, but about same size as on 10 mm. squares.
White spots	¼ square cm	Black equals 15 white		Much more black. Fewer white areas, but about same size as on 5 mm. squares.
Solid black, no figures.				Very dark, nearly uniform, save usually a light area near pectoral fin, and in some specimens a number elsewhere.
Solid white, no figures.				Very light, nearly uniform, usually some light grayish patches.

[a] In this test the background was continuously rotated.

TABLE III.—RELATION BETWEEN THE PATTERN IN THE SKIN OF FLOUNDERS AND THE SIZE AND TOTAL RELATIVE AREA OF BLACK CIRCULAR FIGURES ON A WHITE BACKGROUND.

Diameter.	Distance apart both ways.	Percentage of black.	Effect on pattern in fish.
	Millimeters.		
0.5 millimeter	20	0.0535	No effect; same as on all white background.
Do	10	.2121	No effect.
Do	5	.8484	Do.
Do	2.5	3.3936	No effect, except probably slightly grayish, no spots.
1 millimeter	20	.1964	No effect.
Do	10	.7856	One small black spot.
Do	5	3.1424	Three small black spots.
2 millimeters	20	.7856	No effect.
Do	10	3.1424	Three small black spots.
3 millimeters	20	1.7175	Do.
Do	10	6.87	Three larger and denser black spots and numerous small ones.
5 millimeters	20	5.302	Do.
Do	10	21.21	Numerous black spots.

By referring to table II and plates XX–XXXV, it will be seen at once that there is, on artificial backgrounds as on natural bottoms, a tendency in the skin of the fish to assume an appearance somewhat similar to that of the environment. On a white background all of the black areas in the skin disappear; on a black one frequently all of the white areas except one near the pectoral fin disappear. In general, it may be said that the larger the proportion of the background covered by the black areas the larger the proportion of black in the skin and vice versa, and the smaller the black and white areas in the background the smaller those in the skin. This is well shown in figures 9–17.

These statements hold, however, only within certain limits. If the black areas are small it requires a larger proportion of black, under certain conditions, to produce the same effect than it does if they are larger. This is shown in some of the records in table III and in plates XXXI, XXXII. A background with dots 3 mm. in diameter, 20 mm. apart, produces very nearly as much black in the skin as one with dots 2 mm. in diameter and 10 mm. apart (fig. 52, 54), although in the former there is only 1.71 per cent black while in the latter there is 3.14 per cent black. And if the dots are very small there are no black areas produced in the skin, no matter how great the proportion of the background covered with black (fig. 49). In the specimen used in obtaining the results recorded in table III, dots 0.5 mm. in diameter, 2.5 mm. apart, produced no black spots in the skin, while dots 1 mm. in diameter, 10 mm. apart, did, although in the former case 3.39 per cent of the background was black and in the latter only 0.78 per cent. If the figures are very small the black acts just as it does if uniformly distributed. That is, a background containing numerous very small spots has the same effect as a uniform gray background. This matter was, however, tested only in a single individual.

If the light and dark areas are excessively large the skin also tends to assume a uniform shade; or, at any rate, there is no simulation of the background. The size of the figures required to produce this varies with the size of the fish. The 2 cm. squares represented in figures 11 and 15 are very near if not slightly beyond the limit in size for simulation in specimens of the size, 14 cm. long, shown in these figures; while in smaller specimens, 10 cm. long, represented in figure 18, the limit in size, of the figures simulated is about one-fourth as great. The effect of relatively coarse-grained bottoms like these depends, however, upon the position of the fish. If the fish is held so that the head is on a black area and the edge of the anterior end of the animal is on white, as in figure 15, the skin assumes a much larger proportion of white than it does if the head is held on a white area and the edge is on black. The production of a uniform shade results if the figures are so large compared with the size of the fish, that one eye is ordinarily affected mainly by black and the other mainly by white. We shall consider the cause of this later.

While large specimens come to resemble the background more closely than small ones if it contains relatively large configurations, the opposite is true if the configurations are small. In the smaller specimens, 5–15 cm. long, adaptation also proceeds more rapidly than in the larger ones, 20 cm. and up.

Relation between the pattern in the skin and that in the background.—Our evidence shows conclusively that both on natural and on artificial backgrounds there is a configuration produced in the skin which resembles that of the background. This is clearly shown in the photographs already referred to. This resemblance between the fish and the background was, however, even more remarkable in specimens which had been for several weeks in a variegated dark blue and white granite pan. (Pl. XXVII, XXVIII.) Is this resemblance due to an actual reproduction of the configurations in the background, as maintained by Pitkin and Loeb, pointed out in the introduction, or is it the result of some other phenomena?

By referring to table II and comparing figures 12, 26, and 27, all reproductions of photographs of the same individual on backgrounds having black and white areas equal in size but different in form, it will be seen that the pattern in the skin of the fish is practically identical in all. The same dark spots and patches are found in all, and they have the same form and relative position, although in the different backgrounds the light and dark areas differ greatly both in form and in spacial interrelationship.

The same will be found to be true in comparing figures 23, 24, and 25. In figure 23 the background was changed every time the fish moved, so as continuously to keep the long axis of the fish parallel with the short axis of the light and dark areas; in figure 24 it was so regulated as to keep this axis parallel with the long axis of these areas; and in figure 25 the background was continuously but very slowly rotated. Thus, in figure 23 the light and dark areas, owing to foreshortening from the flounder's angle of vision, appeared nearly square, in figure 24 very much elongated, and in figure 25 the appearance changed continuously. Yet the pattern produced in the skin by these different backgrounds appeared to be the same, even in details visible only under considerable magnification. This may be seen by comparing with a lens the photographs reproduced in the three figures mentioned above, and even more clearly by studying those reproduced in figures 31–40.

Figures 33 and 34 represent the same individual on different backgrounds. In figure 33 the specimen was in a shallow granite pan which was dark blue speckled with white. The white spots, as shown in the photograph, varied in form and size and were scattered promiscuously over the surface. Figure 34 represents the same individual on an artificial black and white background. The white areas in this background covered about the same proportion of the whole as the white areas did in the granite pan, and they were on an average about the same size on the two backgrounds; but in the former they were regularly arranged and fairly uniform in shape, while in the latter they were irregularly arranged and varied much in form.

By examining these two figures it will be seen, however, that there is a striking similarity in the patterns produced in the skin. On the artificial background there are in the skin a number of light areas which resemble the white spots in the background quite closely in size but not at all in form and arrangement. In the pattern produced in the pan these light areas are all present, moreover they are practically the same in size and form and have precisely the same relative position, respectively, as those in the pattern produced by the artificial background, although the form and arrangement of the white spots in the two backgrounds differ greatly. This is well illustrated in figures 39 and 40, which are photographic enlargements of a small region taken somewhat above the ventral ocellus in figures 33 and 34, respectively. The same characteristic is shown in figures 31 and 32. In figure 32 the white areas in the background are somewhat larger than they are in the pan, represented in figure 31. The white spots in the skin are likewise somewhat larger in the former, but they have precisely the same spacial interrelationship in both. In neither, however, is there any similarity in arrangement between the spots in the skin and those in the background. This is clearly shown in figures 35, 36, 37, and 38. These figures are photographic enlargements of certain areas in figures 31 and 32. The magnification in all is approximately nine diameters. Figures

35 and 38 represent the background and figures 36 and 37 a small portion of the surface of the fish shown in figures 31 and 32, respectively. The section of the skin enlarged in these figures is found in the same relative position as that enlarged in figures 39 and 40.

A glance at these figures shows at once that there is no indication of an actual reproduction of the background. In the granite pan the adaptation of the fishes to the background in color and shade, as well as in pattern, was, as previously stated,[a] most remarkable. So closely did they resemble the bottom, in most instances, that strangers rarely saw them until they were pointed out, and yet a comparison of figures 35 and 36 shows conclusively that the configuration of the light and dark areas in the skin is strikingly different from that in the background. The pattern in the skin, on the other hand, is almost identical, even in minute details, with that produced by the artificial background. The different black and white areas in one are practically identical in form and spacial interrelationship with those in the other, although some are considerably larger on the artificial background than they are in the pan. This is especially true of the prominent white spots, two of which are included in the areas enlarged.

The simulation of the background in *Paralichthys*, in so far as the pattern in the skin is concerned, is due merely to the formation in the skin of light and dark areas similar in size to those in the background. On a background with large figures the light and dark areas in the skin become relatively large. On one with small figures the pattern breaks up into small areas, black dots appearing in the larger white areas and white ones in the larger black areas. The location of these dots and their form are morphologically fixed. They are essentially the same in fishes over a background consisting of alternate black and white stripes as they are over one consisting of alternate black and white squares, or one consisting of black spots on a white field, or white spots on a black field, or one consisting of light and dark areas irregular in form and arrangement, as found in granite pans and on natural bottoms.

All our evidence supports the general conclusion of Sumner with reference to *Rhomboidichthys*, stated in the following words (1911, p. 468): "Squares, crossbands, circles, etc., were never copied in any true sense," and contradicts the contention of Pitkin and Loeb that there is an actual reproduction of the figures in the background. It supports only with certain limitations Sumner's contention (p. 472) "that there may be very specific relations between the distribution of light and shade in the background and the pigment pattern assumed by the fish." *The size of the light and dark areas in the background and the relative amount of surface covered by them have a profound effect on the pattern produced in the skin, but the form and arrangement of these areas have, at least within rather wide limits, none.*

Individuality of the pattern.—In some individuals adaptation is very much more precise and is attained much more rapidly than in others. This, however, I think is largely due, as I shall show later, to difference in experience.

The characteristic markings in the skin of different individuals of the same species appear very much alike, provided they are on the same background. This is clearly seen by comparing figures 10, 19, 20, and 30, all photographs of different individuals of the same species on similar backgrounds. In detail, however, there is considerable variation in the patterns of these individuals, as a comparative examination with a lens

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[a] See the autochrome, fig. 66.

of the same area in the different photographs mentioned will show. In all of the specimens of this species there are three small but prominent black areas, ocelli, which stand out rather conspicuously, especially in animals adapted to a background containing relatively little black. They are well shown in some of the figures on plates XXVI and XXXII, and also in many other figures. In individuals adapted to a white background they are light gray and quite indistinct, but they can still be seen. On backgrounds containing much black, however, these areas become continuous, with larger black patches, and can no longer be distinguished.

Without a lens it can be readily seen that the ventral one of these ocelli is elliptical in outline in figure 9, and in all of the other photographs of this individual in which it can be seen at all (fig. 9–17, 23–29, 49–55). In figure 19, which represents a different individual, this area is, however, very nearly circular, and the posterior border contains a small but conspicuous white spot. These characteristics are seen in all of the photographs of this individual. They are particularly prominent in figures 33 and 34. In figures 31 and 32, photographs of still a different individual, this area has other distinguishing features. Thus any individual could be recognized by the characteristics of this area alone. There is probably quite as much individual difference in every other section of the surface, so that the patterns of different individuals of the same species which superficially appear so nearly alike are, in detail, so different that every individual could be recognized by a thorough examination of any small area of the pigmented surface probably not larger than 0.5 mm. square. This individual variation becomes very evident in a comparison of figures 36 and 37 with figures 39 and 40; the former represent enlargements of a given area of one individual on two different backgrounds, the latter enlargements of the same area of another individual of the same species, *P. albiguttus*, on similar backgrounds. By examining these figures closely it will be seen that while nearly all of the light and the dark areas and spots found in one individual are also found in the other, they differ considerably in form. There is, in fact, more difference in the details of the patterns in the two individuals on the same background (granite pan) than there is in the patterns of the same individuals on the different backgrounds.

Effect of mechanical and other stimuli on the pattern.—If *Paralichthys* or *Ancylopsetta* is mechanically stimulated, contrastive patches suddenly appear in the skin. If the fish are adapted to a dark background, numerous white spots appear, and if adapted to a white background numerous black spots appear. In either case the animal becomes very conspicuous. This is especially marked in *Paralichthys*. (Fig. 21, 22.) The degree of stimulation required to produce the reaction varies greatly. In animals that have not been handled much it ordinarily requires only a light touch. Strange objects brought in the field of vision also induce this reaction. Thus, to cause the reaction, it is often only necessary to bend over the aquarium or to bring a strange specimen within a distance of 15 to 30 cm. In such cases the change in the chromatophores is clearly due to stimuli received through the eyes. Similar changes usually occur during the process of feeding. This is particularly marked in specimens adapted to white. No new spots originate in any of these cases. That is, the spots, both black and white, appear in the same relative regions in all specimens and in the same regions in which they appear when they are caused by any other stimulating agents. As to the biological significance of these phenomena, if there really is any, we are quite in the dark.

COLORED BACKGROUND, ARTIFICIAL.

General statements.—Among those who hold that fishes simulate the background in color, Frisch (1912, 1913) has probably presented the most conclusive evidence. He made an extensive study of the reactions to color in *Phoxinus* and *Crenilabrus* and maintains that there is in these forms clearly adaptation to color. (Farbenanpassung.) Hess, however (1913), while admitting that fishes change color, maintains that there is no evidence showing that these changes bear any specific relation to the color of the environment. He asserts that the strongest point Frisch has in favor of his contention is found in his statement that *Phoxinus* on a yellow bottom becomes yellow, but, he concludes, after working on this form one and one-half years, that Frisch is in error. He kept specimens over colored bottoms for several weeks and found no specific effect of the color of the bottom on that assumed by the fish. He says (p. 407): "I did indeed find that after having been over red, yellow, or orange bottoms for a number of hours some of the specimens appeared slightly more yellow than those kept over gray bottoms, but often the opposite was true." And those on blue, he maintains, frequently appeared more yellow than those on red. Hess asserts that his opinion regarding the color of these specimens was confirmed by his colleagues, and he says that one of them even maintained that those on the gray were more yellow than those on the yellow bottom.

After the appearance of the criticism of Hess, Frisch repeated some of his experiments. He tested 22 specimens of *Phoxinus* on yellow, and asserts that 20 became yellowish and 2 did not. One of these, he says, was later found to be sick and the other abnormal, in that it contained only a very small amount of yellow pigment. Frisch states that his judgment concerning the color of these fish was confirmed at the time by his colleagues, Hertwig, Goldschmidt, and Buchner.

While the results recorded in table 1 include neither *Phoxinus* nor *Crenilabrus*, they indicate clearly, as previously stated, that adaptive color changes do occur in some fishes. A thorough study of *Paralichthys* and *Ancylopsetta*, on artificial backgrounds variously colored, proves that this conclusion is correct and shows that color-adaptation in these forms, especially in *Paralichthys*, is highly developed and extends over a wide range.

In this study nine wooden boxes, 30 cm. long, 25 cm. wide, and 7.5 cm. deep, were used. Each box was colored on the inside with oil paint ranging from dark red to very dark blue. There were thus nine boxes in all, each differing in color from the rest. The nine different colors represented in these boxes were compared with Bradley's standard colors. The common name of each and that in Bradley's classification with which it most nearly corresponds follows: Maroon (red, shade no. 2), vermilion (orange red), dark brown (orange, shade no. 2), light brown (orange, shade no. 1), chrome yellow (orange yellow), light yellow (yellow, tint no. 2), chrome green (yellow green, shade no. 2), light blue (green blue, tint no. 1), dark blue (blue, shade no. 2).

These boxes were all placed in strong diffused sunlight and so arranged that the water in them was constantly about 4 cm. deep. All of them received a constant supply of sea water from the storage tank. One or more moderately small specimens of *Paralichthys* were put into each box, and one of *Ancylopsetta* into the maroon, the chrome yellow, the chrome green, and the dark blue. Under these conditions the fish fed normally and thrived, some being in the boxes more than two months. None were lost except by accident.

When the specimens were put into the boxes, the shade, color, and pattern of the skin were nearly alike in all. Nearly all had been in a white aquarium for some time. No color, save gray of various shades, could be detected in any of them except in *Ancylopsetta*, and in these there were only some slightly irridescent patches, and at times a faint trace of brownish color in and around the four conspicuous ocelli, which are responsible for the common name "four spot," by which the members of this genus are known.

Immediately after they were put into the boxes they still appeared alike. There was no evidence whatever that colored light reflected from the sides of the boxes or transmitted through the fish from the bottom affected in any way the appearance of the fish, with the exception of the fins and tail. Within half an hour, however, there was a marked difference. There was much individual variation, but in general those in the yellow boxes were distinctly yellowish; those in the brown, brownish; those in the red, grayish or brownish; and those in the blue and green, grayish.[a] The pattern in the skin of all the specimens remained essentially the same throughout the experiment, but the shade and color continued to change greatly in all until, in the course of from a few days to several weeks, the skin in most of them came to resemble the background in color, as well as in shade to a most remarkable degree. This was especially true of those on various shades of yellow and brown, and of those on light and dark blue and chrome green.[b] (Pl. XXXIII–XXXV.) It was in general more marked in *Paralichthys* than in *Ancylopsetta*.

On red of different shades and dark green, tested in another connection, the fish did not assume a color very much like that of the background, but in each case, including the different shades of brown, red, and yellow, the color of the skin was unquestionably different from that in any other case, and it showed no resemblance to anything obtained on any shade or intensity of white, gray, or black.

Thus the effect of each of the nine different colors tested, ranging from dark red to dark blue, is specific, and since no combination of black and white, regardless of the intensity of the light, produces anything similar in effect, it is evident that this specific effect produced by the different colors can not be accounted for on the basis of differences in the intensity or quantity of light reflected by the various colors, but must be due to differences in the length of the waves. The fact that the light reflected from the colored paint was not monochromatic can affect in no way the validity of this conclusion. Pure colors, so necessary in much of the work on color-vision, are not even essential in work of this sort.

Experiments and results in detail.—These general statements and conclusions are supported by the following details regarding changes in color under different conditions, selected from my notes and by the autochromes[c] and photographs reproduced on plates XXXIII–XXXV.

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[a] The tendency to become gray is particularly marked on those colors which are apparently not readily simulated. On such backgrounds the animals become adapted in shade first and later in color, if at all. The response resulting in a gray shade is undoubtedly, in some way, associated with the quantity of light reflected from the background regardless of its quality, i. e., the length of the waves. The response, on the other hand, which results in the production of color is associated with the quality of the light. There are therefore two mechanisms involved in the process of adjustment on colored backgrounds.

[b] After this part was completed the same was found to be true for pink.

[c] It is a pleasure to acknowledge my indebtedness to W. P. Hay for his generosity in putting at my command an excellent rapid lens, without which the autochromes would have been practically impossible. Even with this lens the plates, all of which were Lumiére, required, under most favorable conditions, an exposure of nearly a minute, and it was often necessary to exercise no small amount of patience to keep the fish quiet that long. After this part was written some exposures were made in direct sunlight and in this way the time necessary was greatly reduced.

The photographs show that the light reflected from the fish had very nearly the same chemical effect on the plates as that reflected by the background, no matter what color it was, indicating that the fish were well adapted with reference to brightness or shade. By examining the autochromes it will be seen at once that the color of the fishes differs greatly. The specimens on the blue appear blue, those on the green appear green, those on the yellow appear yellow, and those on the red appear brownish. This becomes strikingly evident if the plate is covered with the gray sheet fastened to it so as to eliminate the background from view. There can be no question but that the autochromes show a correlation between the color in the background and that in the skin of the fishes, but the correlation seen in these autochromes is not as marked in many respects as it actually was in the living specimens. The blue, the pink, and the green are fairly accurately reproduced; the red and the yellow not so accurately. This may have been due, at least in part, to the action of the water on the light; for in order to prevent the formation of waves by the water forced through the gills in the process of respiration it was necessary to have the water over the fish 1–2 cm. deep.

Autochromes were taken of specimens on all of the nine different colors or shades, a total of nineteen, but those of the two shades of brown could scarcely be distinguished and there was very little difference between them and those of the two shades of yellow. The difference between the vermilion and the maroon was also much greater than the autochromes indicate. In general, there was actually much more difference in the color of the fishes than the reproductions indicate.

The original plates of nine of the autochromes reproduced on plates XXXIII–XXXV were exhibited at the meeting of the American Society of Zoologists held in Philadelphia in January, 1914. There was much surprise expressed at the remarkable contrast in the color of the fishes and the correlation between it and that of the different backgrounds, but in spite of the fact that the autochromes show less difference in color than there actually was in the living specimens and minimize the correlation between their color and that of the background, it seemed inconceivable to many that there could have been even as much as shown; and not a few suggested that the animals must have been translucent so that the background showed through them, or that the color must have been due to the reflection of light from the sides and the bottoms of the boxes.

I shall present evidence showing conclusively that these suggestions are not valid. An autochrome of a specimen of a given color in a box of a different color would have settled this whole matter, but there was so much difficulty in keeping the specimens quiet long enough for the purpose required, without removing them from the box in which they were, that, owing largely to lack of time, this was not attempted.[a] Fortunately, however, in one of the autochromes on the green color taken at the close

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[a] During my second season at Beaufort (1914) after this section of the paper was completed, W. P. Hay very generously took a number of autochromes of flounders of a given color on backgrounds of a different color. Nearly all of these autochromes were taken in direct sunlight. Thus the time of exposure was greatly reduced, and consequently much of the trouble experienced during the preceding season in keeping the animals quiet was eliminated.

Several of these autochromes are reproduced on plates XXXIII-XXXV (fig. 60, 64, 65, 66, 67). Figure 64 represents a specimen autochromed in a green box immediately after it had been taken from a blue box in which it was fully adapted. Figure 65 represents four specimens autochromed in a green box immediately after they had been taken from blue, green, yellow, and pink boxes, respectively. Figure 67 represents the same individuals autochromed on a white background. These three figures show conclusively that the color seen in the autochromes of the fishes is not due to reflection of colored light from the background, and that it therefore must be due to the structure of the skin. I shall not, however, eliminate the other evidence presented in favor of this conclusion, since it is of value in elucidating other characteristics associated with the process of adaptation.

of the season (fig. 62) the specimen had not had time to become fully adapted. This specimen, taken from the dark-blue box, appeared dark blue in color when first put into the green box and, although it had been in this box nearly four days and had changed color considerably, it was still distinctly blue when it was autochromed. This is fairly well seen in the reproduction. A comparison of this figure with figure 61, which represents the same specimen fully adapted to blue, and with figure 63, which represents one fully adapted to yellow, shows fairly conclusively that if the light reflected from the sides of the boxes or transmitted through the animals has any effect at all on their apparent color it is, with the exception of that in the fins and tail, of minor consequence. And even the fins and tail in *Paralichthys* are so nearly opaque that very little light is reflected through them from the bottom, as can be seen clearly by examining the photographs on artificial backgrounds, especially figures 17 and 26.

The best evidence in support of this contention, however, is found in the following detailed account of the changes in color, observed during the process of adaptation in the individuals on the various backgrounds. This account also throws some light on the nature of these changes and on the rate of adaptation. It will be given essentially in the form in which it was written at the time the observations were made.

Light brown.—July 27, *Paralichthys albiguttus*, 15 cm. long, taken from the white aquarium and put into the light-brown box (considerably darker than Bradley's orange, shade no. 1); it rapidly assumed a brownish color. July 31, simulation of background in shade and color, good. August 10, 12.07 p. m., color yellowish brown with numerous small bluish spots, excellent color adaptation as seen from a distance of about 75 cm. Autochromed and photographed; put into dark-blue box and compared with specimen fully adapted to blue, it still appears brown, striking contrast. August 11, bluish gray but not nearly so blue as the specimen fully adapted. At 2 p. m. it jumped into the brown box, changed back to brown almost at once. Returned to the blue box. August 12, more blue than on preceding day. August 19, simulation of background in color and shade remarkably good.

Dark blue.—August 7, a. m., *P. albiguttus*, 19 cm. long, taken from white aquarium and put on dark blue (darker than Bradley's blue, shade no. 2). Became dark gray almost at once. August 8, 10.37 a. m., autochromed. (Fig. 58.) Simulation of background in color and shade excellent. August 11, if any change, somewhat darker and bluer; pattern more nearly uniform. Put into the light-blue box.

August 11, 5 p. m., a specimen of *P. albiguttus* which had been in the green box since July 27 and appeared distinctly green was put into the dark-blue box. In this box it appeared quite as green as it did in the green box. At 6 p. m. it was still distinctly green, showing a marked contrast with the specimen autochromed on the blue. August 12, 2 p. m., much grayer but still has slight greenish tint. August 19, no longer greenish; appears much like specimen autochromed on the blue, which is still in the box. There is no evidence indicating that the color of the fish is due to colored light reflected from sides of box or transmitted through the animals, except in the fins and tails of some specimens.

On August 19 a specimen of *P. albiguttus*, thoroughly adapted in color to a brown, water-soaked, cypress board, was put into the dark-blue box. In this box it appeared as brown as it did when on the cypress board. A bright yellowish-brown stripe about 0.5 mm. wide, extending along the entire margins of the ocular opening in the skin, was particularly conspicuous. There was no indication of blue. On August 22 it was dark grayish blue, with still some evidence of brown, but not in the stripe bordering the ocular openings. This stripe was now grayish blue. It was put into the green box and compared with specimen adapted to green. Marked contrast between color of the two individuals compared. No indication of green in the specimen adapted to blue. August 27, autochromed. Color about same as August 22, brownish tinge[a] still visible, giving the animal a slightly greenish tint not seen in the other specimen on the dark blue.

Dark red.—August 2, *P. dentatus*, 14 cm. long, taken from white aquarium, put into dark red (Bradley's red, shade no. 2). August 12, rich sepia color, not red; there is a tendency to have a row of whitish spots along the fin. Rather prominent white area at the base of the pectoral fin. Three large and several smaller black spots, darker than the rest of the surface and surrounded by yellowish rings, stand out quite conspicuously. This specimen was put into the dark brown and the vermilion boxes and compared with those fully adapted to these colors. It was found to be unquestionably darker than either, but it did not show the slightest indication of any similarity to the color of the skin produced by black. This shows that the relatively long waves of light found in the dark-red color have a specific effect and that the spectrum is probably not shortened at the red end. August 29, color dark rust brown, particularly striking when compared with specimens in boxes of other colors. The pattern was very uniform and inconspicuous, and the tips of fins and tail were yellow. Autochromed and photographed. There was much difficulty in keeping the specimen quiet. It was forcibly held for some time before the autochrome was taken. This caused the skin to become abnormally mottled. The dark patches around the ocelli, shown in figure 70, are due to this.

Green and yellow.—July 27, *P. albiguttus*, 15 cm. long, taken from the white aquarium and put into the light-yellow box (Bradley's yellow, tint no. 2). August 11, adaptation very good, very little contrast in different regions of the skin, but uniformly of a slightly darker shade than background. Autochromed, photographed (fig. 56), and put into the green box. The color in all the autochromes taken on light yellow is so faint it can scarcely be seen.

When first put into the green box there was great contrast in color between this specimen and those adapted to the green. August 12, much darker, color grayish, with distinct greenish tint. In this specimen the green is more pronounced than it is in other specimens in the same box, taken from gray sand several days earlier. August 26, very good simulation of background, color yellowish grayish green. The green in the fish becomes very evident when it is compared with specimens adapted to other colors. Autochromed and photographed; colors very faithfully reproduced. (Fig. 57, 71.)

Vermilion.—July 27, *P. albiguttus*, 19 cm. long, taken from white aquarium and put into vermilion box (slightly darker than Bradley's orange red). July 31, pinkish gray, contrasting strongly with the background. August 12, general appearance when viewed from a distance of 75–100 cm. uniform sepia, contrasting considerably with background. Close examination shows a sort of network consisting of dark-brown stripes about 0.5 mm. wide which surround grayish green areas 1.5 mm. or less in diameter. White patch at the base of the pectoral fin, about 6 mm. in diameter. The three ocelli, characteristic of the species, are dark brown, not black. Put into dark-brown box and compared

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[a] This can be distinctly seen in the autochrome taken at this time but not reproduced.

with a specimen adapted to this color. It is clearly darker and more reddish. No indication whatever of black in the skin of the specimens in either the brown or the red box, showing clearly that brown or red does not have the same effect as black or gray, and that the color assumed on them is correlated with the length of the waves of light. August 26, general color rich sepia brown, having slightly greenish tint. Scattered all over the surface are small spots varying considerably in size and color; some are brown, others greenish or pinkish, and still others brown with a greenish border or greenish with a brown border. Considerable contrast between the color of the fish and that of the background. Autochromed[a] and photographed. (Fig. 59, 72.) August 30, conspicuously reddish brown with slight greenish tinge. My colleagues all remark about the redness of this specimen and the striking contrast it shows when compared with specimens of the same species adapted to other colors.

Two other specimens were kept in the vermilion box with the one referred to above. One of these was of the same species but much smaller (9 cm. long); the other (17 cm. long) was *P. dentatus*. The color in both was very much like that described, but in *dentatus* the markings in the skin were smaller and less conspicuous, and the color and shade more uniform.

Light blue.—August 12, 3 p. m., *P. albiguttus* taken from the dark-blue box and put into the light-blue box (Bradley's green blue, tint no. 1). Half hour later much lighter, grayish blue. August 27, simulation of the background excellent, finely mottled grayish blue. Pattern remarkably uniform, no light or dark areas visible. (Fig. 73.) A number of nemerteans which appear dark are seen in the fins. August 29, autochromed and photographed.

Dark blue.—August 22, *A. quadrocellatta*, 17 cm. long, caught in the seine and at once put into the dark-blue box (considerably darker than Bradley's blue, shade no. 2). This specimen changed rapidly to a dark bluish gray, except two large areas which remained very light and somewhat iridescent. August 24, the fish is more bluish; the light areas have a decidedly bluish tint; the tips of fins and tail are bright yellow. August 26, somewhat darker and more bluish. Autochromed and photographed. (Fig. 61, 74.) The colors as they appeared in the fish are fairly faithfully reproduced in the autochrome. There is, however, probably a little too much of a greenish tint in the light areas. This specimen was, at this time, transferred to the green box.

Green.—August 26, *A. quadrocellata*, the same specimen as shown in figure 61, taken from the dark-blue and put into the green box (Bradley's yellow green, shade no. 2). After it was transferred it appeared quite as blue as before. The four ocelli were distinctly blue. There was no indication of a greenish tint in any part of the surface except the fins and the tail, which were somewhat translucent. August 30, still distinctly bluish but has more of a greenish tint. The four ocelli are greenish dark gray surrounded by greenish yellow rings about 1.5 mm. wide. The large light areas have a pinkish cast. The tips of the fins and tail are bright yellow. In general, the specimen is not nearly so intensely green as the *P. albiguttus* shown in figure 57, which is still in the green box. Autochromed and photographed. (Fig. 62, 75.)

Owing to the fact that it was necessary for me to leave Beaufort at this time, this specimen was autochromed after it had been on the green less than four days, not nearly

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[a] Too much green in autochrome.

long enough to become fully adjusted to the new color. The autochrome shows that the fish was still bluish and does not indicate that there was any marked adaptation to the green. The autochrome is valuable, however, in that it demonstrates fairly conclusively that the color represented in the various autochromes is due to the structure of the skin and not to light reflected from the sides of the boxes or transmitted through the fish from the bottom, as many who have seen them intimated.

Yellow.—July 27, *A. quadrocellata*, 16 cm. long, taken from the white aquarium and put into the chrome-yellow box (slightly darker than Bradley's orange yellow). It became distinctly yellowish within a few hours, as did also a specimen of *P. albiguttus* put in at the same time. Adaptation on yellow occurs much more rapidly than it does on blue, green, or red, and there is no indication of adaptation in shade before adaptation in color occurs, as appears to be true for some of the other colors. August 7, the color of the skin is very much like that in the background except in the two large light areas and in the four ocelli, but as a whole *Ancylopsetta* is much more conspicuous than *Paralichthys*, the color of which is remarkably similar to that of the background and very uniformly distributed, making the animal very inconspicuous. *Ancylopsetta* autochromed and photographed. The colors are quite faithfully reproduced. (Fig. 63, 76.)

On a background consisting of alternate black and yellow squares the skin of *Paralichthys* assumes a conspicuous pattern consisting of black and yellow patches similar in size, form, and arrangement to the black and white patches assumed on a background consisting of alternate black and white squares of the same size.

Conclusions.—The evidence which we have presented leaves no reasonable doubt that in both *Paralichthys* and *Ancylopsetta* the skin simulates the background in color as well as in shade and pattern, and that the colors which are simulated range at least from dark blue to dark red. It shows that adaptation in shade ordinarily occurs more rapidly than adaptation in color and that adaptation to yellow is ordinarily attained in a much shorter time than adaptation to most of the other colors tested. In the case of yellow it may occur in a few minutes, while in the case of the other color it takes days and even weeks.

Thus it is evident that both the quality and the quantity of the light, the length of the waves, and the energy are functional in adaptive processes that occur in the skin. Concerning the question as to how these characteristics of light function and the question as to the process and mechanism involved, we shall have something to say later.

RATE OF ADAPTATION TO BACKGROUND.

The difference in the time required for different individuals of a given species to simulate the background is very great. This has been noted by practically all who have investigated the subject. This great difference is largely due, not to innate individual variation, but to variation in the experience of the individual; to training, if you please. Van Rynberk (1906), Sumner (1911), and others maintain that the reaction time of the chromatophores is much reduced by repetition. Sumner, referring to flatfishes, says (p. 469): "The same fish acquired with practice (if this word may be allowed) the power of changing much more rapidly than before. The time required for a radical change of shade or of pattern ranged from a fraction of a minute to several days."

The results of my observations are in harmony with the statements presented above. The time required to produce adaptive changes in the skin, both in *Paralichthys* and in *Ancylopsetta*, varies greatly. Under some conditions changes resulting in maximum adjustment in shade to a given background occur in two minutes or less; under others it requires several days. In general, the time required for adjustment is considerably longer for large specimens than it is for small ones. It is much longer for individuals kept continuously on a given background than it is for those frequently changed from one background to another. That is, the time required for adaptation is greatly reduced by practice. This is clearly shown in the following experiment.

A *P. albiguttus*, 12 cm. long, after having been in a white granite pan continuously for two weeks and long since maximum white, was transferred to a black pan August 18, 2.05 p. m. At 4.30 p. m. it was about one-half maximum black; August 19, 12 m., about three-fourths maximum black; August 22, 10 a. m., nearly maximum black; August 23, 10 a. m., maximum black. This same individual, after having been frequently transferred from white to black and vice versa, from August 23 to August 30, was taken from the white background on which it was maximum white and put into the black pan at 7.27 a. m. One minute later, 7.28, it was already five-sixths maximum black, and after one minute more, 7.29, it was maximum black. The change from black to white, however, was never observed to be so rapid as this; it was never observed to occur in less than an hour. Thus, while it required five days to produce a complete change in the skin from white to black, after continuous sojourn of two weeks on white it required only two minutes, after repeated transfer, to change from one to the other. This is a most remarkable change in the reaction to a given stimulus. Such a change in the reaction of man would undoubtedly be called learning. Are the processes involved in changes in reactions in these widely different organisms fundamentally the same as they are in man?

No specific observations were made on the effect of repetition on the time required for adaptation in pattern and color, but judging from superficial observations on this point made in connection with experiments on the degree of adaptation, it appears probable that repetition has the same, or at least a similar, effect on adaptation to these characteristics as it has on adaptation in shade.

Changes in color require, in general, much more time than changes in shade or changes in pattern. There is, however, much variation regarding this among the different colors. Yellow, for example, is a color that the fish assume much more readily and rapidly than green or blue. This may be due to the fact that yellow ordinarily predominates in their environment. I have seen specimens which had been kept on various black and white backgrounds for weeks, showing no trace of yellow, become almost at once distinctly yellowish when put on a yellow background.

FACTORS INVOLVED IN THE PROCESS OF ADAPTATION.

CHROMATOPHORES IN THE SKIN.

The skin of the fishes contains several different sorts of colored cells or groups of cells known as chromatophores. These cells are much branched, some contain melanin granules, which are brown or black in color, others contain xanthine granules, which vary from yellow to orange, and still others contain iridescent guanin crystals. Ballowitz (1913) refers to these cells or groups of cells as melanophores, xanthophores, erythrophores, and guanophores, respectively. The pigment granules in these cells are sometimes found massed together in a small space and at others spread out over a considerable area. The color, the shade, and the pattern in the skin depend mainly upon the relative position of these granules and the guanin crystals.[a] Changes in these features consequently depend upon their movements. Some maintain that the cells are ameboid and that the movement of the granules is caused by changes in the state of ameboid processes; others maintain that they are fixed in form and that the granules move through the protoplasm or through fixed canals in it. Hooker (1914) has recently reviewed the literature on this subject. It will, therefore, not be necessary to go into details regarding this matter. I shall, moreover, treat this whole matter in a subsequent paper.

EYES, NERVOUS SYSTEM, AND DIRECT ACTION OF STIMULATING AGENTS AS FACTORS IN ADAPTATION TO BACKGROUNDS.

Ballowitz (1893) and others have shown that the chromatophores are surrounded by a dense network of nerve fibers; and the results of operations on the eyes and the nerves by Pouchet (1876), Šečerov (1909, 1913), Frisch (1912), Sumner (1911), and others indicate that these fibers are part of the sympathetic system and that the adaptive movements of the pigment granules are largely, if not entirely, controlled by stimuli received through the eyes. It has been found by these investigators and others that if the eyes are destroyed, or if the optic nerves or the sympathetic trunks are cut, adaptive changes in the chromatophores of the skin cease.

The results which we obtained by means of operations on the eyes in flounders confirm these conclusions in so far as they refer to the function of the eyes. In *Paralichthys*, it was found that the removal of either eye alone interferes only temporarily with adaptive processes in the skin, but that such processes cease permanently after the removal of both eyes, although blind specimens learn to move about in aquaria without any apparent difficulty, and in some instances they even learn to capture minnows. One such specimen was kept for over three weeks. At the end of this time the wounds had healed, the eye sockets had become pigmented, and the fish appeared to be in perfect condition. Changes in the background, however, had no apparent effect on the appearance of the skin.

There is always some degree of uncertainty as to the cause of negative results after operations. Regarding some of the experiments mentioned above, Sumner (p. 473) and others have raised the question as to whether the effect of the operations on the chromatophores was due to the elimination of the action of the sympathetic system and the eyes, in accord with the conclusions stated above, or to the injury involved in the operation. Moreover, Spaeth (1913), Šečerov (1913), and others maintain that light, temperature, chemicals, and other agents affect the movement of pigment in the chromatophores directly. They found that the chromatophores in small pieces of skin separated from the body still respond to these agents. Thus the question arises

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[a] Frisch (1913) maintains that in addition to the pigment granules there is in some forms a blue-green substance probably in solution. He says (p. 156) that in *Crenilabrus*, after having been on a blue background for two weeks, pigment in the chromatophores was much condensed thus exposing the blue-green substance, and he also maintains that the flesh in these individuals had a distinct blue-green cast not found in others. This, he holds, indicates that the blue-green substance increases when the fish is on a blue background.

as to what part the direct responses of the chromatophores to the stimulating agents may play in the process of adaptation in normal animals. The results obtained in the following experiments seem to give precise and conclusive answers to some of these, as well as to other questions.

A specimen of *Paralichthys*, 5 cm. long, in which adjustment to a black or a white background occurred rapidly, was put into a glass dish on the stage of a binocular and so arranged that the head was over a black surface and the tail over the opening in the stage. The mirror was then adjusted so as to reflect strong diffused light up through the opening, thus strongly illuminating the tail without affecting the head. The fish was kept in this position an hour, which was much longer than was necessary for marked changes in adjustment to either black or white. It was carefully examined under low magnification from time to time and finally put entirely on a black surface and again examined. No difference whatever was detected in the shade of the two ends of the fish. This experiment was repeated several times with this specimen and also with two others of about the same size. Those which were adapted to black remained uniformly dark throughout the experiment and those which were adapted to white became uniformly dark over the entire surface of the body. There was no indication that the intense reflected light had any direct effect on any of the chromatophores, although many of them, especially those in the fins and the tail, were strongly illuminated and all of them were unquestionably in stronger light than those on the opaque surface, for much light penetrated the tissue even where it was thickest. If light of this intensity does not under normal conditions appreciably affect the movement of the pigment granules directly, there is no probability that light reflected from the bottom will do so. This conclusion, moreover, is supported by the following observations and experiments.

Specimens free in an aquarium, half of which was black and the other half white, were repeatedly seen to come to rest with the head either on the black or on the white and to remain long enough for adaptation to occur. In every instance observed in which there was any response at all the entire fish assumed a shade corresponding to that of the bottom under the head. Thus the posterior end of the animal in every instance stood out in striking contrast against the background, while the anterior end corresponded well with it. In no case was there any evidence of a line of demarcation on the body corresponding with that in the background below. The same was found to be true, no matter what position the fish had with respect to this line. If it was parallel with the dividing line in the background so that one eye was over black and the other over white, the skin assumed a gray shade of equal intensity on both halves of the body. This also occurred if only the tip of the head was on the black or white and in some instances even if the line between black and white was some little distance in front of the anterior end.

These statements are supported by the following detailed account of individual observations and by the photographs reproduced on plate XXX.

On July 3 a specimen of *P. albiguttus*, 11 cm. long, was closely observed for several hours in an aquarium one half of which was white and the other half black. It usually moved about near the bottom very slowly for a period, then came to rest and remained a variable length of time, and then moved away again, repeating this process. Adaptation to black or white occurred remarkably rapidly in this specimen. So rapid were the changes in the skin that in slowly swimming from black to white or vice versa the animal became almost fully adjusted in the time it required the body to cross the line. As the fish went from the black to the white it appeared as though the black chromatophores were being rapidly buried in a white substance; and, as it returned to the black, as though they were being rapidly uncovered.

At 10.30 a. m. this specimen came to rest with the head on the white and the body and tail on the black, in such a position that the longitudinal axis made an angle of about 30 degrees with the line between the two halves of the aquarium. One eye was 2 cm. from this line and the other farther away. The skin immediately became much lighter. The fish remained in this position until 12.45 p. m. At this time it was much darker than when fully adapted to the white and much lighter than when fully adapted to the black bottom. It was gray, somewhat mottled but not contrastive, and the same over the entire pigmented surface. At 12.45 p. m. the specimen moved forward 15 cm. so that it was entirely on the white. It at once became much whiter, and soon appeared maximum white. At 1.15 p. m. it returned to the black bottom and at once became much darker. At 1.50 p. m., when the observations were closed, it was still on the black bottom and it appeared maximum black, having, as usual when in this condition, a number of conspicuous white spots scattered over the surface.

During the course of these observations, while this specimen was on the white bottom, a large dark four spot, 20 cm. long, several times swam slowly toward it. Each time, as the four spot approached a point approximately 10 cm. from the anterior end of the specimen of *Paralichthys* under observation, this specimen suddenly became much darker. Whether this change in shade was due to the darkness of the four spot and the consequent reduction in reflected light, or the excitement caused by its presence, I am unable to say, but other observations show that dark objects at a distance sometimes do have an effect owing to the reduction of light. Similar phenomena were observed in a considerable number of other specimens. Details in reference to one of these follow:

A specimen of *P. albiguttus* 21 cm. long was kept for several weeks in a large quarium, one half of which was black and the other half yellowish white. On August 19 and 20 it was frequently transferred from the black to the white bottom and vice versa. Adaptation to black and white, at the end of this period, was found to be rapid. On August 21, 2.30 p. m., it was found on the black bottom fully adapted. It was at once put into water about 4 cm. deep in a glass crystallizing dish 50 cm. in diameter. This dish was placed in water in strong diffused light, on a sheet of bristol board half black and half white, and so adjusted as to continuously keep the anterior half of the animal over the white and the posterior half over the black bottom. The entire surface of the fish became light grayish white almost at once, and it soon appeared to be maximum white. The fish was held in this position until 4.55, photographed (fig. 44), and then rotated until the anterior end was on the black.

At 7 p. m. it was nearly maximum dark. At this time it was set free in the dish and left. At 10 p. m. it was found with the anterior end on the white and the entire surface appeared to be, if anything, whiter than it had been at any time previous, although the light was so weak that during most of this time only that part of the fish which differed in shade from the background could be seen.

The following morning it was still maximum white. At 8 a. m. the anterior end was put and held on black. At 10 a. m. the entire surface was nearly maximum black. It was then turned until the longitudinal axis was parallel with the dividing line in the background, so that one eye was on the black and the other on the white bottom. The entire surface soon became gray of a shade about halfway between maximum white and maximum black. No further change occurred, although it was held in this position until 11.55 a. m. At this time it was photographed (fig. 45) and then set free in the dish.

The following morning at 6 a. m. it was found, with only the head to a point a trifle over a centimeter back of the eyes, on the white. The specimen appeared nearly if not quite maximum white. It was kept in this position until 9.20 a. m. and then photographed (fig. 46), after which it was rotated until the anterior end was on the black bottom. In this position it was held until 12 m. and then again photographed (fig. 47). This photograph shows several light lines crossing each other in the central part of the surface of the fish. These lines are not normal; they are due to abrasions in the skin and do not show in the other photograph because of the light shade.

The animal was now moved backward until the dividing line in the background was below a point about 1 cm. back of the eyes. The entire surface became distinctly whiter. The fish was then moved forward again, and the entire surface soon became distinctly darker. This was repeated several times with the same results.

The fish was then put entirely on the white with the head directed from the black, and left until it became maximum white. It was then turned through an angle of 180 degrees and moved forward so that the anterior end faced the black and was 2 cm. from the dividing line. In the course of a few minutes the entire surface became distinctly darker. This entire experiment was repeated several times with the same results.

Similar results were also obtained with color. On August 22, I was much surprised to find a specimen of *P. albiguttus* on a black and white checkered background distinctly yellowish. This specimen had been used in experimental work on black and white backgrounds almost continuously since July 22, and at no time before was there any evidence of yellow or any other color in the skin. When this specimen was discovered in the yellow state it was in a crystallizing dish in close contact with the edge. The dish was on an artificial black and white background, which at this point extended 2.5 cm. beyond the edge. Beyond this a brownish-yellow water-soaked cypress board, on which it rested, was exposed. This board, which was somewhat over 2.5 cm. from the eyes of the fish, evidently caused the flounder to become yellowish.

At 3.10 p. m. the dish was moved farther from the exposed part of the board. Fifteen minutes later there was only a trace of yellow left in the skin of the fish, and the following morning there was nothing more to be seen of it. At 9.30 a. m. the fish was so placed that the exposed part of the cypress board was 6 cm. from the anterior end of the fish and directly in front of it. In this position it was held until 10.45 a. m. There was no apparent effect of the yellow color. The fish was then moved forward until it was 5 cm. from the exposed part of the board and held until 12 m. Still there was no visible effect. It was then moved forward 2 cm., i. e., 3 cm. from the board, and held. An hour later, at 1 p. m., the skin of the fish was distinctly yellowish.

These results, without further analysis, show very clearly that under normal conditions the shade and the color in the skin of *Paralichthys* are regulated by the effect of light received by the eyes. There is no evidence whatever indicating that the simulation of the background, so marvelously developed in these creatures, is in any way influenced or affected to an appreciable extent by any direct action which the stimulating agents in the environment may have on the chromatophores. Consequently if we are ever to obtain an insight into the mechanism of this phenomenon of adaptation it must be through a study of the chromatophores in their relation to the nervous system, the eyes, and the environment. The reaction of isolated chromatophores to various stimulating agents, recently so much studied, can throw but little light on the problems concerning the evolution, the mechanism, and the function of the adaptive processes in question.

EXTENT OF DISTRIBUTION OF STIMULI FROM EITHER EYE.

Sumner asserts (p. 459) that the flatfish *Lophopsetta*, with either eye removed, responds normally in reference to adaptation to the background. The results of my experiments on *Paralichthys* with but one eye are in harmony with this contention. In these experiments, which unfortunately were not very extensive and refer only to changes in shade, the responses appeared to be normal both in time and degree. Similar responses have been observed by other investigators in a number of different fishes. There are, however, some species in which the removal of one eye greatly alters the reactions in the skin. Thus while Šećerov (1909) maintains that the chromatophores in *Nemachilus barbatula* with but one functional eye respond normally over the entire surface, and Frisch (1911) holds that the same occurs in *Phoxinus* and in *Carassius*, Pouchet (1876) asserts that in trout, with one eye blinded, only those chromatophores on the opposite side respond normally, and Frisch (1911) confirmes this assertion in experiments on "Forellen" and "Cyprinoiden." Semper also maintains that the chromatophores in "Makropoden" and "Teleskopfishen" having but one eye respond differently on opposite sides of the body.

In all of the species in which adaptation to the background is normal after the destruction of one eye, the shade, the pattern, and the color assumed on any given background must be the result of an integration of the stimuli received individually by each of the two eyes. This is clearly shown in reference to shade and pattern for *Paralichthys* in plates XXIX, XXX.

If a *Paralichthys* is held with one eye on a black and the other on a white background the skin assumes a gray shade, much lighter than it does when both eyes are over black and much darker than when both eyes are over white. Obviously, then, the effect of the stimuli received by the chromatophores from one eye is modified by the effect of the stimuli received from the other eye. (Fig. 45.)

The same is true with reference to pattern. If one eye is held over a background with large figures and the other eye over one with small figures, the pattern in the skin becomes intermediate in texture between that produced by the effect of the large figures and that produced by the effect of the small figures acting alone. (Fig. 41, 42, 43.) When the specimen represented in these figures was fully adapted to the background containing the large figures, the skin had relatively large white and black patches. (Fig. 42.) A few minutes later it was so arranged that one eye was on this background and the other was on the background with the small figures. It then could be seen clearly that both the large white and the large black patches were breaking up, dark spots appearing in the former and light spots in the latter. It is consequently evident that a given stimulus in the process of simulation of the background does not have the same effect when both eyes are functional as it has when but one is functional. In other words, the pattern and the shade assumed are the result of a sort of superimposition of the effects of the stimuli received by each of the two eyes.

RELATION BETWEEN THE INTENSITY OF LIGHT AND THE REACTION OF CHROMATOPHORES.

Keeble and Gamble (1904, p. 353) maintain that the response of the chromatophores in higher crustacea, under normal conditions, is independent of the intensity of the light. They found that specimens in a white porcelain jar covered with black paper "pierced with several pinholes" became just as pale as others of the same species in the same kind of jar uncovered.

Sumner (1911, p. 460) obtained similar results in experiments on the flatfishes, *Rhomboidichthys* and *Lophopsetta*. In these experiments he used two boxes, one painted gray, the other white. To the latter so little light was admitted that the white surface appeared distinctly darker than the gray surface in the other box, and by means of a photographic method it was proved that less light was reflected from the white than from the gray surface. He found, however, that specimens became maximum white on the former and gray on the latter.

I was able to confirm these results in experiments on *Paralichthys*. In addition to tests similar to those described above, numerous observations were made at night, usually about 10 p. m., on animals in various stages of adaptation to backgrounds differing in shade, color, and pattern. In making these observations a strong electric light was momentarily turned on. In all cases in which adaptation was complete the shade, color, and pattern of the skin appeared to be the same as it had been during the preceding evening. If there was any change it consisted in slight contractions of the chromatophores. These statements apply especially to *Paralichthys*.

In those specimens in which adaptation was not complete there were usually marked changes of such a nature as to show that the adaptive process continues in very weak light. This was repeatedly observed in specimens changed from dark to light backgrounds or vice versa late in the evening. Thus, to cite one instance, August 21, a *Paralichthys* very dark in shade was put upon a white background at 7 p. m. At this time it was already so dark that the fish could be seen only against the white background, and later it became still darker. At 10 p. m., however, when the fish was examined in strong electric light, it appeared maximum white.

There is some evidence indicating that the pattern assumed in weak light is not as conspicuous as is that assumed in strong light. This was most evident in specimens on backgrounds containing small black dots, of such a number as to produce relatively few black spots in the skin. For example, *Paralichthys*, individual (B), on a white background containing black dots 2 mm. in diameter and 10 mm. apart, regularly had in the skin a number of distinct black spots (fig. 54), but when examined in artificial light, at 10 p. m. on two different occasions, not a trace of these spots was found.

Ancylopsetta becomes much darker at night. This was repeatedly seen in various specimens in the colored boxes. Verrill (1897) observed similar phenomena in other forms. I was unable, however, to see any change in *Paralichthys* in the same boxes with *Ancylopsetta*. Moreover, both in *Paralichthys* and in *Ancylopsetta*, the shade assumed on any given background is the same in direct as it is in diffused sunlight. It, therefore, seems well established, at least for *Paralichthys*, that the shade assumed by the animal is independent of the intensity of the light. How is it possible to explain this phenomenon?

LIGHT REFLECTED FROM THE SKIN AS A FACTOR IN ADAPTATION.

Sumner says (1911, p. 463) that to account for adaptation in shade "we are limited to two alternative explanations: Either (1) the fish takes into account the degree of illumination, just as we do, and makes due allowance for this in judging of the paleness or darkness of the background; or (2) it makes a direct visual comparison between its own surface and that of the background and endeavors to bring the former into harmony with the latter."

To test the second hypothesis he made numerous observations on specimens, some of which had an opaque cloth fastened over them so as to conceal all but the eyes, and others had the pigmented surface stained. The results of all of these experiments he considers inconclusive owing to the possible effect of the treatment. He holds, however, that adaptation occurs normally in specimens bedded in sand, and concludes that this comes "very near to refuting the visual hypothesis altogether."

This would no doubt be true if all of the skin within the range of vision were concealed when the animals are bedded, but this does not appear to be the case. While I have not seen *Rhomboidichthys*, the form used by Sumner in his experiments, I have made numerous observations on *Paralichthys*, a similar form, and I have never found one, except for very short periods, in which the skin along the margin of the mouth was not exposed. Moreover, the skin bordering the lower margin of the eye is also usually exposed. Since both of these regions are within the range of vision, the fact that adaptation occurs in flounders after they are bedded does not seem to warrant Sumner's conclusion.

By removing the eye situated near the mouth and by taking special precautions to keep the lower margin of the other eye well covered, I was able to correct the defects in Sumner's method, and I found that after thus totally eliminating all of the skin from the view of the fish, it still simulated the background, and, moreover, simulation was quite as rapid and as extensive as it had been before the skin was covered. This was observed in several different experiments, one of which follows:

On September 3 the ventral eye of a specimen of *P. albiguttus* 27 cm. long was entirely removed. On September 12 the wound was thoroughly healed and the specimen fed and acted normally in every way. It was put into a black aquarium, and after it had become maximum black it was, at 9.40 a. m., suddenly entirely buried with gray sand. The fish soon shook enough sand off to admit of respiration, but the eye remained covered. At this time the sand was washed from the posterior portion of the animal, so as to admit of direct observation of the skin. This was found to be still maximum black, showing that no change occurs when the eye is entirely covered. Soon after this the fish moved slightly and the eye was raised sufficiently to be seen, but it was still covered with a thin layer of sand, and the upper surface was still somewhat below the surface of the sand. The skin, however, began to turn lighter, and half an hour later, 10.40 a. m., it was clearly somewhat lighter. At 11.30 the shade of the skin was considerably lighter and the pattern much broken so as to simulate the sand fairly accurately. During this entire time the eye projected only very little above the surface of the sand. The lower margin of the eye was continuously well covered with sand, as was also all of the rest of the skin within the range of vision. It is consequently evident that adaptation can occur with the skin entirely concealed and that light reflected from the skin or received by it plays no appreciable part in the process.

THE DIRECTION OF THE LIGHT AS A FACTOR IN ADAPTATION.

The fact that flounders and crustacea become maximum white on a white background and gray on a gray background even if the former, owing to weak illumination, reflects less light than the latter, shows conclusively that the shade assumed by these creatures is not proportional to the absolute amounts of light received from below. Keeble and Gamble (1904, p. 354) maintain, for crustacea, that it bears a specific relation to the ratio between the light received by the eyes direct from above and that received from below after reflection from the background—i. e., the "ratio $\frac{\text{direct}}{\text{reflected}}$ light." Sumner inclines to the same view with reference to fishes. He holds that adaptation in shade can not be regulated by a "direct visual comparison [by the fish] between its own body surface and the bottom on which it lies" (p. 476); and he further says:

> May not, then, the ratio between the light reflected from the near-by surfaces within the tank and the light which enters the latter from above be that factor of the total stimulus which renders possible these accurate adjustments of the shade of the fish's body to that of its background? I think that this is the true solution of the problem.

This hypothesis seems to meet all the requirements of the phenomena in question; but neither Keeble and Gamble nor Sumner succeeded in establishing it experimentally, although Sumner says that he constructed apparatus for this purpose, but was unable to make the necessary tests, owing to lack of material. The following experimental results throw some light on the problem in hand:

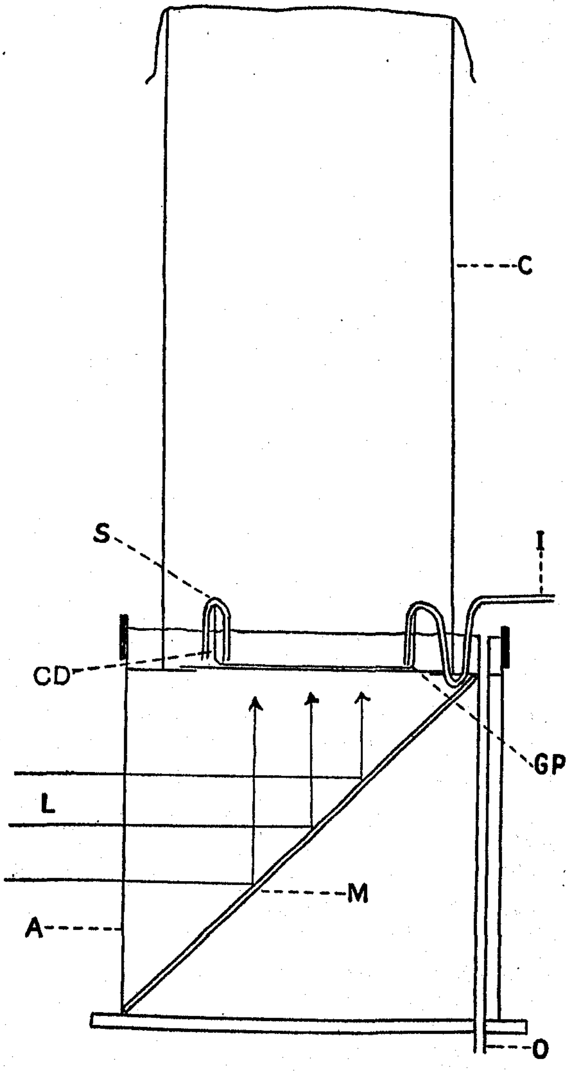

FIG. 2.—Vertical section of apparatus used in testing, in flounders, the effect of abnormally increasing the relative amount of light received by the eyes from below. A, glass aquarium; CD, crystallizing dish; S, siphon; I, inlet for water; O, outlet; GP, glass plate; C, opaque cylinder; M, mirror; L, light.

If the shade of the animal depends upon the ratio between the amount of light received by the eyes direct from the source above and that received by the reflection from the background below, in accord with Keeble and Gamble's hypothesis, then an increase in the amount received from below, without any change or with a decrease in the amount received from above, ought to cause the animals to become abnormally pale, no matter what the shade of the background may be. On a gray background the animals ought to become maximum white. On the other hand, if this hypothesis holds, an increase in the amount of light received from above, without any change or with a decrease in the amount received from below, ought to cause the animals to become abnormally dark. Under these conditions they ought to become gray on a white background.

In the following experiments these conditions of illumination were produced, but not all of the results obtained support the hypothesis in question. It was found that abnormally increasing the reflected light induces the fish to become abnormally pale, but that abnormally decreasing it has no effect. It was also found under the former conditions that black spots in the background affect but little the pattern in the skin and that color in the background is simulated only to a slight degree.

Reference to text figures 2 and 3 (p. 207, 213) will make clear the essential features of the apparatus used in these experiments. We shall refer to the two sets of experiments performed by means of the apparatus represented in these figures as (A) and (B), respectively. In (A) the background was illuminated from below, thus making the "ratio $\frac{\text{direct}}{\text{reflected}}$ light" abnormally small. In (B) the eyes were more highly illuminated from above than was the background, making the reflected light received by them relatively low. Thus the "ratio $\frac{\text{direct}}{\text{reflected}}$ light" became abnormally large.

EXPERIMENTS (A), LIGHT FROM BELOW RELATIVELY STRONGER THAN NORMAL.

1. *White background.*—On August 10, 9 a. m., a specimen of *P. albiguttus* 18 cm. long was taken from a yellowish white aquarium and put into the glass crystallizing dish, over an ordinary sheet of white writing paper 25 cm. square in the apparatus shown in text figure 2. When the specimen was put into the apparatus it was yellowish white. All the air was removed from under the dish, so as to avoid any interference with the light reflected from the mirror below. The black cylinder was then put in place and the upper end closed with a piece of opaque cloth. At 12 m. the specimen was very light gray with a brownish cast. The cloth was then removed, admitting light from above. No appreciable change occurred either in the shade or the color of the fish.

August 11 the cylinder was removed and the light from the mirror intercepted by inserting a piece of bristol board under the dish. The brownish color disappeared, and the fish consequently became slightly paler. These tests were repeated several times under other conditions with different individuals and similar results were obtained. The brownish color was, no doubt, due to the collection of brown sediment on the mirror. The water contained so much solid material, ooze, diatoms, and the like that it required only a very short time to form a perceptible layer on everything submerged. On a white background, then, increase in the relative amount of light from below does not appreciably alter the reactions of the chromatophores.

2. *Gray background.*—On August 16, at 10.30 a. m., the sheet of white paper with black spots was replaced with one which had been made uniformly gray of a medium shade (Ridgway's pale neutral gray). The light from the mirror was intercepted, and the fish was fully illuminated from above. At 1 p. m. the entire surface was fairly uniformly gray, and the fish was quite inconspicuous. At this time the cylinder was put in place and covered and the light from the mirror turned on. The background, as seen from the top of the cylinder, appeared distinctly gray, not white. At 2 p. m. the fish was nearly maximum white. There were no dark spots and the three ocelli were very light gray. The following morning, 6 a. m., the fish was fully as white as it had been at any time on a pure white background. The cylinder was now removed and the light from the mirror intercepted. At 10 a. m. the fish was well adapted to the gray again. The background was now again illuminated from below, and also left exposed to light from above. The fish seemed to turn a shade lighter, although there was some question concerning this. It was left until 3 p. m., then a sheet of gray tracing paper and another sheet of white paper were added to the gray paper under the dish, making the background much darker and nearly opaque. The cylinder was then put in place, covered, and the light from the mirror turned on. The background, as seen from above, appeared nearly black. At 5 p. m. the fish was nearly if not quite maximum white, and the following morning it was unquestionably maximum white.

Thus we see that if the light from above is abnormally low in comparison with that from below, *Paralichthys* may become white on a background which appears dark gray to the human eye. This strongly supports the idea that the shade assumed by the skin in these creatures under normal conditions depends upon the amount of light received by the eyes from above, as well as upon the amount received from below; for under such conditions animals on a gray background always become gray. This idea is also supported by the results obtained in the following experiment, in which the background contained numerous black spots:

3. *White background containing black spots.*—On August 11, 2 p. m., the sheet of white paper under the crystallizing dish in the first experiment was replaced by one of the same kind and size containing dense black dots 5 mm. in diameter. These dots were made with india ink, and they were such a distance apart that they covered one-half of the entire surface. The opaque cylinder was removed and the light from the mirror was not obstructed. Thus the background was illuminated both with light from below and from above, but it appeared much as it did under normal conditions of illumination, the spots being merely relatively somewhat darker. Numerous black spots appeared almost at once in the skin of the fish, just as under normal conditions, except that the spots were slightly more conspicuous. At 2.15 p. m. the cylinder was put in place and closed so as to cut off all light from above. Under these conditions of illumination the spots in the background, as seen from above, were still very prominent. At 2.30 p. m. no change had taken place in the skin. At 8 p. m. all of the black spots except three, the ocelli, had disappeared, and the fish was nearly if not quite as pale as it had been in the preceding test on a pure white background. The three ocelli were, however, somewhat darker. This shows that simulation of the pattern in the background is dependent upon light received from above; and it shows again that decrease in the illumination from above tends to cause the skin of the fish to become abnormally light.

Even if this illumination is only slightly reduced the effect becomes quite evident, as seen in the following observations:

On August 15, 11 a. m., the side wall of the crystallizing dish was covered with black paper, thus forming a black cylinder 6 cm. high in order to slightly reduce the illumination from above. The fish at this time was fully adapted to the spotted background fully illuminated from above and below. It had numerous dark brownish spots and the three ocelli also had a brownish cast. At 5 p. m. the fish in general had become much lighter. The three ocelli were at this time nearly black, but the dark regions around them and the dark spots were much smaller and much less distinct. The light from the mirror was now again intercepted and at 6.30 p. m. the surface was again about the same as it was in the beginning of the experiment. These tests were repeated several times the following day and in general it was found that the fish assumed a lighter shade when the background was illuminated from below in addition to the illumination from above, and in general the pattern in the skin appeared to be less conspicuous, although the spots in the background, as seen from above, appeared much more conspicuous. The ocelli and spots in the skin did not appear quite as large or as dense as they did when adapted to the background illuminated only from above, but the light regions appeared somewhat whiter.

It is consequently evident that a slight reduction of light from above has a marked effect on the reactions in the skin; but the following observations indicate that there is no strict proportionality between these reactions and the amount of light received from above compared with that received from below.

On August 12, 6 a. m., the cylinder was removed, admitting light from above. The skin of the fish immediately became speckled. The three ocelli became black, a row of five conspicuous black spots appeared near the base of the dorsal fin and another row of the same number near that of the ventral; and some spots also appeared in the fins and the tail. When the cylinder was put in place and closed these spots rapidly disappeared again and the ocelli became lighter. This change required less than two minutes. When the cylinder was removed the spots appeared again but not quite so rapidly. With the cylinder open on top, admitting some light from above, the results appeared to be the same as they were when it was closed, admitting no light from above. This was tried several times between 6 and 10 a. m., after which the cylinder was put in place, closed and left. At 11.45 a. m. there was no change; the ocelli were still clearly visible, the rest of the surface was very light gray with a slight brownish cast. There was much reddish sediment on the mirror. This was removed and the entire aquarium cleaned. At 1.15 p. m. the three areas apparently had become somewhat darker and the rest of the surface lighter, the brownish cast having entirely disappeared. After the cylinder had been removed a row of dark spots appeared almost at once along the edge of the body near the fins, and the three ocelli became much darker. The light from the mirror was now intercepted so that the background was illuminated only from above. At 1.22 p. m. the dark spots had become darker and many more had appeared and each of the three ocelli was surrounded by a dark patch fully 1 cm. in diameter. Observations were made from time to time during the afternoon, but no further changes were seen. At 5 p. m. the light from the mirror was again turned on and left. At 6.10 p. m., however, no reduction in the number or the size of the dark spots was detected. This test was repeated August 14, with essentially the same results, although according to my notes there was a tendency in the fish to become darker with the light from the mirror intercepted. There was little or no difference noted in the shade of the light regions, but the ocelli and spots appeared to become somewhat less dense and brownish when the background was illuminated from below.

4. *Background consisting of direct reflection from the mirror.*—August 13, 5.30 a. m., the cylinder was put in place and covered. The sheet of white paper with black spots was still under the fish. At 8.30 a. m. the three ocelli appeared black and the rest of the surface very light gray. The sheet of paper was then removed, exposing the fish directly to the light from the sky reflected by the mirror. At 9.15 a. m. the ocelli were light grayish and the rest of the surface light reddish gray. The reddish cast was probably due to the reddish sediment on the mirror. The cylinder was now removed, a sheet of white paper put under the dish, and the light from the mirror intercepted. At 2.45 the reddish cast had disappeared and the fish was maximum white. This shows that the effect of illumination from below is in all probability due solely to the increase in the amount of light from the background.

5. *Colored background.*—I have in several places pointed out that when the light from the mirror was colored the skin of the fish also became colored. On August 18, 4.30 p. m., a piece of brown wrapping paper was put under the dish, the cylinder covered and put in place, and the light from the mirror turned on. After the paper became wet it was considerably lighter in shade, but it still appeared distinctly brown as seen through the cylinder. August 19, 3 p. m., the fish was very light gray, probably maximum white, with no indication of a brownish cast.

The brown paper was now replaced by a maroon-colored glass. As seen from the opening at the upper end of the cylinder, the background appeared bright red. August 20, 9 a. m., the fish was maximum white, except the three ocelli and a row of ten spots about 1 mm. in diameter near the base of the fins. All of these were brown, not black or gray, as they had been on the gray and the white and black backgrounds. August 21, 11 a. m., no change could be detected. August 22, 8.30 a. m., it was still the same. At this time the cylinder was removed and the light from the mirror intercepted. The fish very quickly became much darker and assumed a distinct brownish color. So rapid was the change that it could be readily detected within two minutes after the illumination had been altered. No further change occurred during the following three days, except an increase in the density of the shade. The fish became dark brown in color, but it was not so reddish as those which had been on a red background for several weeks. These tests were repeated several times during the following five days with essentially the same results. The brownish ocelli and spots mentioned never failed to appear. These were not seen in any of the tests with a gray background illuminated only from below, no matter how dense it was.

It is therefore evident that the appearance of the brownish ocelli and spots on the red background could not have been due to the quantity of light transmitted by the colored glass, and that it must have been due to the quality of the light—i. e., the length of the waves. But, under normal conditions on a maroon background, with certainly no more colored light striking the eyes from below and none received from above, just as in these tests, the effect of the color is very much greater. The entire surface becomes reddish brown. This marked difference in effect must be due to the difference in the illumination from above.[a] How can this be explained?

Under normal conditions adaptation to a colored background, as demonstrated elsewhere, involves two processes. One results in adaptation in shade, the other in adaptation in color. Adaptation in shade, as the tests with the gray in particular indicate, is, at least to some extent, dependent upon the ratio between the intensity of the direct and the reflected light. A decrease in this ratio causes concentration and an increase causes distribution of the black pigment in the melanophores. The distribution of the guanin crystals may also be affected but in the reverse manner, so that when the dark melanin granules become concentrated the white guanin crystals spread out and cover them over. When the red background was illuminated only from below, this ratio became very small, and therefore adaptation in shade required concentration of the melanin and distribution of the guanin; but adaptation in color required just the reverse, together with distribution of the red and yellow pigment. Thus under the conditions of the tests there was an antagonism between the two processes involved; and this accounts for the resulting limitation of the brown color to the ocelli and dark spots, in which it requires less stimulation than elsewhere to cause an expansion of the melanin. Distribution of the red and yellow pigment was no doubt masked in all other regions by the distribution of the guanin which lies nearer the surface. Hence the extreme whiteness in these regions.

This leads directly to a discussion of the whole question concerning the relation between the different structures in the skin and the production of the different shades, colors, and patterns that have been observed in fishes. This question, however, I hope to treat more fully in a later paper.

EXPERIMENTS (B), LIGHT FROM ABOVE RELATIVELY STRONGER THAN NORMAL.

In these experiments a specimen of *P. albiguttus* 20 cm. long was used. This specimen had previously been transferred frequently from a white to a black background and vice versa; and at the time the experiments were made adaptation in shade to either of these backgrounds occurred very rapidly.

The fish was put into a 22 cm. crystallizing dish on a pure white background and covered with the black cylinder, which was lined with white cloth extending from the bottom to a line several centimeters above the surface of the water. A piece of white wire screen was so bent and adjusted in the glass dish as to prevent the fish from turning. The top of the cylinder was nearly closed with opaque cloth, making the intensity of the light within, so low that the white background appeared decidedly gray. A tube 3 cm. in diameter and 45 cm. long was fastened so as to extend down through an opening in the opaque cloth, directly over the eyes of the fish. Through this tube a beam of light from the sky was reflected, by means of mirrors (fig. 3, p. 213). This tube was so adjusted that the beam of reflected light illuminated the eyes and the skin about them, but not the background, and it was readjusted whenever the fish moved. In

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[a] The fact that the fish became nearly maximum white on the red background illuminated from below indicates that the melanophores, groups of black pigment-bearing cells, respond to monochromatic light much as they do to white light; that the stimulus which affects these organs bears a definite relation to the quantity of light regardless of the quality. It would be interesting to ascertain whether or not this relation is the same for all colors—that is, if a given amount of light energy has the same stimulating effect regardless of the length of the waves.

some tests a black cork containing two small holes was inserted in the bottom of the tube. These holes were of such a size and were so located that the two beams of light passing through just covered the two eyes.

In all of the tests the light received by the eyes from above, compared with that received from the background, was abnormally intense; and in accord with the hypothesis under consideration the fish should have become abnormally dark. This, however, did not occur. In most of the tests the fish was allowed to become maximum white in the cylinder in low light intensity before the eyes were illuminated from above; but in other tests a piece of black cloth was put under the crystallizing dish and the fish was allowed to become maximum black; then the cloth was removed from under the dish and the light from the tube turned on. In still other tests a piece of bristol board containing black and white 5 mm. squares was put under the glass dish and the fish was allowed to become mottled before turning on the light through the tube. Without going further into details, the results may be summed up by saying that the increase in illumination from above induced no observable change, although the beam of light was directed on the eyes, in some instances, continuously for over two hours, a period much longer than was necessary for a complete change in this individual from black to white or vice versa.

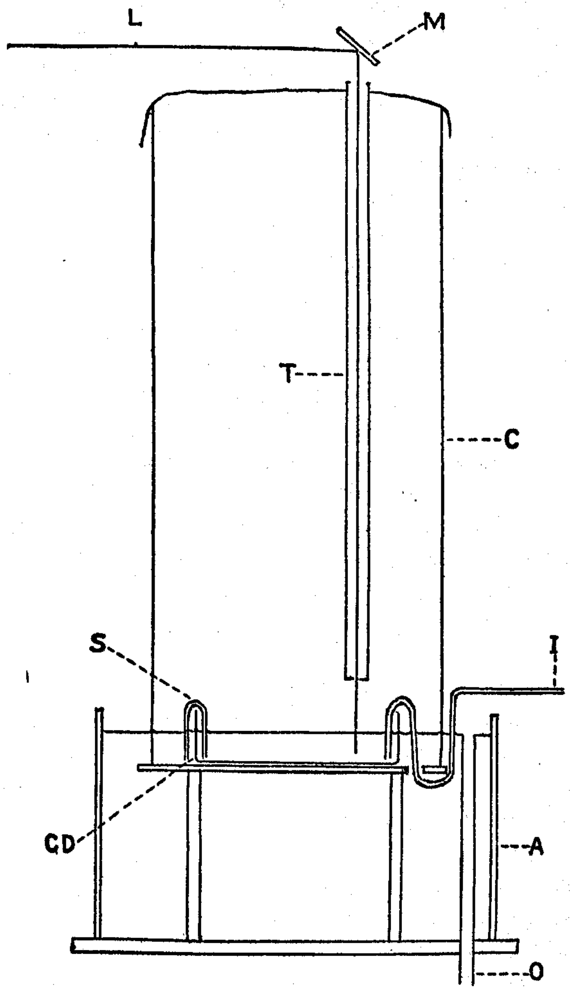

FIG. 3.—Vertical section of apparatus used in testing, in flounders, the effect of abnormally increasing the relative amount of light received by the eyes from above. A, aquarium; CD, crystallizing dish; S, siphon; I, inlet for water; O, outlet; C, opaque cylinder; T, iron tube; M, mirror; L, small beam of light.

At first thought, these results appear to contradict the idea that the shade assumed by the fish depends upon the ratio between direct and reflected light. The fact, however, that in all of these tests the fish retained the shade it had at the beginning of the increase in illumination from above, no matter whether it was dark or light or mottled, indicates merely that under the conditions of the experiment the chromatophores did not respond at all. The excessive illumination of the eyes from above entirely prevented stimulation by light reflected from the white background; for without this illumination the reflected light from a white background always caused the fish to become maximum white.

These experiments were later somewhat modified and repeated with an individual having but one eye. Adaptation in this individual occurred very rapidly. When transferred from a white background to a black, or vice versa, marked changes in shade could be detected at once. In preparation for the experiment the specimen, *P. albiguttus*, 27 cm. long, was put into an aquarium containing gray sand. In a short time it assumed a gray shade very similar to that of the sand. It was in rather low diffused daylight. By means of the apparatus described above and an additional mirror, a vertical beam of direct sunlight 3 mm. in diameter was reflected down into the eye. The beam of light was so small that none of the skin around the eye, except the projected margin over it, became illuminated. The illumination was continued for 30 minutes. During this time the fish did not move and there was but little movement in the eye, which was merely drawn down into the socket occasionally, as it ordinarily is when stimulated by contact. Thus the illumination from above as compared with the reflected light from the background was very much stronger than it normally is and, in accord with Keeble and Gamble's ratio theory, the fish should have become darker, but no change in shade was detected.

The same was, however, also true when the experiment was repeated beginning with the animal adapted to a black background. In this experiment the fish was put into a black aquarium, and after it became adapted it was suddenly and entirely covered with gray sand. The apparatus was previously adjusted, so that as soon as the sand was removed from the eye the beam of light entered it. The posterior portion of the animal was uncovered for observation as in the preceding experiment. The illumination was continued from 11.35 a. m. to 12 m. No appreciable change occurred in the skin. If anything it became somewhat lighter.

At 12 m. the beam of light was intercepted without making any other change. At 12.10 p. m. the fish had clearly become somewhat lighter, and at 1 p. m. much lighter, showing that the absence of changes in the skin under the apparatus was in all probability not due to lack of time.

These experiments were again repeated with the same individual, but with the beam of light entering the eye at an angle of 35 degrees with the horizontal. There was, however, no difference in the results obtained. Moreover, the fish was placed in direct sunlight and a small shadow cast on the eye so as to reduce the light received from above without decreasing that received from the background. Under these conditions, in accord with the Keeble and Gamble's ratio hypothesis, the fish should have become lighter, but, although the shadow was held continuously on the eye for 40 minutes, no appreciable change in the shade of the skin occurred. While these results are not conclusive, they do throw considerable doubt on the validity of this hypothesis. It is, however, certain, as previously demonstrated, that simulation of the background is not controlled solely by light reflected from the bottom; i. e., the effect of the light received from the background must be modified, in some way, by light received from some other source. This modification is, however, in all probability, not so simple as is demanded by the hypothesis in question.

VISION.

COLOR-VISION.

Several investigators have maintained that they have experimentally demonstrated that fishes have color-vision, but in every case the validity of the evidence has been seriously questioned.

Washburn and Bentley (1908, p. 140), working with the creek chub (*Semotilus atromaculatus*), found that it could be trained to distinguish food associated with green from food associated with red of different shades; and Reighard (1908) found, in experiments on feeding, that the gray snapper (*Lutianus griseus*) can distinguish blue as well as green from red, even if the red appears much darker or much brighter than the blue.

The fact that these animals distinguish the blue from red that is brighter, as well as from red that is darker than the blue, shows, the authors maintain, that the selection could not have been solely on the basis of difference of intensity or brightness such as a color-blind person can perceive in the different colors, and that the animals consequently have color-vision. This conclusion is valid, however, only if the brightness at the red end of the spectrum is practically the same for the fishes as it is for man. If this end has a lower stimulating efficiency for fishes, as is found to be true in color-blind persons, it is evident that the red which, to the normal human eye, appeared brighter than the blue may have actually appeared darker to the fishes; and if this is true the discrimination observed may have been made on the basis of brightness.

This idea is in full harmony with the conclusion reached by Hess, who has probably done more work on vision in animals in general than anyone else. In his experiments on fishes (1913) he studied their response in the spectrum as well as their reactions to colored objects. In these experiments he tested *Atherina*, *Phoxinus*, and *Mugil*. Young *Atherinas* are positive in white light of all intensities above the threshold. When they are exposed in a spectrum, Hess maintains, they aggregate in the yellow near the green, but that they aggregate in any other region except the red if it is made more intense than the rest. This, he asserts, is true for light-adapted as well as for dark-adapted specimens, provided the spectrum is sufficiently strong. He holds that they respond just as color-blind organisms would be expected to respond, and, he contends, the same is true in regard to the reactions of adult *Atherina*, *Phoxinus*, and *Mugil* to colored objects, in feeding experiments. In the feeding experiments he used food and other objects colored red, yellow, green, blue, and gray of different shades, in various combinations. He maintains that he found no evidence whatever of discrimination on the basis of color. He asserts that he has demonstrated that the methods of earlier investigators, supporting the idea of color-vision, were inadequate, and concludes that fishes, contrary to other vertebrates, are color-blind. In this conclusion, however, Hess seems to stand practically alone among investigators of this subject.

Bauer (1913), on the basis of results obtained by means of methods similar to those used by Hess, concludes that fishes have color-vision when their eyes are adapted to light but not when they are adapted to darkness. And Frisch is even stronger in his support of color-vision. He bases his conclusion on three lines of evidence—discrimination of food of different colors, change in color during the breeding season, and adaptation in color to the bottom.

He maintains (1912) that *Phoxinus* fed for some time exclusively on yellow meat was able to distinguish between yellow and any one of 24 different shades of gray, some of which were very much darker and others very much lighter than the yellow. This discrimination, he holds, could only have been made on the basis of difference in color. He further contends that it is possible to understand the changes in color during the breeding season, so conspicuous in the males, and adaptation in color to the bottom only on the assumption that fishes have color-vision.

All of this evidence, however, does not convince Hess. He maintains (1913) that some of the fishes, which during the breeding season become most highly colored, red and yellow predominating, live at such a depth that these colors are entirely eliminated by absorption and consequently that they can have no bearing on vision whatever. He repeated and extended Frisch's experiments on feeding and adaptation, using the same species but, he asserts, improved methods, and maintains that he obtained no evidence of discrimination among different colors and no evidence of adaptation in color to the bottom. He concludes (p. 439) that Frisch's statements regarding the behavior of *Phoxinus* are wrong, "sämtlich unrichtig."

In order to answer these charges Frisch extended his feeding and other experiments on *Phoxinus*. He used 50 shades of gray ranging from black to white and also blue, green, yellow, and red. He maintains that the fish distinguished between any of these colors and all the shades of gray, also between any combination of blue, green, and red, but not between yellow and red. He also maintains, as previously stated, that the fish assumed a color similar to that of the bottom; and that, while Hess may be right in his assertion that some species which become highly colored during the breeding season live in water so deep that yellow and red rays do not penetrate, nearly all fishes in which this occurs live in shallow water. Moreover, he holds that the fact that yellow and red at a given depth appear gray to the human eye does not prove that they affect the eye of the fish in the same way.

Unless the results of Frisch's observations, especially those on feeding, can be shown to be erroneous they seem to support strongly the idea of color-vision in fishes. The experiments here made on *Paralichthys* and *Ancylopsetta* support this idea quite as strongly and prove conclusively that *Paralichthys* and *Ancylopsetta* assume a color similar to that of the background, ranging from dark blue to dark red, and that this correlation can not be accounted for on the basis of difference in brightness or energy, and that it is dependent upon the length of the light-waves, and, moreover, that the color assumed is dependent upon stimuli received through the eyes.

Now the essential objective characteristic of color-vision in man consists in the fact that the stimulation resulting in sensation of color is dependent upon the length of the waves and not upon luminous intensity, at least not in certain respects. On the basis of this phenomenon as a criterion it necessarily follows, from the facts stated above, that flounders also have color-vision. It may, however, be contended that this is not a satisfactory criterion of color-vision, and, in a certain sense, this is perfectly true. But is there any criterion that is more satisfactory?

In the process of adaptation in color we have a response dependent upon the quality of light, wave-length, and upon the visual apparatus in the eyes. It is known that the stimuli involved pass through the optic nerves to the brain and that they are distributed through the spinal cord and the sympathetic nervous system to the cells in the skin, where they induce coordinated responses. It is also known that these responses may be influenced by other stimuli, physiological states, and processes in general. Essentially the same is true, with the exception of the part played by the sympathetic system, regarding every other reaction that has been used as a criterion of color-vision in animals. Nothing is known, in any case, as to what part, if any, the brain may play in the process.

The principal difference between this criterion and that which involves muscular activity is found in the course of transmission of the impulses from the brain to the reacting organs. In the latter this transmission is accomplished through the motor nerves; in the former, at least in part, through the sympathetic nerves. Whether or not both sorts of reactions should be marshaled under the term "color-vision" is, at present, very largely a matter of personal opinion. But whatever conclusion may be reached regarding this, neither criterion throws any light on the question as to whether or not animals have sensations of color similar to those in man, or of any other sort. That is, the term "color-vision" must be used in a purely objective sense regardless of which of these kinds of reaction is meant.

In a study of the question concerning the selection of backgrounds, pursued after the preceding pages were written, results were obtained which have a further bearing on the problem of color-vision. In this study one specimen of *Paralichthys* and one of *Ancylopsetta* were confined for about six weeks in each of four boxes. These boxes were painted on the inside, blue, green, yellow, and red, respectively; the red, however, turned pink in the course of a few weeks. At the close of this period each individual was tested as to the selection of colors on three consecutive days (Sept. 16, 17, and 18) as follows:

Boxes of the same kind as those mentioned above, and previously described in the section on colored backgrounds, were divided crosswise in the center. One half was covered with paint of one of the four colors mentioned and the other half with paint of another color. In this way boxes were prepared to represent all possible pairs of the four colors and one in addition, which was black and white.

In making the tests each specimen was gently placed directly over and parallel with the dividing line in the box. It was then released and the color toward which it turned recorded. Each individual was given 20 trials (10 with the head facing in one direction and 10 with it facing in the opposite direction) in each box that contained the color to which the animal was adapted, and also, on the second and third days, in the black and white box. Thus each individual was given a total of 60 trials in each colored box and 40 trials in the black and white box. The results obtained in these trials are summarized in table IV. The responses of *Paralichthys* and *Ancylopsetta* in each box were essentially the same. They have been added in the table, making a total of 120 tests in each box, except the black and white, for the two individuals adapted to a given color.

By referring to the table it will be seen that the individuals adapted to pink turned, in the red and yellow box, toward the red 50 times and toward the yellow 70 times; in the red and green box, toward red 40 times and the green 80 times; in the red and blue box, toward the red 5 and the blue 115 times; and in the black and white box, toward the black 1 and the white 79 times. Thus they turned toward the color to which they were adapted fewer times than toward any other color.

TABLE IV.—EFFECT OF ADAPTATION TO A GIVEN COLOR ON THE SELECTION OF COLORS.

Adapted to background colored.	Relation in brightness.	Number of times the fish turned toward—					
		Red.	Yellow.	Green.	Blue.	Black.	White.
Red	1	50	70				
		40		80			
		5			115		
						1	79
Yellow	4	29	91				
			60	60			
			63		57		
						3	77
Green	2	21		99			
			36	84			
				69	51		
						6	74
Blue	3	5			115		
			11		109		
				27	93		
						1	79

This was true, however, only for those specimens adapted to pink, and the fact that these specimens were adapted to pink (Ridgway's alizarin pink) and that the test boxes were still the original red (Bradley's red, shade no. 2) may have had something to do with it. The preponderance of turning toward the yellow in individuals adapted to yellow was also insignifiant. But in those adapted to green and blue the selection of these colors, respectively, was quite marked, especially the latter. In all the selection of white was practically perfect.

The order of brightness of these four colors, beginning with the darkest, was as follows: Red, green, blue, yellow. Between the red and green and especially between the green and the pink, which was considerably lighter than the red, the difference was not great, but it was marked in reference to the other three colors.

The fact that the individuals adapted to green selected green in preference to red, yellow, or blue, seems to indicate that the selection was not made on the basis of brightness, for the green was lighter than the red and darker than the yellow and the blue. The same argument applies to the reaction of those adapted to blue.

The only way that these reactions could be accounted for, solely on the basis of brightness, would be to assume that the animals were adapted to a color of a given degree of brightness, and they reacted negatively to colors either darker or brighter than the one to which they were adapted. This assumption, however, does not accord well with the results obtained in the black and white box; for it demands that the brighter the color to which the animal is adapted the greater the tendency to turn toward the white. Thus one would expect the greatest relative number of positive reactions to white in individuals adapted to yellow and the least in those adapted to red. This expectation, however, was not realized. These results are not in themselves absolutely conclusive regarding color-vision, but they do seem to lend support to the conclusion reached with reference to the problem in the study of the simulation of colors in the background.

Hess (1913b) holds that the spectrum for certain fishes is shortened at the red end and that the region of maximum brightness is shifted toward the blue. That is, he maintains that the distribution of brightness for these animals is similar to that for color-blind persons. But even if this is true for flounders, the reactions recorded in table IV can not be accounted for solely on the basis of brightness, nor can they be accounted for on this basis on the assumption that the brightness values for fishes, of the four colors used, differ in any other way from their values in man; for in accord with all such assumptions the reactions in each box should have been the same for all of the individuals tested. The reactions in the blue-green box, e. g., should have been the same for the individuals adapted to blue as they were for those adapted to green. This, however, was not the case; the former were positive to blue, while the latter were positive to green.

VISION OF MOTION, SIZE, AND FORM.

Much more work has been done on color-vision in fishes than on any other phase of the subject. It is well known, however, that many species in securing food regulate their movements by vision and that smell and taste play a minor rôle in the process, if indeed they play any. This is true for *Paralichthys* and *Ancylopsetta*. It is also well known that these fishes see other objects, especially such as may be injurious. It is known, moreover, that the movement of the object seen is an essential factor in the process of vision. Very little, however, is known as to what rôle in the process is played by form, size, and surface characteristics.

The following observations throw some light on these questions. A fiddler crab of moderate size was thrown into an aquarium containing a number of hungry specimens of *Paralichthys*. The crab was seized at once, partly swallowed, and then thrown out. It was then taken by another specimen and again rejected. Neither of these specimens nor any of the others in the aquarium was again seen to attack a crab, although during the following few days specimens of various sizes were repeatedly thrown in. Minnows of the same size, however, were invariably taken during this time. Thus it is evident that the crabs were recognized, and this recognition, no doubt, was made on the basis of form.

Size, however, is also a distinguishing characteristic for these animals, as shown by the fact that they rarely attack minnows which are so large that they can not be swallowed. But if the simulation of patterns in the background in *Paralichthys* may be used as a criterion of vision, we have evidence of far greater significance regarding this matter.

By referring to plates XXXI, XXXII, figures 49–55 and the legends accompanying them, it will be seen that dots 0.5 mm. in diameter produce no specific effect, but that those 1 mm. in diameter do. It will also be seen that the effect of dots 2 mm. in diameter differs from that of those 3 mm. in diameter, and that the effect of these dots differs from the effect of those 5 mm. in diameter. These results, as I have shown elsewhere, are due to stimuli received through the eyes, and impulses passed through the brain and the central and sympathetic nervous systems. These responses may be and probably are purely reflex. But, however that may be, they indicate as clearly as any other responses can that these animals recognize the difference between spots 2 mm. and 3 mm. in diameter, and that they do not recognize spots 0.5 mm. in diameter. Regarding subjectivity in these animals, we know next to nothing, if not actually nothing. It is consequently evident that, until this state of affairs is changed, the term recognition should be used strictly in an objective sense.

FUSION RATE OF IMAGES ON THE RETINA.

It is well known that if a disk containing alternate black and white sectors is rotated rapidly enough the sectors become invisible and the disk appears uniformly gray. This is due to the fusion of the images on the retina. If the images on the retina in fishes fuse somewhat as they do in man, a flounder over such a disk, at a certain rate of rotation, ought to become uniformly gray. And if the fusion rate is the same for fishes as it is for man the flounder ought to become, when the disk is rotated fast enough to appear gray to the human eye, as uniformly gray as it does on a stationary gray background. The results of the following experiments show that this actually occurs.

In these experiments a disk, 25 cm. in diameter, was fastened to a vertical shaft and so arranged in a wooden vessel that it rotated immediately under a stationary horizontal glass plate. The shaft extended down through the bottom of the vessel, where a pulley was attached to it. The disk was divided into 32 equal sectors, half of which were painted with white enamel and the rest, alternating with these, with black engine paint. The vessel contained flowing water extending to a point a few centimeters above the glass plate. The specimens to be tested were put on this plate in a glass inclosure of such a form and so arranged that the head was held continuously over the center of the disk. All air bubbles were carefully removed from under the plate. The disk was turned by means of a water motor, the speed of which could be altered as desired.

Four individuals were tested, three *P. albiguttus*, 16, 20, and 27 cm. long, respectively, and one *P. dentatus*, 14 cm. long. The specimen 20 cm. long was more thoroughly studied than any of the others. This specimen had been changed frequently during several weeks from a white to a black aquarium and vice versa until adaptation to these shades occured moderately rapidly. It was kept over the disk continuously, with the exception of a few short intervals, for five days. During this period the rate of rotation of the disk was changed at intervals varying from a few moments to an hour or more, and the effect on the pattern of the skin was noted and recorded. Without going into details regarding these records the results may be summarized as follows:

When the disk was not rotating the pattern in the skin became very conspicuous. The three ocelli became black and numerous other black spots of about the same size as the ocelli appeared. Numerous larger irregular light and dark patches also appeared, giving the fish a contrastive mottled appearance. Rotations of the disk up to about 50 revolutions per minute did not cause, in strong diffused sunlight, any appreciable alterations in the pattern. If anything, it became more conspicuous. As the rate of revolution increased above this, the pattern became less and less conspicuous until at 200 revolutions, in strong, diffused sunlight, the fish became as nearly uniformly gray as it did on a stationary gray background. Under both conditions the entire surface, with the exception of the ocelli and spots mentioned above, became, in the same length of time, almost uniformly gray. The ocelli and spots were in all cases considerably darker than the rest of the surface but not nearly so dark as they were when the disk rotated more slowly.

Thus, in moderately strong light the images produced on the retina of the fish fused completely when the disk made 200 revolutions a minute, or, since the disk contained 32 sectors, when the images were superimposed at the rate of 6,400 per minute.

In lower light intensity the fusion rate was lower. According to notes taken at 6 p. m. on the third day of the experiment, September 12, the rate was found to be about 4,800 per minute, and the following day the same rate was obtained between 11 a. m. and 1 p. m. by reducing the light intensity by means of an opaque screen. When the screen was removed, without changing the rate of rotation of the disk, the fish could be seen to become almost at once distinctly more conspicuous. When the light was thus increased the dark spots and patches became markedly darker, and when it was again decreased by replacing the screen they rapidly faded again. With full illumination, moderately strong indirect sunlight, the fusion rate was found during this period to be approximately 6,400 per minute.

The fusion rate for the human eye in all of these tests was apparently the same as that for the eye of the fish. At 50 revolutions per minute and below the sectors appeared nearly, if not quite, as black and white as they did when the disk was not rotating, although they appeared considerably narrower. As the rate of rotation increased, the sectors appeared to become narrower and narrower, and to become more and more nearly alike in shade, until they finally merged entirely and the disk assumed a uniformly gray shade. This occurred at about 200 revolutions per minute in strong, diffused light, and at a lower rate in weaker light, just as in the case of the fish. In other words, the disk appeared uniformly gray whenever the fish became maximum gray. Under no circumstances did the fish become maximum gray before the sectors on the disk had entirely disappeared.

The results obtained with the other three specimens were in all essentials like those set forth above. Two of them, however, did not appear to become quite as gray over the disk rotated fast enough to appear uniformly gray to the human eye as they did on a gray bottom. In these individuals, however, the changes in the skin proceeded so slowly that it was exceedingly difficult to detect slight changes which may have occurred in the shade and the pattern. Consequently, there is some doubt concerning these results which, if valid, would indicate that the fusion rate for some specimens may be higher than it is for man.

SUMMARY.

1. The evidence presented above indicates that fishes have color-vision and that the spectrum for them is, objectively, essentially the same as it is for man.

2. It indicates that they do not recognize dots 0.5 mm. in diameter as individuals, but that they do recognize dots 1 mm. in diameter and that they distinguish between dots 2 mm. in diameter and dots 3 mm. in diameter. In this respect vision does not appear to be as keen in fishes as it is in man.

3. It indicates further that fishes recognize differences in form, that the difference in the reaction to a crab and a minnow is on the basis of difference in form.

4. It also indicates that the fusion rate of images on the retina is essentially the same for fishes as it is for man, and consequently, that motion as a factor in vision is approximately the same for both.

SELECTION OF BACKGROUND.

No one has heretofore obtained any evidence indicating that fish show any tendency to select a background which harmonizes with the shade, color, or pattern of the skin. Sumner (1911, p. 443) made a number of tests with *Rhomboidichthys* and obtained negative results. He is very conservative, however, in his conclusion based upon these results, stating merely that they "render it improbable that the fish exercises much selection in respect to the shade of its background." The results here noted of experiments on both *Paralichthys* and *Ancylopsetta* show very clearly that such selection occurs. They throw but little light, however, on the question as to the extent and the significance of the selection.

In these experiments two methods were pursued. One may be called the group method and the other the individual method.

GROUP METHOD.

In the group method a given number of specimens, usually 10, which had been either on a white or a black background continuously for several days or longer, were released in an aquarium one half of which was black and the other white. Their movements were then studied and their positions at given intervals were recorded. The aquarium used for this purpose was 55 by 70 cm. The bottom of this aquarium was divided lengthwise into four equal areas. Two of these, with the adjoining side walls, were painted white and the other two, alternating with the first, were painted black. In these tests, specimens of *Paralichthys* were exclusively used. They varied in length from 12 to 20 cm. At the close of the first test two new individuals were added. With this exception the same individuals were used throughout the tests. In making these tests the individuals were put into the aquarium and left undisturbed. At intervals of about five minutes their positions were noted and the number on the white and on the black, respectively, was recorded. At the close of each test these numbers were added. The resulting sums appear in table V.

TABLE V.—THE RELATION BETWEEN THE SHADE OF THE SKIN AND THAT OF THE BACKGROUND SELECTED.

Number of test.	Time covered by test.	Number of specimens used.	Shade of background and time on same before tests.	Total number of readings.	Position of specimens at time of readings.	
					On black.	On white.
I	July 14, 10.28 a. m. to 12.49 p. m.	8	Black, 3 days or over	30	160	80
II	July 15, 9.47 to 11.58 a. m.	10	do	88	616	264
	Total				776	344
III	July 18, 2.31 to 5 p. m.	10	White, 3 days	37	139	231
IV	July 20, 11.30 a. m. to 4.15 p. m.	10	White, 5 days	67	218	452
	Total				357	683
V	July 15, 12.03 to 1.55 p. m.	10	Continuation of test II	6	31	29
VI	July 22, 6 to 7.30 a. m.	10	In a half black and half white aquarium, 2 days.	4	20	20
	Total				51	49

INDIVIDUAL METHOD.

A number of specimens of *Paralichthys* and *Ancylopsetta* were kept for several weeks in a shallow wooden aquarium 2.6 meters long and 1.3 meters wide. One half of this aquarium, sides as well as bottom, was painted black and the other half white, with the dividing line extending crosswise.

It was repeatedly noted that most of the specimens in the aquarium persistently remained on the white, but a few tended to remain on the black. When those on the white background were forced over onto the black they almost invariably returned at once, and the same was found to be true for those on the black background, indicating a selection of background in harmony with the shade of their skin.

More detailed results regarding this, however, were obtained as follows: Individuals fully adapted to either white or black were placed on the dividing line in the aquarium in such a position that one eye was over black and the other over white. In this position they were held with the hands until they became quiet, which usually occurred in a very few moments, and then released. In some instances they remained quiet after being released. Whenever this occurred the tip of the tail was touched repeatedly until they started off. The direction in which they turned was then noted and recorded, after which the whole process was repeated. In returning the animal, in about half of the individual tests it was moved across the line to the opposite end of the aquarium and then brought back onto the line so as to counteract any possible influence of the direction of movement before the test, on the direction of turning during the test. The results of nearly all of these tests are summarized in table VI.

TABLE VI.—THE RELATION BETWEEN THE SHADE OF THE SKIN AND THAT OF THE BACKGROUND SELECTED.

Number of test.	Designation of individual used.	Shade of background and time on same before test.	Time tests were made.	Number of times and direction of turning.			
				Ventral surface on black.		Ventral surface on white.	
				Toward black.	Toward white.	Toward black.	Toward white.
1	Paralichthys, 30 cm	Black, 1 day	July 9, 2.30 p. m.	8	2	7	3
2	.....do	Black, 2 days	July 10, 5 p. m.	15	0	12	3
3	.....do	Black, nearly 6 days	July 16, 5 p. m.	20	0	15	5
4	Paralichthys, 33 cm	Black, 1 week or over	July 8, 11.45 a. m.	12	3	14	1
5	.....do	Black, over 1 week	July 9, 4.15 p. m.	14	1	11	4
6	.....do	White, 1 day	July 10, 5.30 p. m.	5	8	6	7
7	.....do	White, 7 days	July 17, a. m.	7	33	7	33
8	Ancylopsetta (A)	Black, 1 week or over	July 9, 3 p. m.	29	0	15	14
9	.....do	.....do	July 9, 4.45 p. m.	16	0	5	11
10	.....do	White, 1 day	July 10	8	5	0	13
11	.....do	White, 7 days	July 16, 5.15 p. m.	5	20	3	22
12	.....do	White, 8 days	July 17, 3 p. m.	0	15	0	15
13	Ancylopsetta (B)	White, most of time for 1 week.	July 9, 3.30 p. m.	0	8	0	8
14	.....do	.....do	July 9, 3.40 p. m.	12	0	12	0
15	.....do	.....do	July 9, 4.30 p. m.	0	6	0	6
16	.....do	.....do	July 9, 4.40 p. m.	9	0	9	0
17	.....do	Black, 1 day	July 10, 4 p. m.	1	13	2	12
18	.....do	Black, 6 days	July 16, 5 p. m.	10	0	10	0

These results, without further analysis, show clearly that there is a tendency, both in *Paralichthys* and *Ancylopsetta*, to turn toward that shade to which they are adapted.

The only results which do not support this statement were obtained with *Ancylopsetta* (B). This individual, as the table shows, turned frequently and persistently toward a given shade for a considerable period of time and then suddenly stopped and turned as persistently in the opposite direction. The results obtained with all of the other individuals are, however, so consistent that not much weight can be placed on those obtained with this one. The tabulated results also show that, especially in *Ancylopsetta*, there is a tendency to turn toward the ventral surface. Thus it is evident that these creatures select, to some degree, that background on which they are least conspicuous. Whether or not this selection has reference to color and pattern as well as to shade remains to be ascertained.

COLORED BACKGROUND.

After this section of the work was completed opportunity presented itself to extend this investigation so as to include color. This study was carried on in the same way as that described above, bearing on the selection of backgrounds on the basis of difference in shade. The details regarding the experiments and the results obtained are presented under color-vision in the section on vision. By referring to table IV in that section, it will be seen that the individuals adapted to blue and to green showed a strong tendency to go toward the background with which they harmonized in color, that those adapted to yellow showed very little of this tendency, and that those adapted to red showed none. Thus it would seem that there is some evidence indicating that color is a factor in the selection of backgrounds. The whole subject, however, is in need of further investigation before hard and fast conclusions can be reached.

SUMMARY.

1. Adaptive changes in shade occur in the skin of practically all of the different fishes found in the region of Beaufort, N. C.; adaptive changes in color occur in many; but adaptive changes in pattern in only a few.

2. The flounders *Paralichthys* and *Ancylopsetta* simulate the background over a wider range and more closely than any other forms studied. In nature they resemble the bottom so much that it is difficult to see them, especially when they are partly buried, as they usually are. They are the only forms found in which the skin changes so as to resemble the bottom in pattern as well as in shade and color.

3. Simulation of the background in *Paralichthys* is more extensive and more nearly perfect than in *Ancylopsetta*. The range of changes in the skin in members of this genus is most remarkable. On a white background they become almost pure white, on a black background nearly black, and on gray backgrounds of various shades they become gray of very nearly the same shade.

4. On blue, green, yellow, orange, pink, or brown of various hues they assume a color remarkably similar to that of the background. Reds of various tints and shades, however, are not very accurately simulated; but the color produced in the skin by each tint or shade of red is different from that produced by any other color and very different from that produced by gray regardless of the intensity.

5. On bottoms containing black and white squares or circles, the skin breaks up into similar areas both in size and shade, but in no case is there any indication of an actual reproduction of the form of the areas, as maintained by Pitkin and Loeb. Large figures in the background produce a coarse pattern in the skin, and small figures a fine pattern, but squares of a given size produce essentially the same pattern as circles or stripes, or within certain limits any other figures of the same size.

6. The size of the light and dark areas in the background and the relative amount of surface covered by them have a profound effect on the pattern produced in the skin, but the form and arrangement have little or no effect.

7. The large features in the pattern are essentially the same in different individuals of the same species, but the details differ so much that any individual could readily be recognized by a careful study of less than a square millimeter of any portion of the pigmented surface.

8. The time required for adaptation to colors is, in general, much longer than that required for adaptation in shade or pattern. On the reds, greens, and blues adaptive changes still appear to continue after a sojourn on them of between two and three months. On yellows and browns adaptation occurs in much shorter time. This may be due to the predominance of these colors in the normal environment of the flounders.

9. The time required for adaptive changes in shade may be greatly reduced by repetition. In one individual, in the course of a week, it was reduced from five days to less than two minutes by repeated changes from black to white and vice versa.

10. Changes in shade, pattern, and color result from concentration or distribution of pigment granules in groups of cells known as chromatophores, in connection with highly reflective and refractive guanin crystals found in other cells known as guanophores.

11. The pigment granules in some of the chromatophores are black. In others they are yellow, varying from yellowish green to deep orange, depending upon the color of the background.

12. The movement of the granules resulting in adaptation is under the control of stimuli received through the eyes by way of the central and sympathetic nervous system.

13. If there is any direct effect of the stimulating agents in the environment on the adaptive reaction of the chromatophores it is insignificant.

14. Stimuli received through either eye are distributed equally over the entire pigmented surface. The shade, color, and pattern assumed is the result of stimuli received through one eye modified by those received through the other.

15. In *Paralichthys* the shade assumed in low luminous intensity on a given background is practically the same as that assumed in high intensity on the same background. It therefore bears no proportional relation to the amount of light received from the background. *Ancylopsetta*, however, assumes a much darker shade in very weak light than it does in strong light.

16. Light reflected from the skin to the eyes plays no part in adaptation to the background. Simulation of the background is not controlled by visual comparison of the skin with the background.

17. On a white background flounders become maximum white and on a gray background maximum gray, even if the conditions of illumination are such that much more light is reflected from the latter than from the former. The action of the light received by the eyes from the background must therefore be modified by light received from above, but the interaction of the light received from the different immediate sources is probably not so simple as is demanded by the ratio hypothesis of Keeble and Gamble.

18. The simulation of the background in color is regulated by stimuli received through the eyes, and it depends upon the length of the light-waves. It can not be accounted for on the basis of differences in the brightness or the intensity of the light. It consequently indicates that these animals have color-vision.

19. This conclusion is, moreover, supported by the fact that flounders adapted to blue or green tend to react positively to these colors when simultaneously subjected to stimuli from one of these and any one of the following colors: Red, green, blue, and yellow, red being the darkest color and the others brighter in the order given.

20. Flounders distinguish differences in size and in form, but the evidence obtained does not indicate that their vision is acute in these respects. The fusion rate of images on the retina, however, is essentially the same in flounders as it is in man, showing that in respect to motions their vision is on a par with human vision.

21. Flounders tend to select a background with which they harmonize in shade and in color.

DISCUSSION.

What sort of mechanism is necessary to account for the reactions of the chromatophores resulting in adaptation in shade, in pattern, and in color? Let us consider this question with reference to these different characteristics in the order given:

Adaptation in shade.—Different shades in the skin of flounders depend upon the degree of concentration of the melanin granules in the melanophores. The movement of these granules, which regulates the degree of concentration, is controlled by stimuli received through the eyes and the nervous system.

If this movement were proportional to the light received by the eyes from the background, and if each melanophore were connected with receptors in only one of the retinas, one could readily account for adaptation in shade, but such is not the case. The movement of the melanin granules is not proportional to the light received from the background, for the degree of concentration of these granules on a background of a given shade is the same, no matter how strong or how weak the light is; and each melanophore is probably connected with receptors in both eyes, for if one eye receives light from a black and the other from a white background the skin assumes an intermediate shade. To account for the regulation of the movement of the granules it is consequently necessary to assume a mechanism, such that the effect of the light reflected from the background on the movement of the melanin, is modified by the action of light received from other sources; and to account for the intermediate shades reproduced when one eye receives stimuli from a background of a given shade and the other from one of a different shade, it seems necessary to assume that the effective stimulus bears a definite relation to the arithmetical means of the light received from the background by each of the two eyes, modified by light received from other sources. It can not be proportional to the summation of the light received by both eyes, for if this were true a greater concentration of the melanin and a more rapid reaction would be expected, under given conditions, if both eyes are functional, than would be if only one is functional. This, however, does not occur; consequently it must be further assumed that the effect on a melanophore of a given amount of light received by a retina from the background modified by light recieved from other sources is twice as great if only one eye is functional as it is if both are functional.

Without attempting any further analysis, it is evident that to account for the observed phenomena concerning adaptation in shade it is necessary to postulate a rather complex mechanism, the working of which is as yet not altogether clear. The difficulties encountered in attempting to elucidate the physiology of adaptation in this respect, however, are much less perplexing than are those encountered in attempting mechanically to explain adaptation in pattern and color. In these we have to account for all of the phenomena regarding the compromise in the effect of direct and reflected light and in the action of the two eyes and others as well. In other words, adaptation in shade is always present.

Adaptation in color.—The observations on adaptive simulation of colors show that the reactions of the chromatophores depend upon the length of the waves of light regardless of the intensity. Each wave-length, within certain limits, has a specific effect. Thus the red causes extension of the pigment granules in the xanthophores and the melanophores, yellow causes greater extension in the former and less in the latter, etc.

If each chromatophore is connected directly with given cells in the retina, it must be assumed that the impulses which travel through a given nerve fiber from the retina to the skin differ and that the character of each impulse depends upon the length of the waves. Thus adaptation to monochromatic light might be explained, but colors produced by mixtures of light waves of different lengths are also simulated. As a matter of fact, most of the colors tested were not monochromatic. The different shades of brown, e. g., which were very accurately simulated, were produced by mixing red and yellow pigments. These pigments on drying aggregated in such a way as to form small adjoining red and yellow areas, distinctly visible under a magnification of 50 diameters; the brown color, therefore, consisted of a mixture of red and yellow rays. It thus becomes evident that a given reaction of a chromatophore is not necessarily specifically associated with a given length of light-wave. In other words, the effect of light consisting of waves of a given length is modified by the presence of light consisting of waves of a different length, and the modification is different for every wave-length. Where and how this process of modification occurs is unknown, but it seems most natural to refer it to the activity of cells in the brain.

The melanophores, as well as the xanthophores, take part in the production of colors in the skin. Their reactions are consequently dependent upon the length of the waves of light as well as upon the intensity, and to account for this as well as to account for the response of the xanthophores it is necessary to add to the complexity of the mechanism postulated to explain adaptation in shade. The nature of this addition is at present quite obscure.

Adaptation in pattern.—In the case of adaptation in pattern there is an integration of the action of impulses from the two eyes similar to that considered under adaptation in shade. If one eye receives stimuli from a background having a coarse pattern and the other from one having a fine one, the skin assumes a pattern intermediate in texture. Thus it is evident that the stimuli from either eye modify the effect of those from the other eye. With reference to the action of each eye alone it was found that, while the dark and light areas produced in the skin bear to those of the images in the retina a definite relation in size, they bear no such relation in form or in special interrelation. Obviously, then, the regulations of patterns can not be explained on the assumption of a direct and specific nervous connection between the chromatophores in the skin and the cells in the retina. An illuminated spot of a given size and intensity produces the same effect on the chromatophores in the skin, no matter where it may be located or what form, within certain limits, it may have. Different configurations (a, b, c, d, e, f, etc.) in the retina, no matter where they are located, all may result in the same configuration in the skin. Consequently, if the pattern in the skin depends upon the spacial interrelation of the impulses, their interrelation must be reorganized somewhere between the retina and the skin, probably in the brain.

Concerning the details of the processes involved nothing is yet known. Driesch, however, would probably hold that it can not be explained on purely mechanical grounds. It is well known that in man the image of an object may result in the same sensations, no matter from what angle the object is viewed. Thus a dog seen from the side may cause the same sensation as one seen from in front or from any other point of view, although the image on the retina in each case differs greatly from that in any other case. This phenomenon is like that just discussed in fishes. Driesch holds that in man it can not be explained on a purely mechanical basis. We should consequently expect him to maintain the same view for the phenomenon in fishes.

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EXPLANATION OF PLATES.

All of the figures found in the following plates are reproductions of photographs and autochromes from life, none of which have been retouched, tinted, or altered in any way.

Plates XIX, XX.—Adaptation on natural backgrounds.

PLATE XIX.

FIG. 1. *Paralichthys albiguttus*, 20 cm. long, on fine variegated shells, yellow predominating, partly buried as usually found in nature.

FIG. 2. Same individual two minutes later with the shells removed.

FIG. 3. *P. albiguttus*, 21 cm. long, on coarse shells of the same kind, partly buried, from August 16 to 19.

FIG. 4. Same individual two minutes later with shells removed. Note that the pattern is much coarser than in figure 2 on the fine shells. In both the skin was distinctly yellowish in color.

PLATE XX.

FIG. 5. Same individual as in figure 4 on very fine gray sand, almost entirely covered with sand. From August 19 to 21. Note the two small depressions in the sand at the base of the caudal fin. The lower one is much more prominent than the other. This individual breathed only through the lower gill. The water which entered the mouth passed back under the body and oozed up through the sand, forming the depressions. The animal was very effectively concealed.

FIG. 6. Same individual uncovered. Compare with figure 4 and note what a great change took place in the pattern. The skin also changed very much in color. All the yellow had disappeared and it had assumed a light gray shade.

FIG. 7. *P. albiguttus*, 13 cm. long, in a glass dish over very fine black sand. Note the remarkable similarity between the pattern and the shade in the fish, especially the central part of the body, and those of the sand. The tips of the fins and the tail have no pigment and consequently stand out boldly against the background.

FIG. 8. *P. albiguttus*, 16 and 10 cm. long, on a smooth jet black background. Note the conspicuous white spots. In some instances all of these, except a trace of the one at the base of the pectoral fin, disappeared entirely.

Plates XXI–XXIII.—Adaptation on artificial black and white backgrounds.

PLATE XXI.

FIG. 9. *Paralichthys albiguttus*, 14 cm. long, individual (B), on black and white background (2 mm. squares) from July 29, 11 a. m., to July 30, 3 p. m., after having been adapted to the background shown in figure 10. This individual was extensively used in the study of adaption on artificial backgrounds. It is represented in many of the following figures. Note that numerous dark spots have appeared in the light areas shown in figure 10, and that the light spots in the dark areas have become more numerous and more conspicuous.

FIG. 10. Individual (B) on black and white background (5 mm. squares) from July 25, 2 p. m., to July 26, 11.30 a. m., after having been adapted to a white background. Note that the three very light gray areas around the ocelli, shown in figure 13, have become much darker and other dark spots have appeared.

FIG. 11. Individual (B) on black and white background (2 cm. squares) from August 1, 9 a. m., to 4.30 p. m., after having been adapted to 1 cm. squares, shown in figure 12. Note that the pattern has changed very little.

FIG. 12. Individual (B) on black and white background (1 cm. squares) from July 31, 11.40 a. m., to August 1, 9 a. m., after having been on (1 sq. cm. circles) from July 30, 3. p. m., to July 31, 11.40 a. m. Note that the dark areas are darker than in figure 10.

PLATE XXII.

FIG. 13. Individual (B) on a smooth white background continuously from July 23, 2 p. m., to July 25, 10 a. m. It was alternately on white and on black about equal time during the preceding seven days. The skin actually appeared much whiter and less mottled and the animal less conspicuous than the photograph indicates. This is partly due to the shadow in the background along the ventral side. In specimens kept continuously on white for two months the skin became much more uniformly white.

FIG. 14. Individual (B) on black and white background (circles 5 mm. in diameter) from August 11, 12 m., to August 13, 1.30 p. m. Note the remarkable difference between the pattern in this figure and that in figures 9 and 13.

FIG. 15. Individual (B) on black and white background 2 cm. squares from August 24, 11 a. m., to August 27, a. m., after having been adapted to white. Note that the light areas are much larger than on figure 15, which shows the same specimen on the same background at a different time. A great variation was observed in the size of these areas during the time the fish was on this background. There is some evidence indicating that the relative amount of black and white produced in the skin depends upon whether the head is over a black square or over a white square. If it is over a white square there is considerably more black near the eyes than white, and if it is over a black square the opposite is true. While in other positions one eye may be influenced mainly by black and the other mainly by white. This no doubt accounts for the variation mentioned. In other words, a fish 14 cm. long can not simulate light and dark areas of this size as accurately as smaller ones, although larger specimens can.

FIG. 16. Individual (B) on black and white background (circles 5 mm. in diameter) from August 15, 10 a. m., to August 16, 9 a. m. This photograph shows one of the most remarkable concealing patterns observed. The fish appeared to contain numerous holes.

PLATE XXIII.

FIG. 17. Individual (B) on black and white background (1 sq. cm. circles) from August 1, 4.30 p. m., to August 2, 11 a. m. Probably not fully adapted.

FIG. 18. *P. albiguttus* (E), 10 cm. long, on black and white background (1 sq. cm. circles) from August 1, 11 a. m., to August 5, 9.40 a. m. On this background the specimen was nearly uniformly gray much of the time, and the simulation of the figures in this background was at no time as good as it was in larger specimens, although on the finer-grained backgrounds it was quite good, showing that the maximum area of figures successfully simulated depends upon the size of the fish.

FIG. 19. *P. albiguttus*, individual (C), 14 cm. long, on black and white background (1 cm. squares) from July 25, 2 p. m., to July 28, 10.30 a. m. Note that the pattern is similar to that in individual (B), figure 12, although specific individual characteristics can readily be found. Compare, e. g., the ventral ocellus in these two figures.

FIG. 20. *P. albiguttus* (E), 10 cm. long, on black and white background (5 mm. squares) from August 6, 12.30 p. m., to August 8, 10 a. m.

Plate XXIV.—Effect of mechanical stimulation on the pattern produced in the fish.

FIG. 21. *P. albiguttus*, 16 cm. long, in shallow bluish-gray mottled granite pan from August 1 to August 4, 10.30 a. m. Excellent simulation of the background on the entire surface except the three ocelli, which are nearly black.

FIG. 22. Same specimen photographed in the granite pan, August 5, 4 p. m., very shortly after mechanical stimulation. Note the contrast due to the enlargement of the regions around the ocelli and the appearance of numerous dark and light spots. These regions and spots were considerably more

pronounced immediately after stimulation. They become less conspicuous rapidly but it usually requires several minutes for them to disappear completely. They usually also appear when the animal is feeding.

Plates XXV, XXVI.—Adaptation on artificial black and white backgrounds, showing that the patterns on them is not actually reproduced in the skin.

PLATE XXV.

FIG. 23. Individual (B) on black and white background (5 by 10 mm. rectangular), long axis of the fish parallel with short axis of rectangles, continuously August 21, from 10 a. m. to 2.30 p. m., and August 22 from 11 to 11.30 a. m. No change in pattern could be detected from that assumed when the fish was free on this background.

FIG. 24. Individual (B) on same background, long axis of fish continuously parallel with long axis of rectangles, August 22 from 3.10 to 5 p. m., and August 23 from 6 to 9.15 a. m.

FIG. 25. Individual (B) on the same background continuously rotated on a disk under the crystallizing dish August 21 from 2.30 to 4.45 p. m. Note that the pattern is essentially the same as that shown in figures 23 and 24, although the apparent forms of the figures were continuously changing from long narrow to short and broad rectangles and vice versa.

FIG. 26. Individual (B) on black and white background (1 sq. cm. circles, area of white equal to that of black) from August 7, 11.30 a. m., to August 8, 10.15 a. m.

PLATE XXVI.

FIG. 27. Individual (B) on black and white background (1 sq. cm. circles, area of black equal to that of white) from July 30, 3 p. m., to July 31, 11.40 a. m.

FIG. 28. Individual (B) on black and white background (stripes 1 cm. wide) from August 4, 5.15 p. m., to August 5, 9.45 a. m.

FIG. 29. Individual (B) on black and white background (stripes 5 mm. wide) from August 5, 4 p. m., to August 6, 4 p. m. Note that the pattern produced by stripes is essentially the same as that produced by white circles on a black field (fig. 26) or black circles on a white field (fig. 27) or square or elongated rectangles, foreshortened in either direction or constantly rotated so as to continuously change the perspective. There is no evidence whatever indicating an actual reproduction in the skin of the figures in the background.

FIG. 30. *P. albiguttus* (A), 15 cm. long, on black and white background (5 mm. square) from July 23, 2 p. m., to July 25, 10 a. m. This specimen was tested on larger and on smaller squares and also on stripes. The pattern produced in the skin was essentially the same as in individual (B), shown in the preceding figures.

Plates XXVII, XXVIII.—Photographs showing more in detail the relation between the pattern in the skin and that in the background.

PLATE XXVII.

FIG. 31. *P. albiguttus* (F), 14 cm. long, in large, shallow granite pan (variegated, dark blue and white) from July 31 to August 14. Note the small white spots shown in irregular rows across the fish.

FIG. 32. Individual (F) on black and white background (dots 2 mm. in diameter) from August 23 to 27, 10 a. m. The white spots in the irregular rows have become more conspicuous, but the pattern is essentially the same, although the spacial interrelationship of the light and dark areas in the background is very different. This is very clearly shown in the enlarged photographs reproduced in figures 35, 36, 38, and 39.

FIG. 33. Individual (C) same specimen shown in figure 19 in the granite pan represented in figure 31 from August 1, 9 a. m., to August 14, after having been on various backgrounds during the preceding week. All the individuals in the granite pan after being fully adjusted were so inconspicuous that it required considerable attention to see them. (See autochrome fig. 66.)

FIG. 34. Individual (C) on black and white background (2 mm. squares) from August 25, 8 a. m., to August 27, 10.18 a. m. Note that the patterns produced by these two very different backgrounds are essentially the same.

PLATE XXVIII.

FIG. 35. A small section of the background shown in figure 31, enlarged. × 9.

FIG. 36. Enlargement of a small section of figure 31 taken slightly above the ventro-anterior ocellus. × 9.

FIG. 37. Enlargement of a section taken from the same relative place in figure 32. × 9.

FIG. 38. A small section of the background shown in figure 32, enlarged. × 9. Note that the details of the pattern in the skin (fig. 36, 37) assumed on these two different backgrounds (fig. 35, 38) are strikingly similar. Practically all of the dark and the light areas found in one are also found in the other, and the forms of these are, respectively, very nearly the same, although in the two backgrounds the dark and the light areas differ greatly, both in form and in spacial arrangement. The same is true with reference to individual (C), figures 33, 34, 39, and 40. On neither background is there any evidence of an actual reproduction in the skin of the configuration in the background.

FIG. 39. Enlargement of a small section of figure 33 located in the same relative position as that reproduced in figures 36 and 37. × 9.

FIG. 40. Enlargement of the same relative section of figure 34. × 9. Note that the patterns shown in figures 39 and 40 are essentially the same, although the backgrounds on which they were produced differ greatly. Note also that the patterns shown in figures 36 and 39 differ considerably in detail, although produced by the same background but in different individuals. While the large features in the pattern of the skin of all individuals of this species are essentially the same, there is sufficient specific individuality in the smaller features to make it possible to recognize every individual by a thorough study of the pattern found on a square millimeter or less of any part of the pigmented surface.

Plates XXIX, XXX.—The photographs on these plates show that simulation of the background is dependent upon stimuli received through the eyes and that the stimuli from each eye are distributed over the entire pigmented surface.

PLATE XXIX.

FIG. 41. Individual (B) (same specimen shown in many other figures), on black and white background (2 mm. squares) from July 29, 11 a. m., to July 30, 3 p. m.

FIG. 42. Individual (B) on black and white background (circles 1 sq. cm.) from July 30, 3 p. m., to July 31, 11.40 a. m.

FIG. 43. Individual (B), one eye continuously on a coarse and the other on a fine-grained background, on August 29, 8 to 11.20 a. m. No further appreciable change occurred in the pattern after 8.30 a. m. Thus it is clear that the fish was fully adapted long before the photograph was taken. This rapid adaptation was no doubt due to the fact that this animal had been used in the study of patterns produced by different backgrounds almost continuously for a month or more. Note that the pattern is the same over the entire surface and that it is intermediate in texture between those shown in figures 41 and 42. It appears to be a sort of superimposition of these two patterns.

PLATE XXX.

FIG. 44. *P. albiguttus* (G), 22 cm. long, head continuously on white and tail on black, on August 21, 2.30 to 4.55 p. m. This specimen was taken from a black aquarium and was fully adapted to black in the beginning of the experiment.

FIG. 45. Individual (G), one eye on white the other on black continuously, on August 22, 10 to 11.55 a. m. The fish was nearly maximum black at 10 a. m.

FIG. 46. Individual (G), continuously with head on white, body on black, on August 23, 6 to 9.20 a. m.

FIG. 47. Individual (G), head on black, body on white, on August 23, 9.20 a. m. to 12 m.

Plates XXXI, XXXII.—Limits of vision, keenness of discrimination, and adaptation to gray background.

PLATE XXXI.

FIG. 48. *P. albiguttus*, 12 cm. long, fully adapted to a very light gray background. This specimen continuously appeared somewhat darker than the background. Note that the three ocelli have almost entirely disappeared.

FIG. 49. Individual (B) (fig. 9), on black and white background (dots 0.5 mm. in diameter) from August 16, 2 p. m., to August 17, 9 a. m. Dots of this size, no matter how numerous, had no effect except perhaps to cause the skin to become uniformly slightly grayer.

FIG. 50. Individual (B) on black and white background (dots 1 mm. in diameter) on August 5, 9.45 a. m. to 4 p. m., after having been fully adapted to 1 cm. squares. These spots have no appreciable effect on the skin unless they are more numerous than they are in this background.

FIG. 51. Individual (B) on black and white background (dots 1 mm. in diameter) on August 20, 10 a. m. to 4.45 p. m., after having been fully adapted to dots 2 mm. in diameter. Note that the posterior ocellus is much darker than on white, but that the two anterior ones are not.

In the production of a pattern in individuals which are maximum white the posterior ocellus always becomes dark first, then the two anterior ocelli and then a row of ten dark spots appears along the base of the fins. Following this two dark spots appear in the tail and two in the central part of the body, after which others appear in the fins, the tail, and elsewhere.

PLATE XXXII.

FIG. 52. Individual (B), on black and white background (dots 3 mm. in diameter) on August 14, 7 a. m. to 1.30 p. m., after having been fully adapted to white.

FIG. 53. Individual (B), on black and white background (dots 3 mm. in diameter) from August 16, 10 a. m., to August 19, 12 m. The black spots are clearly somewhat larger and denser than those produced on dots 2 mm. in diameter (fig. 54).

FIG. 54. Individual (B), on black and white background (dots 2 mm. in diameter) from August 19, 3 p. m., to August 20, 10 a. m., after having been fully adapted to white. On this background the same number of black spots are produced as on that in figure 52, but the spots are slightly larger and more dense. This statement and all others of a similar nature are based upon a comparative study of a series of prints made from each of the different negatives, and upon descriptions of the effect of the different backgrounds written during the process of the experiments.

FIG. 55. Individual (B), on black and white background (dots 5 mm. in diameter) from August 2, 12 m., to August 3, 1 p. m.; no observable change after 8 a. m. The black spots are practically the same as those produced on dots 2 mm. in diameter, but only half as far apart (fig. 54).

Putting the matter in subjective terms this work shows that these animals do not recognize dots 0.5 mm. in diameter as individuals, but that they do recognize those 1 mm. in diameter and that they distinguish dots 2 mm. in diameter from those 3 mm. in diameter and dots 3 mm. in diameter from those 5 mm. in diameter.

Plates XXXIII–XXXV.—Simulation of colors in the background.

PLATE XXXIII.

For a fuller account of the environment of the specimens autochromed see text.

To compare the color of the different individuals eliminate the background by covering the autochromes with the accompanying gray sheet containing holes. These autochromes prove conclusively that the color in *Paralichthys* and *Ancylopsetta* changes within wide limits so as to harmonize fairly accurately with that of the background.

FIG. 56. *P. albiguttus*, 17 cm. long, on chrome yellow from September 1 to 11. The color is only fairly accurately reproduced.

FIG. 57. *P. albiguttus*, 15 cm. long, on green from August 11 to 26.

FIG. 58. *P. albiguttus*, 19 cm. long, on dark blue from August 7 to 8. This specimen became bluish exceptionally rapidly. It remained on dark blue four days longer and became but little more blue than it was when autochromed.

FIG. 59. *P. albiguttus*, 20 cm. long, on vermilion from July 27 to August 26.

PLATE XXXIV.

FIG. 60. *Ancylopsetta quadrocellata*, 14 cm. long, on pink (Ridgway's alizarin pink) from August 3 to September 11. Excellent reproduction.

FIG. 61. *A. quadrocellata*, 17 cm. long, on dark blue from August 22 to 26.

FIG. 62. Same specimen on green from August 26, 4 p. m. to August 30, 2.30 p. m. When first transferred, this fish appeared even bluer in the green box than it did when it was in the blue box, and there was no evidence of green whatever. During the following four days the blue became fainter and the fish gradually assumed a greenish tint. But at the end of this time there was still considerable blue in the skin, as the autochrome shows. This demonstrates conclusively that the color of the skin as reproduced in all of the figures on this plate is due to internal structures and not to colored light reflected from the surface or transmitted through the fish, as has been suggested by a number of those who have seen the original autochromes. This is more conclusively demonstrated in the reproduction of autochromes taken later (figs. 64, 65, and 67).

FIG. 63. *A. quadrocellata*, 16 cm. long, on chrome yellow from July 27 to August 26.

PLATE XXXV.

FIG. 64. *P. albiguttus*, 15 cm. long, on blue from August 20 to September 11; autochromed in a green box. This proves that the color shown in the autochromes is due to the structure of the skin and not to light reflected from the background as many who saw the originals maintained.

FIG. 65. Four specimens of *P. albiguttus*, adapted to blue, green, yellow, and pink backgrounds, respectively, autochromed on green. Color in all but the yellow one is quite faithfully reproduced.

FIG. 66. *P. dentatus*, 14 cm. long, in a variegated blue and white granite pan from August 19 to September 10. The brown spots are due to particles of rust. Colors faithfully reproduced.

FIG. 67. *Paralichthys*, same individuals adapted to the same backgrounds as in figure 65. Autochromed on a white background. The color in all but the smallest specimen is fairly faithfully reproduced. The smallest specimen appeared much greener in life and also in another autochrome taken at the same time than it does in this figure.

Plate XXXVI.

FIGS. 68–76. Photographs taken with orthonon plates of specimens adapted to colored backgrounds. Fig. 68, brown; 69, dark blue; 70, maroon; 71, green; 72, vermilion; 73, light blue; 74, dark blue; 75, green; 76, chrome yellow. Note the remarkable simulation of the background in shade and the absence of conspicuous patterns, especially in *Paralichthys*. The conspicuous dark areas and light spots shown in figure 70 were present only after abnormal stimulation.

Plate XXXVII.

FIG. 77. Photograph of a group of *Paralichthys* on a white background containing considerable débris scattered over it. All of the specimens are *albiguttus* except the large one above and to the left, which is *dentatus*. Note that this specimen has five dark areas, two rather inconspicous ones near the head and three near the posterior end. In some specimens there are several others nearly as conspicuous as these. In *albiguttus* there are but three, the two near the posterior end at the base of the fin being absent.

The difference in shade in the different individuals is largely due to difference in their past experience.

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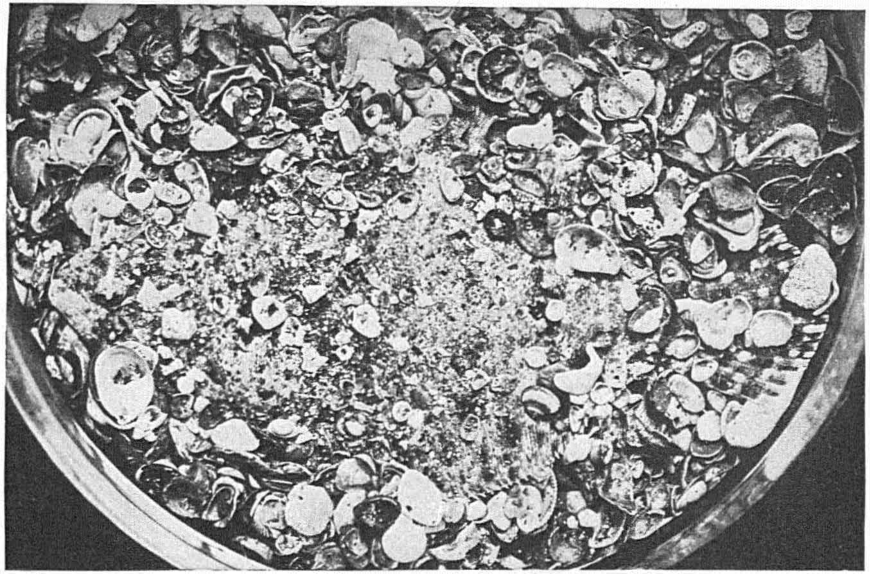

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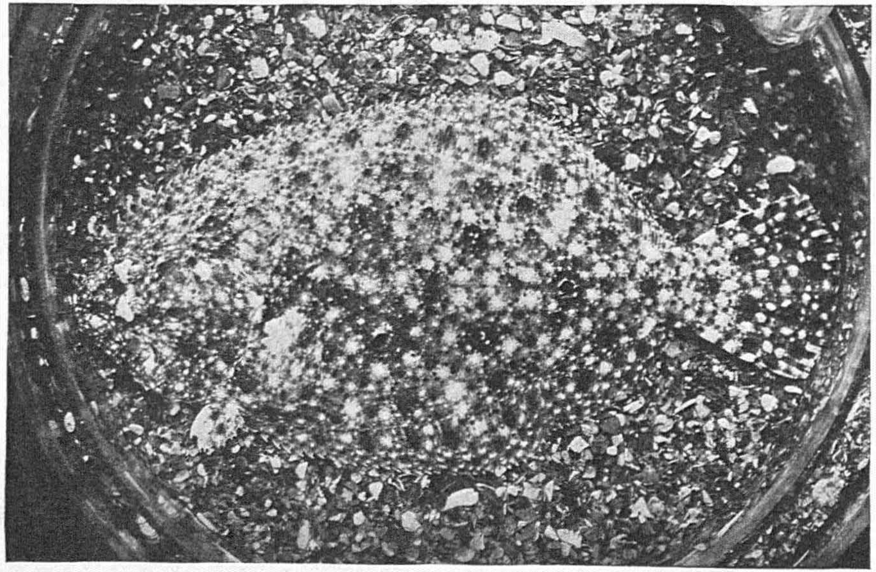

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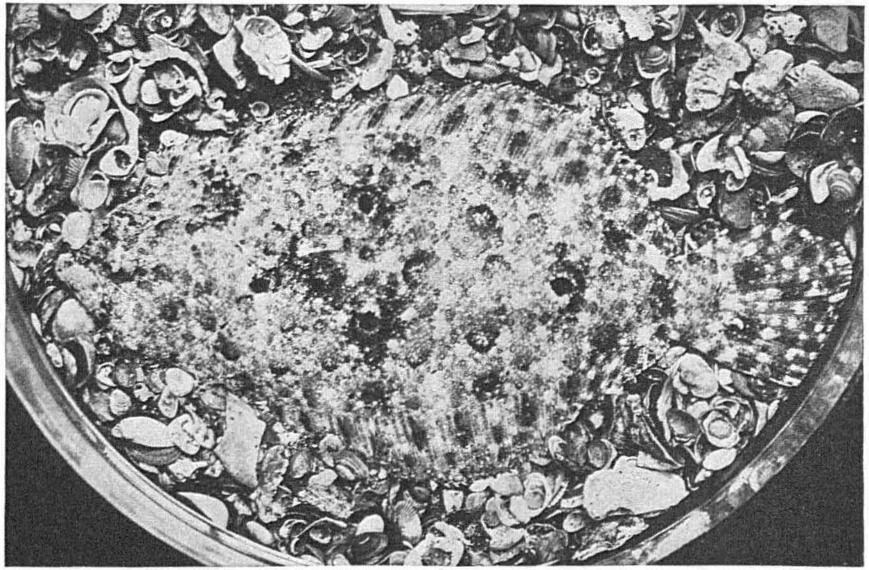

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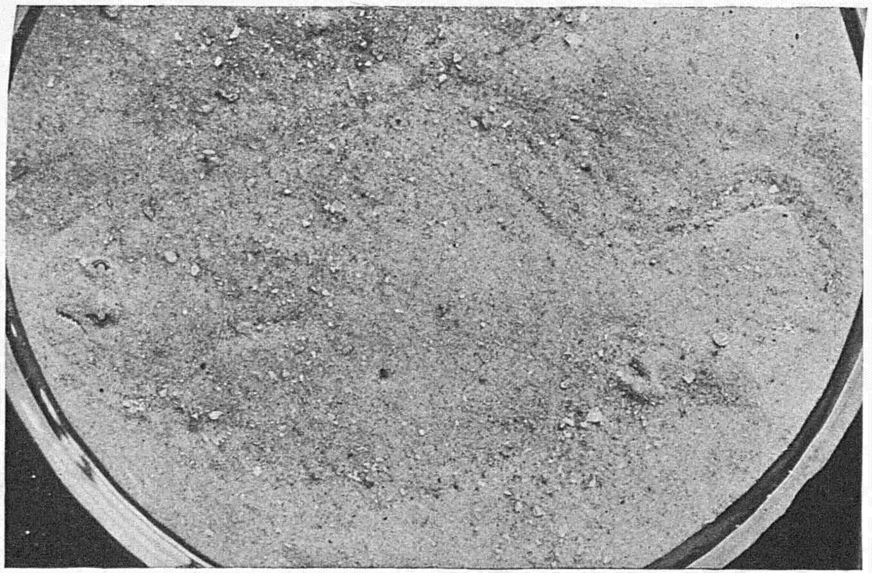

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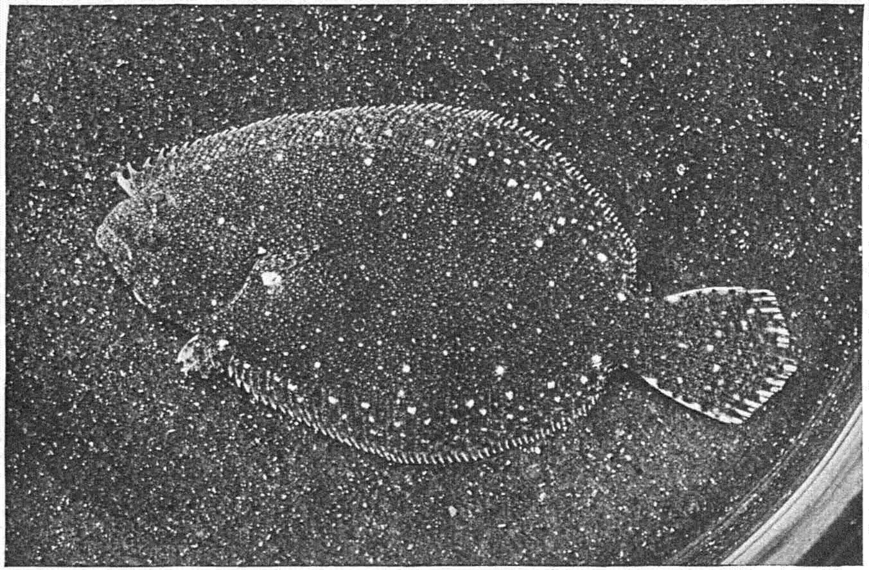

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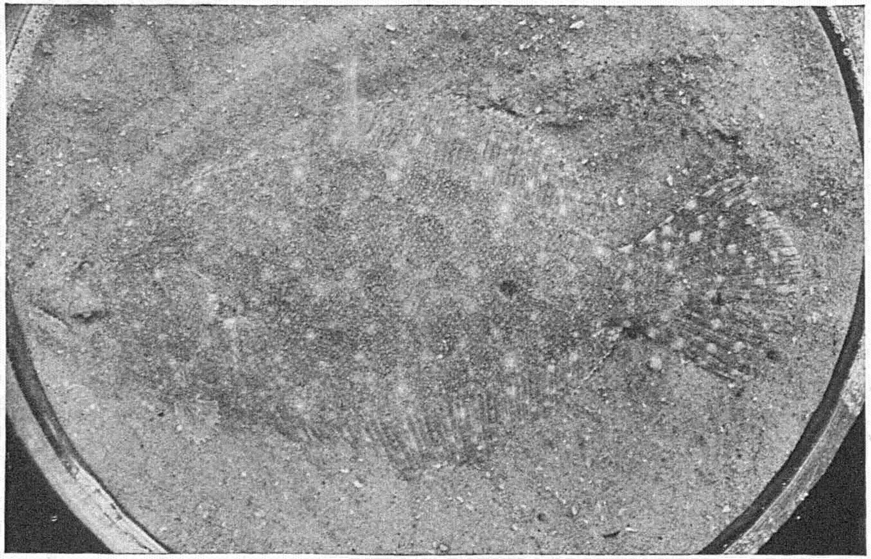

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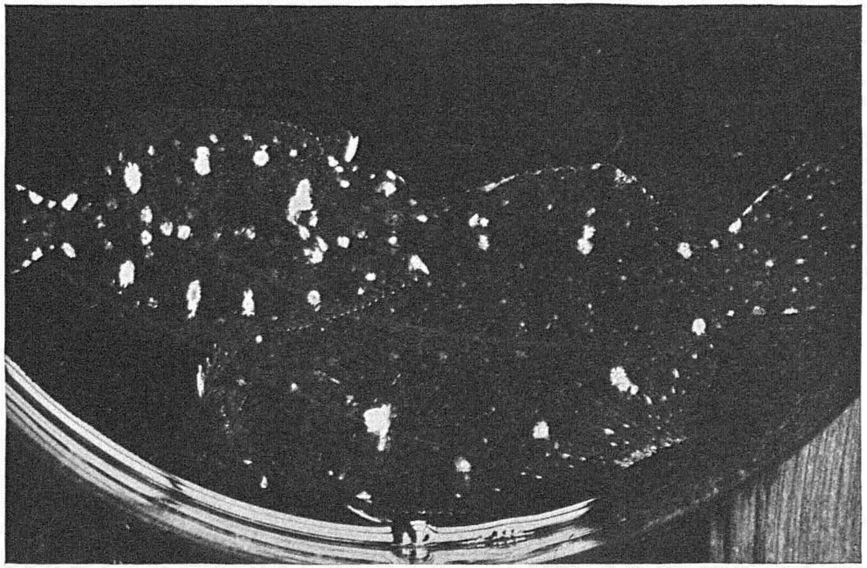

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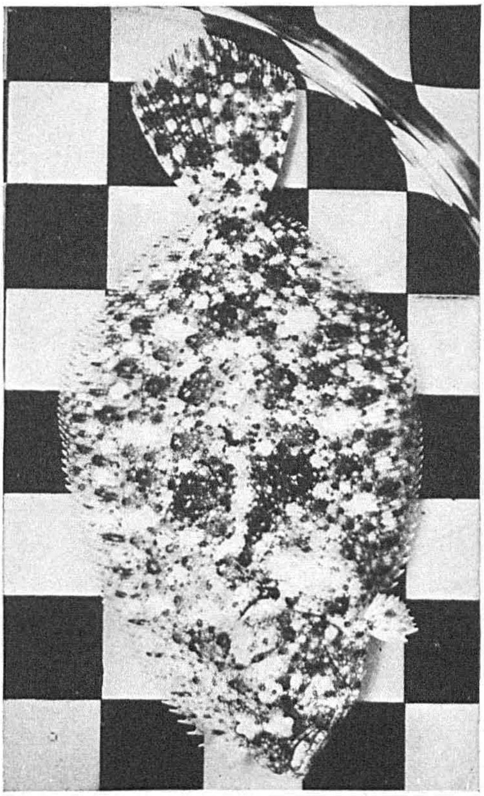

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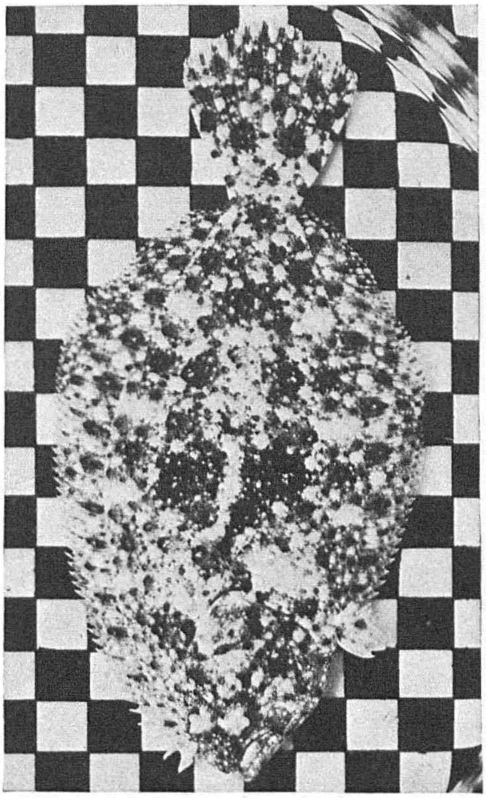

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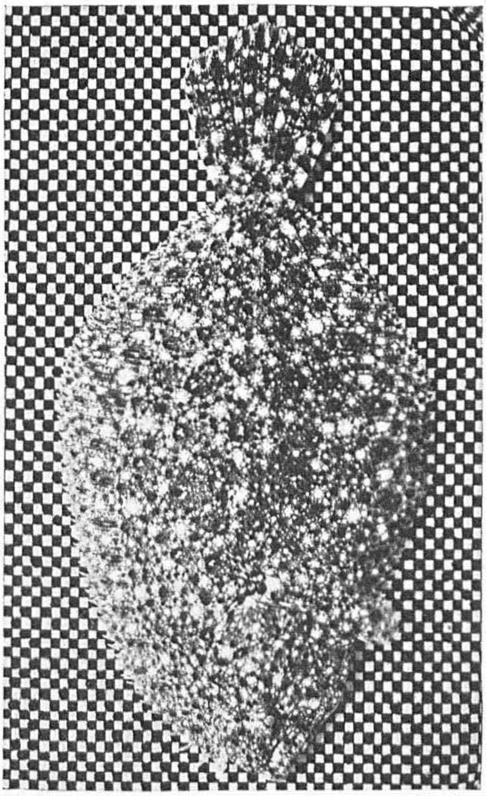

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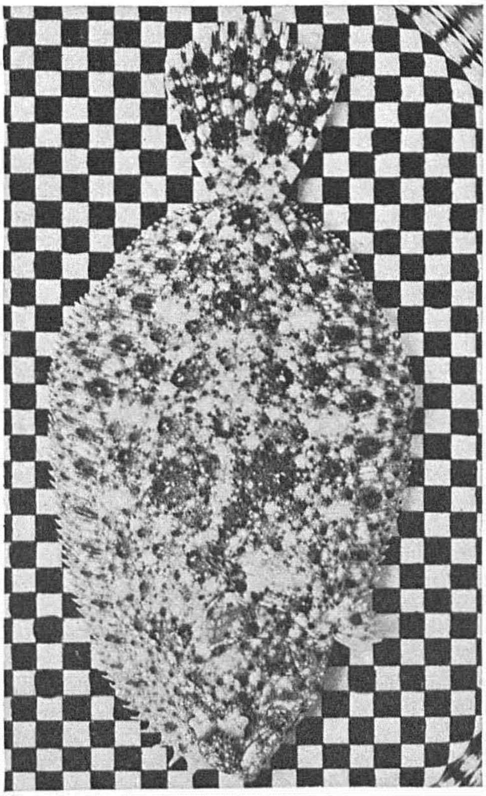

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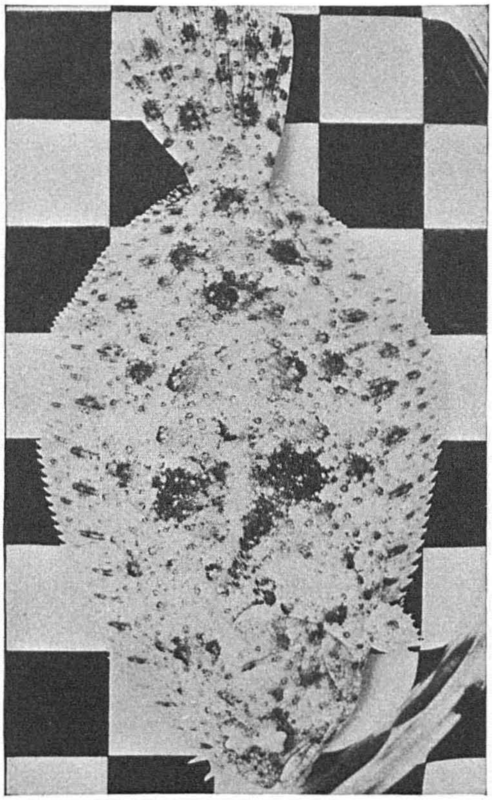

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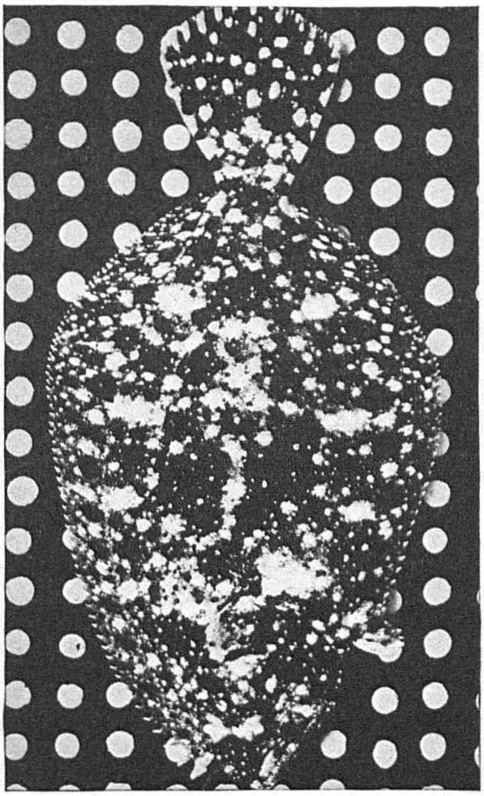

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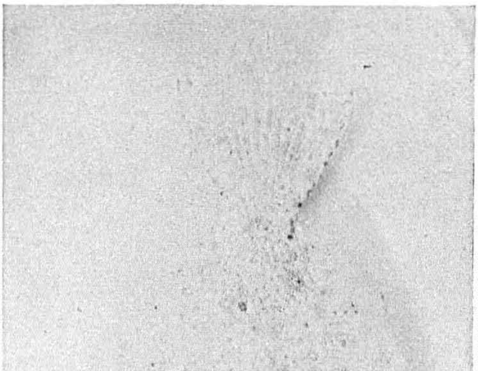

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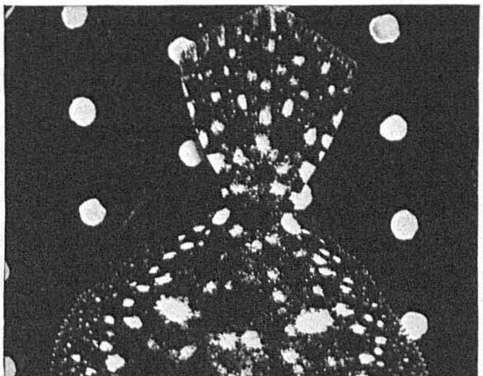

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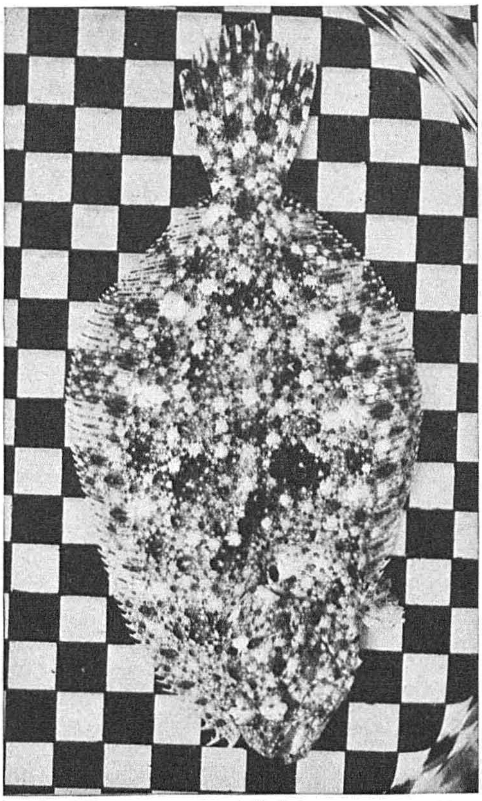

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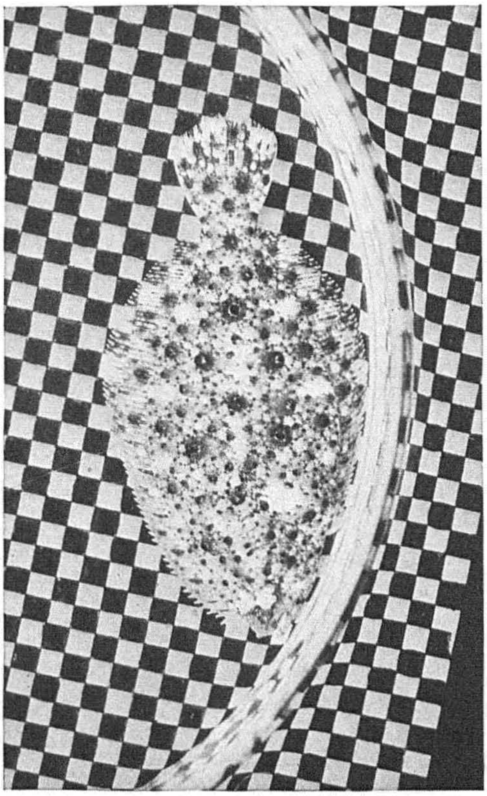

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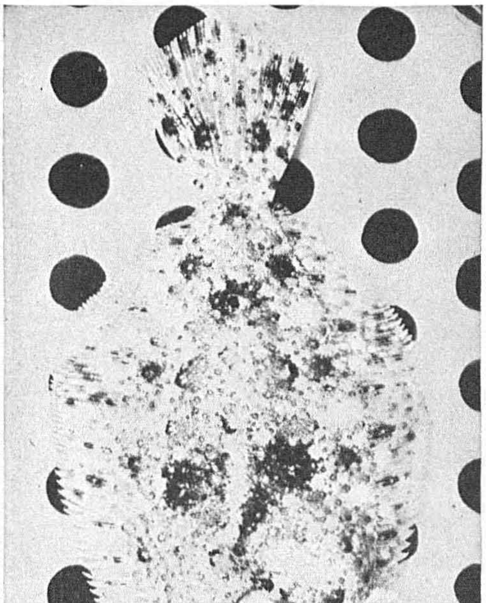

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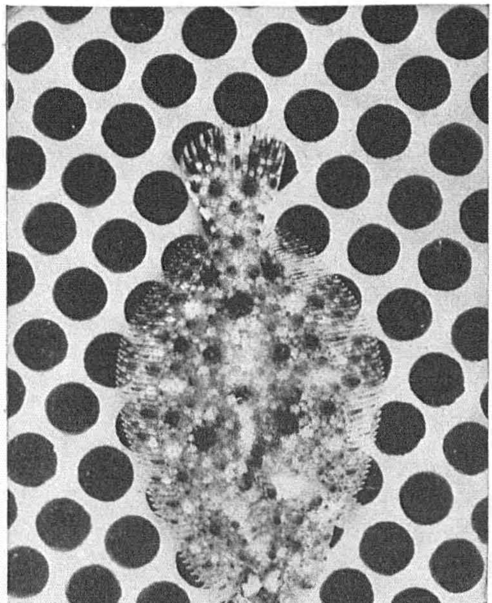

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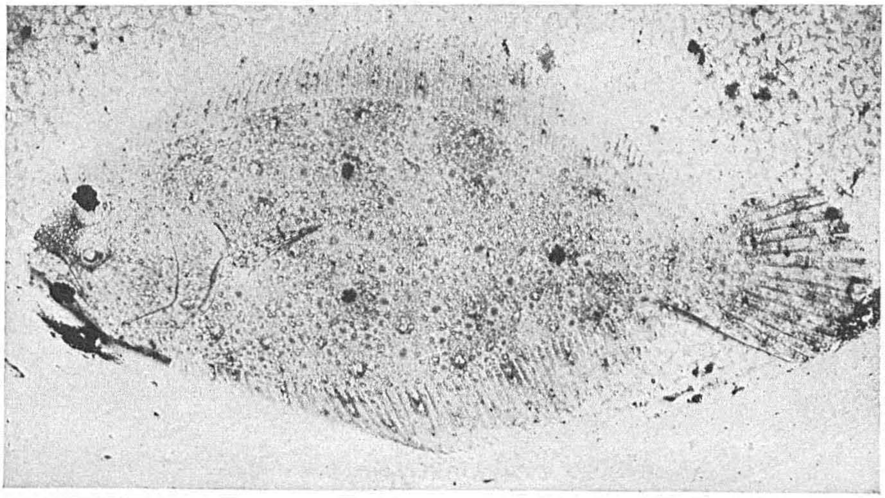

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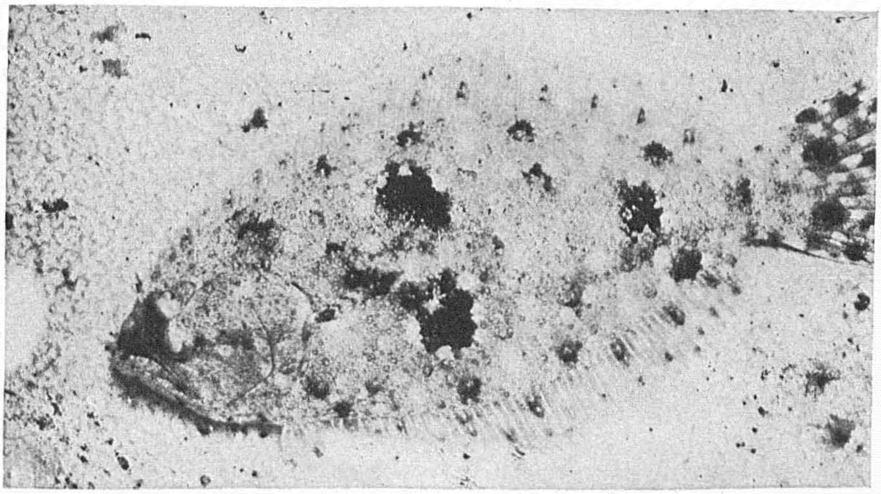

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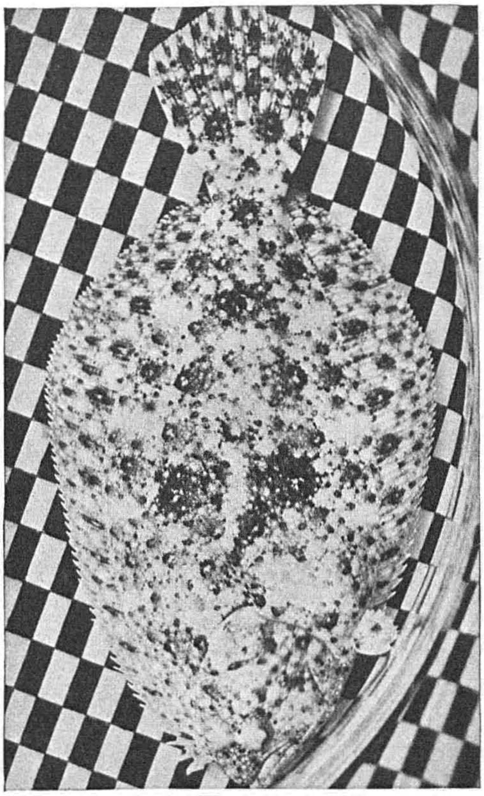

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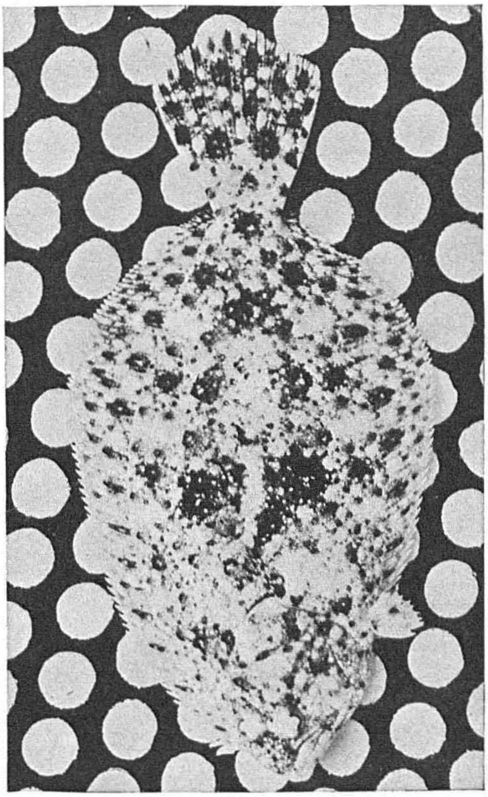

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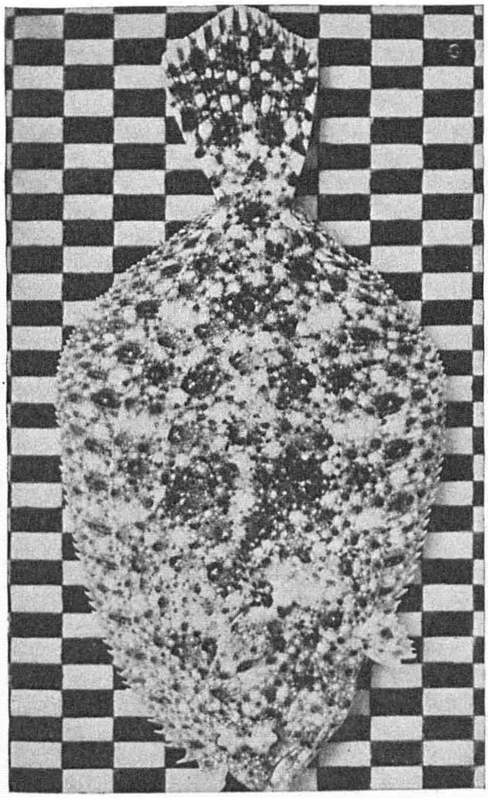

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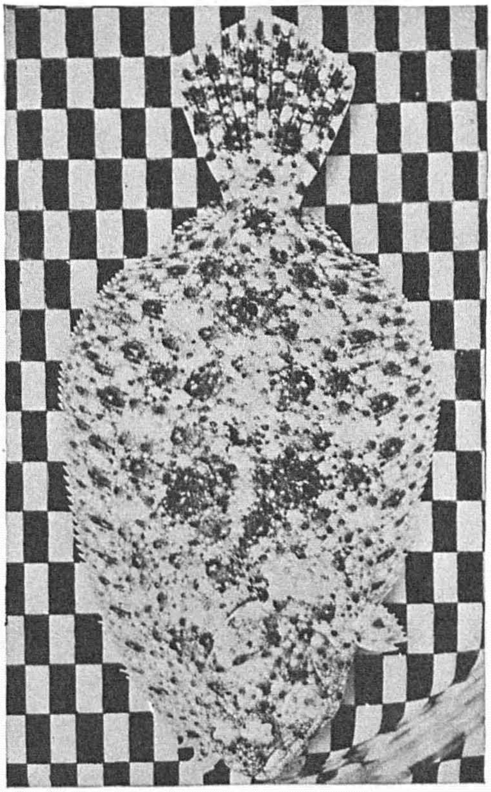

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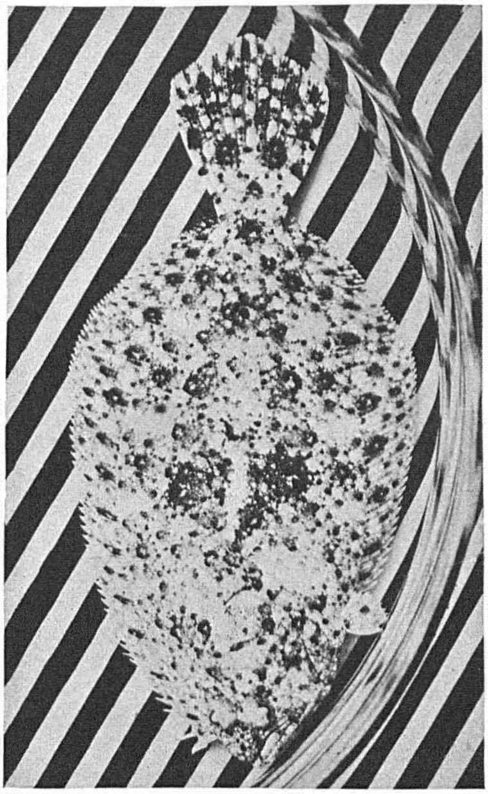

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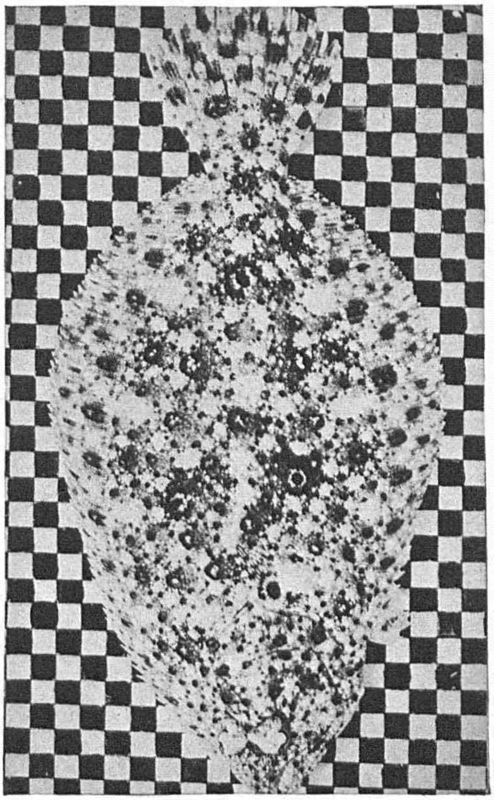

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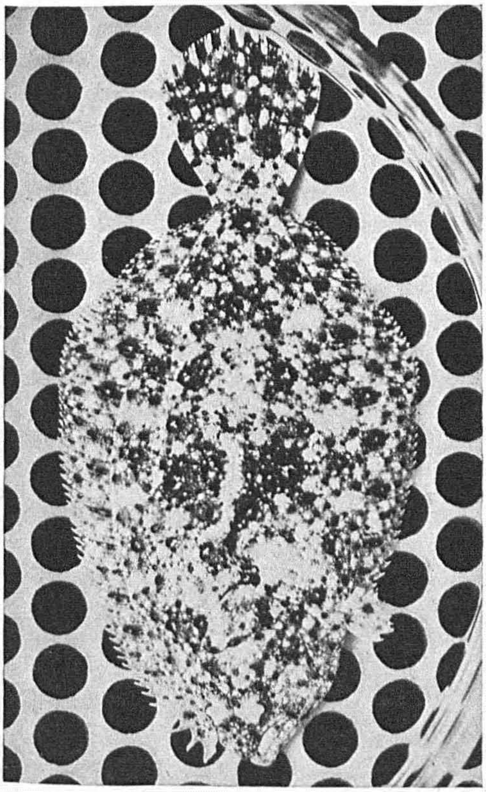

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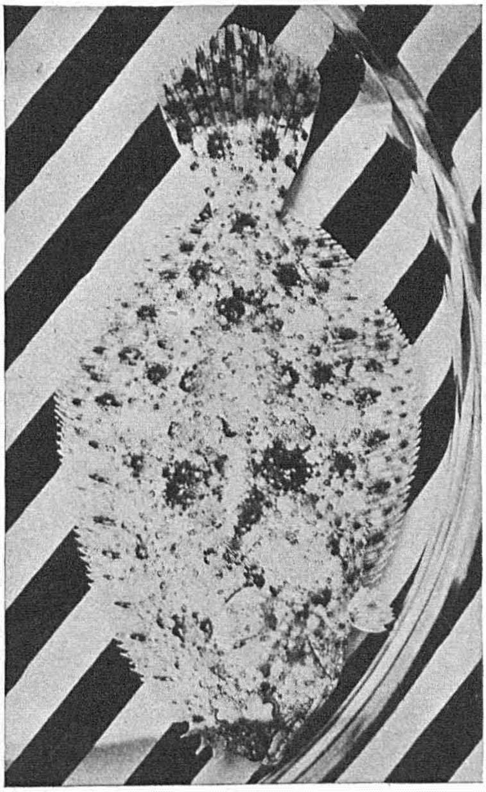

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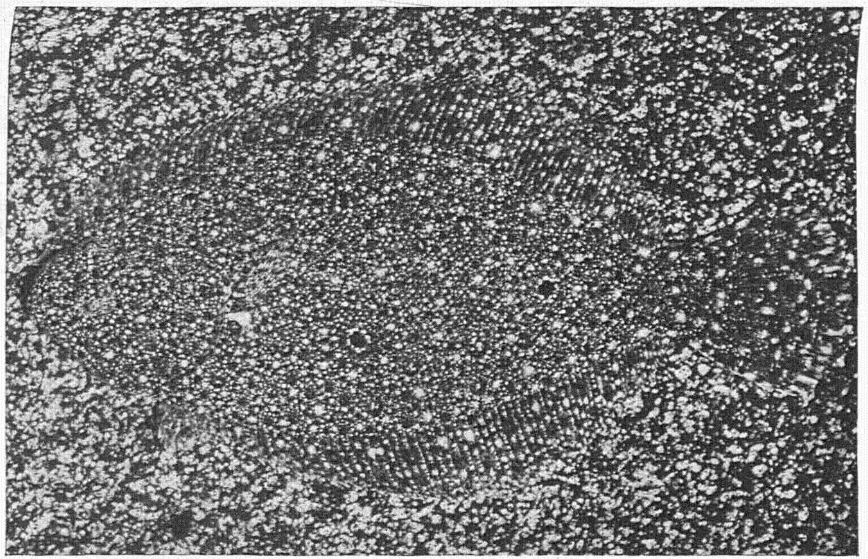

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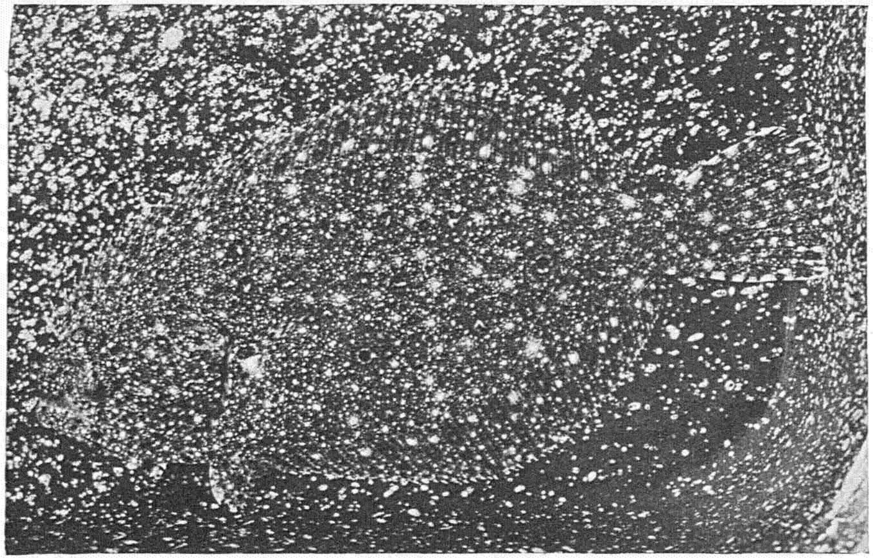

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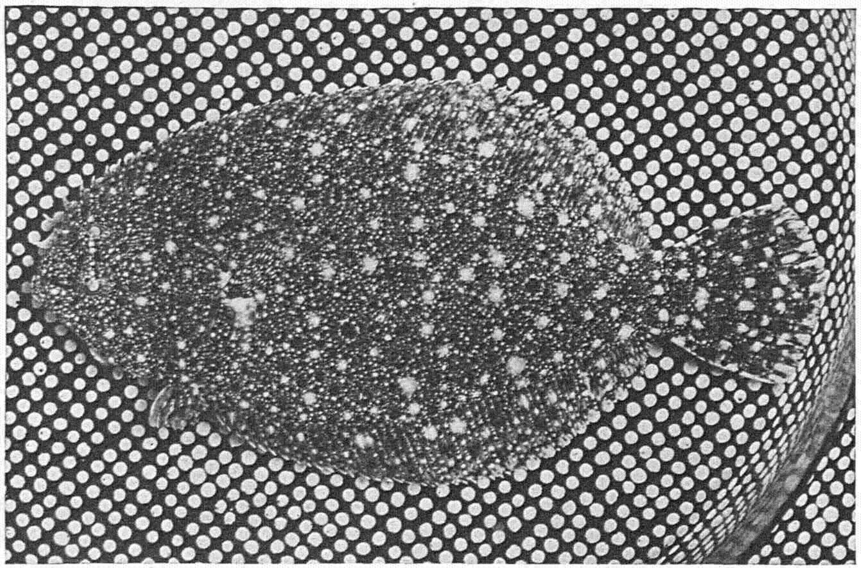

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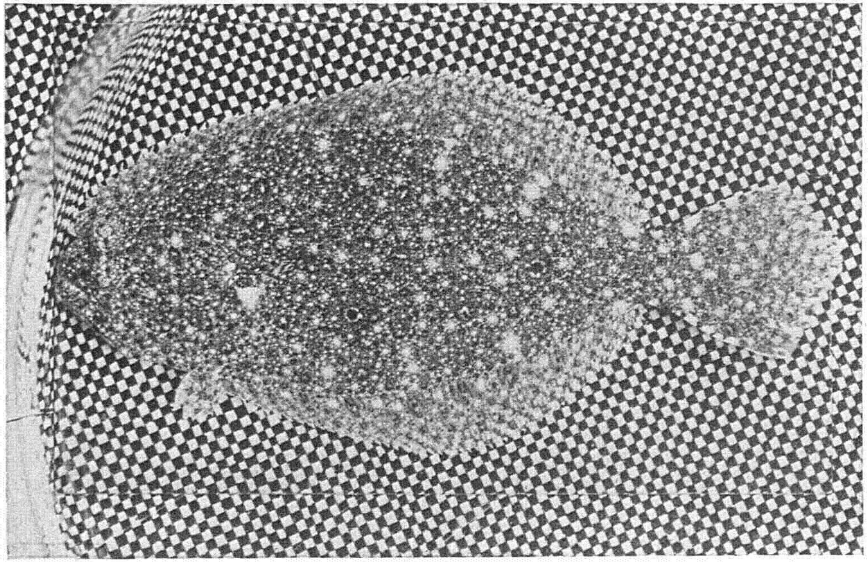

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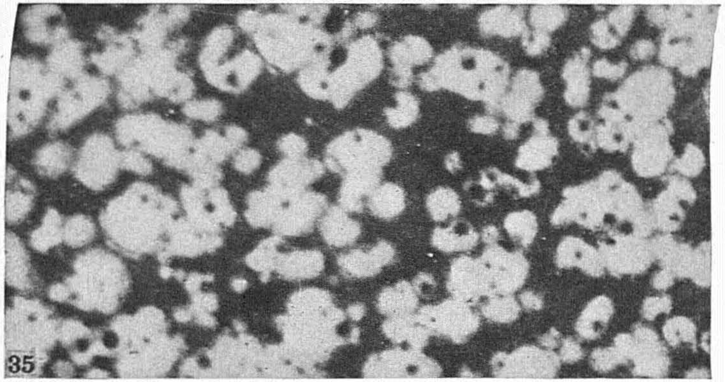
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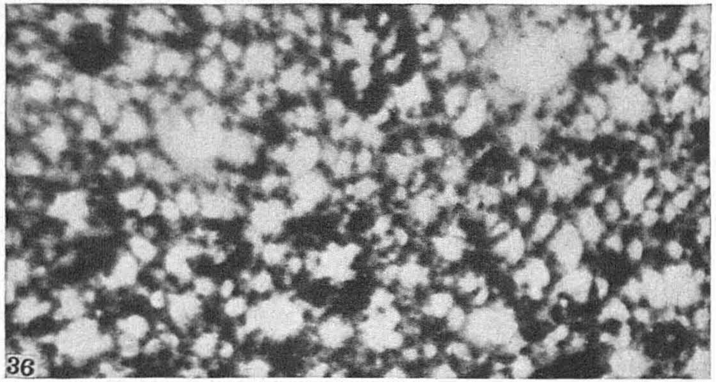
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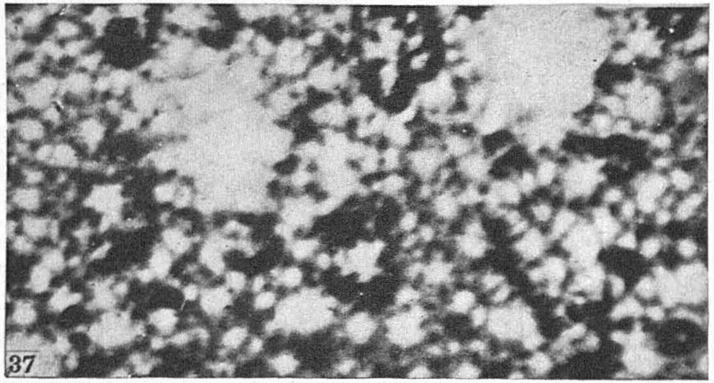
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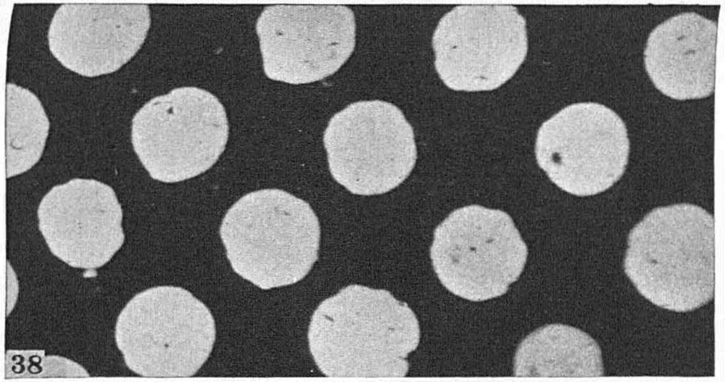
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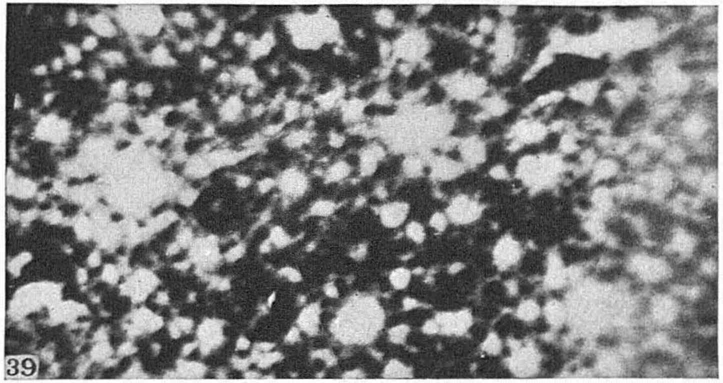
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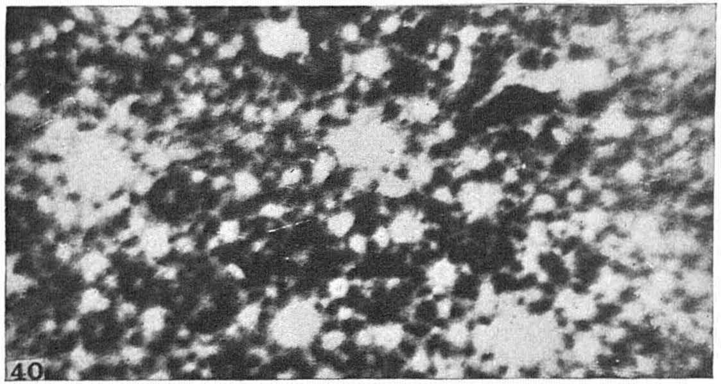
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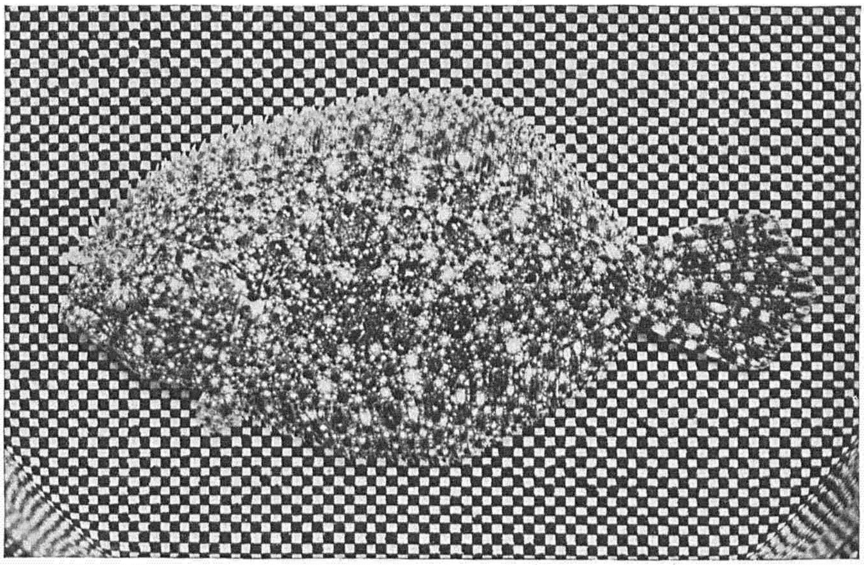

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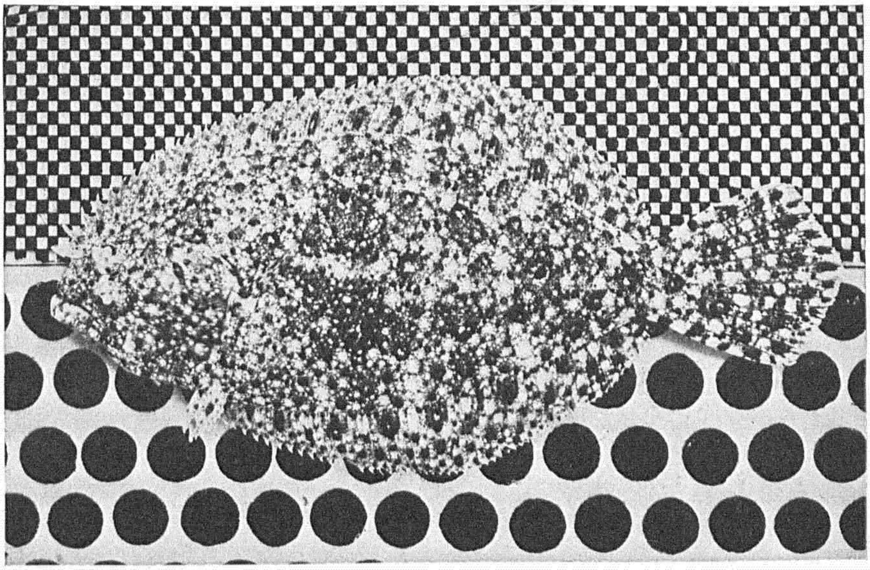

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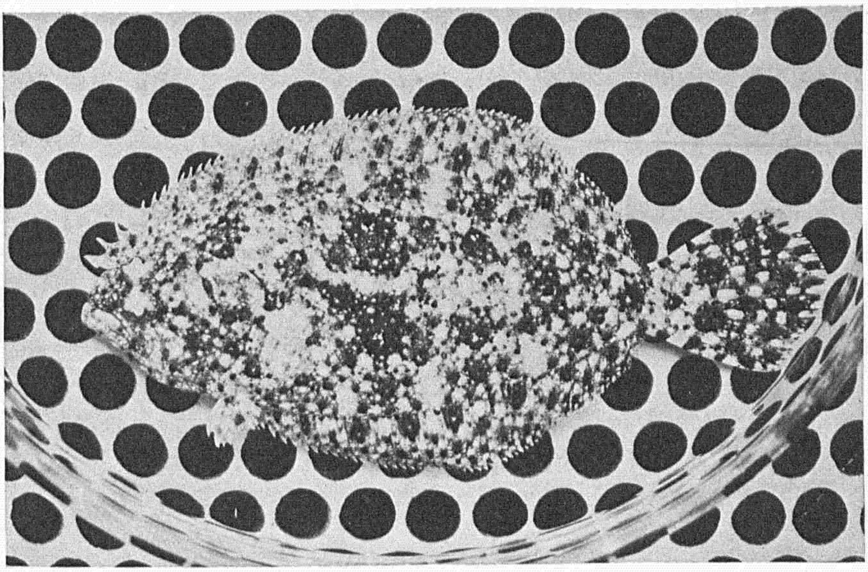

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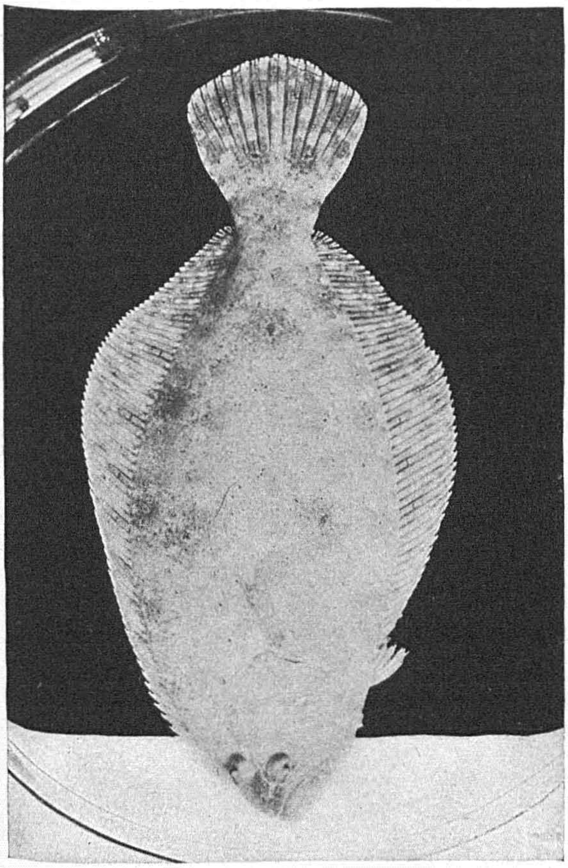

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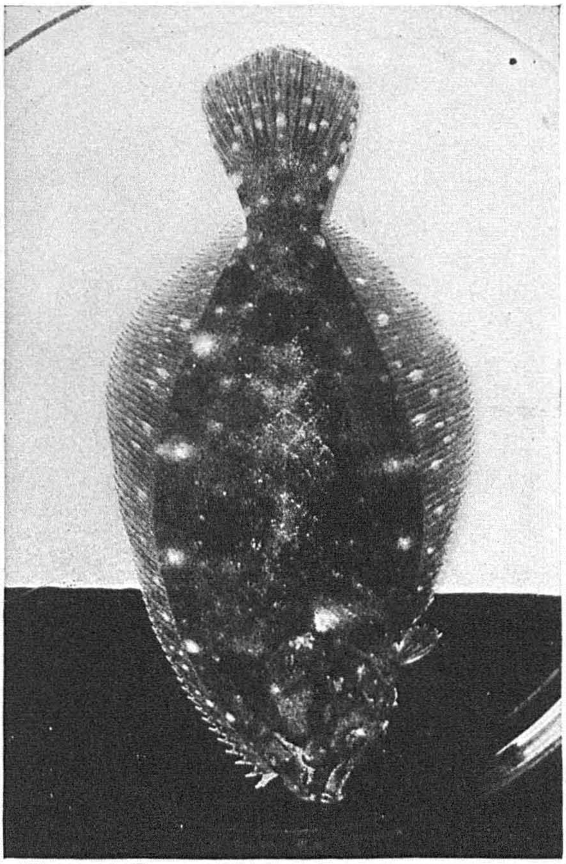

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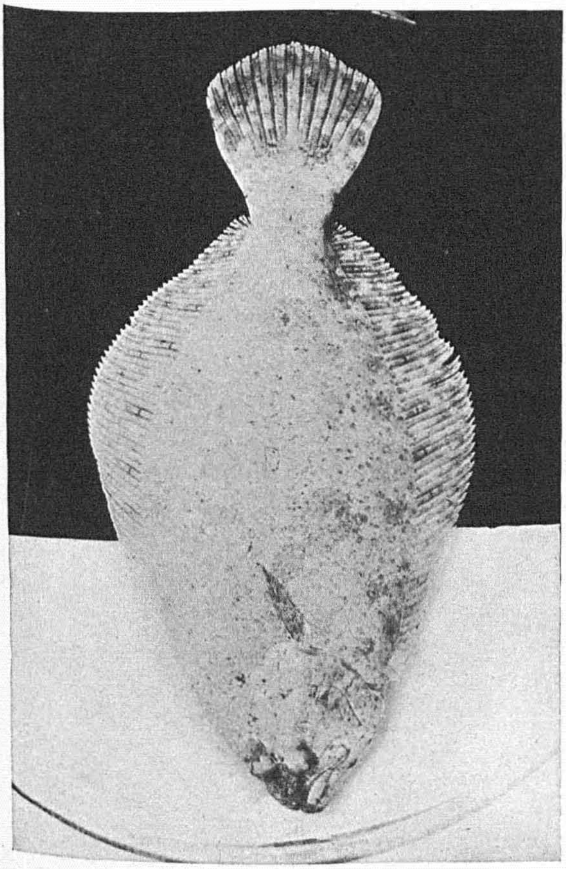

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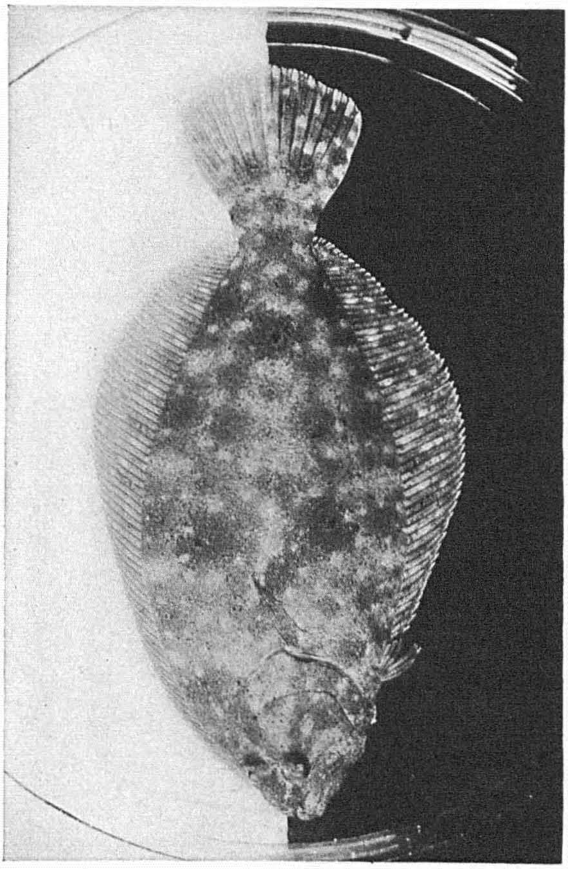

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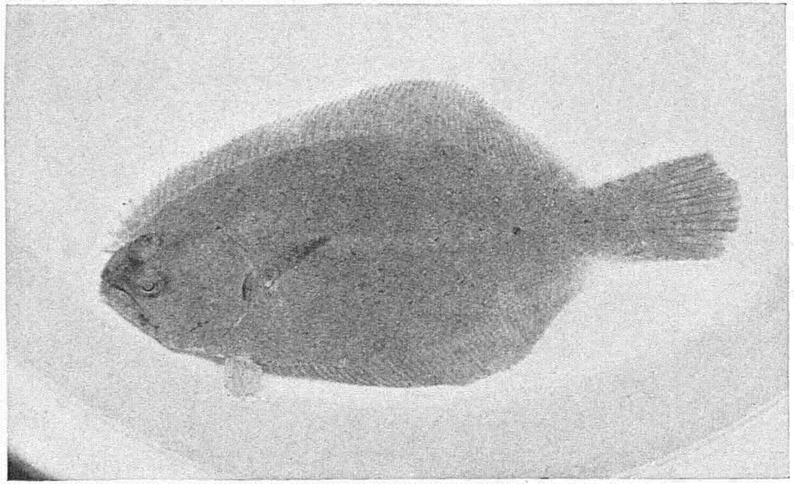

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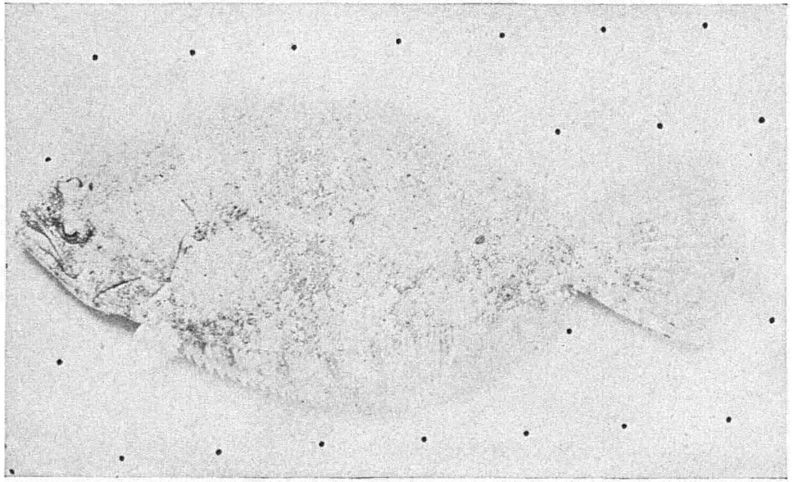

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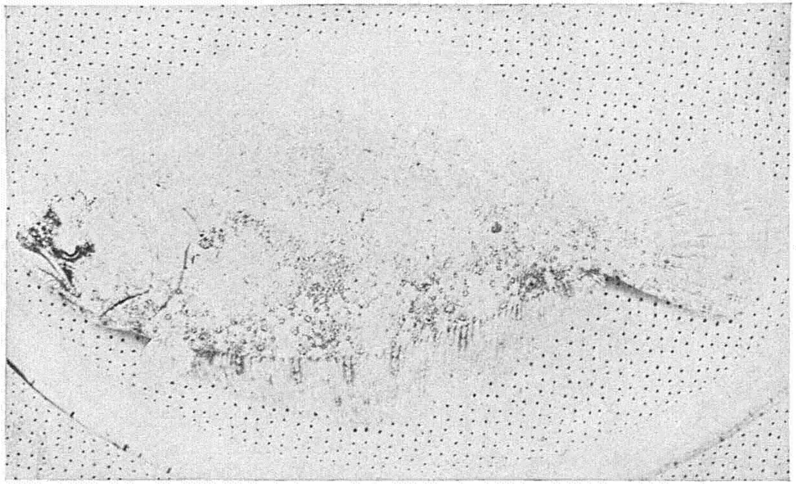

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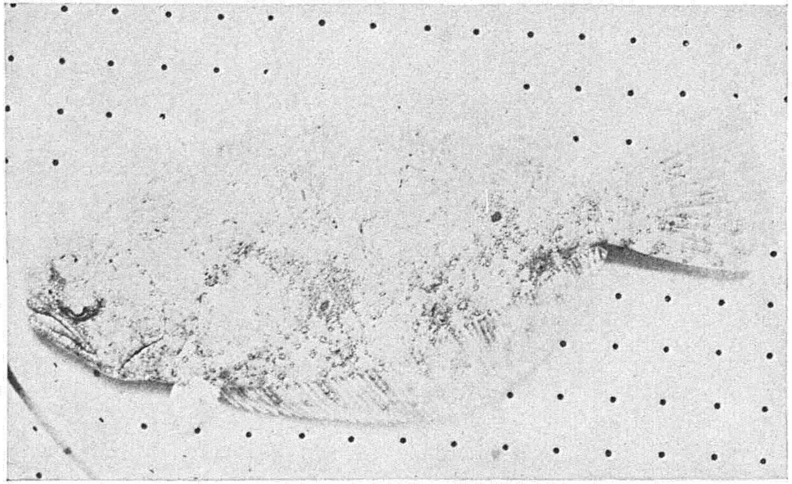

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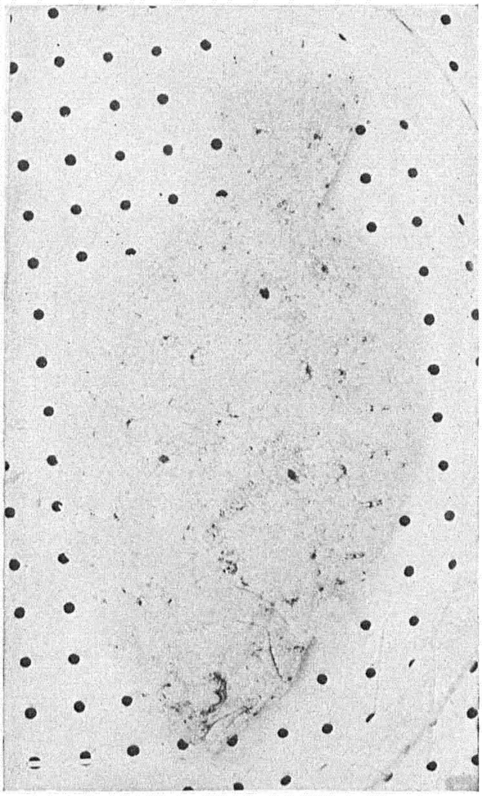

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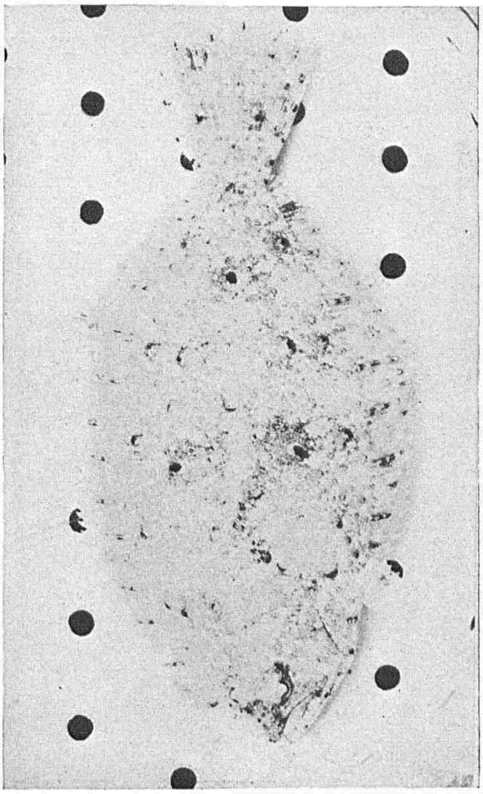

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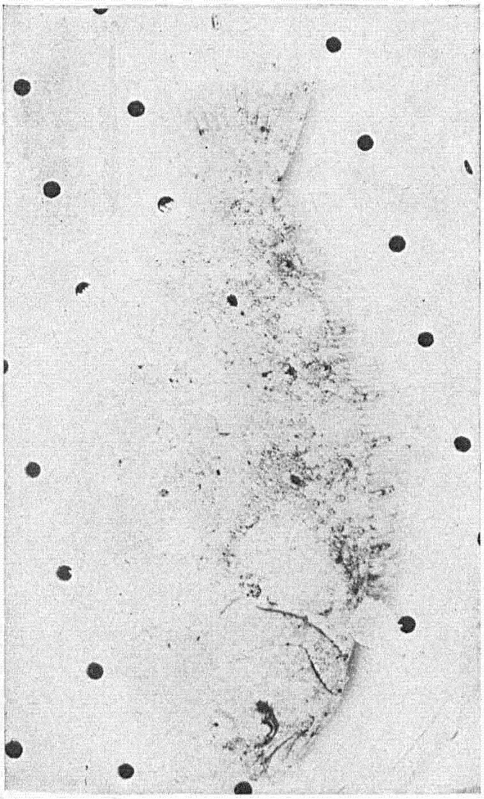

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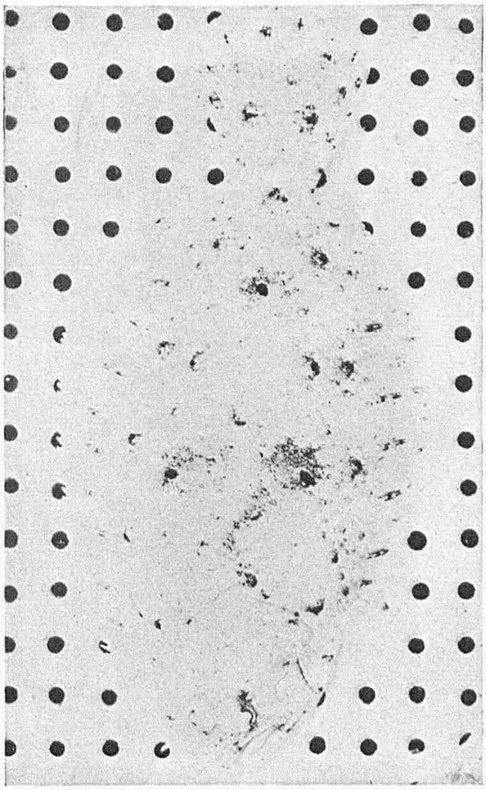

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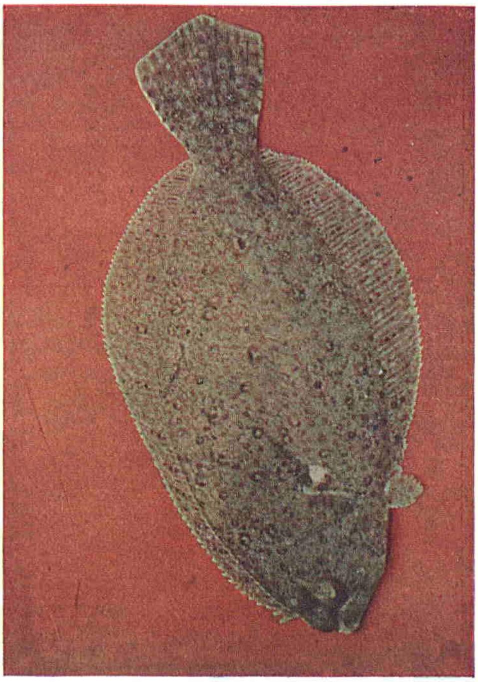

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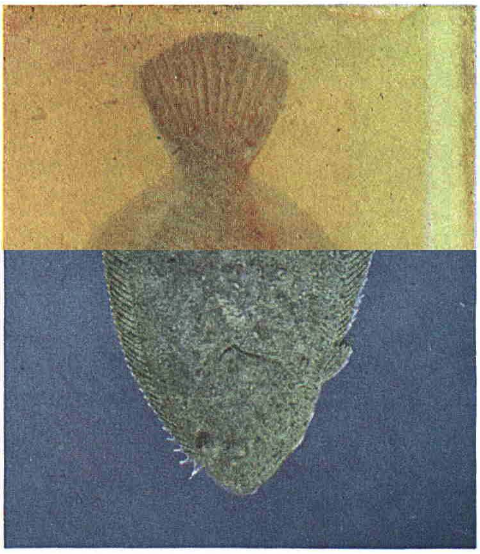


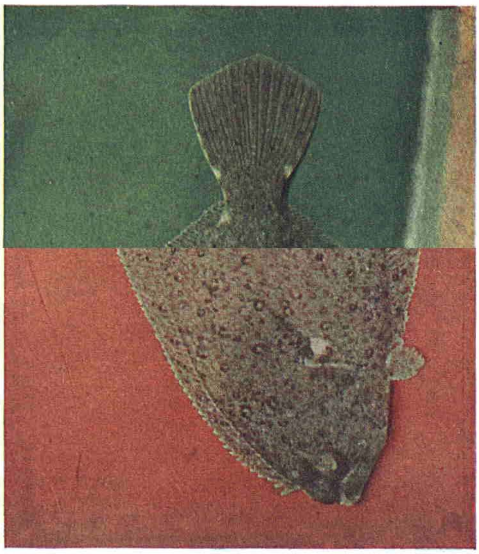
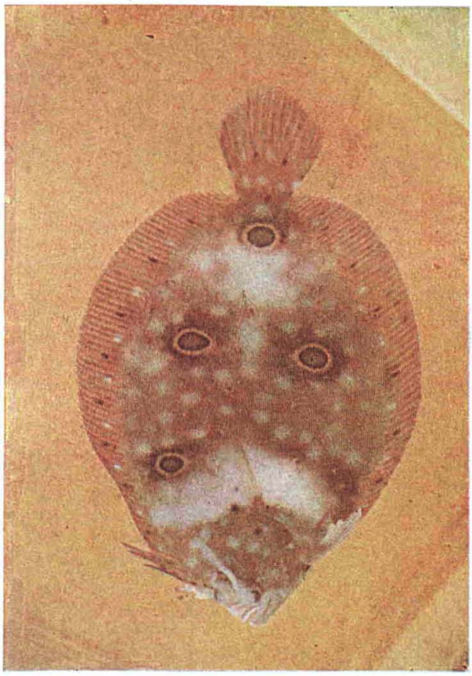


PLATE XXXIV.

61



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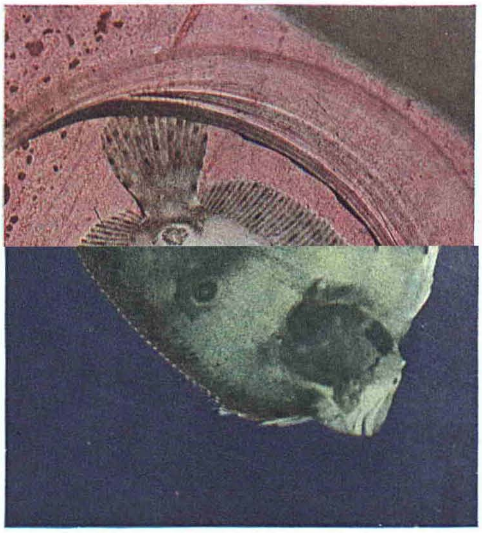

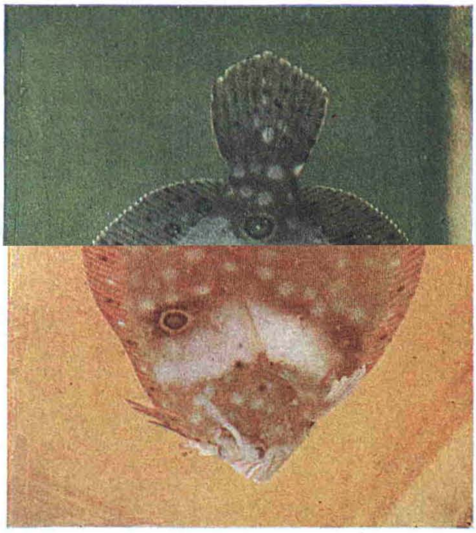

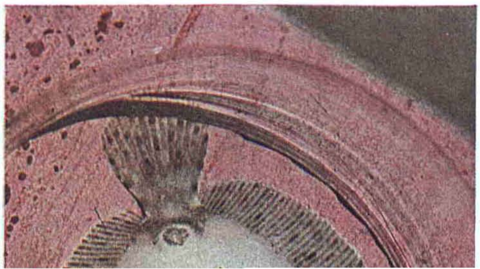

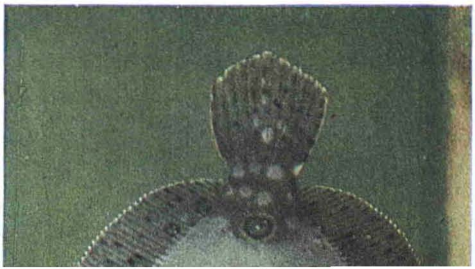

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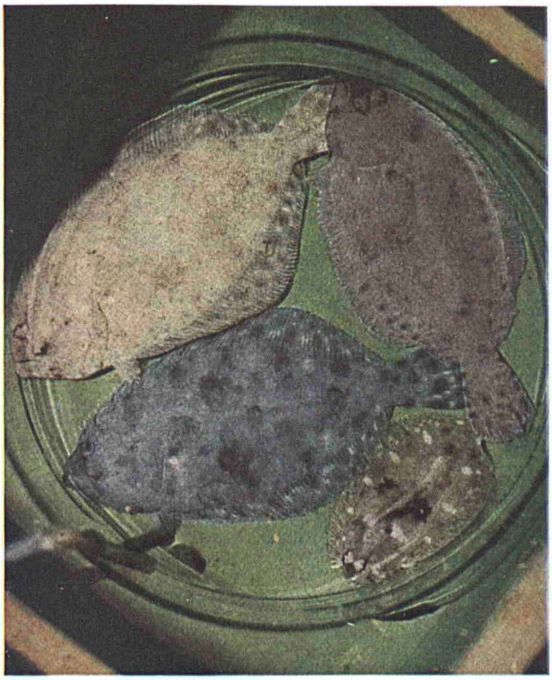

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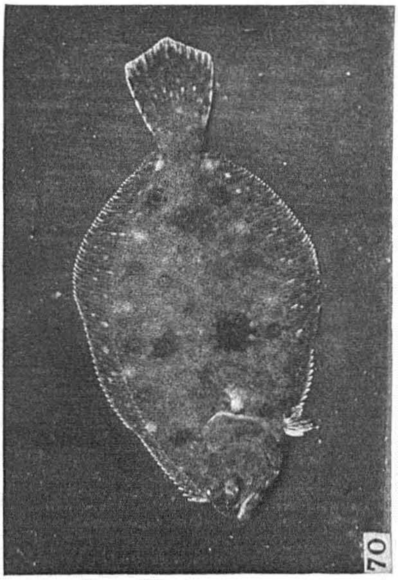
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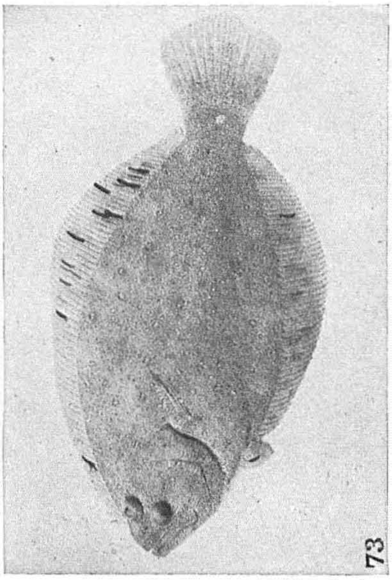
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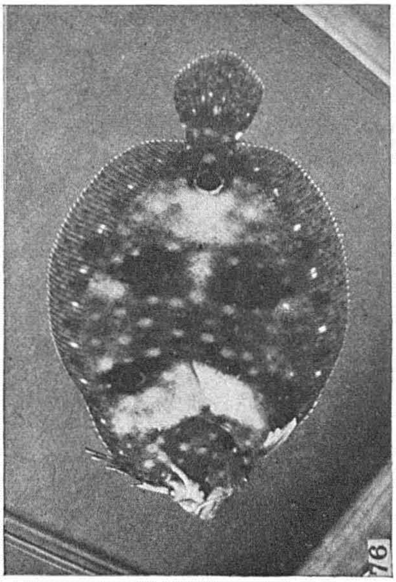
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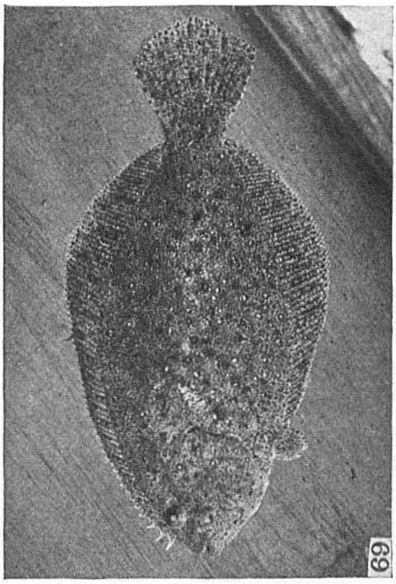
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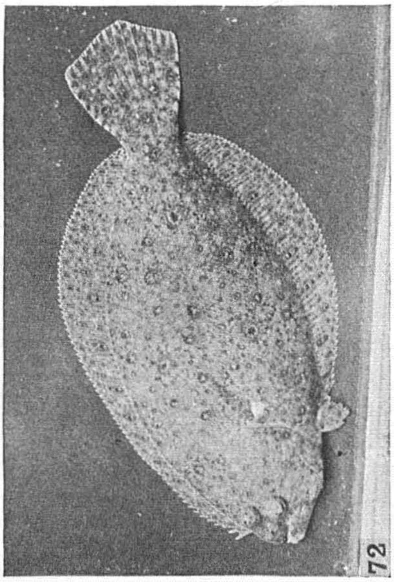
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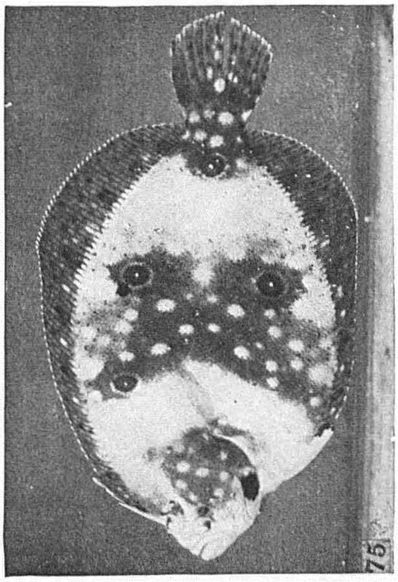
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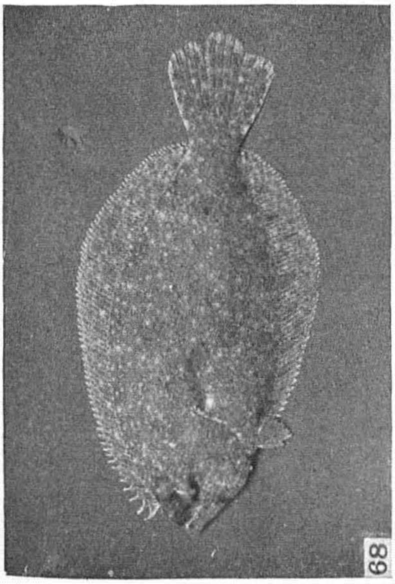
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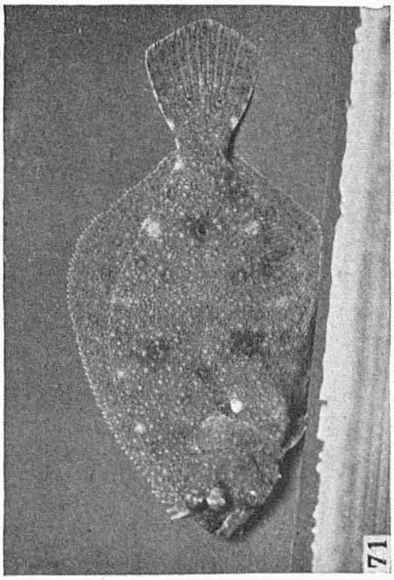
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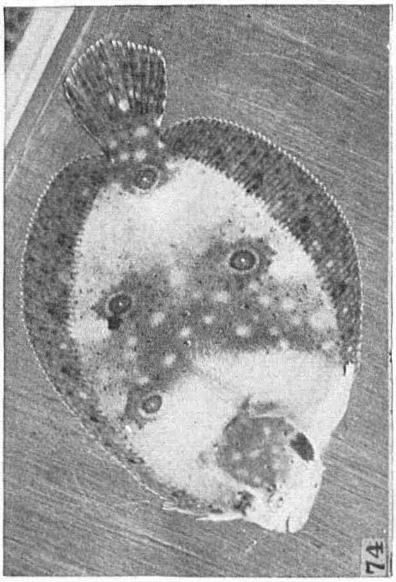
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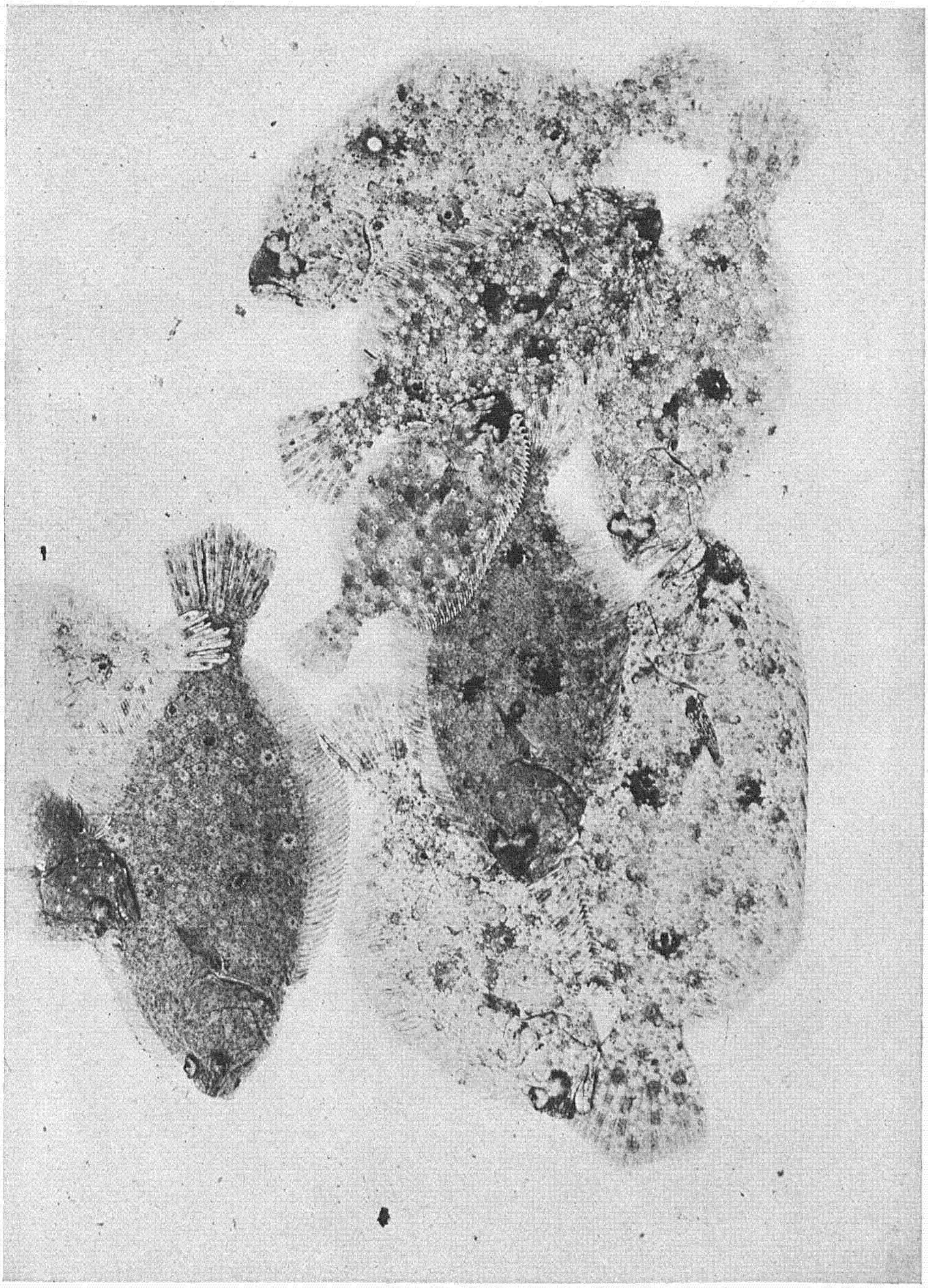
Plate XXXVII.



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