3. The Colour Changes and Colour Patterns of *Sepia officinalis* L.

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(Plates I.–III.† ; Text-figures 1–5.)

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1. INTRODUCTION.

The cuttlefish, *Sepia* (*Eusepia*) *officinalis* L., has always attracted the interest of naturalists by the remarkable rapidity with which it changes colour ; and it has been suggested that the variety of colours which it can assume is of protective value, each colour rendering it inconspicuous in a particular environment, both to its predators and to its prey. Among those who have taken this view was Aristotle. In 'Historia Animalium' (Thompson, 1910) he says : "Of molluscs the sepia is the most cunning . . . (the octopus) seeks its prey by so changing its colour as to render it like the colour of the stones adjacent to it ; it does so also when alarmed. By some the sepia is said to perform the same trick ; that is, they say it can change its colour so as to make it resemble the colour of its habitat."

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† For explanation of the Plates, see p. 34.

But no attempt has yet been made to investigate fully the view that each of the colorations of *Sepia* renders the animal inconspicuous in the specific environment in which it is assumed. Indeed, a complete account of the animal's colour changes has never yet been given. One of the most striking features of the colour change is the repeated reappearance of various patterns of colour on the animal's body, each unit of each pattern occupying the same position whenever the pattern appears: and these patterns are either but briefly noticed, or inaccurately described, in the literature of the subject. The older descriptions of Delle Chiaje (1823), Wagner (1833), and de Férussac and d'Orbigny (1835–48) are very incomplete ; and although Hofmann (1907 *a* & *b* ; 1910) has photographs of *Sepia* showing a stripe and a black spot pattern, he was concerned rather with the physiological aspects of colour change, and does not devote much attention to them. Finally, only very brief reference to the animal's colour behaviour is made in the recent L.M.B.C. Memoir on *Sepia* (Tompsett, 1939).

The incompleteness of the previous descriptions makes it desirable that the colorations and colour patterns of *Sepia* should be fully described. This done, it will be possible to consider more profitably whether they are allæsthetic characters ; whether, that is, they have an effect on other animals, and are thus of importance to the cuttlefish in its ecological relations. It may be the case that, as is so in many other animals, *Sepia*'s colorations have not only a protective, or " cryptic " effect, as Aristotle suggests, but also fall into the further classical categories of " warning," " mimetic," and " sexual " coloration.

The nature of the chromatophores and of the way in which they co-operate to produce colour changes were long in dispute, and the history of the problem is reviewed by van Rynberk (1906). The more recent investigations which have contributed to our knowledge are described by Baglioni (1913), Bozler (1928), Fuchs (1914), and Sereni (1930). We now know that each chromatophore is a pigment-containing sac, acted upon by a system of muscles, inserted radially upon it. The sac is thus pulled out to cover a maximal area of the body surface when the muscles are fully contracted ; and when they are relaxed, the elasticity of the walls of the sac itself makes it assume a contracted spherical state, covering a minimal area. The chromatophore muscles are directly innervated by nerve fibres of which the cell bodies lie in the central nervous system.

The extreme rapidity with which complete and general colour changes take place, in a way quite unknown in any other animals than Cephalopods, has already been mentioned. A clear idea of the speed of the process can be gained from the work of Hill and Solandt (1935). These workers show graphs of the time relations of colour change in *Sepia*, as obtained by photo-electric measurement. The change from complete contraction to complete expansion in a chromatophore can take place in two-thirds of a second ; that is, with a rapidity unparalleled by any other type of chromatophore mechanism.

Close examination of the chromatophores of a living animal shows that waves of slight contraction and expansion of the chromatophores pass all over the body, even when the animal is not changing colour. The fact that the chromatophores are directly controlled by the nervous system means that the rapid changes of colour, the colour patterns, and these waves of pulsation of the chromatophores are all manifestations of waves of activity, and of patterns in the excitation of the chromatophore motor neurons in the central nervous system.

The chromatophores lie in three layers parallel with the outer surface of the animal, and these layers can be distinguished from each other by the colour of the pigment in their chromatophores. Those of the outer layer contain a bright yellow pigment ; in the middle layer the pigment is orange-red ; and in the basal layer the chromatophore pigment is brown, sometimes with a red tinge, sometimes almost black (Naef, 1921–28 : Kühn and Heberdey, 1929).

The colour patterns owe nothing of their form of patterning in the distribution of the chromatophores, for such variations as there are in their numerical distribution over different areas of the body surface bear no relation to the various patterns.

But the colour of the animal is not produced only by the reflection of light from the chromatophores. Throughout the epithelial tissues of the animal, lying below the chromatophores, is a layer of immobile reflector cells, the iridocytes or iridophores. The structure, development, and optical properties of these structures have been investigated by Schäfer (1937). Over most of the body surface their distribution is unpatterned, but at some points unusually dense groups of them lie above the chromatophores. Here they form distinct white markings, as on the fins (Pl. III. fig. C ; text-fig. 1), where they make a regular pattern ; and similar markings are also found at points all over the dorsal surface of the mantle, at the places where the skin papillæ arise (p. 26 ; Pl. III. fig. C), and at points on the tentacles and head. But apart from these white markings, and from the general greenish iridescence which is contributed by reflection from such of the deep iridophores as are exposed by contraction of the chromatophores, the iridophore system, being immobile, makes no contribution to colour change and pattern. There is thus no major pattern intrinsic in the distribution of either chromatophores or iridophores which can be related to the colour patterns. These must therefore be entirely the result of expansion and contraction of the chromatophores, and are a display on the surface of the body of patterns in the activity of the central nervous system.

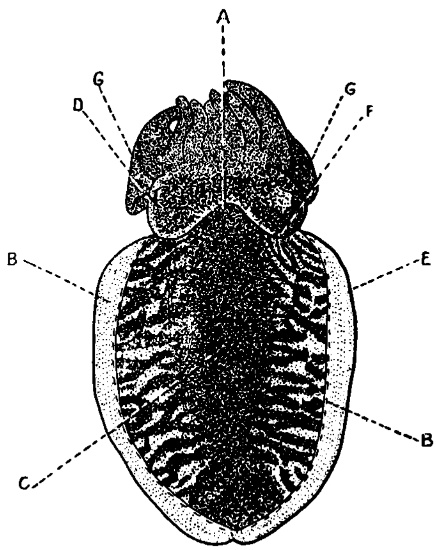
The observations upon which the following account is based were made at the Laboratory of the Marine Biological Association at Plymouth. I am grateful to Professor E. S. Goodrich for his permission to use the Oxford table there, to the Director and Staff of the Laboratory for their help, and to my father for financial assistance. My chief debt is to Mr. J. Z. Young for suggesting the problem, and for the system of ideas, derived from his studies on the nervous system of *Sepia*, with which I approached the work. And his practical experience with the Cephalopods and his advice in the writing of the paper have both been invaluable to me. Professor Goodrich has assisted me by reading and criticizing the manuscript, and Dr. H. B. Cott has kindly given me the benefit of his special knowledge on the subject of animal coloration, with several suggestions.

2. The Coloration of *Sepia* under Various Conditions.

(i.) *Free-swimming in an Aquarium.*

In the largest aquarium tanks at Plymouth an actively swimming *Sepia* has a striking colour pattern on the dorsal surface of its mantle (text-fig. 1 ; *cf.* Pl. I. fig. A). Dorsally a central region, shaped like the cuttle-bone above which it lies, is of a dark brown colour. In this part of the pattern all the dark chromatophores are expanded to approximately two-thirds of their maximal diameter, while the other chromatophores are almost completely contracted. On both sides of this central area in a pattern in which stripes of dark chromatophores almost fully expanded alternate with stripes in which the dark chromatophores are completely contracted. Over the whole of the striped area the orange and yellow chromatophores are slightly expanded. Thus this pattern is made up of alternate dark brown and almost white stripes and has been compared with that of the zebra (Hofmann, 1907 *b*). As text-fig. 1 shows, the stripes are not uniform in shape and size, and they often branch and join. But it is remarkable that, in spite of this irregularity, the details of the pattern shown by an individual are always the same and always located in the same position on the mantle whenever the pattern appears. Stripes are visible also on the dorsal surface of the large ventral arms ; but on the other arms and on the head there is no definite pattern,

Text-figure 1.



Sepia officinalis, dorsal view, showing the " zebra " pattern.

A = anterior point of the mantle and cuttlebone ; *B* = white markings on fin, formed by superficial iridophores ; *C* = central dark region of the mantle ; *D* = the eye ; *E* = the fin ; *F* = the aperture of the mantle cavity ; *G* = the ventral large sickle-shaped arms.

Approximately one-third natural size.

the colour being that of the central region of the back. On the ventral surface of the body no chromatophores are expanded, and its colour is that produced by the reflection of light from the iridophore layer.

It is a salient point in the theory of animal camouflage that in order that an animal may be protectively coloured it is not necessary that its colour shall be an exact match of that of the environment ; indeed, such a resemblance would be ineffective. Instead, the animal should have such gradations of shading and colouring on its body that the gradations of light and shade produced on it under normal conditions of illumination, and which give it its characteristic three-dimensional form, are eliminated. In this way the form and outlines of the animal, as well as its colour variations, are made invisible, for it becomes monochrome and flat in appearance (Cott, 1940: Thayer, 1918). The fact that it is very usual for animals to be more lightly coloured on their ventral than on their dorsal surface when they are, like *Sepia*, normally lit by much more light from above than from below is almost certainly a demonstration of this principle. The study of fish in a new American aquarium of great size has convinced Breder (1938) that the shading of fish from a dark coloured back to a light belly is extremely effective in making the outlines of the fish hazy and indistinct, even to a close observer. *Sepia* shows well this " obliterative counter-shading." For the mid-dorsal region of the mantle, which receives the most incident light, is darkest in colour ; the sides of the mantle, which are less well lit—as light from above is incident at a more acute angle—are less dark ; and the ventral surface, which receives only reflected light from the under-water surroundings, is quite pale.

In this connection it is interesting that when *Sepia* is turned on its back in the water all the chromatophores of its ventral surface expand fully ; and if it is turned half over on to its side, the upper half of its ventral surface darkens, while the lower half remains pale. The ability to react in this way to an upset from its normal posture is perhaps valuable to the animal, for if turned upside down by an enemy's attack it would be rendered extremely conspicuous by the reversal of its normal obliterative shading relations, if the ventral surface remained pale.

The monochrome, flat appearance given by obliterative shading is only an adequate concealment for the animal if the environment itself also seems monochrome and without brightness variations. Conditions in the sea cannot often be thus ; so one may suggest that the zebra pattern is a further protective device, depending on the well-known principle of camouflage that a strongly contrasted pattern of stripes or other shapes on an animal's body breaks up its outline. The boundaries between the light and dark stripes are so much more clearly marked than is the outline of the animal, that the latter becomes inconspicuous, and although the fins bear no disruptive pattern, their outline is obliterated, for when the animal is showing the zebra pattern, all the chromatophores of the fins are contracted, so that the latter are transparent. Further, among beds of sea-weed on the sea-floor, in which *Sepia* often swims (Cuénot, 1916–18), the stripe pattern must be most valuable, for when the environment is made up of dark stripes of weed against the lighter water, any outline which interrupts these stripes is made immediately most conspicuous. *Sepia*, however, will not be so betrayed, for, being striped itself, its outline will remain indistinct.

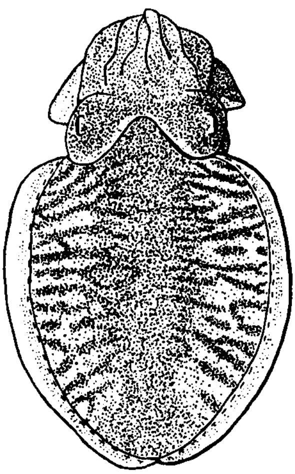
An observation of Breder (1938) suggests another type of environment in which the stripes of *Sepia* would protect it. When a shark is swimming a few feet below the surface of water which is disturbed into ripples, and on which the sunlight is falling, there plays over its back a pattern of golden stripes of light. In these circumstances *Sepia* would not be made conspicuous, as the shark is ; for the stripes already present on its back would so combine with those falling on it as to break up the outline of the animal.

(ii.) *Swimming near the Floor of a Sandy Tank.*

In nature *Sepia* is found, during the summer months, in shallow coastal waters, where it swims about near the bottom, at depths of about ten metres. One of the localities near Plymouth from which it is often obtained is Cawsand Bay, where the sea-floor is sandy ; and it seems that it often inhabits similar environments elsewhere (Cuénot, 1916–18; de Férussac and d'Orbigny, 1835–48; Lo Bianco, 1909).

When swimming at the bottom of an aquarium tank with a sandy, shell-gravel floor, *Sepia* shows a stripe pattern, similar in form to the zebra, but much less contrasted in coloration (Pl. I. fig. A) (text-fig. 2). This may be described as a " pale zebra " pattern, for all the units of the zebra striping are here made paler by the less full expansion of the dark chromatophores; and this combines with the half-expanded yellow and orange ones to give a sandy brown colour to the animal.

Text-figure 2.



Sepia, dorsal view, showing a very pale zebra pattern. Compare Pl. I. fig. A.

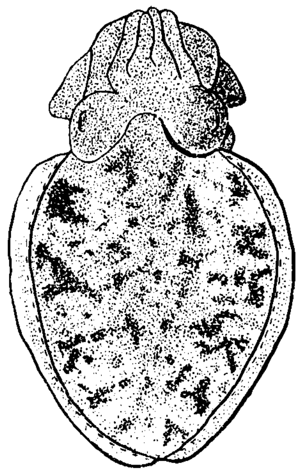
This colour, assumed by the animal when near a sandy bottom, may well be a protective resemblance, for any coloration markedly different from that of the environment would make the outlines of the animal very conspicuous. The stripes still retained will help to break up the animal's outline as before, and this they must do even more effectively when the sand is disturbed into ripples by movement of the water.

The various forms of the zebra and light mottle patterns make up a continuous series of pattern change, as is shown by Pl. I. figs. A & B; Pl. III. fig. B; and text-figs. 1 & 2. It is thus impossible clearly to differentiate any one of these patterns from those nearest akin to it either on its composition or on the environmental circumstances in which it is produced.

(iii.) *At Rest on a Sandy Bottom.*

When *Sepia* is at rest on the sandy floor of a tank, the stripe pattern is seldom shown and there appears instead a mottle over the whole dorsal surface of the animal, of very light and slightly darker browns (Pl. I. fig. B). The orange and yellow chromatophores are considerably expanded all over, and the dark chromatophores are fully contracted in the pale regions of the mottle, very slightly expanded in the darker ones. The general coloration given to the animal by this light mottle pattern is very close to that of sand. Further, when it is at rest, *Sepia* has the habit of digging itself into the sand, by washing a concavity in it by the movement of its fins, at the same time throwing the excavated sand on to its back. Thus the animal lies not only with most of its body below the level of the sea-floor, but also with its back partially covered by a thin layer of sand ; and even those parts of its mantle which are exposed have in their coloration a close protective resemblance to the environment.

Text-figure 3.



Sepia, dorsal view, showing a form of the " light mottle " pattern

When the animal is thus buried, the light mottle pattern is sometimes modified by the appearance on the mantle of a series of dark brown markings, roughly tri-radiate in form, along the base of the fin. At the same time the rest of the mantle becomes almost uniformly sandy brown, very little mottling remaining in the coloration (text-fig. 3). These markings are not often seen, and there is no evidence as to under what special circumstances they appear.

(iv.) *In a Dark Environment.*

The colour behaviour of *Sepia* under conditions in which it is much less brightly illuminated than in the previous instances, has been investigated by the use of a black tank ; that is, of a tank of which the sides and bottom are painted black so as to absorb all light incident on to them, and with a close-fitting lid. When the animal is left in such a tank for a few minutes, with the lid closed, it is only with the greatest difficulty that it can subsequently be seen by the observer, even by the light admitted by partial removal of the lid. The details of the coloration of the animal under these circumstances can be revealed by sudden bright illumination and observation before they are much changed. It is found that the body is very dark in colour, and this effect is produced by a pattern composed of the same units as the light mottle, but differing from it in that all parts of the mottle have become much darker, by the further expansion of the dark chromatophores. The distinction of lighter and darker areas in the pattern, however, still remains.

The colour of the whole body of the animal in the black tank is that shown on the dark parts of the mantle of the individual in Pl. II. fig. B. When more light is admitted to the tank, by the further removal of the lid, the animal becomes less dark in appearance, by a general slight paling of all the units of the mottle, produced by a decrease in the degree of expansion of the dark chromatophores.

It seems that *Sepia* often inhabits regions of considerable darkness on the sea-bottom, as under rocks, or among weed, or in crevices ; and its ability to become dark in colour under these circumstances must be of considerable procryptic value to it. In such a situation, where there is very little light incident on to the animal, its dark colour will enable it to absorb this light, and thus to prevent its outlines from being visible against the background, as would those of a light coloured animal. Further, any distinct form which might be given to the animal if there were a slight difference between the amount of light reflected by it and by its environment, will tend to be obliterated by the mottle pattern, which will break up the shading on the animal, taking from it the solid appearance it would have if uniformly coloured.

(v.) *In a Black-and-White Environment.*

When the lid is taken completely off from the black tank, the outlines of the *Sepia* become clearly visible, and it responds to illumination of this intensity by producing a transverse grey band along the dorsal surface of its head, between its eyes. This band is produced by a local complete contraction of the orange and yellow chromatophores, and the almost complete contraction of the dark ones.

If still more light is admitted, or a white object such as a porcelain square placed in the tank, further changes in the colour of the animal take place, and these, together with the head band, compose the " white square " pattern (Pl. I. fig. C ; Pl. II. fig. A). A large median white square appears on the dorsal surface of the mantle, and a median white area on its posterior tip. At the same time the head band also becomes a clear white. The pallor in the three areas is produced by the complete contraction of all chromatophores in them, light being then reflected only from the iridophores, and perhaps also from the cuttlebone, which lies below the square and posterior white area. The rows of iridophore groups on the fin (p. 19) are conspicuously white under these conditions of illumination, and may be considered as supplementing the white square pattern.

The production of this pattern takes place usually in a very few seconds after the alteration of the conditions of illumination ; and it can be elicited from animals showing the mottle or zebra patterns, as well as from dark ones, if when showing these patterns they are placed in a black environment containing a white object. The white regions appear first by a local paling of the original pattern, as can be seen in Pl. I. fig. D, where the pallor is spreading over the white square. This photograph brings out a point of considerable interest regarding the nervous mechanism underlying colour change, for a transient phase in the production of the pattern has been captured, and the paling is seen to be taking place first on that side of the animal which is nearer to the white object.

Corresponding to each white area in the pattern there must be a group of chromatophore motor neurons in the central nervous system which is in a state of inhibition, so that it does not discharge nerve impulses. It is notable that this inhibition momentarily disappears when the animal is stimulated by a sharp blow against the side of the tank in which it is resting, for there is a transient darkening of all the white regions on the mantle and the head.

Further evidence as to the environmental circumstances which usually accompany the production of this pattern can be obtained from the study of animals in conditions more natural than those in the black tank. One of the tanks in which *Sepia* is kept at Plymouth is out of doors, and is much shallower than those in the aquarium. Thus, although it is shaded from the direct rays of the sun, it is much more brightly lit than the deeper indoor tanks. The sides of the tank are black, and its floor is covered with stones, mixed with sand and shells. The animals live well in this tank, and when they are resting on the bottom almost always show the white square pattern.

Another pattern which is often seen in the outdoor tank, and which appears as an extension of the white square, is the " white stripe " pattern (Pl. II. fig. C). In this, two wide bands of completely contracted chromatophores extend laterally from the white square down the sides of the mantle. The white stripes never appear in the absence of the white square, and when they do appear, it is usually at some time after the latter, although no visible change in the environment has taken place. Pl. III. fig. C shows the first appearance of the white stripes as a slight paling of the local colour, accompanied at the same time by the production of a dark line marking off the boundaries of the stripe. Pl. II. fig. B shows a further stage in the development of the pattern, which usually takes place relatively slowly.

The fact that *Sepia* does not show the white square when brilliantly illuminated from all sides shows that it is not merely the bright light reflected from the porcelain plate that initiates the pattern formation. The evidence of the black tank, and of the shallow open-air tank with black sides and a floor with many light and dark features, suggests that the quality of the illumination that accompanies the production of the pattern is always that of the presence of contrasts of light and dark. Relatively brightly illuminated objects and dark ones must be present in the animal's visual field at the same time. Therefore, in a black-and-white environment *Sepia* assumes a pattern different from that manifested in either a black or a white environment.

On the sea-bottom conditions must very often be such that the visual field of the animal contains light coloured objects such as white stones, reflecting all the small amount of light present, and dark objects reflecting none of it. If a uniformly coloured *Sepia* were lying on black and white pebbles, its outline would be clearly seen. But when the white square or stripe patterns are shown, its form is broken up just as is that of the environment. This procrypsis is not a case of detailed patterned resemblance, and it is only manifested when the animal is undisturbed ; that is, when its enemies are at some distance from it and unable to inspect it closely. The brilliant white markings strike sharply into the shape of the animal and distract attention from its outlines by superposing on them a pattern similar to the pattern of the environment.

(vi.) *In a White Environment.*

If *Sepia* is kept for some time in a tank of which the walls are painted white, the colour of the whole of its body grows progressively more pale, by a general decrease in the degree of expansion of all the chromatophores. Eventually the animal shows no colour other than the iridescent whiteness produced by the reflection of light from the iridophores. It does not seem likely, however, that this coloration is often manifested in nature, for the conditions found in the white tank are hardly natural.

(vii.) *Patterns shown on Disturbance.*

(a) *The Papillæ.*

Sepia reacts to a very slight disturbance, whatever colour pattern it is showing, not by abandoning the pattern, but by adding to it by an alteration of its skin musculature which produces its effect without any change in the degree of expansion of the chromatophores. Scattered over the dorsal surface of the mantle, as has already been mentioned, are white markings formed by aggregations of iridophores which lie above the chromatophore layers. These markings are distributed irregularly except along the outer edge of the mantle, parallel with the base of the fin, where they form a regular row of white lines. The muscular change following slight disturbance of the animal results in the elevation of the skin in the region of each iridophore group, so that a number of papillæ are formed all over the mantle surface, each with a bright white tip.

The papillæ at the base of the fin are larger and more conspicuous than those over the rest of the mantle and they may arise alone (Pl. II. fig. A), or at the same time as the smaller ones, which have been described by German authors as " skin-warts " (Pl. III. fig. C).

The papillæ are produced after such a slight disturbance of the animal as is involved in the movement of another creature in the water close to it, or in touching of the water surface by the observer. The white markings, which are made so conspicuous by being raised up on papillæ, form a distinct and striking pattern, quite different from that made by the outlines of the animal before the change was made. This suggests that the reaction has a protective function. For the substitution of a new pattern causes the *Sepia* to " disappear," its place being taken by something different, characterized by a pattern of bright white marks. And the " disappearance " will be much more effective than would be the simple act of swimming away, for in that case the predator might very well follow, without losing sight of its prey.

(b) *The Black Spots.*

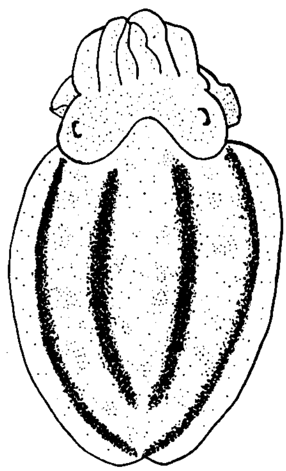
Strong optic, static, or tactile stimulation of *Sepia*, such as is the result of a violent movement in its visual field or of touching it with the hand, is always followed by a series of colour changes of remarkable rapidity and completeness, involving the whole body of the animal ; and in which a succession of patterns is displayed, each one enduring only for a few seconds.

The first result of the stimulation is usually the appearance of the " black spot " pattern, consisting of two black spots which arise in an invariable position on the dorsal surface of the mantle, one a little to each side of the middle line (Pl. III. fig. A). Normally the two spots arise simultaneously, but if the animal is stimulated just adequately on one side only of its body, as by scratching the side of its head, the ipselateral black spot only is produced (Pl. III. fig. B).

Slightly stronger stimulation, or a repetition of the same adequate stimulus, causes a rapid and total paling of the rest of the animal, and the accentuation of the black spots themselves by the still further expansion of the dark chromatophores which produce them. Thus for a moment the two black spots stand out most vividly on the background of the iridescent white animal. The total pallor is never maintained for more than a few seconds, but its transitoriness makes it the more striking. Often this is followed by the animal's contracting its mantle violently and shooting away by the action of its siphon, and this movement is accompanied by a colour change which makes it amazingly difficult to follow, even to the human eye. For while at one moment one's eyes are fixed on a white animal with two black spots, at the next it seems to have disappeared, for its rapid movement is accompanied by total darkening of its body, by full expansion of all chromatophores. This complete colour change, most deceptive to a human observer, must be even more effective in nature in deluding predators. The colour of the animal on darkening in this way is different from the darkness shown in a black tank, in that, in the present instance, the animal has a purplish tinge due to the expansion of the orange and yellow chromatophores, which does not take place in a dark environment.

If further irritated, the animal may respond by a total paling of the whole of its body, and upon this background may appear longitudinal black stripes, at the base of the fins and along the middle of the back (text-fig. 4). These lines flicker vividly over the pallid back, and then suddenly disappear, to be followed perhaps by a reappearance of the black spots, another total darkening,

Text-figure 4.



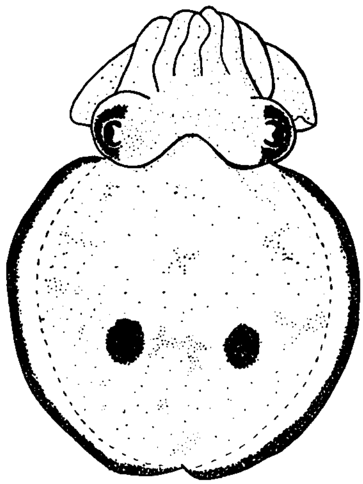
Sepia, dorsal view, showing the longitudinal black stripes and total pallor produced on disturbance.

or a brief reappearance of the zebra pattern. All this time the animal darts about rapidly, as if to avoid the irritation, and its final action when it cannot do so is to eject a cloud of ink. Then at once it becomes motionless, and hides below the black cloud which it has produced, and its colour can be observed no more.

(c) *The Flattened Posture and its Colour Pattern.*

Sometimes, when *Sepia* is resting in a corner, or behind stones, it does not move away when irritated strongly, but instead shows a strange reaction involving the flattening of its body and the appearance of a striking colour pattern. The whole animal broadens itself and decreases in thickness, so that it seems to shrink against the sea floor. The change in the shape of its head which results from the flattening brings its eyes into such a position that they are directed upwards rather than in the normal lateral direction (text-fig. 5), and they are made still more conspicuous by the raising up of the iris which normally covers most of the eye. At the same time, a black line of fully expanded chromatophores appears along the outer edges of the fins, and striking black rings are similarly formed around the sides and lower edges of its eyes. This remarkable colour pattern is always accentuated by the total paling of the rest of the body, and this combines with the black markings and the

Text-figure 5.



Sepia, dorsal view of an animal in the flattened posture, showing the accompanying colour-pattern.

condition of the eye to give the animal the appearance of "threatening" the disturber. It seems not unreasonable to suppose that those features of this pattern that make the animal seem so "fierce" to human observers have a special protective function in nature.

(viii.) *Colour Changes shown when "Hunting."*

When *Sepia* is hunting its prey, that is, when it has located it, and is moving into a position suitable for attack, its arms assume a characteristic posture. The two most dorsal are raised up almost vertically, the sickle-shaped ones are held out laterally, and the rest also are held in those positions most convenient for securing the prey when it has been seized by the ejectile tentacles. During this manœuvring the most brilliant play of colour goes on over the arms.

No definite pattern is visible, and the colour change seems to result from the passage over the head and arms of waves of contraction and expansion of the chromatophores. To a lesser degree a similar activity takes place on the rest of the body.

Capture of the prey is brought about by the long ejectile tentacles, which shoot out from each side of the mouth, within the outer rings of arms on which the colour change takes place ; and it may be suggested that the colour movements in this case serve to distract the attention of the prey from the tentacles which spring out towards it. For the impression of movement given by the waves of colour is much more striking than the movement involved in the appearance of the tentacles.

(ix.) *Colour Changes shown during Sexual Activity.*

These colour changes are dealt with by Tinbergen (1939) in his recent account of the sexual habits of *Sepia*, and I can add nothing to his description as I have not seen the animal's mating behaviour, which is rarely observed at Plymouth.

3. Discussion.

(i.) *Evidence that the Colorations are Protective.*

In order to prove conclusively that the colours and patterns of *Sepia* are allæsthetic characters with a protective value, it would be necessary to make a complete ecological and behavioural investigation of the relations between the animal and its predators, and all other animals likely to be sensitive to its coloration. Further, the sensory capacities of *Sepia* itself would have to be studied, to find what colours and patterns of light it is capable of distinguishing, and so to what extent it is capable of reacting to colour and pattern in its environment. The work of Kühn (1930), and of Kühn and Heberdey (1929), is an attempt to determine the sensitivity of *Sepia* to colour ; and it brings out clearly the difficulty of the problem, for the criterion of the sensitivity of the animal to light of different wave-lengths which they used was the "amount of movement" of the animal when in the different types of illumination.

Similarly, the sensory capacities of the predators of *Sepia* must be studied, in order to make sure that our views of the protective nature of its coloration are not invalidated by a considerable difference between the sensory equipment of the predators and that of ourselves. It is therefore of considerable importance that the animals that we have reason to believe are among its principal predators are Cetacea, including whales, dolphins, and porpoises (De Férussac and d'Orbigny, 1835–48 ; Cuénot, 1916–18 : Cuénot, 1933). The Atlantic coasts of France are said by these authors to be commonly littered in the spring with the bodies of *Sepia* of which the heads only have been eaten by the dolphins. It is very likely that the larger fish also eat *Sepia*, but the fact that mammals are, so far as we know, its chief enemies is probably significant, for the factors concerned in their visual perception must be much more nearly like those in ourselves than are those of fish. Thus human judgments on the protection afforded to the animal by its colours can reasonably be considered as valuable evidence.

As our knowledge of the habits of *Sepia* is somewhat limited, it may be objected that many of the suggestions here put forward are not valid under the conditions in which it lives. Thus, for example, there is the problem as to whether sufficient light penetrates through the water to make the animal's complex patterns visible at the depths at which it lives. Russell (1936) points out that in the sea some colours of light do not penetrate as far as others : thus the red component of daylight is completely eliminated from the light that penetrates beyond a depth of ten metres in inshore waters (Atkins and Poole, 1933).

However, the evidence bearing on this problem of light penetration gives some assurance that *Sepia* is usually sufficiently illuminated for its patterns to be visible to its predators, if these are sensitive to the colours of which they are composed. On the Atlantic and North sea coasts of Europe, and at Naples, *Sepia* is found during the summer months in shallow coastal waters, often where the bottom is sandy, but also where there is mud or seaweed

(De Férussac and d'Orbigny, 1835–48 : Cuénot, 1916–18 : Lo Bianco, 1909). Here it swims about on the sea-floor, usually at a depth of about ten metres, and never below nineteen metres (Cuénot, 1933). In the autumn it migrates out into deeper waters, but even there it has never been found below a hundred metres (Lo Bianco, 1909), and it is usually at from fifty to eighty metres below the surface at this time (Cuénot, 1916–18).

The information at present available as to the penetration of light into the sea is not extensive, but Clarke (1936) finds a great disparity, which is said to obtain all over the world, between the transparency of coastal waters and that of the mid-ocean. In Woods Hole harbour, the reduction of the blue component of daylight to one per cent. of its value at the surface takes place at a depth of eight metres ; while in the Sargasso Sea such a reduction is not encountered till a depth of a hundred and fifty metres is reached. Divers report that tools can be seen at arm's length for several hours a day during the summer, at a depth of twenty-nine metres (Clarke, 1936). One may conclude that at nineteen metres in coastal water the illumination is not such as to invalidate the suggestions of the procryptic value of *Sepia's* coloration : this must also be true in the deeper waters that the animal inhabits, the sea there being much more transparent. And even if the reliance here placed on human perception is unjustified, Clarke (1936) suggests that the work of Grundfest (1931–2) on *Lepomis*, the sun-fish, shows that this animal is sufficiently sensitive to light of low intensities to be able to 'see' objects on the sea-floor in coastal waters for much of the daytime.

Evidence which may be considered to substantiate claims that the colour patterns are a protective device comes from observations on other Cephalopods. In no other member of this group than *Sepia officinalis* are colour patterns found of the variety and complexity of those here described. This fact may tentatively be related to differences between the habits of *Sepia* and those of the other members of the group. For to the former complicated colour patterns could be protective, while to the latter they could not be so. Three species of Cephalopod found at Plymouth are :—*Loligo forbesi*, the squid ; *Sepia* (*Parasepia*) *elegans*, a form about four inches in length ; and *Heterosepiola atlantica*, which is never more than an inch and a half long. Of these three animals the squid is shoal-forming and swims about continuously below the surface of the sea, in water of varying depths. When doing so most of the chromatophores on its body are contracted, and it is extremely transparent, much as in Pl. II. fig. D. This animal contrasts with *Sepia officinalis*, in that it never seems to lie on the sea-floor, and therefore in its encounters with its enemies it is never compelled by limited space to frighten the predator away, for it can swim away itself in any direction. Thus the only power of colour change which it possesses is that of undergoing darkening by expansion of all chromatophores either when disturbed, or in a dark environment (Pl. II. fig. E). The same is also true of *Heterosepiola atlantica*, which, although like *S. officinalis* it lives in summer on the sea-floor in coastal waters, is perhaps rendered by its small size able to conceal itself without complicated colour patterns, for its ability to darken completely when frightened or in dark situations is alone sufficient to make it very elusive. *Sepia elegans* is intermediate in respect of pattern formation, for it has a row of white iridophore groups along the mantle at the base of the fins, and it can elevate these on papillæ. Also it shows a very slight suggestion of a white square and stripe pattern when placed in a black bowl; but it seems to be capable of producing no other pattern. This species seems to have habits similar to those of *S. officinalis*, and the difference between them may be attributed to the larger size of the latter, which renders it more conspicuous to enemies, and therefore more in need of protection.

(ii.) *The Manner in which Protection is afforded by the Colorations and by sudden Colour Change.*

Animal colorations that are considered to produce an effect on individuals other than those manifesting them were classified by Poulton (1890) as follows:—

1. Apatetic colorations—protective resemblances.
   - A. Cryptic coloration, concealing the animal by giving it a resemblance to its environment.
     - i. Procryptic coloration, concealing it in this way from its predators.
     - ii. *Anticryptic coloration, concealing either the whole animal, or its weapons* of aggression only, from its prey.
   - B. Pseudosematic, or mimetic coloration, giving the animal a resemblance to a warningly coloured individual.
2. Sematic, or warning colorations.
3. Epigamic colorations.

In *Sepia* there is no evidence that any of the colours are mimetic, for no animal is known that might be the subject of the imitation.

Also there is strong presumption against the colours having a warning effect. For warning coloration as originally defined is that which is successful in frightening away a potential predator because the predator has learnt by experience that the coloration is borne by an animal capable of defending itself successfully from attack, or undesirable as food. The brilliant coloration of such forms serves to decrease the time taken for the predator to learn its lesson. The multiplicity of patterns shown by *Sepia* can hardly be effective in this way, for the predator would learn only very slowly to avoid an animal that manifested such different colorations at different times.

However, consideration must be given to the possibility that certain of the colour patterns have a protective value which derives specifically from the form of the colorations which compose them. Thus it may be that the colorations shown with the flattening reaction and the black spots, for example, are protective because their pattern has a particular form, not solely because it is conspicuous. In higher animals certain patterns of stimulation in the visual field have a much higher stimulatory value than others, and they produce the avoiding reactions that are in man associated with the subjective experience of "fright." It is thus, perhaps, not unimportant that human beings have described the flattening reaction and its colorations as "menacing." Colorations affording protection in this way should be described as "warning" in a new extended sense.

The colorations already described as manifested during sexual activity are undoubtedly epigamic.

The colour patterns of *Sepia* that appear to be cryptic in function may be classified according to Poulton's scheme.

A. *Cryptic colorations.*

i. Procryptic colorations. These may have their effect :

a. By colour resemblance to the surroundings, as in a dark environment.

b. By obliterative shading concealing the form of the animal by breaking-up the normal effects of light and shade upon it. This is seen in the zebra pattern.

c. By breaking-up the outlines of the animal

(α) by ruptive patterns, such as the zebra, the white stripe and square, and the longitudinal black lines, or

(β) by close imitation of a patterned environment, as by the sandy colorations.

ii. Anticryptic colorations. These include

a. Concealment of the whole *Sepia* from its prey by any of the methods which are procryptic.

b. Concealment of *Sepia*'s aggressive weapons by the colour movements shown when it is hunting prey.

The multiplicity of colour patterns which the animal is capable of showing gives to the cryptic resemblances an increased effectiveness, for if one cryptic coloration does not succeed in concealing *Sepia*, then the animal may change its pattern, and the act of doing so makes it seem to disappear. For to the potential predator it will seem that the animal which it recognized as possible food, and distinguished by a particular colour pattern, has moved away and cannot be seen.

But the categories " apatetic," " sematic," and " epigamic " do not include every means by which *Sepia* protects itself through its coloration, and there must therefore be added to the classical classification :—

4. Sudden colour change, which affords protection by initiating a flight reaction in the predator.

Sepia makes use of its special ability to change colour with great rapidity by muscular action not only to increase the protective efficiency of its cryptic resemblances, but also as an independent protective device, in association with special colour patterns, to cause the flight of a predator. It is to include this mode of self-protection that the new category is created, and into it may fall also the colour behaviour of some of those animals which suddenly display previously concealed colorations, or emit flashes of light from photogenic organs, if in these cases the effect is not simply an aposematic one (see Cott, 1940). Although all the patterns exhibited in such quick succession when the animal is violently disturbed probably do have a cryptic effect by breaking-up the animal's outline, their chief protective effect probably lies rather in their ability to induce a " flight reaction " in the predator, by virtue of the rapid change which their appearance causes in its visual field.

The flight reaction in fish, for example, seems to be initiated by any sudden change in the visual field, and it is thus the result of a sudden discharge of nervous impulses from the eye. The colour patterns of *Sepia*, such as the black spots and longitudinal black lines, are so conspicuous that their sudden appearance and disappearance must be very effective in producing an optic discharge. Thus these patterns serve their protective function through their conspicuity and the rapidity with which they appear.

It may be concluded that *Sepia* offers perhaps the most complex example of a system of protective coloration shown by any animal. And this is only one aspect of the complexity of the animal's behaviour, which is again the result of the possession of a nervous system as highly organized as any in the invertebrate kingdom.

5. Summary.

1. The nature of the colour changes shown by *Sepia officinalis* L. in different environments is discussed.

2. Several patterns in the coloration of the animal, each appearing under certain specific conditions of stimulation, are described.

3. Each pattern is formed by a pattern of expansion and contraction of the chromatophores, supplemented by reflection from the immobile iridophores which lie below them.

4. The state of expansion of each chromatophore is determined by its musculature, which is under nervous control ; and therefore each colour pattern is a manifestation of a pattern in the process of excitation of the chromatophore motor neurons in the central nervous system.

5. In no other Cephalopod than *Sepia* have such colour patterns been described, and they form a complex and highly developed system of protective coloration, adapted to the conditions under which *Sepia* lives.

6. The types of protection afforded by the colorations are discussed. Cryptic patterns are found affording protection through obliterative shading, close environmental resemblance, and striking ruptive patterns.

7. Concealment is made more effective by the animal's ability to change its coloration from one pattern to another in times as short as two-thirds of a second.

8. Certain of the colour changes probably protect *Sepia* by virtue of their great rapidity for, like any sudden change in the visual field, they produce a flight reaction in the predator.

9. Such rapid change of colour thus forms a new category in the classification of the means by which colour can afford protection to animals.

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EXPLANATION OF THE PLATES.

All the figures, except Pl. II. figs. D and E, are dorsal views of *Sepia officinalis* L., shown at from one-half to one-third natural size.

The processes involved in the production of the plates have been directed rather towards revealing the details of the colour patterns than to showing their protective effects in the different environments.

PLATE I.

Fig. A. A form of the zebra pattern in which the stripes are less contrasted than in text-fig. 1, but more so than in text-fig. 2.

B. A form of sandy mottle pattern showing less trace of striping than that in text-fig. 2.

C. The white square pattern, shown by an animal resting on a white plate in a black bowl.

D. The first appearance of the white square pattern by a paling of the median square first on that side of the mantle nearest the white plate. The mantle is showing a sandy stripe pattern, and skin papillæ have appeared on the right side.

PLATE II.

Fig. A. The white square pattern, shown by an animal otherwise very dark in colour. The single row of papillæ is shown on the right edge of the mantle.

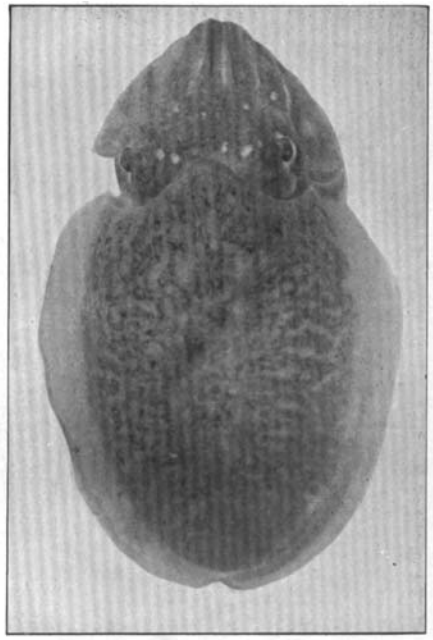
B. The formation of the white stripe pattern, by the extension of the pale area from the central square.

C. The full white stripe pattern.

D. *Loligo forbesi* in a white bowl, with most of its chromatophores in a contracted state.

E. *Loligo forbesi* in a black bowl, with its chromatophores expanded.

A



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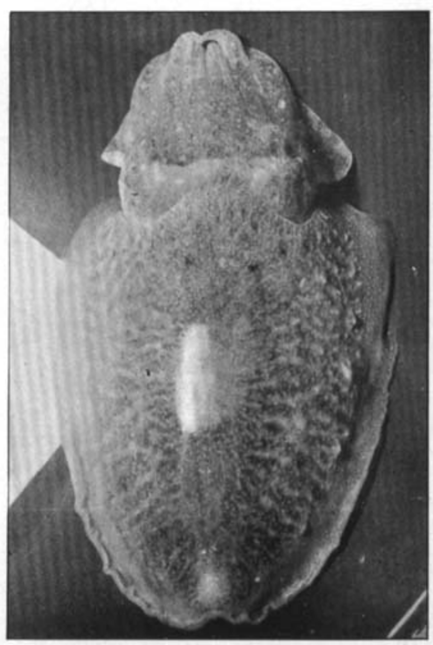

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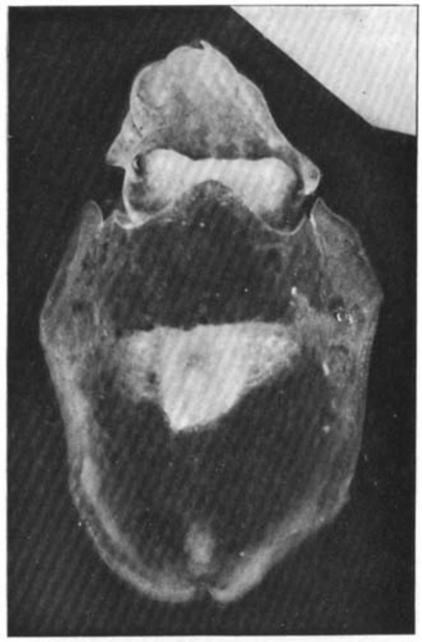

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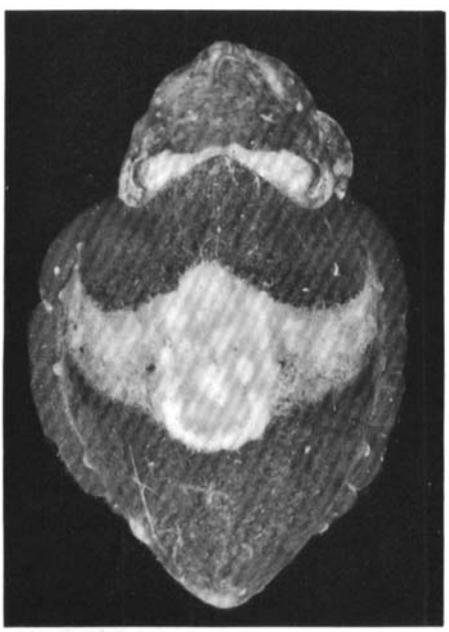

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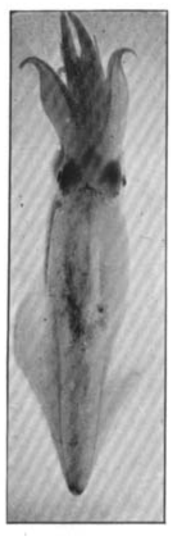

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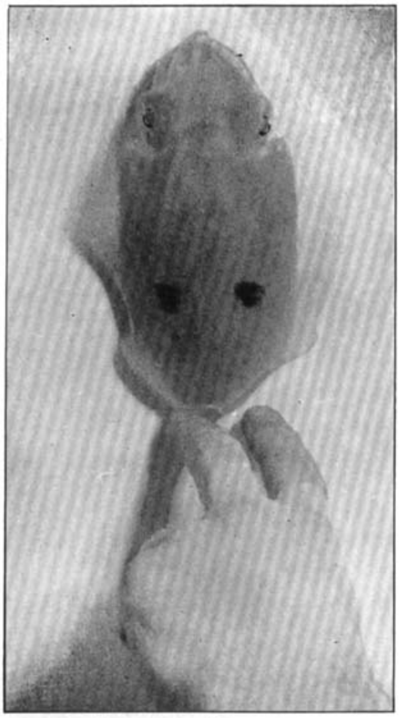

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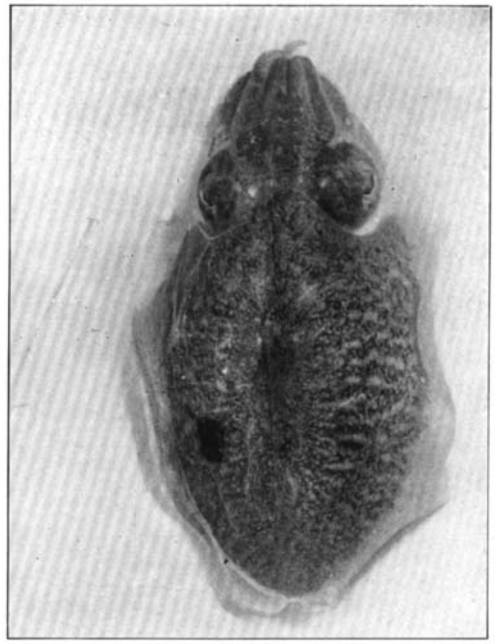

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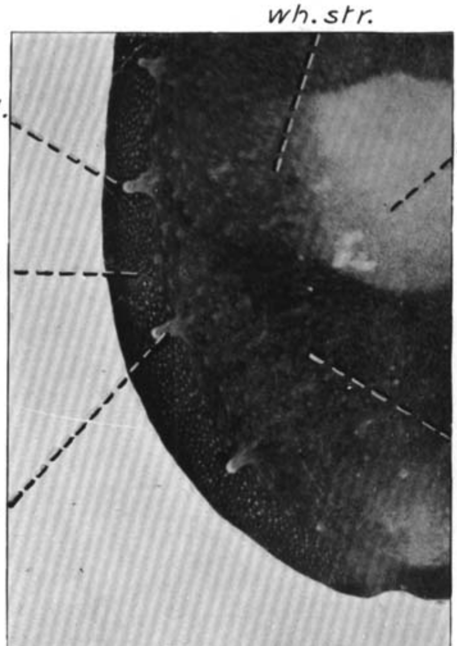

C

Plate III.

Fig. A. The black spot pattern, showing the general paling which often accompanies it.

B. The production of a single black spot by an animal showing a sandy stripe pattern. The animal is being stimulated on that side of its body on which the spot has appeared. On the other side the point at which the second spot will soon appear is visible as a local darkening of the stripes.

C. Detail of the left half of the mantle of a dark animal, showing the white square, the beginnings of a white stripe, and the skin papillæ.

fin irid. = white markings on the fin, formed by groups of iridophores ; *irid.* = iridophore line at the tip of the papilla ; *pap.* = papilla of the row at the base of the fin. ; *sm. pap.* = small papillæ, or skin warts ; *wh. sq.* = the white square ; *wh. str.* = the white stripe, in the first stage of its appearance.