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Review Lecture: On the Organization of Reflecting Surfaces in Some Marine Animals

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REVIEW LECTURE

ON THE ORGANIZATION OF REFLECTING SURFACES IN SOME MARINE ANIMALS

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[Plates 58 and 59]

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Reflecting surfaces of fish are formed of stacks of thin, flat crystals composed of guanine, as the major component, and hypoxanthine, as the minor component. The broad surfaces of these crystals are not, in general, parallel to the surfaces in which they lie in the fish but they are orientated at angles which depend on the function which they serve. The stacks of crystals in different situations also differ in the number and thickness of crystals and in spectral reflectivity. The organization of these crystals is described, in relation to function, for the silvery surfaces of bony fish, the herring and mackerel, for the reflecting tapeta found in the shark and dogfish, for the photophores of the deep-sea hatchet fish and, finally, for the eye of the scallop.

I. The reflecting system in a sprat scale

I shall begin by describing in some detail the properties of one particular reflecting surface, a scale from the ventral 'keel' of a juvenile sprat (*Clupea sprattus*). Figures 1 *a*, *b*, plate 58 show such a fish which has been illuminated with white light at near normal incidence. By reflexion the ventral scales appear coppery coloured: by transmission they appear green-blue. These colours, like those found in some other natural reflecting surfaces, e.g. the iridescent surfaces of insects, are given by interference and, since there is little absorption of light, the reflected and transmitted colours are complementary (for accounts of reflectors of this kind see Lord Rayleigh (1919), Mason (1927), Franz (1907), Fox (1953) and Fox & Vevers (1960)).

A sprat scale can readily be detached from the fish and studied alone (figure 1 *d*, plate 58). We find that its colour changes with angle of viewing moving progressively further towards the shorter wavelength end of the spectrum as we view it by reflexion more and more obliquely. With light falling at angles other than normal or glancing incidence, the reflected light and transmitted light are both polarized. These are properties expected of interference (structural) colours (see, for example, Boys 1924). At higher magnifications the reflecting material can be seen to be numerous elongated 'platelets' whose long axes all run parallel to each other at an oblique angle across the scale. These platelets are only about 25 × 5 μm in size so that almost a million are needed to cover each square centimetre of reflecting surface. If the scale is scratched

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Description of plate 58

Figure 1. (*a*) Reflected light. Photograph in white light of the flank of a juvenile sprat, *Clupea sprattus*. The lines which can be seen running diagonally across the ventral scales show the orientations of the long axes of the platelets.

(*b*) Like (*a*) but with transmitted white light.

(*c*) and (*d*) Transmitted light. Parts of anterior region of single ventral scales from a sprat like that shown in (*a*). In (*c*) the scale was immersed in a solution of concentration double that of marine teleost Ringer; in (*d*) the scale was in marine teleost Ringer. Curves showing the change in spectral reflectivity caused by such a change in the medium are given in figure 3 *b*.

(*e*) and (*f*) Reflected light. Photographs taken with a directional white light of a piece of skin from the flank of a mackerel (*Scomber scombrus*). The orientation of the tissue with respect to the light source has been varied to display successively (*e*) a layer of red reflecting platelets and (*f*) a deeper layer of green reflecting platelets. Both photographs were taken with light falling on the platelets at close to normal incidence.

(*g*) Reflected light. Photograph of some of the mouthparts of a herring; taken, as in (*e*) and (*f*) by means of a directional light source. The orientation of the tissue with respect to the light source is that which shows a red reflecting layer: at a different orientation a green-blue reflecting layer (not shown here) could be seen.

(*h*) Photograph of the eye of a sprat. The platelets of the iris run generally dorso-ventrally and not, as we might expect, either radially or tangentially to the centre of the eye.

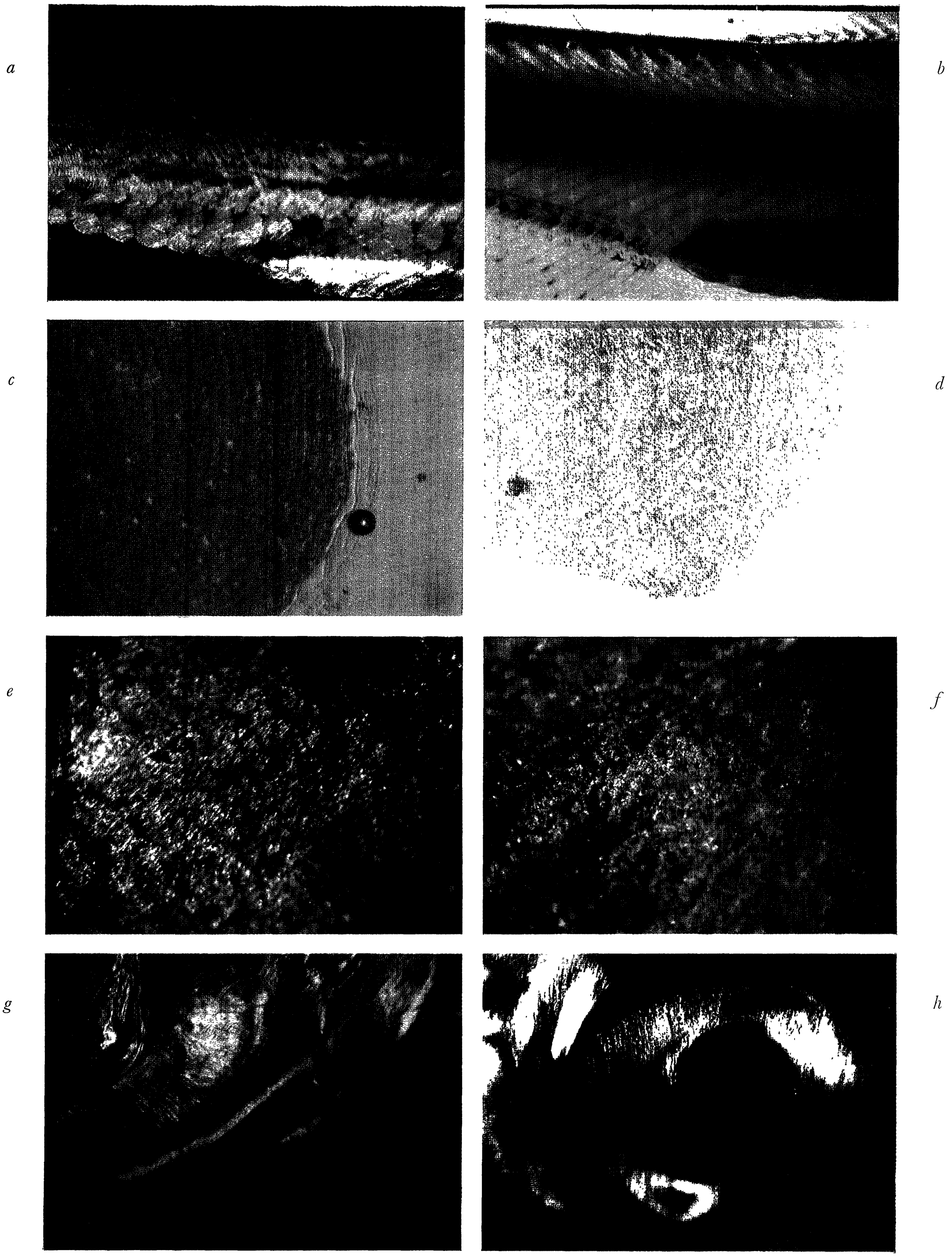

FIGURE 1. (For legend see facing page.)

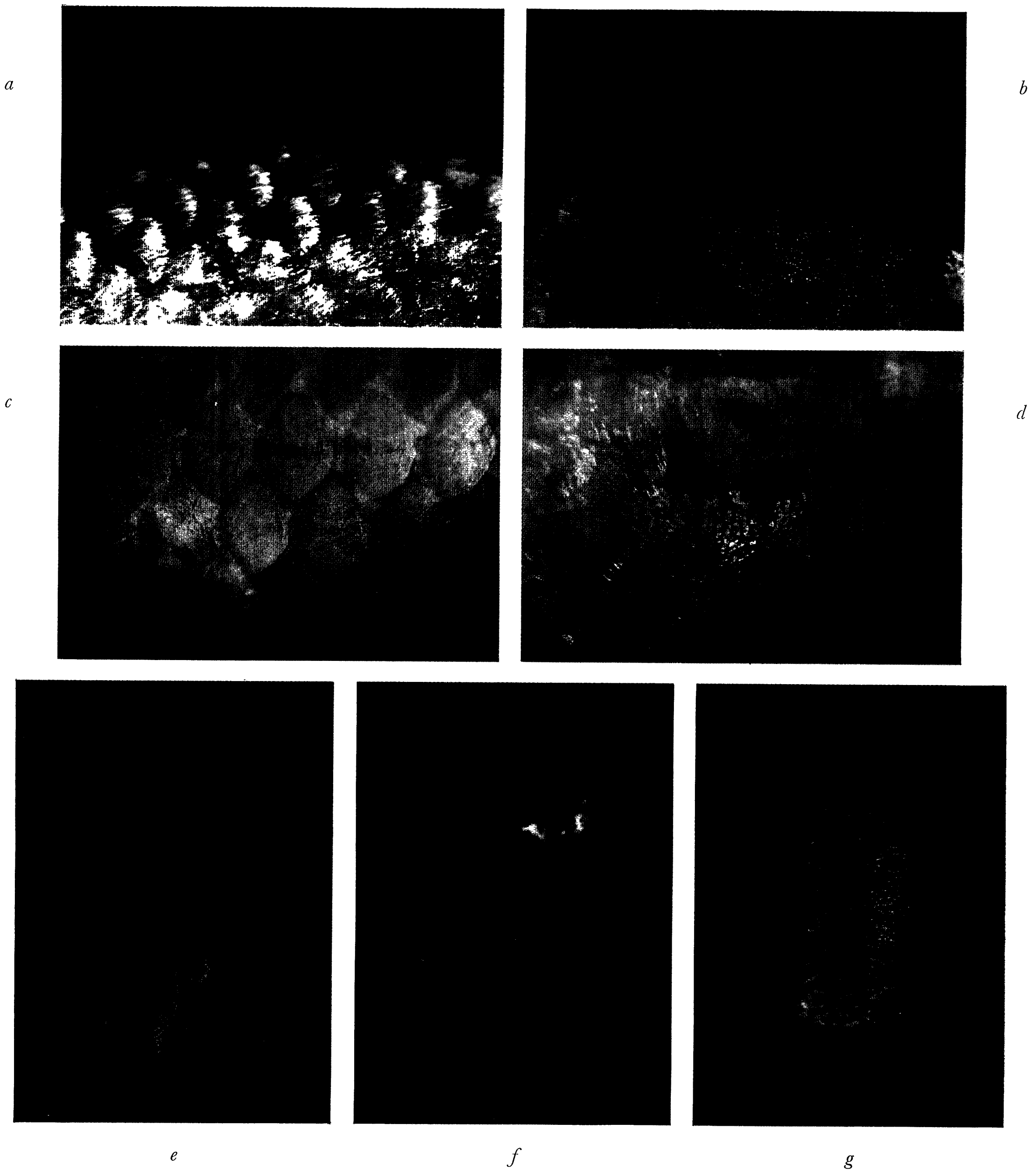

FIGURE 8. (For legend see facing page.)

on its inside surface, the reflecting material comes away and the remaining part of the scale is almost transparent. The scratchings dispersed in water do not contain the brightly coloured platelets but numerous crystals which have approximately the same dimensions as the platelets (figure 2) yet only a low reflectivity changing little throughout the visible spectrum. Whilst dispersed and spinning in the water the crystals reflect light only in flashes which show their full surfaces and they can, when studied in this way, be seen to be flat and almost certainly less than 1 μm thick. With such an upper limit to thickness a fairly uniform reflectivity throughout the visible spectrum is only consistent with an optical thickness (thickness × refractive index) of a quarter of a wavelength for visible light (figure 2*c*, curve for $p = 1$). This conclusion is confirmed by the fact that where one crystal lies on another their combined reflectivity is much less than that of a single crystal. This is what we should expect if together they made a single reflecting structure one half-wavelength thick. Direct measurements with the high-power interference microscope designed by A. F. Huxley (1954) showed that single crystals from scales like that shown in figure 1*d* were all of an optical thickness close to 0.18 μm (Denton & Land 1967). This thickness is a quarter wavelength for light of wavelength 720 μm (i.e. light at the far red end of the visible spectrum). By estimating the number of crystals from a given area of scale and finding the average area of a crystal it was shown that they must be piled 4 or 5 deep over the whole reflecting area and that, since the platelets almost touch but do not overlap, each platelet must consist of 4 or 5 crystals (figure 2*b*), numbers confirmed by electron microscope studies on small areas of scales. Piles of thin films with alternate layers of high and low refractive index material have recently been employed industrially, for example as colour-selective mirrors and coatings for the ends of lasers. They have been studied theoretically by Rayleigh (1919), Heveans (1955–60) and Vašíček (1960). By far the most convenient treatment for biologists is, however, that given by Huxley (1968). He shows that the highest reflectivity at a given wavelength λ_0, together with the widest waveband of

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DESCRIPTION OF PLATE 59

FIGURE 8 (*a*) to (*d*). Herring, *Clupea harengus* (photographs in white light; magnification, × 6).

(*a*) Reflected light. An array of scales on the dorsal region. The reflecting regions do not overlap.

(*b*) Reflected light. The same region as (*a*) but some scales have been pulled off and the direction of illumination changed so as to display some of the iridiocytes which lie in the skin under the scales.

(*c*) Reflected light. This shows an array of scales on the lower ventral flank. The illumination has been arranged to display the orange-yellow anterior parts of the scales. In this array of scales the anterior parts always lie underneath the posterior parts of other scales.

(*d*) Reflected light. This shows a region on the flank from which many of the scales have been pulled off so that the layer of golden platelets which lie in the skin under the scales can be clearly seen. The golden layer is only found in the more ventral regions of the fish. In the vertical flanks of the fish (the upper part of this photograph) this layer is absent.

(*e*) and (*f*) *Argyropelecus arculeatus*. Photographs of a group of reflecting tubes in the postanal group of photophores. The illumination in (*e*) has been chosen so as to display the reflexion of the front 'half-silvered' surface of the reflecting tube. This appears orange when it reflects at near normal incidence. Between (*e*) and (*f*) the direction of illumination has been changed so that in (*f*) we see the inner argenteal reflector o the tube. This reflector possesses some melanophores. The anatomy of these wedge-shaped tubes is shown diagrammatically in figure 12.

(*g*) A photograph of the external 'half-silvered' surface from one of the reflecting tubes of *Argyropelecus*. The lines of platelets can easily be seen. This particular tube reflects best in the green when viewed at near normal incidence. With a different illumination an observer can see the inner argenteal reflector through this surface.

high reflectivity, is given when all these alternate layers have an optical thickness of $\frac{1}{4}\lambda_0$, and, on figure 2*c*, we show (after Land 1966*b*) the estimated reflectivities at normal incidence for such '$\frac{1}{4}\lambda_0$ stacks' containing from 1 to 5 crystals of guanine spaced with cytoplasm. It may be seen that for a stack of this kind the reflectivity rises very sharply with number. Thus whilst a single crystal has only a low reflectivity, 5 crystals suitably spaced can reflect about 80 % of the incident light over a band of the spectrum approximately equal to $\lambda_0 \pm \frac{1}{10}\lambda_0$. We may notice that if the ratio of refractive indices of crystals and cytoplasm were greater fewer crystals would be needed to achieve a given reflectivity at the wavelength λ_0 but the width of the band of high reflectivity would be reduced. On figure 3*a* we give the spectral *loss* of light *by reflexion* on going through single sprat scales like that of figure 1*d*, plate 58. We see that these do show a waveband of high reflectivity between 600 and 800 μm of approximately the kind expected if both the crystals and the cytoplasmic spaces of the platelets were all of an optical thickness

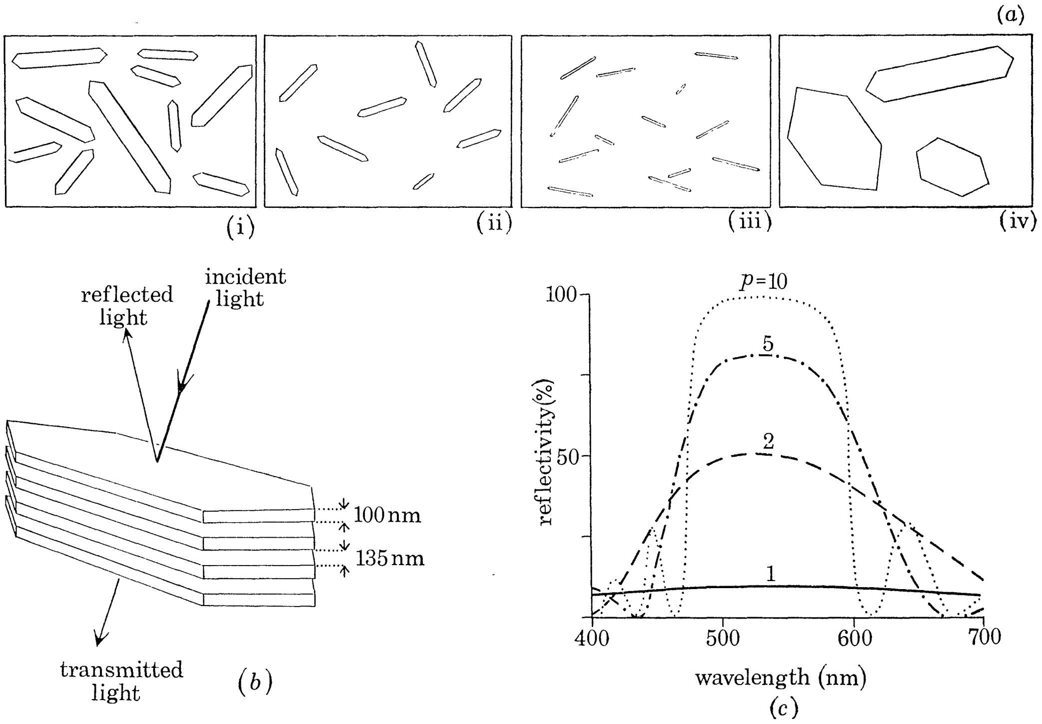


FIGURE 2. (*a*) Diagram showing broad surfaces of crystals from different situations on the bleak, *Alburnus alburnus*, compared with some from the eye of a dogfish. (i) Crystals from a scale taken from a region close to the lateral line. (ii) Crystals from a scale taken from the lowermost row of scales on the belly. (iii) Crystals from the argenteum on the flank. (iv) Crystals from the tapetum of *Scyliorhinus canicula*. (i), (ii) and (iii) are after Denton & Nicol (1965*b*) and (iv) after Best & Nicol (1967). In figure 12 are shown drawings of crystals taken from different regions of a photophore of a deep-sea hatchet fish. These various examples show how specialized are the reflecting systems possessed by fishes.

(*b*) Diagram of a platelet showing a stack of crystals of thickness and spacing to give the best reflexion for light of 720 μm. The broad surfaces of the crystals have been less magnified than the thicknesses of the crystals. A typical platelet from a scale like that of figure 1*a* would have a broad surface of about 25 μm × 5 μm and the whole stack of crystals and spaces would be about 1 μm thick.

(*c*) This shows [after Land (1966*b*) calculated from equations given by A. F. Huxley (1968)] reflectivities at normal incidence for various numbers of crystals arranged in $\frac{1}{4}\lambda$ stacks where both crystal and space have an optical thickness of $\frac{1}{4}\lambda$ for light of wavelength 530 nm. It may be seen that reflectivity rises very quickly as the number of crystals (p) goes from 1 to 5.

approximately equal to $\frac{1}{4}\lambda$ for light of wavelength 720 μm and electron microscope studies confirm that the spacings are about this in thickness.

If the osmotic strength of the medium in which the scale is placed is changed, the colour of the scale changes in the way which we should expect if the cells containing the crystals either swelled or shrank and the crystals of guanine became further, or less far, apart (figures 1*c* and *d*, plate 58; and 3*b*).

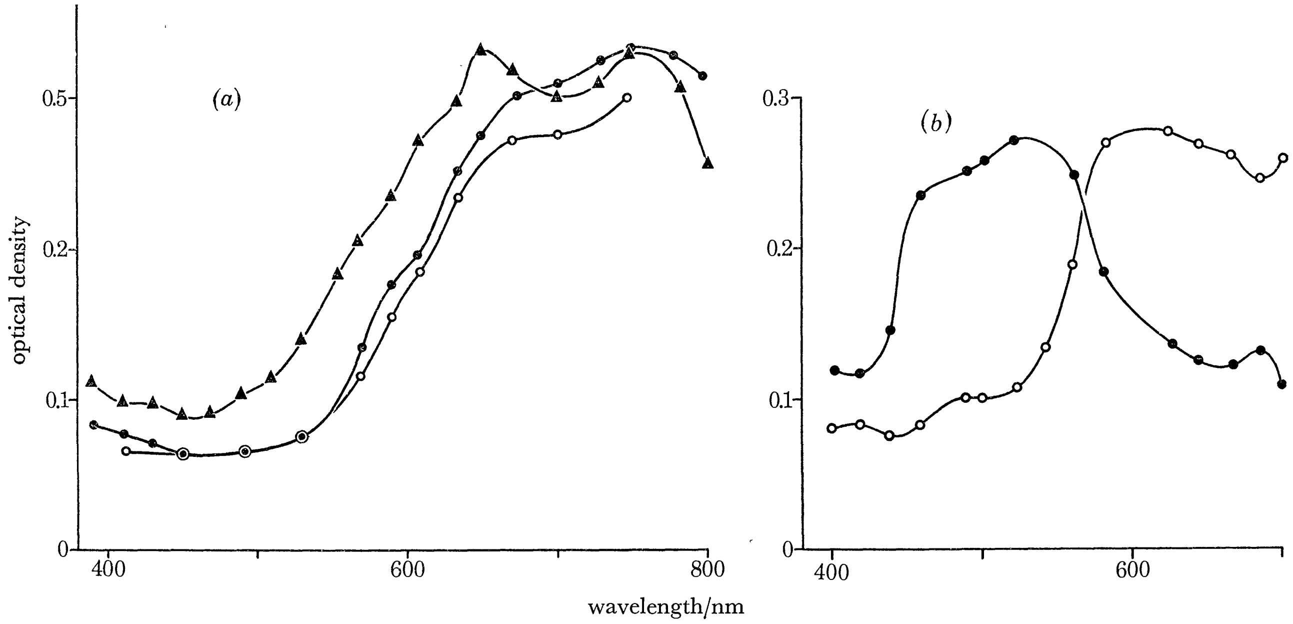


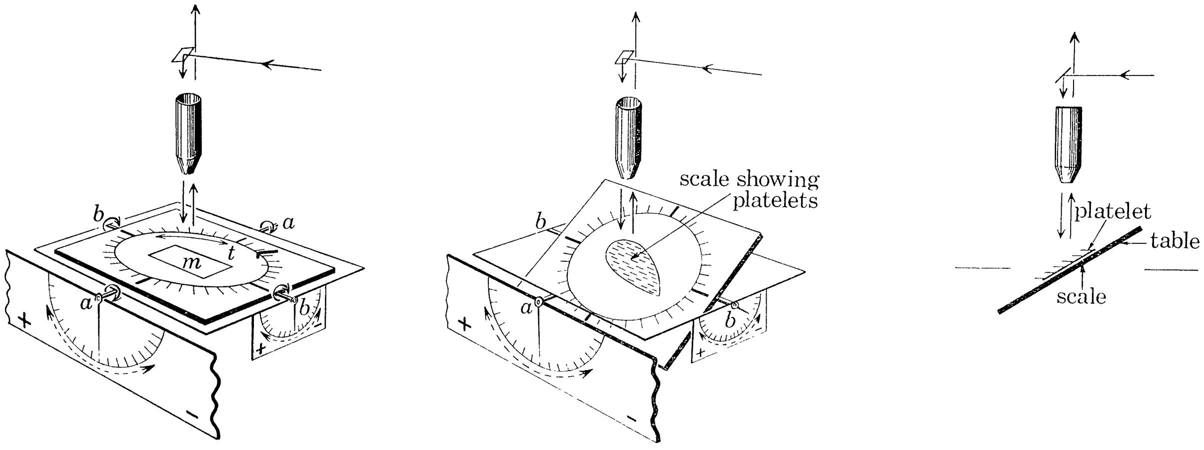
FIGURE 3. The loss of light due to reflexion is plotted against wavelength. The ordinate is optical density and the higher its value, the higher is the reflexion of light by the scale. These measurements were made with the light falling at near normal incidence on the scales.

(*a*) Ventral scales from three specimens of sprat in marine teleost Ringer. (A scale in this medium is shown in figure 1*d*, plate 58.)

(*b*) A ventral scale from the sprat. ○, in marine teleost Ringer (see figure 1*d*, plate 58); ●, in a solution in which the salts of marine teleost Ringer were doubled in concentration (see figure 1*c*, plate 58) (Bone & Denton, unpublished work).

We may notice that, if a dielectric like guanine is used, high reflectivity can only be achieved with a few reflecting surfaces by using thin films of the kind described above. Whilst 5 crystals can give a reflectivity of over 80 % when they are spaced in a $\frac{1}{4}\lambda$ stack, a similar pile of 'thick' crystals, i.e. over 1 μm in thickness, would reflect less than 20 % of normally incident light (Land 1956*b*).

Following this account of the reflective properties of individual platelets we shall look again at the properties of the complete scale. If a scale, like that of figure 1*d*, is placed under an appropriate physiological solution on a small tilting table similar to that shown in figure 4*a* and viewed with vertical illumination we can compare its reflective properties with those of a small flat metallic mirror. (The scale can be rotated on the table and the table itself can be inclined at any chosen angle with respect to the horizontal.) It is found that while the mirror gives its highest reflectivity when it is horizontal (figure 4*a*), the scale appears completely dark when horizontal and has to be tilted appreciably away from the vertical before its platelets reflect well. We find that although there are so many platelets on the scale their surfaces are all approximately parallel to each other so that an orientation can usually be found at which the scale appears bright all over its surface. If the scale is now turned on the tilting table so that the long axes of the platelets lie parallel to one axis of rotation, say *bb* of figure 4*b*, then it is only necessary to rotate the turntable about this axis to obtain the best average reflexion of the scale and the position of the other axis can be left at that which gives the best reflexion for a plane mirror. This shows that the long axes of the platelets all lie parallel to the plane of the scale but that the platelets are tipped away from the scale around these axes (figure 4*c*). The orientation of the platelets is such that, with the scale in its natural position on the fish, their reflecting surfaces are closer to being perpendicular to the surface of the sea than are the scales under which they lie (see figures 7*b* and *c* which show the dispositions of platelets in cross-sections of fish).



(*a*) (*b*) (*c*)

FIGURE 4. (*a*) Diagram of a tilting table used to determine the relative planes of the surfaces of scales and reflecting platelets. *t* is the table, the central part of which can be rotated. This table can be tilted about the two axes *aa* and *bb*. With a flat mirror *m* on the table the best reflexion is given with the table horizontal.

(*b*) A fish scale has been placed on the table. The central part of the table has been rotated so as to bring the long axes of the reflecting platelets on the scale parallel to the axis *bb*. These platelets can now be made to give their best reflexion by rotating the table about the axis *bb* and leaving the axis *aa* in the position shown in (*a*).

(*c*) Cross-section through the tilting table in a vertical plane containing the axis *aa*. This shows, diagrammatically, the relative positions of table, scale and reflecting platelets at the setting of axis *bb* for which the platelets of the scale shown in (*b*) give their best reflexion.

Observations of the kind described in this figure were usually made with the scale under an appropriate Ringer solution (Denton & Nicol 1965*a*).

We are now in a position where we can usefully summarize the properties of the reflecting system of this particular scale. These are: (1) The reflecting units, the platelets, are very small in area (about 100 μm^2). Each platelet consists of a few alternate layers of high refractive index material, guanine crystals, and low refractive index material, cytoplasm. All these layers have a thickness of approximately a quarter of a wavelength of visible (here red) light and the platelet is only about 1 μm thick. [1 μm seems a thin structure to give a high reflectivity of light but silver mirrors of only 0.1 μm can reflect well (Draper & Common, cited by Shackleton 1923)]. (2) The surfaces of the platelets are not parallel to the surface of the scale under which they lie but are tilted in a regular way across their long axes; these long axes being themselves parallel to the plane of the scale. (3) The platelets reflect a wide band from the spectrum fairly well and the waveband reflected moves towards the blue end of the spectrum the more obliquely that we view the scale. (4) The platelets polarize light that falls on them at angles other than normal and glancing incidence.

In some ways these seem complicated properties with which to work but we shall see how they are exploited for special purposes extremely effectively and how their apparent disadvantages are often put to good use.

II. Reflectors in external surfaces of fishes

(1) *Underwater daylight and fish behaviour*

It is a striking fact that while silvery animals are very common in the sea and in fresh water, they are relatively rarely found on land. We shall seek, as did earlier workers (e.g. Popoff 1906; Franz 1907; Ward 1919) the explanation in terms of the differences in illumination between the terrestrial and underwater environments. We are very greatly aided in this by recent work by Jerlov & Fukuda (1960) and Tyler (1960) on the distribution of light under the sea and in deep freshwater lakes. These workers found very good agreement between theoretical and experimental results, and we now have a good understanding of how radiance (radiant flux per unit solid angle per unit projected area of surface) is distributed at different depths in a homogeneous water mass. This makes a discussion of problems of fish camouflage, to which we have devoted most of this section, more profitable than it could have been earlier.

On cloudy days, when the sun is obscured, radiance in a water mass is distributed fairly symmetrically about a normal to the surface, even when relatively near the surface. Thus Tyler (1960), working in Lake Pend Oreille in Idaho, found for an overcast day with the sun's altitude at 40°, i.e. 50° from the normal to the surface, that the direction of maximum radiance at only 6.1 m depth was only about 10° from this normal. On clear sunny days the greatest radiance just under a water surface is found in the direction in which the sunlight is refracted on entering the water mass. However, with increasing depth the radiance distribution becomes progressively more and more symmetrical with respect to a normal to the surface until, as Preisendorfer (1959) has shown, the diffuse field settles down to a pattern in which the relative radiances in different directions remain constant and independent of the position of the sun or the cloudiness of the sky. Thus, for example, the radiance directly downward might be always 100 times that directly upward with both falling together at an exponential rate with increase in depth. If a sunny sky clouded over this ratio would remain constant, both upward and downward intensities falling by an equal factor to perhaps one-third of their former values. Figure 5*a* explains how a direction in which a measurement of radiance at a given point is defined and on figures 5*b* and *c* are given examples of the way in which radiance distribution changes with depth and angle of tilt. Curves *B*, *C* and *D* of figure 5*c* are for the plane in which the sun lies and for which the symmetry about the vertical will be the worst possible. Nevertheless, they show that even in the clear waters studied by Jerlov & Fukuda and by Tyler the light distribution had always gone a long way towards a symmetry around the vertical even at moderate depths, e.g. 30 m. In the arguments which follow the symmetry of light distribution assumed is, moreover not, with respect to the sea surface but with respect to the body of the fish itself. Many fish turn their backs, at least partly, towards the direction from which the most intense light comes (von Holst 1950). If this turning were complete a symmetry of light around the body would be achieved. Other fish point their heads either towards or away from the direction of the sun

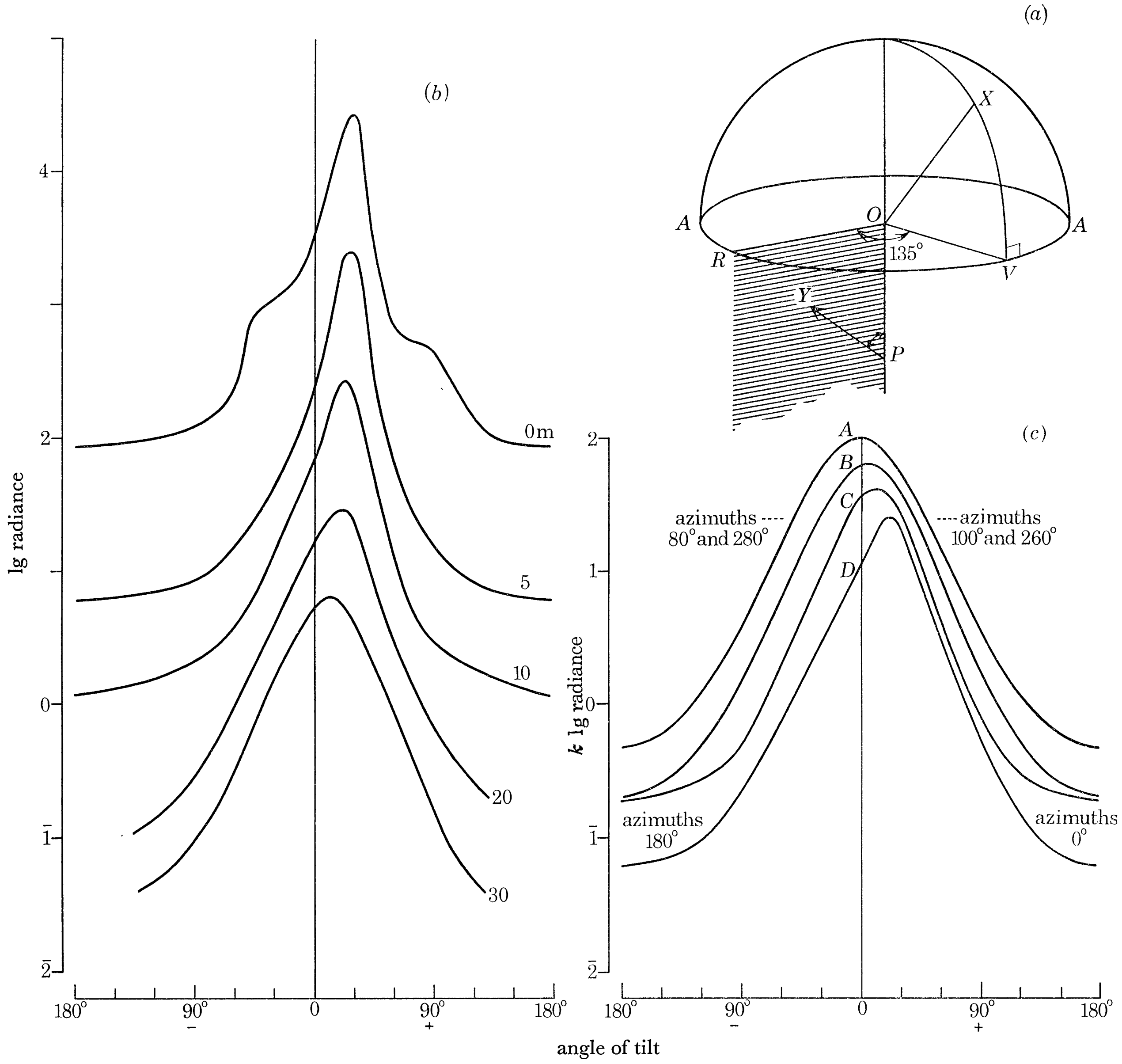


Figure 5. (*a*) To explain how a direction in which a measurement of radiance at a given point in the water mass is defined. Let *P* be the point in the water mass and *PY* the direction in which the measurement is made. *O* is a point in the water mass directly above *P* and the plane of the sea surface contains *A*, *R*, *O*, *A′* and *V*. *OX* is the direction of the sun. *PY* is defined by the azimuth angle *VOR* (here 135°), the tilt angle *OPY* (here 60°) and the depth *OP*.

(*b*) Angular distribution of observed radiance (λ = 535 nm) followed down to 30 m depth in order to illustrate the approach to a distribution symmetrical around the vertical. Abscissa is angle of tilt. These measurements by Jerlov & Fukuda (1960) were made in the azimuth 0 to 180° with a clear sky with the sun's altitude 48 to 58°.

(*c*) Data from Jerlov & Fukuda (1960) and Tyler (1960). The ordinate is *k* lg radiance where the factor *k* has been chosen to make the maxima of the curves equal to 2, 1.8, 1.6 and 1.4 for curves *A*, *B*, *C and D* respectively. (*A*) After Tyler, depth 55 m, sun's altitude 40°, overcast sky. (*B*) After Tyler, depth 66 m, sun's altitude 56.6°, clear sky. (*C*) After Jerlov & Fukuda, depth 30 m, sun's altitude 48–58°, clear sky. (*D*) After Tyler, depth 29 m, sun's altitude 56.6°, clear sky. The azimuths in which the measurements were made are given at the sides of the lines.

(Johnson 1939). This will give a symmetry of light around the flanks of the fish if not about a vertical to its mid-dorsal surface. Mr Gene Henderson of the Biological Laboratory, St Andrews, New Brunswick, Canada, has recently given me an interesting example of this. He tells me that in Passamaquoddy Bay herring are caught in 'weirs'. Fish which enter the holding region of a weir will generally stay within it, but if its opening faces eastwards the fish which enter overnight leave at dawn. Fishermen know that it is important to clear such weirs (but not those facing in other directions) before the sun comes up.

Because of the natural distribution of submarine light and the behaviour of fish to light we can, for very many mid-water marine fish, assume, as a first approximation, that they live for much of their lives in an environment where the light distribution is symmetrical with respect to the plane containing their mid-dorsal and mid-ventral lines and of the general type given by line A of figure 5c.

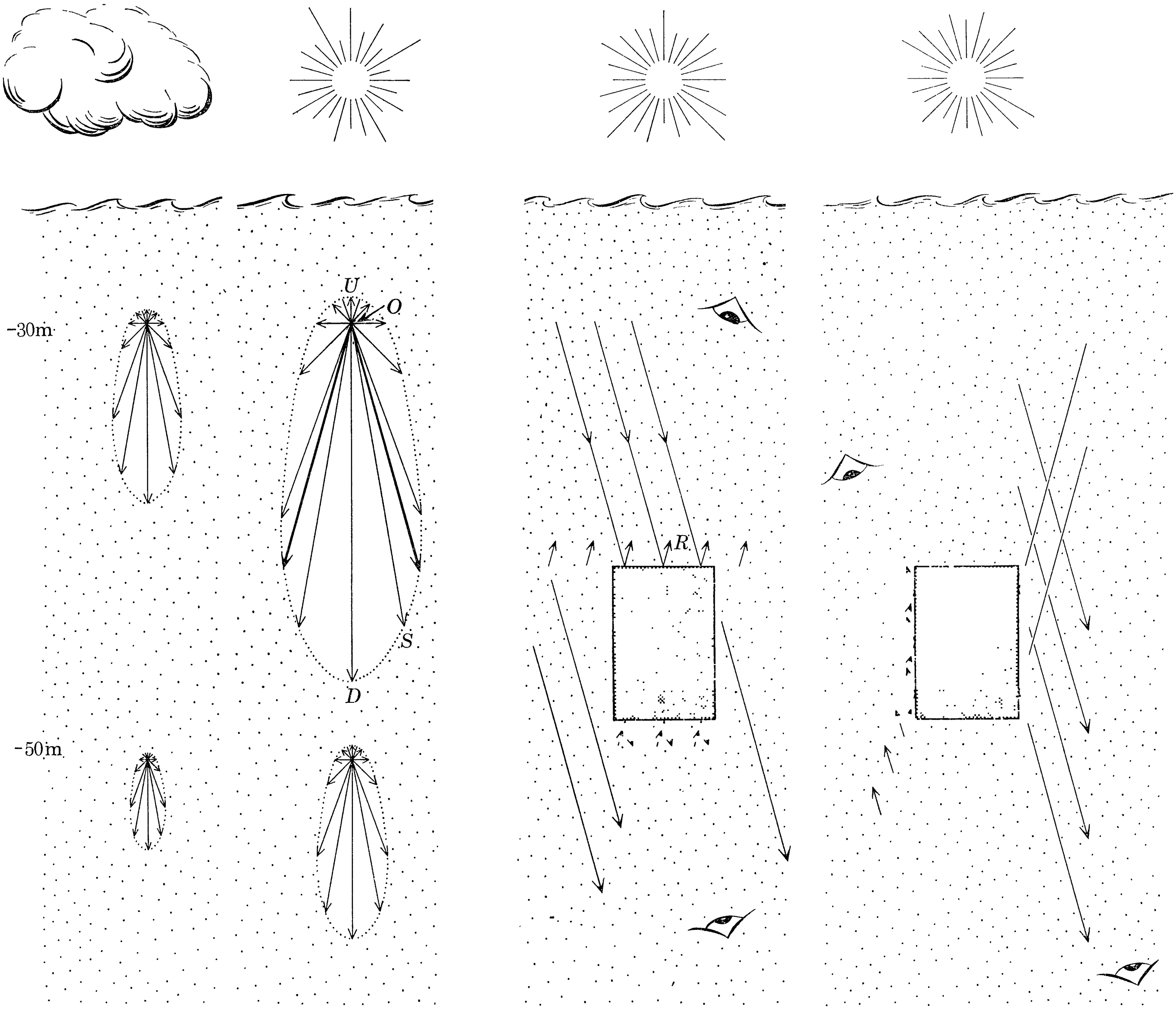
(2) *Fish camouflage in mid-water*

It is evident that the relative constancy of the light distribution in the sea (figure 5) will greatly simplify the problem of camouflaging a marine animal. This can be illustrated by considering how a 'fish' of rectangular cross-section might be made invisible in an environment in which the distribution of radiance with angle is of the general kind shown diagrammatically in figure 6a. Now the 'fish' will certainly be invisible from a given direction if the light reaching the eye of an observer is the same whether the fish is present or not.

To be invisible from above the dorsal surface need only be made dark, reflecting that fraction of the bright incident downward light which will match the dim upward scattered light seen on either side of the fish (figure 6b). In clear oceanic waters, where the 'downward' light may be 200 times more intense than the 'upward' light, this surface would have to be very dark indeed; in turbid lakes where the light is very much more scattered it would need to be only slightly darkened.

The vertical sides of the rectangular 'fish' could be made invisible if they were covered with perfectly reflecting mirrors. This condition is shown in figure 6c where it can be seen that no matter from where a vertical mirror is viewed it always reflects to an observer an intensity of light which is the same as that which would be found if the mirror were not present. If the illumination is strong the camouflaging of the bottom of the fish cannot be effective because the light passing on either side of the fish is so much brighter than the upward light which is available for reflexion (figure 6b). We shall see later that at appreciable depths in the ocean, where the intensity of daylight is very small, some fish have luminescent organs which could send light downwards and sideways so as to match the light passing on either side of the fish. Leaving aside this special case, the problem of camouflaging the 'bottom' of a silvery fish can be partially solved by the fish having a keel instead of a rectangular bottom and such a keel is found in many fish, including most clupeids, e.g. the herring and the pilchard. However, if the dorsal surface of a fish absorbs any light at all the presence of the fish must cause a diminution of the intensity of light at least in some directions below the fish and no redirection of light by mirrors can then make it invisible from every direction.

For a given volume of fish with a dark back and silvery sides, the best shape for camouflage is clearly one in which the fish is very much flattened laterally so as to have the least possible absorption of light by the dorsal surface and present the least possible projected area to an observer below the fish. Although such a flattened body is the easiest one to camouflage, and is



(a) (b) (c)

FIGURE 6. (a) Diagram showing the kind of distribution of radiance in the sea which is assumed in this review. For a given point, e.g. O on the upper right of the diagram, the distribution in three dimensions is given by the surface formed by revolving the dotted curve S around the axis UD. The relative radiance in a given direction is given by the length of line in that direction joining the point O to a point on the surface S. Thus the ratio of radiances of light in the directions vertically up and down are as OU:OD. In the ocean this ratio is approximately 1:200. The diagram shows that although light intensity falls both with increasing depth and with cloudiness of the sky, the polar diagram of radiance distribution remains constant and does not depend on depth, on the intensity of daylight above the surface, on the position of the sun in the sky or on the cloudiness of the sky.

(b) A 'fish' of rectangular cross-section. The back of the fish will be invisible to an observer above it if the reflected light R equals the light passing on either side of the fish. The bottom of the fish cannot be made invisible by reflecting light since the light which can be reflected must be less than that passing on either side of the fish.

(c) The vertical sides of the 'fish' will be invisible if they are perfect mirrors for, in a light field of the kind shown in (a), they will always reflect to any observer an intensity of light which he would see if the 'fish' were not there at all.

possessed by some fish, e.g. the Indian glass fish and the deep-sea hatchet fish, it is not the one which allows a fish to swim through the water most easily; all of the most rapidly swimming marine animals, e.g. dolphins and tunny fish, have a much more nearly circular cross-section.

Although silvery fish are generally flattened laterally to some extent they do have curved surfaces and these present special problems of camouflage. Thus if the upper flank of a fish

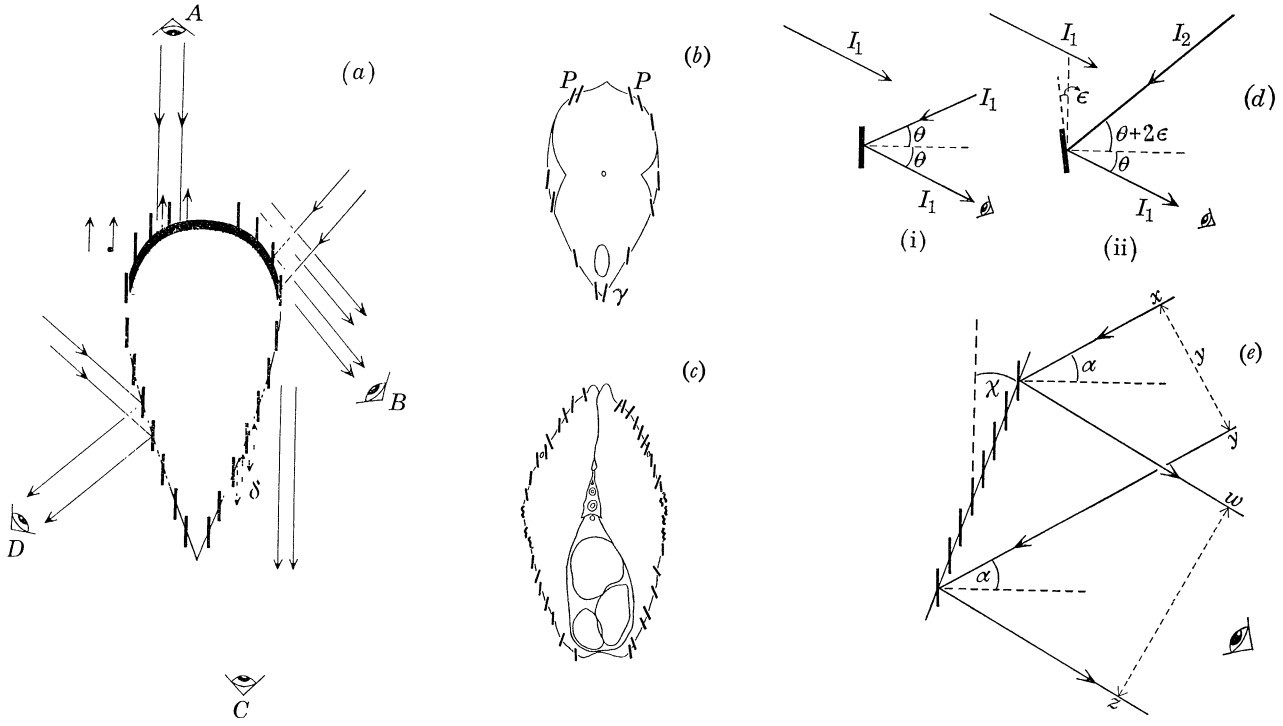


FIGURE 7. In *a*, *b*, *c* and *e* the orientations of reflecting platelets are indicated by heavy black lines—the platelets are, in fact, very small and very numerous.

(*a*) Diagram of a cross-section of a fish in which the orientated platelets all have their surfaces vertical to the surface of the sea. An observer (*A*) above the fish will look between the platelets on the back and see only the light reflected by the black pigment beneath them. An observer (*B*) looking at the same region from the side and below will see the light reflected by the platelets. An observer (*C*) directly below the fish will not see the light reflected by the orientated platelets but that reflected by the argenteum beneath these platelets, whilst an observer (*D*) looking at the same region to the side of the fish will see the light reflected by the platelets.

(*b*) Diagram of the cross-section through the body of the herring, *Clupea harengus*, showing the orientation of the reflecting platelets which are found under the scales. On the lower flanks because of the overlap of scales there are several orientated layers superposed (see figure 8, plate 59).

(*c*) Diagram of the cross-section through the body of the horse mackerel, *Trachurus trachurus* showing the orientation of the reflecting platelets. On the lower flanks there are several layers of orientated cells set at slightly different angles with respect to the surface of the fish. A similar disposition is found in the mackerel, *Scomber scombrus* (see figure 1*e* and *f*, plate 58, and figure 9*b*).

Letter δ marks a region corresponding approximately to that of figure 1*e* and *f*, plate 58. Letter γ marks the region from which the scales of figure 1*c* and *d* were taken.

(*d*) Diagram showing how the tilt of the platelets away from the vertical position affects the direction from which an observer receives light. (i) shows how a vertical mirror can match the background light I_1 if it reflects all of the incident light. (ii) shows how a mirror a little inclined to the vertical can match the background light by reflecting a part only of the incident light I_2. In a light field such as that shown in figure 6*a*, I_2 will be greater in intensity than I_1.

(*e*) Diagram of a section through a ventral surface of a fish which is inclined downwards towards the sea bed, e.g. that marked δ in (*a*). This shows that if the reflecting platelets are perpendicular to the surface of the sea, as shown in (*a*), the reflected light is spread over a wider projected area than the incident light (xy is less than wz) and this surface must appear less bright than the background against which it is seen even if the platelets reflect all the light which strikes them.

is to be generally invisible it needs to have different reflectivities in different directions appearing dark from above and silvery from the side and below. By taking a roach, mackerel, bass, bream, salmon, herring or any similar fish and turning it over against a white wall it can readily be seen that all these fish have this property. Such effects are achieved by tilting the very small reflecting platelets with respect to the surfaces in which they lie (see figures 4 and 7*a*) (Denton & Nicol 1965*a*). We can show this by two different methods.

In some fish, e.g. the mackerel (*Scomber scombrus*) and the horse mackerel (*Trachurus trachurus*), the scales are transparent and the reflecting material is all found in the subdermis. The reflecting cells can easily be seen in histological preparations. Sometimes the platelets themselves remain intact and their orientations can be found, but even when the guanine crystals dissolve while the histological sections are being made, the planes in which the platelets originally lay can still be determined. Other fish, e.g. herring, salmon, bleak and dace, have reflecting material on the under sides of their scales as well as in the subdermis. Using the apparatus of figure 4 it is easy to study the properties of individual scales and then, from a knowledge of the shape of the fish and the positions from which the scales were taken, to determine the pattern of orientation of platelets. Such patterns for vertical cross-sections of horse mackerel and herring are shown in figure 7.

In addition to the reflecting layers described above, fish usually have other layers which are also important in our present discussion. On the upper surfaces of the body there are usually numerous melanophores, some in the epidermis and some beneath the layer of reflecting cells. (Such pigment layers are described by Schnakenbeck (1925).) Here, there are also beautifully coloured iridiocytes similar to those studied by Kawaguti (1965) (figure 8*b*, plate 59). An observer looking downwards on these surfaces would look between the reflecting platelets and see the surface as a dark one whilst from the side and below he would see light reflected by the orientated reflecting material (figure 7*a*).

Beginning near the centres of their sides and extending over the lower flanks and ventral surface there is another silvery surface, the argenteum, lying beneath the orientated reflecting layers. This has numerous thin elongate cells containing slivers of guanine which lie more or less parallel to the surface of the body. In an adult *Trachurus* this layer is about 40 μm thick on the lower flank and thins out dorsally. Looking from directly below a fish this is the reflecting surface which would be seen.

In addition to differences in pigmentation there is usually another important difference between the arrangement of reflecting material on the upper and lower flanks. On the upper flank there is usually only one layer of reflecting cells; at normal incidence, this looks bluish in the horse mackerel and magenta in the herring. On the lower flank there are usually several superposed layers of platelets and these do not have their reflecting surfaces or their long axes parallel to each other (figures 1*e*, *f* and 9*b*). By placing a piece of tissue containing such superposed layers on a tilting table (figure 4) and illuminating it with a directional light we can find positions of the table which allow us to see the reflexions of these layers separately from one another. On figure 1, *e* and *f*, we show the two outermost such layers on a skin of a mackerel viewed in this way. We see, and this is a feature common to many fishes, that these layers differ not only in orientation but also in the colour which they reflect at normal incidence. In the mackerel the outermost layer appears red, the next layer, which can be seen through the outermost one by suitably tilting the table, appears green.

The superb play of colours which we sometimes see when a freshly caught mackerel is brought into a boat is given by successive reflexions from such differently coloured and differently orientated layers as the fish twists and turns in the sunlight. Figure 1*g* shows a similar red reflecting layer on the mouthparts of a herring. At a different setting with respect to the light this surface, here red, appears bright green.

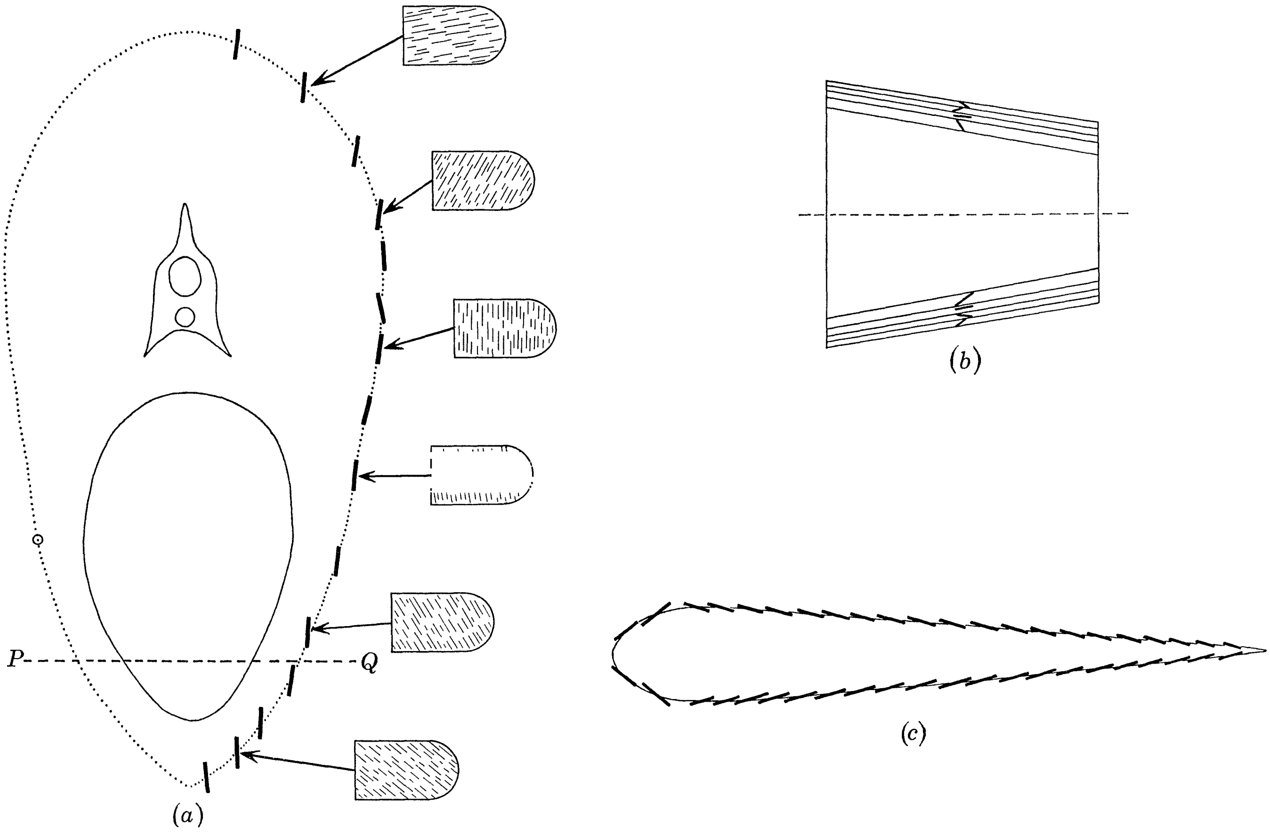


FIGURE 9. (*a*) Diagram of a cross-section through the bleak (*Alburnus alburnus*). The orientations of the platelets under the scales are shown by short heavy black lines around the right side of the section. Some 'scales' are shown as they would appear to an observer looking at the fish from the side, the small lines on these 'scales' show the directions in which the long axes of the platelets are orientated. Arrows connect the 'scales' to their corresponding positions on the cross-section. The platelets run dorso-ventrally on the broad vertical flank of the fish and much more nearly antero-posteriorly on the dorsal and ventral scales.

(*b*) Diagram of a horizontal longitudinal section through the posterior trunk of a horse mackerel, *Trachurus trachurus* (like that indicated by the line *PQ* in (*a*)). This shows the orientations of several superposed orientated layers which are found in the integument in this region. These orientations were determined from histological sections (Denton & Nicol 1966).

(*c*) Shows the orientation of platelets under the scales of the bleak, *Alburnus alburnus* in a horizontal longitudinal section such as *PQ* in (*a*).

Although there are some features in their reflecting systems which are shared between many fishes, the variety of organization is very great. Denton & Nicol (1966) have made a survey covering a number of fishes, here we shall confine ourselves to giving a detailed description of only one fish, the herring, and then discussing, with examples, some general considerations in the arrangement of reflecting material in animals.

(3) *Description of the reflecting system of the herring*

We shall examine in turn various regions around the fish and try to relate the reflecting properties of the structures found in them to the camouflaging of the fish.

(*a*) *The dark mid-dorsal surface*

Although most of the external surface of the herring is covered with reflecting scales, there is a dark dorsal band on either side of the mid-dorsal line where the scales are without reflecting platelets. When the fish is viewed from directly above this band accounts for almost half of the projected area of the fish. Since this surface is almost horizontal it can only be seen by observers in the hemisphere above the fish and, for it to be invisible to such observers, the surface has to match the relatively low radiances of light from angles of tilt between 90° and 180° (see figure 5). For the light distribution of curve *A* (figure 5) these radiances lie between 3.5 %, at 90°, and 0.5 %, at 180°, of the maximum radiance coming from above the fish (angle of tilt = 0°). If the reflexion were specular, $\frac{1}{2}$ % would be an unusually low reflectivity; black paper reflects around 8 % and black velvet 2 % of incident light. The mid-dorsal surface of a fish contains, however, not only numerous melanophores but also iridiocytes and these are mostly orientated so as to reflect light sideways rather than upwards. For such a system an average reflectivity of a few per cent will allow the surface to match the background over a wide range of angles of viewing. By expanding and contracting the melanophores, the fish can also make its back more or less dark; this presumably enables it to adapt to water of different optical properties.

(*b*) *The inclined dorsal surfaces*

On the curved dorsal surfaces only a small part of each scale has reflecting platelets and although the scales overlap, the reflecting parts do not overlap (figure 8*a*, plate 59). The scales appear reddish purple or magenta in colour when the platelets are approximately perpendicular to the incident light and, as figure 7*c*, region *P*, shows, although the platelets are not parallel to the surface of the animal they are still inclined at about 15° to 20° from the vertical to the surface of the sea.

If we consider these properties together we shall see how well they harmonize in making this surface difficult to see. In the vertical plane normal to the flank of the fish if the inclination of the platelets to the vertical is $\epsilon°$ then an observer looking at them will see light which is reflected from an angle of tilt $2\epsilon°$ closer to the vertical than he would if the platelets had their reflecting surfaces parallel to the vertical (see figure 7*d* for diagram showing this effect and Denton & Nicol (1965*b*) for an account of what will happen when the surface is viewed obliquely). Now if platelets were inclined at an angle ϵ to the vertical and reflected all the light striking them then they would appear very much brighter than the background against which they were viewed. They can match the background only by reflecting, as they do, only a fraction of the incident light. For a light distribution of the kind given in curve *A* of figure 5*c* this fraction would have to vary with the angle of viewing and the platelets reflect more strongly for steep angles of incidence than for small angles of incidence. This is exactly what these platelets will do for the blue-green light which penetrates best into the sea. For angles close to normal incidence the platelets reflect red light well; this does not matter because very little red light penetrates into the sea; they reflect, as they should, green light poorly. On moving to oblique angles of incidence the waveband best reflected by this multilayer interference reflector moves to a shorter waveband in the green-blue and has the required property of reflecting green-blue light well. This is an interesting example of the use of the special properties of these reflectors. It certainly could, in principle, lead to the fish almost perfectly matching its dorsal surface to the background from all directions of viewing.

(*c*) *The vertical lateral flank*

In this region the need would seem to be for a vertical mirror reflecting as much as possible of the incident light. Here the platelets cover most of the scales and the scales overlap greatly. High reflectivity is achieved by adding together the reflexion of these scales with that of the argenteum. This is possible because the reflexions are given by interference so that light not reflected by an outer layer can go on to be reflected by a deeper layer. In general the properties of this region are like those of the inclined ventral flank discussed below but the golden reflecting layer of the skin is absent here, and the platelets have their reflecting surfaces approximately perpendicular to the surface of the sea when the animal is in its normal swimming position.

(*d*) *The downwards inclined ventral flank*

Unlike the dorsal scales, the greater part of the area of a scale from this region is covered with reflecting platelets and the spectral waveband reflected varies appreciably over the area of the scale.

The reflectivity of a single scale is much less than 100 % but when the scales are in their natural array the reflecting regions of different scales greatly overlap and at any particular point on the fish the scales are generally three deep.

The platelets on the posterior part of the scale are orientated so as to reflect more posteriorly than those of the rest of the scale so that by examining the side of the fish with a pencil of light whose direction can be changed we can, as we did with the mackerel (figure 1*c* and *f*), pick out the reflexions of different parts of the scales even in the intact array of scales on the side of the fish (figure 8*c*, plate 59). The reflexion of a deeper golden layer can be detected in the same way even without removing scales. When the scales are all removed this layer, which lies in the skin, becomes the outermost one and can be examined without the filtering action of the interposed platelets of the scales (figure 8*d*, plate 59). Its platelets, like those external to it on the scales, are orientated with respect to the surface of the fish being inclined dorsally and inwards.

Beneath the golden layer lies the argenteum containing long thin crystals whose axes lie approximately parallel to the surface under which they lie. A layer of this kind reflects light in the way described later (figure 13).

As we approach the mid-ventral line the shape of the body surface varies greatly from one end of the fish to the other and the scales have correspondingly different reflecting properties. In general these scales show little variation in the colour band which they reflect, being specialized to reflect the red end of the spectrum at normal incidence. The reflectivity of the platelets is, moreover, much greater than for the mid-line scales.

(4) *General considerations in the design of reflecting surfaces*

(*a*) *The colours reflected*

The above description of the properties of these various reflecting layers shows quite clearly that the silveriness for which fish like the salmon, herring and mackerel are so renowned is given by combining the reflexions of overlapping layers of very different spectral reflecting properties. For a fish living near the surface of the sea or of a lake it will be important to reflect light well over the whole of the visible spectrum. But, we might well ask, what is the relevance of the almost complete reflexion of white light in waters where the penetrating daylight is predominantly green or green-blue? The answer must lie in the special properties of the multilayer interference reflectors which the fish uses. We have seen that if a pile of crystals in a platelet is highly organized so as to reflect one spectral waveband efficiently it will reflect others poorly and that the waveband reflected varies with angle of viewing. It is, therefore, evident that even to reflect blue-green light efficiently, over a wide range of angles, several different sets of platelets will be needed. Platelets whose strongest reflectivities at normal incidence are at the red end of the spectrum are a very prominent feature of the reflective systems of fishes. This is not only a waveband to which the eyes of animals are usually relatively insensitive but also one which penetrates poorly even into clear oceanic water. These platelets must certainly be concerned with reflexions at the oblique angles of incidence for which their maximum reflectivity is not in the red but in the green-blue part of the spectrum. We may recall that on the flanks of a fish the brightest incident lights do fall obliquely from above.

(*b*) *Polarization*

We should expect that a platelet would at angles of incidence, other than normal and glancing, reflect one plane of polarization of light (that with its electric vector parallel to the surfaces of the crystals) more strongly than light polarized at an angle perpendicular to this one. If the two materials of which the stack of a platelet consisted were isotropic dielectrics of refractive indices 1.8 and 1.33 then the reflected light would be completely polarized when incident in a parallel beam at an angle of about 54°. The individual platelets of fish do polarize light strongly at such oblique angles of incidence. The surfaces of a fish such as those shown in figure 1*e* to *g*, and figures 8*c* and *d*, plate 59 contain, however, several overlapping layers with their reflecting surfaces set at various angles with respect to each other and in nature, the light falling on a fish is not parallel light but comes from a fairly broad source. In these circumstances the effective polarization of light by reflexion from the side of a fish is not nearly so great as might be expected (Denton & Nicol 1965*a*). Very little of the light which strikes the lower flanks of a herring in the sea can escape reflexion by one or other of the overlapping layers in the scales and skin, but the reflected light is certain to be polarized to some degree and differently in different directions.

(*c*) *Effects of projected areas*

Let us suppose that we have a ventral surface of a fish making an angle χ with the normal to the surface of the sea, with its reflecting platelets normal to this surface being tipped away from the flank in a dorso-ventral direction but not towards either the head or the tail of the fish. We see in figure 7*e* that when light falls from above at an angle α to the horizontal this light is spread and the average intensity of the reflected light must be less than that of the incident light. If all the incident light is reflected the ratio of average intensities of reflected and incident light will be as cos $(\chi+\alpha)/\cos(\chi-\alpha)$. This is an important effect for larger values of α. We may notice that although a surface of this kind with mirrors which have their surfaces perpendicular to the surface of the sea can diminish the brightness of the reflected layer relative to the incident light it cannot increase it. If a surface of a fish is inclined upwards towards the light and has perfectly reflecting vertical platelets there is a loss of light between these platelets so that the intensity of the reflected light merely equals that of the incident light.

We have seen that ventral surfaces set the principal camouflaging problems of a fish like the bleak, salmon and herring. Such fish absorb light on their dorsal surfaces so that there must be a diminution of light intensity in at least some directions beneath them. In general the reflecting material is arranged so as to camouflage the fish very effectively when viewed from above and from the side. It is camouflaged scarcely at all when viewed from directly below but the camouflaging improves as we move away from this position.

For many fishes, e.g. the bleak and the salmon, where the body tapers towards the tail, the orientated platelets of the scales are arranged so that their reflecting surfaces face towards the tail, whilst where the body tapers towards the nose the reflecting platelets are inclined towards the nose (figure 9*b*).

(*d*) *The arrangements of the axes of reflecting crystals*

So far we have mainly dealt with the relationships of the surfaces of reflecting crystals to those of the fish. The arrangement of the platelets and crystals which they contain in terms of their long axes is also interesting. The general rule governing this is simple. The reflecting platelets have their long axes parallel to the surface in which they lie and they are tipped away from this surface only across their short axes. This allows the platelets set at any given orientation to be packed into the least depth in the surface. To give examples:

(1) If a platelet lies in the mid-ventral flank, where its reflecting surface is perpendicular to the surface of the sea but turned towards the tail of the fish, its long axes run dorso-ventrally.

(2) If a platelet lies on the inclined dorsal surface of a fish and is tipped so that its reflecting surface is facing sideways and tailwards at the same time its long axis will run obliquely across the scale (from below and anterior, to above and posterior). In figure 9*a* are shown examples of such orientations in the bleak.

The neat packing of platelets is not the only consideration in these orientations. When we have an array of platelets such as those shown in figure 1*c*, plate 58 their surfaces are not exactly parallel to each other. Their long axes which are approximately parallel to the surface in which they lie are, however, much more nearly parallel to each other than their short axes. Thus when a scale from the flank of a bleak was illuminated with a narrow beam of light on the apparatus of figure 4 the ranges of angles of good reflectivity around that which gave the brightest reflexion were only ±4° in a plane parallel to the long axes of the platelets but ±14° in a plane parallel to the short axes of the platelets. In this scale the long axes of the platelets ran dorso-ventrally. Since the fish mostly swims with its antero-posterior axis horizontal, a lack of constancy in the angle to which the various platelets reflect light coming to it from ahead or behind the fish, i.e. reflexions across the short axes, will be unimportant since the intensity of light will not vary appreciably between various directions in a given horizontal plane. The light does, of course, vary enormously in a dorso-ventral plane (figures 5 and 6) and here, with the long axes of the platelets orientated dorso-ventrally, the scatter of light is small.

(*e*) *Examples of detail and adaptation in reflecting layers*

The above descriptions have given some indication of the high degree of organization of the reflecting layers in fishes. The following examples show how detailed and varied this organization can be:

(1) Where a reflecting scale lies over a curved part of the body the platelets have different and appropriate orientations in different regions of the one scale.

(2) The colours for a given region of a fish are approximately constant and these colours are achieved by the fish manufacturing platelets whose crystal thicknesses and spacings differ in an appropriate way from one region to another (Denton & Land 1967).

(3) The silvery iris of a herring or salmon which might be expected to have the long axes of reflecting platelets either radially or tangentially orientated with respect to the edge of the pupil has these axes running everywhere approximately dorso-ventrally like those on the flank of the fish (figure 1*h*, plate 58).

(4) Whilst on an oceanic cruise aboard R.R.S. *Discovery* in 1967 I noticed a long thin fish which clearly usually swam head upwards for it was dark around it nose and not on its back. All the silvery crystals around the whole of its body had their long axes running antero-posteriorly which would be the best orientation for effective camouflage in this swimming position.

Some fish change their silveriness in life. Thus when the freshwater eel (*Anguilla anguilla*) prepares to migrate from fresh water to the deep oceans its flanks become more silvery and its dorsal surface much darker. The sea lamprey (*Petromyzon marinus*) also shows an increase in silveriness as it goes to the sea. A still more striking example is that of the salmon (*Salmo salar*). The dorsal surfaces of the salmon parr are mottled and broken by a disruptive pattern of bars and red spots. Before leaving the stream the parr metamorphoses to become a smolt and its sides become very silvery and its dorsal side darker as it assumes the camouflage pattern of a pelagic oceanic fish.

Some animal tissues are almost transparent (e.g. the cornea and lens of the vertebrate or cephalopod eye) others are translucent (e.g. muscles and nerve fibre of *Loligo* and the leptocephalus larva of the freshwater eel). If an animal consisted only of such tissues it would certainly be very difficult to see in the diffuse light found under the sea. There are, however, some organs which cannot function properly and still be transparent, e.g. the eye, red muscles and the ink sacs of squid. The camouflaging problem which is set by such tissues is often solved by treating whole organs as if they were entire fish, i.e. their organs are rendered almost invisible by silvering their sides and darkening their tops. Thus the larvae of many fish, e.g. plaice and herring, are almost transparent except for the eyes and digestive tracts and these are silvered on all their outer surfaces except those facing upwards, which are darkened.

(5) *Making fish more conspicuous*

There seems no doubt that many shoaling fish, like the herring, depend on vision to remain in contact with each other, and shoals of fish often disperse at night (Blaxter & Holliday 1963). There is, therefore, a conflict between the need to remain invisible to predators yet to see each other well enough to shoal. The reflecting arrangements which we have described do not render a fish like the herring invisible, although they must reduce its visibility, and we have seen that from some positions, e.g. from directly underneath the fish, the surface reflectors give little help

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in camouflage. The black spot of the pupil must always remain visible from the side and some fish have, in addition, a black spot on their flanks.

Now divers are generally agreed that when silvery fish are swimming quietly they are very difficult to see except when viewed from below and that a shoal of fish can often come quite close to a diver before he realizes that they are present. Occasionally, however, even in quiet conditions, a silvery fish will turn and swim lazily on its side for a little while and then it becomes very conspicuous indeed. Sometimes when a shoal of fish is disturbed by an attacking predator bright flashes can be seen as the fish of the shoal twist and turn and it may be that such flashes distract the predator, and shoals of small juvenile fish swimming near the surface may look like 'rivers' of silver flashes. These phenomena are easy to explain for as soon as a fish turns a silvery side upwards it will inevitably reflect a bright light sideways and become extremely conspicuous to an observer to whom this reflexion happens to be directed and the surface waters are those where the symmetry of light distribution is least perfect.

In other fish, e.g. the neon tetra, some iridescent surfaces are clearly used for display and not for camouflage.

III. Tapetal reflectors of fish

A shining reflecting layer, the tapetum lucidum, is found in the eyes of almost all cartilaginous fishes; these include sharks, dogfish, rays, angel fish, torpedo fish, sting rays and devil fish. Curiously enough, though silvery external surfaces are common in bony fish, reflecting tapeta are relatively rare.

The reflecting material is again principally guanine and if a silvery tapetum is scratched, crystals like those found in the platelets of the fish scales are released. On two species, *Squalus acanthias* and *Scyliorhinus canicula*, these crystals have been shown to have optical thicknesses corresponding to a quarter wavelength for lights of 508 and 544 nm respectively (Denton & Land 1967). These are values close to the wavelengths which the tapeta of these animals reflected best. We are presumably again dealing with quarter wavelength stacks similar to the platelets in the scales of fish. The reflectivity of such tapeta is high and the waveband reflected, although centred close to that of the light which penetrates best into the sea, is quite broad (figure 10) and for this light approaches that of a sputtered aluminium mirror. Although the waveband reflected varies with the angle of viewing, this is not important in the tapetum where the light is always reflected at angles close to normal incidence.

The first step in the detection of light is its absorption by the retinal photosensitive pigments. The reflecting tapetum is placed just behind the retina so that light which is not absorbed by these pigments in its first passage is reflected back through them and so has a second chance of being absorbed. The possession of such a tapetum might, however, have certain disadvantages: first, light might be reflected to other parts of the eye and so make the image of the outside world less sharp, and, secondly, like the eyes of a cat in the headlights of a car, the animal might be made very much more conspicuous.

When the tapeta of cartilaginous fishes were first examined in detail by Franz he found that the reflecting plates (made of a number of platelets), were not always parallel to the retina but sometimes very inclined to it, and that in some fishes, e.g. *Squalus acanthias*, a black pigment migrated over the reflecting plates when the animal was exposed to bright light.

In figure 11 is shown, as an example, a cross-section through the eye of the spur dog (*Squalus*

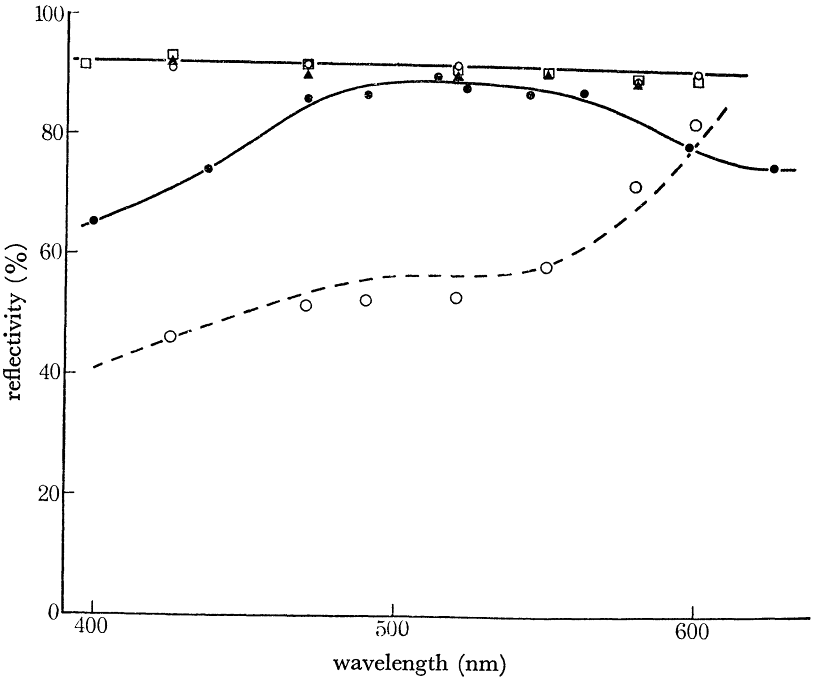

FIGURE 10. The spectral reflectivity of the tapetum of the common dogfish, *Scyliorhinus canicula* (●), is compared with those of a sputtered aluminium surface (□, ○, ▲) and a polished sheet of copper (○) (from Denton & Nicol 1963).

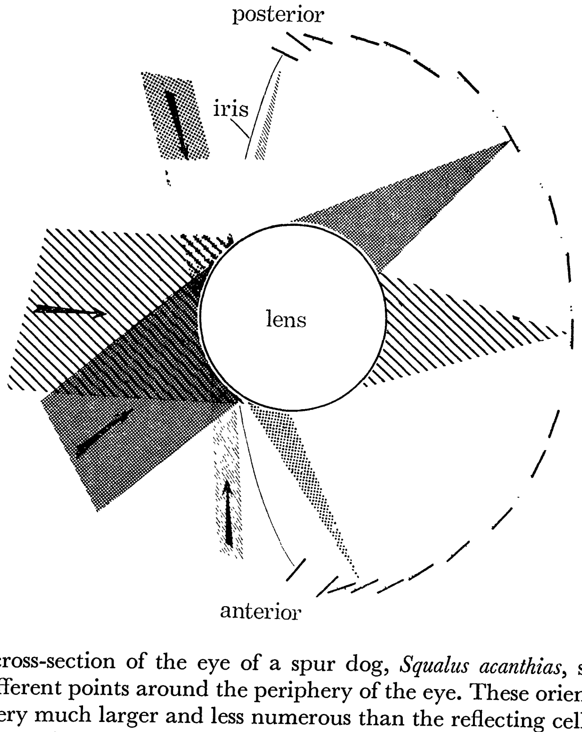

FIGURE 11. Diagram of a cross-section of the eye of a spur dog, *Squalus acanthias*, showing the orientations of reflecting surfaces at different points around the periphery of the eye. These orientations are shown by heavy black lines which are very much larger and less numerous than the reflecting cells. It can be seen that when we take account of the way in which the iris limits light entering the eye, the reflecting surfaces are always approximately perpendicular to the light which can reach them.

acanthias), and it is seen that, because the iris limits the light which enters the eye, the reflecting plates are arranged so that they are everywhere approximately perpendicular to the light which can reach them. The light not absorbed by the visual pigments is, therefore, reflected either back through the pupil (this is why eyes with tapeta sometimes shine so brightly) or on to the black inside surface of the iris. The reflecting plates do not scatter light to other parts of the eye so as to disturb the sharpness of the image.

Now it has usually been thought that the migration of black pigment over the reflecting plates of the tapetum lucidum, which is found to take place in some sharks, was useful in that it limited the sensitivity of the eye. This can scarcely be the true function of this migration for it could only reduce the sensitivity by about 40 % yet the natural light intensity can often be 100 000 times above that at which vision is just possible. It seems much more likely that the true function of the pigment migration is to avoid eyeshine for, as we have seen earlier (figures 5 and 6), light in the sea is very directional and so of the kind which would make animals visible in this way. Another unexpected finding was that fish which have reflecting tapeta usually have only about half the amount of visual pigment per unit area of retina (the retinal rods are only about half as long) of fish without tapeta living in the same environment. Thus the function of the tapetum cannot be to increase the total absorption of light by the photosensitive pigments of the eye but to achieve a given absorption with much less visual pigment.

IV. Reflectors in light-producing organs

In the ocean many animals can produce light and very often this light is directed in particular directions by mirrors. In fish these mirrors are made of crystals and needles of the same properties as those found in the external surfaces and tapeta of fish. Bassot (1966) has given us excellent electronmicrographs showing that photophores contain multilayer structures similar to those described above for the fish scale and tapetum. He has also made important contributions to our knowledge of the general histology of luminescent organs or photophores.

Sometimes the functions of the photophores are quite unknown; sometimes they are quite obvious. Thus there can be little doubt as to the purpose of those seen in an eel-shaped fish which E.R. Gunther saw feeding whilst he was aboard R.R.S. *William Scoresby*. He wrote, 'From a pair of luminous organs in the orbital region, the fish (which was 9–12 inches in length) emitted a beam, of varying intensity, of strong blue light which shone directly forwards a distance of about two feet'. Some of the most specialized of all photophores are found in the deep-sea hatchet fish and these are the ones in which the organization of the reflecting material has been studied in most detail. Figure 12*a* shows a diagram of one species of hatchet fish, *Argyroplecus arculeatus*, showing that the photophores are mainly arranged along its ventral surfaces. A similar distribution of photophores is found in other deep-sea fish and this has suggested to Frazer (1962) and to Clarke (1963) a plausible theory as to their function. It will be remembered that the most difficult surfaces of a fish to camouflage are its lower ventral surfaces for the light which can be reflected is very much less intense than the light passing downwards on either side of the fish. Frazer and Clarke suggested that the ventral photophores of deep sea fish might generate a downwardly directed light whose intensity equalled that passing on either side of its body and so make the fish almost invisible even when viewed from below. This is a method which could not be used by animals living in bright daylight near the surface of the sea, for even the brightest photophores could not produce a sufficiently intense beam of light, but Clarke has shown that a matching of the downward light is certainly possible at the depths at which many deep sea fish live.

Recently, aboard R.R.S. *Discovery*, Dr J. B. Gilpin-Brown, Dr B. L. Roberts and I examined the reflecting layers in the photophores of hatchet fish in some detail. These have a very particular organization which allows us to say how the light which they produce must be distributed, and this distribution suggests that the fish might use the light produced by them to match the background light over a wide range of angles of viewing.

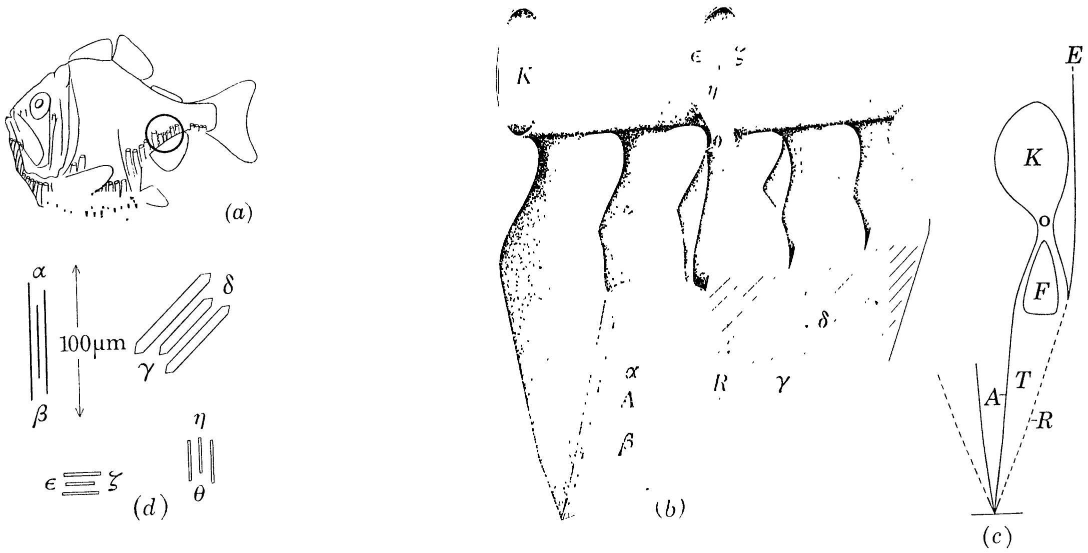

FIGURE 12. *Argyropelecus arculeatus*. (*a*) Diagram of the animal showing that the photophores arranged mainly along the animal's ventral surfaces. The anal group of photophores is ringed. The fish of this species which were studied in *Discovery* (Denton, Gilpin-Brown & Roberts 1969) were up to about 7 cm long. This diagram is after Schultz (1964) and our own observations.

(*b*) and (*c*) Diagrams showing the relations of the various parts of photophore group. *E* is the external surface of the fish, the upper part of the photophore lies beneath this surface. *K* is the chamber within which light is produced, it has highly silvered walls; sometimes one common chamber gives light to reflecting tubes on both sides of the fish. This chamber leads through apertures to all the reflecting tubes of the group. *O* is a small aperture through which light must pass from the light producing chamber *K* on its way to a reflecting tube *T*. *T* is the reflecting tube, it is filled with a viscous liquid which plays an insignificant part in the optics of the tube. *A* is the argenteal surface of the reflecting tube, it contains long thin reflecting crystals. The kind of reflexion given by such a surface is shown in figure 13*a* and *b*. (*d*) Diagram showing the shapes of reflecting crystals from different regions of the photophores shown in (*b*) and (*c*). Directions $\alpha\beta$, $\lambda\delta$, $\epsilon\zeta$ and $\eta\theta$ given here are also shown on (*b*) where they show the orientations of crystals in different regions of the photophore.

The photophores of the hatchet fish (figure 12*a*) are arranged in groups and these groups are specialized for directing their light in particular directions. Thus the light from the ventral photophores shines predominantly downwards, whilst that from the supra-abdominal photophores, which lie above the ventral ones, shines predominantly sideways so that these two groups complement each other. As an example, we shall now describe one group of photophores, the anals, in detail, the other groups share its general properties. The anal group has six reflecting tubes (figure 12*a*). These do not all have the same properties for the most anterior and posterior photophores are longer than those between them and in white light their external surfaces reflect an iridescent blue-green light (figure 8*g*, plate 59) whilst those between them appear orange (figure 8*e*, plate 59). It might be emphasized here that the special shapes and colours of these reflecting surfaces are constant from one specimen to another of a given species. Now the light which is emitted by these six reflecting tubes comes from a common chamber lying above all of them. This chamber is very highly silvered all over its inside walls so that light produced anywhere within its volume must be projected through the small openings in its lower wall into all the reflecting tubes and these must act as if they were all part of a single light producing unit. The tubes are all wedge-shaped in vertical cross-section, the external reflecting surface being almost flat and the internal surface curving to meet it (figures 12 and 13). Figure 12*b* is a perspective diagram of several tubes of this kind which explains the terms used to describe them.

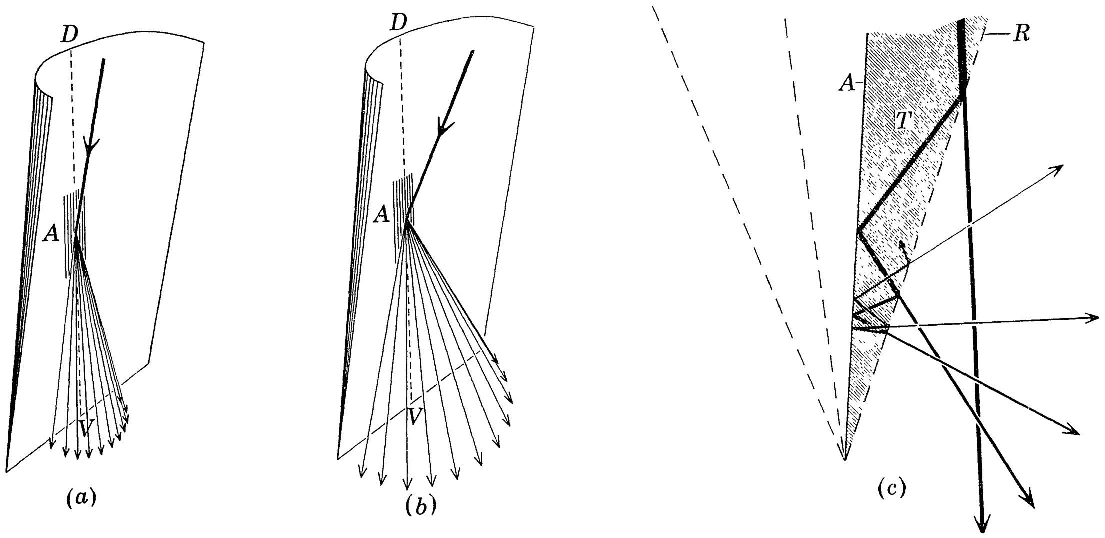

FIGURE 13. (*a*) and (*b*) Diagrams showing the way in which the internal, i.e. argenteal, surface of a reflecting tube reflects light. This surface (see figure 12) consists of long thin crystals running dorso-ventrally. Light striking such a surface is always reflected at the same angle with respect to the dorso-ventral line *DV* but it is spread over an arc anteriorly and posteriorly, i.e. towards the head and tail of the fish.

(*c*) This shows, diagrammatically, what would happen to a pencil of light which is projected into a reflecting tube (like those of figure 12) from above. Here is shown in cross-section that multiple reflexions between the external, half-silvered, surface and the internal, argenteal, surface will take place giving a light distribution in which the light emitted on striking the external surface will progressively fall with each double reflexion. Here no account is taken either of the effect shown in (*a*) and (*b*) or of the change in reflective properties of the external surface with change in the angle of incident light.

The internal surfaces of the reflecting tubes are very highly silvered and made of platelets of very long thin (75 μm × 2 μm) crystals which have their long axes parallel to the surface and alined dorso-ventrally, i.e. along the length of the photophores. Experiments with a piece of this surface on a tilting table (figure 4) showed that this surface had the reflective properties expected if the short axes of the platelets were scattered in angle with respect to the surface on which they lie. This kind of reflexion is shown diagrammatically in figures 13*a* and *b*. The light is always reflected at the same angle with respect to the dorso-ventral line (DV) but it is spread over an arc anteriorly and posteriorly, i.e. towards the head and tail of the fish. The front surface of the reflecting tube has quite different reflecting properties. The platelets are made of broad crystals like those found under scales (figure 2). These platelets are brightly coloured and have their reflecting surfaces parallel to the plane of the front surface of the reflecting tube. This surface is a 'half silvered' mirror reflecting only part of the light which falls on it and, by suitably arranging the lighting, we can see through this surface to that lining the inner 'mirror' (A) of the reflecting tube (figure 8*f*, plate 59). Figure 13*b* shows what must happen to a pencil of light which is projected into the tube from above. It will suffer multiple reflexions between front and back surfaces. Each time that light falls on the front surface a fraction will be transmitted to the external world. If the internal surfaces were completely reflecting and the external surfaces had constant reflective properties with change of angle of incidence, the light emitted would diminish by a constant fraction with each successive reflexion and so build up a roughly exponential decrease in light intensity with the angle between that of viewing and the dorso-ventral axis through the tube. Now the light produced by such photophores is green-blue. The special properties of the external surface, which looks orange at normal incidence and, therefore, will reflect blue-green best at oblique incidence, will tend to increase the amount of light directed sideways as opposed to that directed downwards, any imperfection in the reflectivity of the internal reflector will have the opposite effect.

Now these results accord well with the hypothesis that the function of these photophores is to match the light field around the fish and so help to reduce its visibility over a very wide range of angles. The properties of the internal argenteal reflectors in the reflecting tube will ensure that each tube distributes its light over a wide arc around a vertical through the surface of the sea so that for an observer a little away from the fish it will be the combined emission from all the photophores of the group and not the emission of the separate tubes which will matter.

At first sight an exponential distribution of light would seem to be approximately that which would make the fish invisible in a light field like those of figures 5 and 6. The fish needs, however, to be camouflaged from all directions of viewing and the light which the photophore produces is spread towards the head and tail of the fish by reflexion at the internal (argenteal) surfaces of the reflecting tubes. Taking account of this and the effect of the ventral surfaces projected areas of the fish in different directions it turns out that for effective camouflage the tubes ought to emit less light at the earlier reflexions at the front half-silvered mirrors.

To work out the combined effects of all the photophores on the ventral surface of an *Argyropelecus* would be a very difficult task for the different groups of photophores have different optical properties. However, nearly all have effectively wedge-shaped structures similar to those shown in figure 12 and they must surely all function in approximately the same way.

This account of the structure of the photophores of *Argyropelecus* is moreover simplified for the argenteum possesses melanophores which can obscure its surfaces and colour filters (*F* in figure 12) are interposed between the light-producing mass and the reflecting tubes.

Note added in proof, 5 *February* 1970. In a cruise aboard R.R.S. *Discovery* in the winter of 1969, together with Dr J. B. Gilpin-Brown and Professor P. G. Wright, I measured the angular distributions of light produced by specimens of two species of *Argyropelecus* and one specimen of *Chauliodus sloanei*. Allowing for projected areas these distributions were very close to those of natural light in the sea (figure 5). It was also found that the colour filters (*F* of figure 12*c*) which are found between the light producing chamber (*K*) and the reflecting tubes (*T*) have a transmission band around 480 nm. These filters will therefore ensure that the light produced by *Argyropelecus* matches the blue-green light which penetrates best into the sea. These experiments give very strong support both to the hypothesis that the function of the photophores of fish like *Argyropelecus* is to make the fish hard to see and to the interpretation of the anatomy of the photophores which is given above and illustrated on figures 12 and 13.

V. THE EYE OF THE SCALLOP

M. F. Land has recently studied the physical properties and also the electrophysiological responses of the very tiny eye of the scallop (*Pecten maximus*) and has discussed the behaviour of the scallop in the light of his results (Land 1965, 1966*a*, *b*).

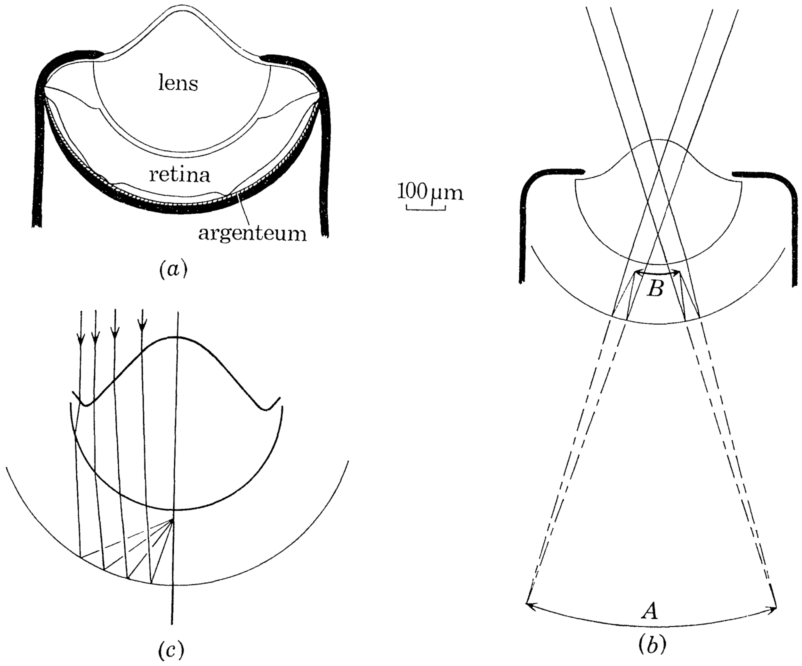

FIGURE 14. (*a*) Diagrammatic median section through the tiny eye of the scallop, *Pecten maximus*.

(*b*) An optical diagram showing that the lens alone would form an image at *A* far behind the retina and that the image *B* on the distal retina is mainly formed by reflexion.

(*c*) Diagram showing the shape of lens which (if it had uniform refractive index) would correct the image on the retina and free it from axial spherical aberration. This constructed lens resembles in shape the actual lens shown in (*a*).

All the diagrams of this figure are after Land (1965).

The scallop eye (figure 14*a*) superficially resembles that of the vertebrate but its lens is not spherical and retinal material occupies the whole space between the lens and the reflecting argentea. There are in fact two retinae; a proximal retina lying against the argentea and a distal retina which lies close to the lens and these two differ greatly in their responses to light (Hartline 1938). Despite these peculiarities it had been generally assumed that the lens forms an image on the back of the scallop eye and that the silvery argenteum acted like the tapetum of the vertebrate eye (see figure 11). Land showed that this was not so. On seven eyes from four animals he found that the average distance between the argenteum and the centre of the lens was 351 μm while the average focal length of the lens was 1238 μm so that even for objects at infinity the lens alone would form an image far behind the argenteum and even further behind the photosensitive cells of the retinae (figure 14*b*). He also found that if a grid is placed in front of the scallop eye an image could be seen in its pupil and proved that this image, which falls on the receptor cells of the distal retina, is produced not by refraction in the lens but by reflexion. We may well ask, before discussing the properties of the argentea, what is the function of the lens? Making reasonable assumptions Land showed that its curious shape is that required to correct spherical aberration in the reflector (figure 14*c*). The arrangement of a spherical mirror with a correcting lens is very like that used in the Schmidt telescope (see, for example, Strong 1946).

The argenteum

Land found that the back of the eye lined with its argenteum is accurately spherical and has a high reflectivity in the blue-green region of the spectrum, its maximum reflectivity to light falling normally upon it being in the waveband 500 to 550 μm. By carefully scraping the argenteum on to a microscope slide and removing the pigment cells, he showed that by transmitted light the reflecting material appeared red, i.e. the complementary colour to the blue-green light which it reflected best. However, if the organization of the argenteum was destroyed in such manipulations high reflectivity and colour were both lost, as we would expect if the colours were structural rather than pigmentary.

On examination of an intact argenteum its surface was seen to be covered by a regular mosaic of squares of sides between 1.1 and 1.3 μm, and that when a dissected argenteum was broken under water very thin square crystals of the same size were released. By interference microscopy these crystals were found to have a refractive index of 1.8 and an average optical thickness of 134 μm. Electron microscopy showed that the argentea consist of 30 to 40 layers of crystals separated by cytoplasm. Now 134 μm is a quarter of a wavelength for light of 536 μm and the spectral reflective properties of the argentea agree very well with those expected if the crystals were spaced by cytoplasmic spaces of the same optical thickness. Evidently the argenteum is a multilayer interference reflector made of 30 to 40 layers of crystals, separated by cytoplasmic spaces, both crystals and spaces being of thicknesses close to one-quarter of the wavelength which the argenteum reflects best. Some other properties supported this conclusion. The colour changes brought about by placing argenteum in solutions of osmotic strength different from sea water were those expected if these changes caused the swelling or shrinking of the cytoplasmic spaces. Again, when white light was reflected obliquely from the argenteum the waveband best reflected moved towards the blue end of the spectrum in the way expected of a quarter-wavelength multilayer reflector.

VI. THE NATURE OF THE REFLECTING CRYSTALS

(1) *Chemical and physical properties*

A variety of substances are used by animals as high refractive index material in multilayer interference reflectors. Thus, some mammals, e.g. the cat, use collagen fibres; the bush baby uses riboflavin whilst the crocodile's tapetum contains guanine. The high refractive index material in the reflecting structures of many marine animals, including copepods, lobsters, *Limulus* and sea anemones, have been shown to be purines. By a variety of tests Millot (1923) and Neckel (1954) showed that the reflectors of fish are composed principally of guanine, and Greenstein (1966) showed that hypoxanthine is the second most important constituent of these crystals and sometimes accounts for about a quarter of the total purine present. In the herring he found that guanine and hypoxanthine account for about 99 % of the weight of the reflecting crystals and that these yield an ash of less than 1 % of their initial weight. The ratio of guanine to hypoxanthine seems to vary with the form of the crystals, broad plate-like crystals contained relatively more hypoxanthine than needle-like crystals.

The optical properties of the iridescent guanine plates found in the copepod, *Sappharina*, were studied by Schmidt (1949). He found that these were strongly birefringent, having a refractive index of 1.79 for rays incident perpendicular to their broad surfaces and a refractive index of 1.55 for rays incident parallel to these surfaces. For crystals from the herring Greenstein (1966) (citing Taylor 1926) gives refractive indexes of 1.85 and 1.81 for light perpendicularly incident on the broad face of a crystal for planes of polarization which are parallel to the long and short axes of the crystal respectively and 1.46 for light incident normal to the broad face, i.e. measured with the crystals supported on edge. From these refractive indexes Greenstein draws the conclusion that the planar purine molecules lie essentially parallel to the broad faces of the crystals. This, he comments, is a most unusual arrangement, for synthetic crystals of planar molecules usually grow more or less perpendicular to the face with the largest surface. Any complete analysis of the reflexion of a surface containing crystals of this kind, e.g. the scale of the herring, would have to take account of the difference in refractive indexes for different planes; so far this has not been attempted. Although not able to identify completely the very small amounts of crystalline material which he obtained from the scallop eye, Land did show that this had some chemical properties compatible with those of purines. He also dissolved the argentea in N/10 NaOH and proved that the dissolved material chromatographed in exactly the same way as guanine and quite unlike uric acid which was his other standard of comparison.

Cephalopods, e.g. *Sepia* and *Ilex*, have very effective multi-layer reflectors which are built of flat lozenge-shaped plates. The plates do not seem, from their shapes, to be crystalline and they are quite unlike crystals in being very flexible. They have a refractive index of 1.56 which means that they could be made of chitin (Denton & Land 1967).

(2) *Development*

Fish have the most highly organized reflecting layers found in the animal kingdom and also the ones for which structures and functions can best be correlated, and they provide very good material for studying the development of multilayer reflecting systems. A. G. C. Best & J. A. C. Nicol (personal communication) and E. J. Denton & Miss J. F. Whish (unpublished work) have studied the development of reflectors in the tapetum and scales respectively. In both situations the reflecting crystals develop intracellularly. In one microscope section of the growing scale we can see, as we move from the edge of the scale towards its centre, successively older stages in the development of the scale and of the reflecting system. In the growing scale three distinct layers are being formed: an external bony layer which is laid down only at the edge of the scale; a layer of collagenous fibres (this layer continues to grow in thickness over the whole surface of the scale and is composed of sublayers of fibres each a few micrometres thick laid down successively with the axes of the fibres running in different directions in successive layers like the wood fibres in plywood); and finally the layer of cells which contain the reflecting guanine crystals. In this layer Denton & Whish found that for a scale like that of figure 1*c* and *d*, plate 58: (1) the crystals are intracellular, one platelet lying entirely in one cell; (2) the number of crystals in a platelet is usually 4 or 5; (3) the plane in which the crystal is laid down is determined before the crystalline material appears; (4) the crystals reach their final thickness relatively rapidly and this thickness does not then change much, if at all, later; (5) the reflecting cells themselves are inclined with respect to the surface of the scale in a similar way but not to precisely the same angle as the crystals; (6) the reflecting cells are held in position with respect to each other by interdigitating ridges and pockets; (7) apart from the reflecting crystals and the sacs within which they are arranged the cells containing these structures are not very rich in cytoplasmic inclusions.

VII. SUMMARY

Recent work has been concerned mainly with the physical and chemical properties and the disposition of reflecting layers. It is shown here that the organization of such layers is often very detailed. For example, in a given situation on the surface of a fish, the crystals of reflecting material will have a particular shape and thickness, they will be arranged in stacks (platelets) of a particular spacing within cytoplasm and the platelets themselves will be orientated at special angles with respect to the surface in which they lie. Layers of such platelets of different but predictable spectral properties and orientations may, moreover, be superposed. In certain cases plausible functions for these complicated reflecting layers have been suggested but these usually remain unproved and it is not possible to assign functions to all the structures which have been found. There has, as yet, been very little advance in our knowledge of the mechanisms whereby crystals and platelets of reflecting material can be manufactured with such precision, nor do we know how the development of the reflecting layers is controlled.

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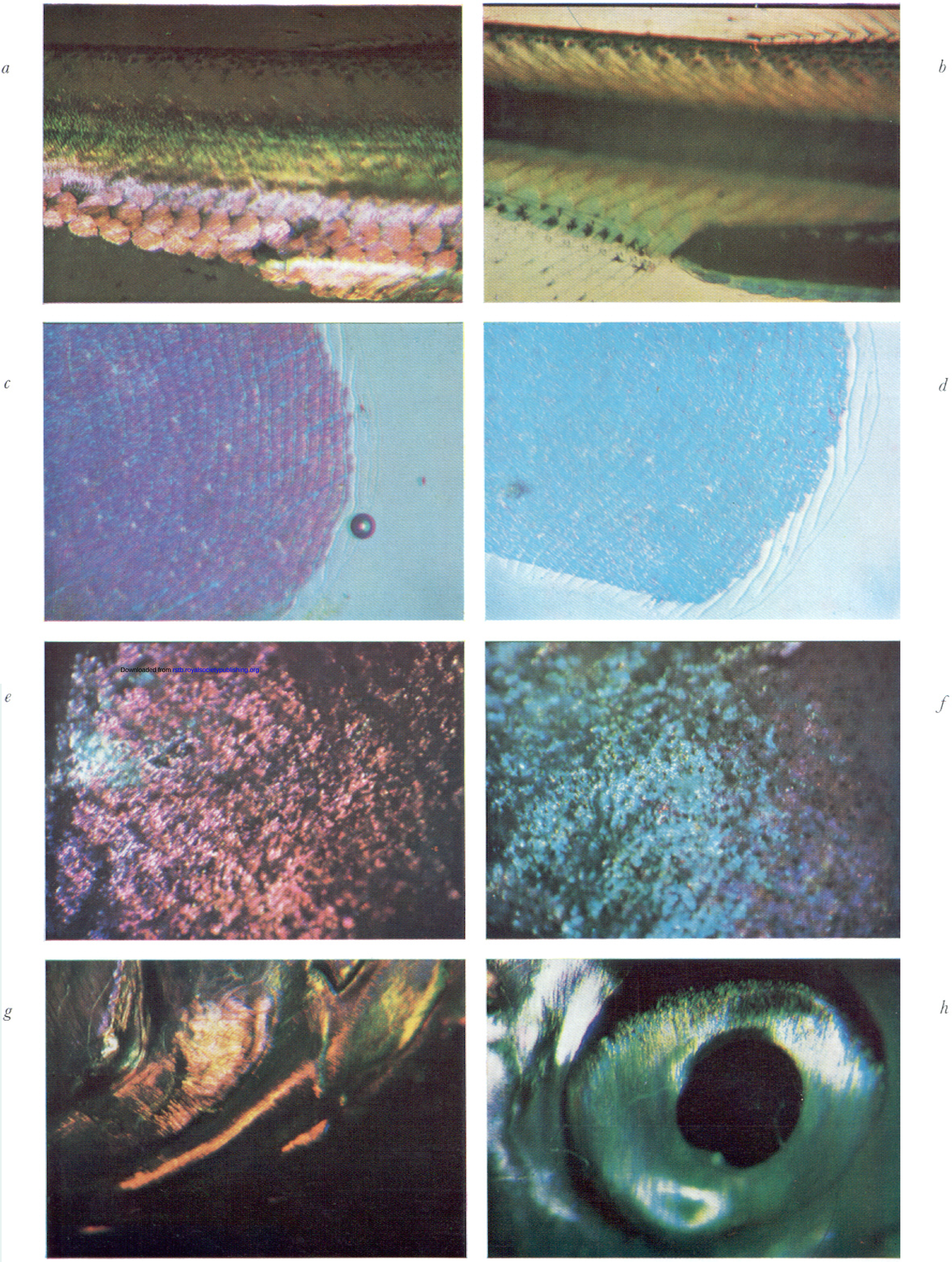

FIGURE 1. (For legend see facing page.)

Figure 8. (For legend see facing page.)