PHILOSOPHICAL TRANSACTIONS.

I.—*On a Periodic Structure in many Insect Scales, and the Cause of their Iridescent Colours.*

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(Received November 7, 1919,—Read January 29, 1920.)

[PLATES 1–3.]

CONTENTS.

I. INTRODUCTION.

Ever since the distinction between the pigmentary and the structural colours of insects was recognised, there has been discussion as to the cause of the latter phenomenon, but no satisfactory explanation has yet been given. A great variety of theories has been suggested, but the very unsatisfactory and controversial state of the problem may be gathered from Prof. R. W. WOOD's statement in a recent paper,[*] to the effect that not only are the existing theories inadequate to explain the phenomena, but that these "cannot be explained by any of the common laws of Optics with which we are familiar."

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[*] WOOD, R. W., 'Phil. Mag.,' London, 6th Ser., vol. 38, p. 98 (July, 1919).

The theories that have been advanced to account for these metallic colours fall under the following headings :—

(1) The diffraction of light at the surface of a grooved structure or "grating."

(2) The interference of light at the surfaces of "thin films," which may be either single or multiple.

(3) The scattering of the shorter light-waves by bodies composed of particles smaller in diameter than the waves themselves, which allow the longer red waves to pass unhindered. The blue of the sea, snow, and sky is of this nature. It has sometimes been called "blue due to scattering by small particles," and that expression will be adopted in this paper.

(4) The selective reflection of light from extremely opaque, highly reflecting surfaces, such as metals, or dry films of aniline dyes that show surface colours.

A complete bibliography of the earlier literature, which is not of great interest, can be found in two papers by BIEDERMANN* on insect colours. The first serious attempt to investigate the matter in a scientific spirit was made by WALTER,† a physicist, who advanced a number of arguments based on the behaviour of polarised light when it is reflected from scales and other iridescent structures. He urged that the colours were caused by selective reflection due to an exceedingly thin layer of a certain material ("*Schillerstoff*"), which acts like a film of dye or a metal, and gives rise to so-called metallic reflection.

A more recent survey of the subject is to be found in the above mentioned articles by BIEDERMANN, who approaches the subject from the point of view of the biologist. He was the first to point out the essential difference between the iridescent scales of Lepidoptera and the metallic wing-cases of scaleless beetles. The change in the colour of all iridescent scales, when they are immersed in liquids of increasing refractivity, is towards the red end of the spectrum ; and, if the fluid approaches the same index as that of chitin (about 1·5),‡ the colour practically vanishes. The wing-cases of beetles, on the other hand, under similar conditions, become even more brilliantly coloured. BIEDERMANN, though he was at first inclined to agree with WALTER, eventually came to the conclusion that the interference of light was responsible for the colour in both cases. Owing to the disappearance of the colour of scales in highly refractive fluids, he came to the conclusion, in some cases no doubt correct, that the colour depends on films of air enclosed between the walls of the scales, which may rapidly be driven out and replaced by any fluid. In the case of beetles, on the contrary, he declared that, since the colours remain practically

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* BIEDERMANN, W., 'Festschrift zum siebzigsten Geburtstage von Haeckel,' Jena, 1904, p. 215 ('Denkschriften d. Med.-Naturwiss. Ges.'); also "Farbe und Zeichnung der Insekten," 'Handbuch der vergleich. Physiologie,' p. 1657, Jena, 1914. Edited by HANS WINTERSTEIN.

† WALTER, B., 'Die Oberflächen- oder Schillerfarben,' Braunschweig, 1895 (Vieweg).

‡ "The chitin from different insects varies slightly ; the average value, however, is about 1·5." SOLLAS, 'Roy. Soc. Proc.,' B, vol. 79, p. 474 (1907).

unaltered in fluids of high refractive index, the plates must be composed of chitin instead of air. He believed that the seat of the colour was usually the surface cuticle of the wing (see p. 27), but, if this were so, the colour would not remain when the wing-case is immersed, and the fluid comes into optical contact with this film. It is true that in a later article* he admits that the above explanation is too sweeping, and that the phenomena are probably more complicated than he had assumed.

Recently, interest in the subject has been very much revived by several papers written from a purely physical standpoint. In a contribution of considerable importance, MICHELSON† unequivocally decides in favour of a theory of metallic reflection for nearly all cases of iridescence. He supports, with the weight of his great authority, the conclusions of WALTER, basing his opinion on the similarity of the behaviour of polarised light when reflected from iridescent structures, and from thin films of aniline dyes. So convinced is he of the accuracy of this opinion, that he even says "it is somewhat surprising to find that the contrary view is still held by eminent naturalists, and it is hoped that the further evidence here presented may serve to emphasise the distinction between 'metallic' or 'surface' colours and the remaining classes of colours (due to pigment, interference, and diffraction)."

BIEDERMANN, who has examined the views of WALTER, is, it is true, a biologist, but others also challenge MICHELSON'S conclusions. Personally, I am unable to criticise the physical arguments, since I can only approach the subject from the biological standpoint. Fortunately, however, the late LORD RAYLEIGH,‡ in a recent paper, gives a most admirable summary and review of all the arguments. He points out that the evidence of MICHELSON, who relies "on the rigorous optical tests of the measurement of the phase difference and the amplitude ratio," when polarised light is reflected, cannot be lightly dismissed; and, if there were no alternative, it might be most difficult to choose between a theory of selective reflection and one of "thin films." LORD RAYLEIGH is impressed by the weakness of the transmission colours, and the similarity of those reflected to the analogous case of the brilliant coloration exhibited by crystals of potassium chlorate, first described by STOKES, and attributed by LORD RAYLEIGH§ to "periodic twinning."

He is able to meet MICHELSON'S objections by supposing that there exist thin layers composed of spheres, or other shaped bodies, with their centres disposed upon a plane. Now, provided that the diameter of the particles is sufficiently small, and

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* BIEDERMANN, W., 'Handbuch der vergleichenden Physiologie,' p. 1657, Jena, 1914. Edited by HANS WINTERSTEIN.

† MICHELSON, A. A., 'Phil. Mag.,' 6th series, vol. 21, p. 554 (1911).

‡ LORD RAYLEIGH, 'Phil. Mag.,' 6th series, vol. 37, p. 98 (January, 1919).

§ LORD RAYLEIGH, 'Phil. Mag.,' 5th series, vol. 26, p. 256 (1888); and 'Scientific Papers,' vol. 3, p. 204. These crystals have since been investigated by Prof. R. W. WOOD ('Physical Optics,' p. 165, 1919). He confirmed LORD RAYLEIGH'S opinion, and calculated that in one specimen the colour was caused by about 700 plates, 0·2 μ (0·002 mm.) in thickness.

that their refractive index differs from that of the medium in which they are embedded, it is possible "to combine a specular and highly coloured reflection with a very imperfectly developed polarisation, and thus to evade the difficulty which meets us, when we confine ourselves to 'thin plates.'"

Both the opinion and experiments of MALLOCK[*] strongly support the interference theory. He points out the fact that the polarisation phenomena (ellipticity, etc., observed by MICHELSON) "may, though functions of the wave length, accompany the production of colour without being necessary to it, that is, may depend on the molecular while the colour depends on the mechanical structure." Moreover, MALLOCK is strongly of the opinion that the disappearance of nearly all colour, when the scales are immersed in highly refractive fluids, is very much in favour of interference being the source of the phenomena. Even stronger evidence is afforded by the behaviour of scales under pressure. He arranged a simple piece of apparatus, by which scales could be brought into the centre of a series of NEWTON's rings, formed between a piece of plate-glass and a lens of suitable curvature. He could thus observe through the microscope the effect of applying pressure to any object. In the case of scales,[†] the colour was always destroyed, but, when feathers were used, it tended to return when the pressure was removed. He was strongly of the opinion that, if the structures giving rise to the colours were of molecular dimensions, *i.e.*, if they were due to selective metallic reflection, pressure insufficient to cause molecular disruption would not destroy the colour. If, on the other hand, the colour were caused by a periodic structure, the pressure would alter the spacing between the plates, thus giving rise either to a change of colour or to its complete disappearance.

Interesting as is the discussion of these rival theories, they cannot fail to appear to the biologist as somewhat abstract and remote from reality. He must feel that there are other avenues for approaching the solution of the problem, and that an increased use of the experimental method, or an extensive investigation of the microscopic structure of the multitudinous objects giving rise to iridescent colours, even if it did not finally decide the question, would at least give valuable evidence, by which the suitability of each theory to a given case might be gauged.

The first point to strike a biologist, on commencing a study of the wealth of forms presented to him, is the impossibility of generalisation, and the danger of invoking one theory to account for all cases, as has generally been done hitherto.

The present investigation, which mainly depends on the description of sections made from a number of scales and other portions of iridescent insects, was undertaken in the hope of illustrating the diversity to which attention has just been drawn; and should a complete solution of the problem prove impossible, of supplying further evidence with which to criticise the adaptability of each theory to the particular case under consideration. It may be objected, with some truth, that the evidence

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[*] MALLOCK, A., 'Roy. Soc. Proc.,' ser. A, vol. 85, p. 598 (1911).

[†] For exceptions to MALLOCK's observations, see the author's experiments on p. 26.

offered by the structures described on p. 35 *et seq.*, is so varied and conflicting that a satisfactory explanation seems further than ever from attainment. Nevertheless, it is claimed, for reasons subsequently given in full: first, that the diversity of forms is so great that every insect or group of insects must be considered on its own merits, for it is possible that in any given case two or more causes of colour may be operating to produce the total effect: secondly, that the periodic structure found at right angles to the surface of many scales (see Plate 1, figs. 1*b*, 2, 3*a*, and 4) is the true cause of iridescence in certain insects: thirdly, that there is another group of iridescent insects which is characterised by a surface layer of transparent chitin, in which the colour is due to a structure analogous to the former one, but parallel to the surface of the scale: fourthly, that many of the objections advanced against the theory of surface colour in the case of scales do not apply to the wing-cases of scaleless beetles, and that, in view of the arguments to be adduced, the theory of surface colour in such beetles accords best with the evidence available: and, finally, that, for a number of reasons, the brilliant colours of the scales of weevils must in part be due to a laminated structure, clearly visible in certain sections, and not entirely to diffraction by "gratings."

The descriptions of all the sections have been given together at the end of the paper, but individual reference is made whenever the necessity arises. In addition to the microscopical investigation, a number of observations and experiments, which contribute certain fresh evidence, were made during the course of this work. In order to deal with these as systematically as possible, an analysis has been made of the factors which contribute to make up the total colour effect of insects, so that each piece of fresh evidence, whether it is in favour of, or adverse to a particular theory, may be dealt with under its appropriate heading. The basis of colour in every insect is considered as due to the action of one or more of the four agencies first mentioned, to which pigmentation must be added. Moreover, there are certain factors which modify the colours already present, and determine the characteristic appearance, tone, quality, etc., of the complete insect. These have been considered first, the principal colour theories subsequently.

II.—Factors which modify the Colours of Insects.

(a) *Position of the Wing and Scales.*—This has a considerable effect on the colour, especially that of iridescent insects; for not only does the angle that the surface of the wing makes with the line of vision alter the colour, but in many cases the appearance of the insect will be totally changed according as the observer looks at the wing parallel to the nervures, or at right angles to them. Similarly, if the observer looks parallel to the nervures, but from the apex of the wing to the base, the colour may be quite different from that seen when looking from the base towards the apex. This is generally due to the fact that the scales are not always set in the same plane as the surface of the wing, but are frequently inclined to it at a definite angle. Thus, though an observer is holding the wing at right angles to his line of vision, the scales may still make an angle with it. In the case of *Ornithoptera poseidon* and others, there are two dark velvety patches on the forewings, which owe their appearance partly to the angle at which the scales are attached to the wing, but chiefly to the fact that the scales form rows which run at right angles to the nervures instead of parallel, as do the other scales.

(b) *Shape and Configuration of the Scales.*—These factors are frequently the cause of the change of colour seen on varying the position of the wing. In this way *Morpho cypris*, the shape of whose scales is convex, may be made to vary from dull purple to electric blue. The well-known appearance like shot silk, shown by *Apatura iris*, LINN., which causes it to seem bright violet in one direction, but black in the opposite, is said to be due to a similar reason. The point of every scale is curved upwards (fig. 1, E, p. 7) like the prow of a gondola, so that only by looking at it from the root should the upper iridescent surface be seen. From the opposite direction the observer should only perceive the brown underside of the upturned tip. This suggestion was made by WALTER,* and it seems to account very well for the appearance of *A. iris* and insects like the purple form of *Euplœa deione*, WESTW. But there is the opposite effect, which must be taken into consideration, shown for instance by the wings of the South American insect *Caligo memnon*, FELDER. The changes of colour exhibited by this insect are similar to those in *E. deione*, except that the purple is only seen when the wing is viewed from the apex to the base, in spite of the fact that the tips of the scales seem to be curved slightly upward. It thus appears that the same shape of scale can produce diametrically opposite effects. A careful scrutiny of these two insects at all angles clearly shows that in one case (*A. iris*) "the black position" is not much more than 45° to one side of the normal, whereas in *C. memnon* it is at about the same inclination, but on exactly the opposite side of the normal, positions in which the upturned tips of the scales could hardly have any effect. These phenomena are very difficult to explain, because when seen in section there is no asymmetry of the striæ† or other part which might produce them.

The shape of the scale may affect the colour in other ways. For instance, since scales are placed in parallel rows, if they are curved as in fig. 1, G and H, so that they rise in one or in two crests, the light will be concentrated in a series of bright lines, corresponding to the high lights on these waves. Further, scales may be convex (fig. 1, A, G, and H), so that there are at all angles a number of rays more or less at right angles to the tangent, and therefore great variations of colour do not follow from changing the angle. On the other hand, if the scales are flat or only slightly concave (fig. 1, C and E), only a small pencil of rays will be normally reflected to the eye, so that the colours which are more intense begin to change rapidly as soon as the wing has been turned through a small angle. There are many other possible

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* WALTER, B., *loc. cit.* (see p. 2).

† It has been suggested that one face of the prism-shaped striæ might be coloured bright blue while the other was brown, see VON ROSENHOF, 'Die monatl. herausgegeb. Insektenbelustigungen,' vol. 3, p. 254 (1755).

modifications in the shape of scales. In *Papilio ulysses*, LINN., for example, the black border of the wing is slashed with markings of a deeper black. The scales forming these streaks have developed into long hairs, which produce an intense velvety black appearance. Again, scales may be twisted corkscrew-wise (fig. 1, I), or they may even be curved in other ways; but the subject has been fully treated by BIEDERMANN.*

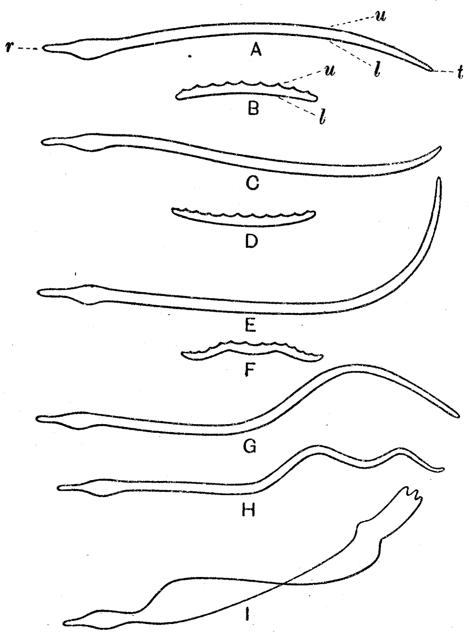

FIG. 1.—Diagram to show shapes of scales. A is a long section, *u*, the upper reflecting surface, *l*, the lower surface, *r*, the root, and *t*, the tip. B is a cross-section of the same scale.

(c) *Modelling and Quality of the Scale Surface.*—These factors exert a profound influence on the colour. As is well known, the surface of most scales is divided by ridges or striæ running parallel to the long axis, and this striation is often converted into a reticulation by fainter ridges crossing it at right angles.† If all the ridges are wave-shaped when seen in section, as in *Papilio ulysses* (see Plate 1, fig. 5), each rectangular field so formed makes a shallow, concave, coloured mirror, the light from which behaves as if it came from a concave scale. When the reticulation is very pronounced, and especially when the striæ themselves appear to give no colour, the light becomes scattered in different directions causing a general dulling effect. The colour may also be rendered matt by numerous small knobs or protuberances, generally situated along the edges and at the corners of each reticulation, as in the scales of *Hypolimnas salmacis*, DRURY, ♂ (Plate 1, fig. 13). These are the "*Höckerchen*" described by SPULER,‡ but they are far less common than he claims them to be.

There can be no doubt that the texture or "quality" of the chitinous surface has a profound effect on the appearance of scales, just as it has on other objects. An extreme instance of this nature is seen in various Lycænidæ of the genus Polyommatus, the sheen of which might at first sight be thought iridescent. As a matter of fact, the pigment of the scales is no brighter than that seen in many dull orange Pierids, and the metallic glitter is entirely due to the highly polished surface, which gives the insect the appearance of burnished copper. In the case of many orange Lycænidæ the violet sheen found is due to a layer of specialised scales.

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* BIEDERMANN, W., *loc. cit.* (see p. 2).

† The structure of ordinary pigmented scales is not minutely described, because an excellent account of the formation and development of the scales of *Danaida plexippus*, LINN., is given by MAYER, 'Bul. Mus. Compar. Zool.,' Harvard College, Cambridge, Mass., vol. 29, No. 5, p. 209 (1896).

‡ SPULER, A., 'Erlangen, Sitzber. physik. Soc.,' vol. 26, p. 111 (1894).

Another remarkable case of surface "quality" is seen in *Dismorphia nemesis*, LATR., ♂ from South America, the shiny appearance of the costa of the hind wings of which might almost be called metallic. Careful observation shows that here the scales lie flat upon the wing, and have smooth, highly polished surfaces, and poorly developed striæ, which are insufficient to give an impression on the collodion films (described on p. 10). On a rough portion of the wing the scales are set at a sharp angle, and the striæ are very pronounced.

(d) *The air-content.*—As in the case of the hair of mammals, the air which is contained within the scales has an important effect. A scale is essentially a flattened sac, and the upper membrane is bound to the lower one by chitinous walls, the summits of which form the reticulation seen on the upper surface. Since they run at right angles, as well as parallel to the long axis, the interior of the scale is divided up into small compartments, or cells. These cells become filled with air which reflects the white light, so that many scales without pigment appear as white as the hairs of some animals. It has been suggested by BIEDERMANN and others that this air, combined with a folding of the scale surface, somewhat in the manner of a sheet of corrugated iron, is sufficient to cause the highly metallic golden and silver colours of certain species, such as the moth *Plusia chrysitis*, LINN. No doubt such a structure would give very brilliant white scales, but unless the air-spaces were very numerous, and not more than several molecules in width, no approach towards the appearance of metallic reflection would be possible. Plate 1, fig. 22, a golden scale of *Dione juno*, CRAMER, with the large air-spaces, *h*, clearly does not show a structure approaching this form.

All white insects do not owe their appearance to the air contained in their scales. Many Pierids, for instance, contain a white pigment (uric acid), as may be seen from the changed appearance of the scales of *P. brassicæ* after treatment with a dilute alkali.

III. FACTORS WHICH PRODUCE THE COLOURS OF INSECTS.

1. *Pigments.*

Pigments give their colours to insects, as to other objects, by absorbing certain rays, the remaining colours of the incident white light being reflected from somewhat below the surface. As a rule, the pigments are mainly situated in the scale, either diffused throughout the chitin or accumulated in granular masses. Nothing is known of the chemistry of these pigments, except those of the Pierids.* Pigments may sometimes be "interlaminar," that is to say, situated between the two wing membranes, as, for instance, the blue-green of the Large White Butterfly, which is only clearly visible when the scales have been removed. The green patches on certain insects, *e.g.*, *Papilio antheus*, R. and J., *P. agamemnon*,

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* HOPKINS, F. G. 'Phil. Trans. Roy. Soc.,' B, vol. 186, p. 661 (1895).

LINN., *Metamorpho dido*, LINN., and others are very striking examples of this effect. As will be described on page 10, these patches are devoid of scales, so that the green pigment, localised in these areas, can be clearly seen. The yellow spots in the small moth *Euchromia polymena*, LINN., from Ceylon, are due to a yellow pigment in a similar position.

Iridescent insects are very often devoid of all except black pigment, which is almost always present, either in the layer of scales below the iridescent ones, or else deposited in the lower portion of the iridescent scales themselves. Here it acts as a background, or absorbing screen, intercepting the white light that would otherwise be reflected to the eye, thus causing a considerable desaturation of colour. This effect is well seen in *Morpho sulkowskyi*, KOLL. (see Plate 1, fig. 2), which owes its shimmering appearance entirely to the absence of pigment.

Similarly, the white scales of *Morpho cypris*, WESTW., differ in no way from the blue ones, except in the entire absence of pigment from the lower membranes. The blue scales can be made to appear similar to the white ones by bleaching the pigment with either chlorine or hydrogen peroxide. The white spots of *Hypolimnas bolina*, LINN. ♂, give the most striking instance of the increase in colour that may be produced by a screen of black scales. The central portion of these spots is a chalky white, whereas the surrounding area is deep purple, the only difference being that in the former the underlying surface of black scales is absent. On the other hand, a matt appearance may sometimes be produced in iridescent insects by the presence of black pigment in the colour-producing structure of the scale itself (see Plate 1, fig. 21).

In Lepidoptera, green colours are seldom due to pigments.* They are usually structural in nature, though frequently a yellow pigment will modify the blue of a structural colour, so as to make the insect appear green. A striking example of this is seen in *Ornithoptera poseidon*, DBLE., ♂ (Plate 3, fig. 2*a*). Other pigments may combine with structural colours to give magentas, etc., as in the case of *Teracolus phlegyas*, BUTL. (Plate 3, fig. 5). The green colour of beetles is sometimes due to a similar cause, as in *Heterorrhina elegans*, FABR., or *H. africana*, DRURY (p. 50). In many red and copper-coloured beetles, which have a burnished yellow or green iridescence, like *Ceroglossus gloriosus*, GERST., from Chile (p. 49), most of the red colour is due to a soluble pigment, the metallic effect alone depending on other causes.

2. *Diffraction.*

As has already been mentioned, most scales have striations parallel to their long axis, which number from 4,000 to 16,000 to the cm. These "gratings" might be

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* According to VON LINDEN (HALLE, 'Leopoldina,' vol. 38, No. 11, p. 124 (1902)), the moths *Hylophila prasinana*, LINN., and *Geometra papilionaria*, LINN., contain an alcohol-soluble yellow pigment with a green fluorescence. It is true that their colour is no doubt pigmentary, but I have been quite

the cause of the colour, but it has been objected that the varying angles of incidence and diffraction would equalise the colour effects. **MICHELSON**, however, has pointed out that this would not be the case if the striations were fine enough to give a single spectrum extending over an angle of 45°. Still, the frequent occurrence of these striæ on scales, whether iridescent or not, is good reason for not regarding them as the sole or even chief explanation of the colour. A number of other objections have been raised,* and among them the difficulty that no spectra are formed by a grating unless the light is broken up into beams; for instance, no colours are shown by a grating under a cloudless sky. Nevertheless, a more rigorous test was considered desirable, and in order to separate effects due to surface contour, etc., from those due to other causes, the obvious method was adopted of taking impressions of the scale surfaces,† as has been done in the case of mother-of-pearl. The best results were obtained with a $2\frac{1}{2}$ per cent. solution of collodion, dissolved in equal volumes of alcohol and ether, containing 0·5 per cent. of glycerol. The solution is used as follows:—

A thin film is poured upon a microscope slide and the pellicle allowed to dry until it no longer adheres to the finger. The wing is now gently pressed upon the surface of the film, where it is allowed to remain for several seconds. It may then be cautiously removed by seizing one of the nervures in a forceps with very little damage to the specimen. The resulting impression is allowed to harden for a few minutes, after which the image sharpens, and a brilliant diffraction spectrum appears. It is impossible to say what occurs during this short lapse of time. The impression in the collodion may actually be modified in some way, so that after an interval the surface assumes a form capable of giving diffraction spectra, though it could not do so before. This supposition does not, however, seem very probable. The film is now ready to be examined microscopically with a 1/6 objective (Zeiss DD), and with the condenser slightly displaced. In this way the minutest details are most faithfully reproduced. A typical example is shown in Plate 3, fig. 9, which represents an impression of one of the green spots of *Papilio agamemnon*, LINN., which are due, as has already been said, to a green interlaminar pigment. The black scales are seen to terminate abruptly, their place being taken by thin silvery hairs, the minute striations on which are clearly visible. Unlike most scales, the

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unable to extract it with alcohol. Many stick insects, grasshoppers, and other Orthopterous insects, as well as some beetles, have green chlorophyll-like colours which fade after death, and are no doubt pigmentary.

* BANCROFT, W., 'J. phys. Chem.,' vol. 23, p. 446 (1919).

† BIEDERMANN made similar attempts with black wax on several beetles' wings, because he was of the opinion that such striking structures as shown by *Cetonia aurata*, LINN., *Potosia preyeri*, JANSON, and others, must give rise to some "grating" colours. I have examined these and other beetles by means of collodion films, but in no case have I obtained evidence of any such colour. Since this method was adopted a paper has appeared, in which dried collodion impressions have been used to study mother-of-pearl (A. PFUND, 'Journ. Franklin Inst.,' April, 1917). This method would obviously have been unsuited to delicate structures like those of the scale and wing-membrane.

black ones are not finely striated, but have two or three equidistant ridges running their full length.

This method, though scarcely original, permits of the investigation of the under as well as the upper sides of the scales, and should prove useful. By gumming the wing on a piece of paper, the wing-membrane may be removed, and impressions taken in the usual way with the undersides of the scales. These lower membranes are free from striations, but are often slightly wrinkled, especially at the base. Unfortunately, notwithstanding the glycerol, these films dry quickly, and eventually become useless. Attempts have been made to preserve them in water, formaldehyde, and chloroform. These did not prove very successful, but since a number of impressions are made with the greatest ease and rapidity from a single piece of wing, it is of no great importance.

Good "gratings" may be made with most Lepidoptera, whether iridescent or not, but butterflies, owing to the more regular organisation of their scales, give the brightest effects. It is scarcely unexpected that most scales give good "gratings," because it is well known that scales mounted between glass, and held before an intense source of illumination, will show brilliant spectra even when pigmented, provided the light is bright enough.

That all insects, the impression of whose scales gives spectra, do not themselves show iridescence, makes it doubtful whether diffraction is ever a main source of colour, especially as it was found that the brilliant scales of *Morpho cypris*, Westw., and others with the same structure, gave an almost flat impression. The probable explanation why black and heavily pigmented scales do not give any diffraction colours is that so little light is reflected to the eye that any colours produced would be imperceptible. This effect may be imitated by preparing a collodion film with a "grating" that gives a good spectrum. If, now, a few drops of an alcoholic solution of an aniline dye are run on the film, so that it is rapidly absorbed without affecting the surface in any way, the colour is seen to disappear, or to become very much reduced in intensity, especially in the region of the spectrum corresponding to the dye used. It might be expected that colour would be seen in white or light scales, and this, as a matter of fact, does sometimes occur. Moreover, when pale scales are looked at under the microscope with oblique illumination, a faint pink and greenish sheen, somewhat like mother-of-pearl, is nearly always observed. In perfectly transparent scales definite spectra sometimes appear, as may be demonstrated by the following experiment. A collodion impression is made with *Morpho achilles*, Linn., which has a layer of transparent, striated scales, care being taken to insure that one or two patches of these blue scales become detached and adhere to the collodion. The film, which should show a bright spectrum, is tipped backwards and forwards, so as to allow the colours to travel across one of the patches of scales. As the pale blue scales fall under the violet end of the spectrum, they are seen to assume a much more intense colour, changing to mauve or pink as the violet is replaced by the red. When the scales finally pass into the infra red region, they assume their original pale colour. Moreover, if the insect itself is carefully scrutinised, at various angles, a pinkish-coloured silky sheen will be seen to play over the scales. These colours change very rapidly with small angles of incidence, and are obviously diffraction effects. The violet end of the spectrum is practically invisible, owing to the deep blue already given by the lower layer of scales. Similar, if not better, effects can be seen in *Hypolimnas bolina*, LINN., ♂.

One of the few exceptions to metallic reflection admitted by MICHELSON occurs in the scales of *Entimus imperialis*, FORSTER, the Brazilian Diamond Beetle, and no doubt in other brilliant weevils as well. He believes that the colours are due to striæ in the interior of the scales, since these lose their colour when highly refractive fluids enter them by some rent or passage in the wall of the scale. MICHELSON calculated that there were from 5,000 to 10,000 striæ to the centimetre, and this figure was found to agree well with actual counts made under a magnification of 1,000 diameters, and oblique reflected illumination. Under these conditions, the striæ appear very sharply defined in small patches. It was necessary to suppose that the "rulings" had an asymmetric saw-tooth shape, since all the light is concentrated in one spectrum.

At first, MICHELSON'S explanation of the colours of *E. imperialis*, which is supported by a similarity between these scales and certain artificial saw-tooth-shaped gratings, certainly appears justifiable, and yet it cannot pass entirely without criticism. By the kindness of Dr. H. SCOTT, I obtained several long series of Curculionidæ, from the Cambridge Museum of Zoology. Among these, many insects tended to be monochromatic, and this was especially the case with the beautiful *Cyphus* 16-*punctatus*, LINN., from the Amazon, which is a soft Eton blue, looking almost as if enamelled. Under the microscope, these scales are spangled, and the striations, instead of being straight, are curved. Another insect, which is monochromatic at all angles, is *Eupholus schönherri*, GUÉR., from the Amazon. The ground colour is a deep blue crossed by bands of vivid green. It is true that artificial gratings can be designed, in which light of certain wave-lengths may be lacking, as, for instance, gratings ruled with more than 20,000 lines to the centimetre. However, not only is it necessary to account for a constancy of colour at all angles, but some explanation must also be given of the very brilliant complementary colours seen in all these scales, whenever they are examined by transmitted light. It is curious that MICHELSON has not dealt with such an obvious difficulty.

It is clear that no grating of the ordinary type, consisting of alternate transparent and opaque strips, can produce these transmission colours. Nevertheless, with "laminary" or "échelette" gratings, which are described in the Appendix (p. 66), some such effects could be obtained. Thus, if it were not for definite microscopical evidence that another type of structure may exist, these colours, seen by transmitted light, would not be conclusive evidence that a structure of the type of the "laminary" grating is absent.

No structure was apparent in sections of some scales, for five or six of the most brilliant insects were examined without result. However, in cutting sections of some of the paler weevils, notably *Hypomeces squamosus*, FABR., var. *durulentus*, HERBST., from Siam, a stratification was most clearly visible, even when sections were mounted in Canada balsam (see p. 53). It is visible in plan (Plate 2, fig. 15*a*), and seems to exist throughout the scale, because, even in thin sections, a second series of striations crossing at right angles can be seen by lowering the objective. This produces the appearance of the strings of a tennis-racket (see Plate 2, figs. 15*b* and 15*c*). Such a stratification may act as a diffraction grating, but, since it obviously exists throughout the body of the scale, it may equally well be a lamination, dividing the scale into strata, though it is of course possible that both interference and diffraction may operate together.

In addition to the above considerations, as well as the theoretical difficulties already mentioned on p. 10, there are certain other peculiarities in these scales, which give added weight to the suggestion that diffraction is not the sole cause of colour, and that the interference of thin films also plays a part. As well as the very bright colours already mentioned, all degrees of pale greens and pinks are to be found, and, in the genus *Platyomus*, grey and even white insects occur. The surfaces of all these scales show patches of the characteristic striation, which is conspicuous for the lack of uniformity in its direction. By transmitted light they all, with the exception of the grey and white scales, show complementary colours. The number of striations varies somewhat, but, on the whole, it is about the same as in *E. imperialis.* The striations can best be seen with oblique reflected illumination, but caution is necessary not to mistake the diffraction fringes on the surface of the scale for a true striation within the scale. It is possible, however, to see the striations with an immersion objective, if the scales are mounted in air, and it is worthy of notice that they are sharper and better defined in some of the pale insects than in the more highly coloured ones. That the structure should appear the same, though the saturation varies so greatly, is difficult to account for, if the colours are produced by diffraction. If, on the other hand, they are the colours of thin films, the pale colours are explicable by supposing that the laminæ vary in thickness; the very bright colours may then be attributed to chitin plates, one-half wave-length in thickness, which would therefore be too close to be resolved by any objective used.

BIEDERMANN and MALLOCK were also of the opinion that the striations are not the main cause of colour, which is, according to them, probably thin films of air, and it must be admitted that the scales are in appearance much like opals* or old decomposed glass, which are thought to owe their colour to air-films.

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* According to a paper by W. BANCROFT, 'J. phys. Chem.,' vol. 23, p. 289, May, 1919, STOKES attributes the colours of opals and of potassium chlorate crystals to the same cause. These papers, entitled "The Colors of Colloids," contain no original matter, but consist of extracts from papers dealing with many obscure points of considerable interest in connection with various colour phenomena.

3. *Interference of Thin Films.*

Some of the evidence in favour of the theory of "thin plates" and against that of selective metallic reflection has already been discussed. Additional arguments may be found in LORD RAYLEIGH'S[*] paper. There is one piece of evidence, appreciated by BIEDERMANN and MALLOCK, not in favour of interference, but which, in the case of scales, seems to be entirely incompatible with the surface colour theory. It is that the transmitted as well as the reflected colours totally vanish when scales are immersed in a sufficiently refractive fluid. If the colours were due to an aniline dye, an increased transparency would be expected, accompanied by an even more brilliant colour, and not by the entire disappearance of colour, as is actually the case. It is hard to understand how both MICHELSON and WALTER can have overlooked so vital a question.

It is true that WALTER believed that "we have to do with solutions of the dyes in chitin, solutions whose refractivity for most part of the spectrum colours is nearly equal to that of benzol." But this seems to increase rather than decrease the difficulty, because, in the first place, solution of the dye in a large volume of chitin would dilute the colour, and, in the second place, when dissolved in chitin, dyes would presumably show their body-colour, as they do when dissolved in water, and not the complementary surface colours seen in thin dry films.

Apart from other arguments for interference, the existence of the periodic structure described on p. 35 *et seq.*, is strong *prima facie* evidence that, in certain insects at least, this structure is the main cause of iridescence; and the evidence would be strengthened if it could be shown that the plates are of the correct magnitude. The first difficulty that requires to be dealt with is that the structure is at right angles, and not parallel, to the wing-surface (fig. 2, p. 36). If the plates are at right angles to the scale, and therefore approximately at right angles to the wing-surface when the latter is normal to the line of vision, the plates must be near grazing incidence, and *vice versâ*. When, therefore, the wing is turned from the normal through an increasing angle, the plates will change from grazing incidence to the normal, but the colour will not change towards the violet or shorter wave-length, as has always been affirmed,[†] but towards the red, because the path of light within the plates is becoming longer. If it can be shown that as a matter of fact the colours do change

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[*] LORD RAYLEIGH, 'Phil. Mag.,' 6th series, vol. 37, p. 98 (January, 1919).

[†] For instance, MICHELSON, A. A., *loc. cit.* (see p. 3), says that in birds and insects "the change of colour with changing incidence strictly follows the law already mentioned—the colour always changing towards the blue end of the spectrum as the incidence increases." WALTER, however (*loc. cit.*, see p. 2), the only physicist who has carefully observed a large number of insects, states that there are exceptions to the general rule, *e.g.*, *Papilio epiphorbas* BOISD., which turns from blue to green at grazing incidence. But he has attributed this anomaly to the fact that "the scales are only coloured slightly and are so raised that at grazing incidence the body-colours are seen, whereby the displacement of the colour becomes quite abnormal." (See BANCROFT, W., 'J. phys. Chem.,' vol. 23, p. 448 (October, 1919).)

towards the red, it appears conclusive proof that these plates are the effective cause of colour.

All the insects that could be obtained were examined and their colour changes noted, but it must be remarked at once that the observation is by no means an easy one, chiefly because the wing is not flat, but usually undulating. Also the plane of the scale is not, as a rule, the same as that of the wing; this causes such a play of colours that an accurate judgment is often impossible, as, for instance, in the case of *Morpho sulkowskyi*, KOLL. In order to make the observations of more value and as accurate as possible, an attempt was made to take colour measurements. A short time ago a method of colour measurement was required for another purpose, and, after a number of careful trials, the "tintometer" was adopted as the most suitable instrument for the occasion. A full description and the method of use will be found in the account of that research.* Briefly, the method of measurement consists in placing the opaque coloured substance in an optical arrangement with two fields, in one of which appears the coloured object, and in the other a standard white background. The colour of this background may be modified by interposing between it and the eye a series of coloured glass slips. These are of three colours—blue, yellow, and red, and each colour is divided into 20 units, and fractions to two places of decimals. These glasses are combined in various proportions until the standard background appears to be exactly the same tone and saturation as the object to be measured. The degree of saturation is regulated by adding black or neutral tint units, which are made by combining equal numbers of units of the three colours, the result being a grey, in which no single tint predominates. The number of units required for a given object analyses the colour, and the corresponding visual impression can be expressed quantitatively by the conversion illustrated in the table below. An obvious difficulty in examining wings of such brilliance is that the percentage of light reflected from their surfaces is much greater than that from the standard chalk background. This might have been overcome by replacing the background with a metallic surface, but it would have introduced an unknown quantity, and it was preferred to adopt the method recommended, of placing neutral tint units in front of the wing until its brightness had been toned down to that of the background. This done, it was quite surprising how accurately, with a little practice, the brightest colours could be matched.

It was considered that the observations would be of more value if they could be given some reference to the normal spectrum. Mr. LOVIBOND, the inventor, published the relationship of the spectrum to a series of tintometer readings.† Since, however, the colours of the insects are not pure spectrum colours, but are generally less saturated, these figures could not be employed directly. It is possible, however, to get a rough idea of the *relative* change of colour by increasing the saturation of the

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* ONSLOW, H., 'Journ. of Genetics,' vol. 8, No. 4, p. 209 (September, 1919).

† LOVIBOND, J. W., 'Light and Colour Theories,' p. 36, *et seq.* (Spon, E. and F. N., London).

readings to equal that of the spectrum colours, while keeping the ratio of the component colours constant. Thus, the colour of *Papilio ulysses* at normal incidence is represented in the visual scale by 8·6 (blue), 7·0 (green), which is in the same proportion as 11·0 (blue), 9·0 (green); the colour is thus equivalent to light of wave-length 5023·0, the position corresponding to the latter tone, with an addition of white to represent the lower degree of saturation in the former. The reading at 45°, after the corresponding adjustment, is 14·3 (blue), 5·7 (green), which is similarly related to wave-length 4903·0. The change of colour on changing from normal to 45° incidence is thus equivalent to a change of 0·012 μ in the wave length towards the violet. This shift up or down the spectrum is given by the figures in the last column of the following table, the unit being a tenth-metre. To take the readings, a simple stage was constructed, with a platform that could be made to revolve on its axis, and a pointer which registered the angle of inclination on a dial. This apparatus could be placed either on the stage of a microscope or on the tintometer. A flat portion of wing was fastened to a glass slide which could be attached to the platform so that the readings might be made at any desired angle. The illumination used was the light from a north window, arranged to avoid all shadows, as suggested by Mr. LOVIBOND. The illumination at acute angles was ensured by the use of a mirror. Changes in the colour of a single scale may be examined in the same way under the microscope. The following observations were made with iridescent insects, sections of whose scales showed that there was no structure at right angles to their surface (see Plate 1, fig. 5).

Insects.	Angle in °.	Coloured glasses.			Light brighter than standard.	Visual colours.			Wave-length in Å.U.	Shift in Å.U.
		Blue.	Yellow.	Red.		Black.	Blue.	Green.		
Papilio ulysses, LINN.	0*	15·6	7·0	—	4·0	—	8·6	7·0	5023·0	—
	45	14·1	4·0	—	4·6	—	10·1	4·0	4903·0	-120·0
	80	13·0	1·3	—	2·0	—	11·7	1·3	4768·0	-135·0
	85	9·8	0·6	—	—	—	9·2	0·6	4740·0	- 28·0
Papilio arjuna, HORSF.	-10	11·4	11·5	—	3·2	—	0·1	11·4	5415·0	—
	0	9·7	10·0	—	3·2	—	0·3	9·7	5401·0	- 14·0
	45	9·0	8·0	—	3·0	—	1·0	8·0	5342·0	- 59·0
	80	8·4	5·3	—	1·3	—	3·1	5·3	5154·0	- 88·0
	85	9·2	5·0	—	1·3	—	4·2	5·0	5090·0	- 64·0
Thecla marsyas, LINN.	0	8·0	4·3	—	1·0	—	3·7	4·3	5086·0	—
	45	7·9	3·0	—	1·2	—	4·9	3·0	4968·0	-118·0
	80	6·0	2·2	—	0·4	—	3·8	2·2	4962·0	- 6·0

* At 0° the wing is normal, and consequently with these insects the interfering surfaces are also normal.

It is clear from the run of the figures for the "visual colours," that, on the whole, the greens get progressively less green, and the blues more blue. Consequently, the wave-length moves steadily towards the violet. The column showing "light brighter than standard" gives an idea of the amount of light reflected from the wing. As a rule, it is at a maximum near normal incidence, but gets progressively less as the angle increases. In the case of *P. arjuna*, it will be noticed that the colour at an angle of 10° on the other side of the normal, *i.e.*, $-10°$, showed the most green. It may consequently be presumed that the angle at which the scales are inserted into the wing membrane accounts for this difference.

The above figures may be contrasted with those on p. 18, which were taken with insects, sections of whose scales all showed periodic structures at right angles to the surface.

The colour in the case of these insects moves in the opposite direction, and the wave-length becomes longer, instead of shorter as in the preceding table. In the case of the first insect, *C. laurentia*, there is no colour at normal incidence, except the deep brown of the pigmented scales surrounding the green spot. A blue colour makes its appearance at a certain angle, and thereafter steadily increases in saturation and in wave-length. (For the explanation of the appearance of this colour, see p. 37, and Plate 1, figs. 3*a* and 3*b*.)

The three large *Ornithoptera*, for which figures are next given, only change colour near grazing incidence, and in order to obtain the best effect, there should be a source of light somewhere on the side of the insect furthest from the observer. The last insect, which is yellow, at first appears to be an anomalous case, because the wave-length becomes shorter, and not longer, although the structure is at right angles to the surface. The probable explanation of this, given on p. 40, suggests that the effect is due to a yellow pigment, and a slight modification of structure, which makes the case somewhat involved.

Many other insects show a similar change of colour towards the red end of the spectrum, among which *Papilio erithalion*, Boisd., is one of the most striking. The carmine spots upon the hind wings are due to pigment, over which in some lights there is an iridescent violet sheen. On tipping the wing, this colour gradually changes to turquoise blue, which passes through all the shades of green, till it reaches an almost pure yellow at grazing incidence.

It should be mentioned that some insects which ought to change colour towards the red, behave anomalously, nor can this be explained in the same way as the case of *Ornithoptera crœsus*. Measurements were made, for instance, of *Morpho cypris*, Westw., and *M. menelaus*, Linn., and it was found that the wave-length of the blue light reflected became longer from 0° to an angle of about 30° to 35°, after which, instead of continuing towards the yellow region, a change takes place in the other direction, and the wave-length gets shorter. After an angle of 90° is reached, the colour becomes a blue-violet. The wave-

Insects.	Angle in °.	Coloured glasses.			Light brighter than standard.	Visual colours.							Wave-length in Å.U.	Shift in Å.U.
		Blue.	Yellow.	Red.		Black.	Violet.	Blue.	Green.	Yellow.	Orange.	Red.		
Chlorippe laurentia, GODART.	0*	No colour visible.												
(blue edge of green spot)	45	10·0	2·0	6·0	—	2·0	4·0	4·0	—	—	—	—	4332·0	—
	52	9·0	0·6	—	0·9	—	—	8·4	0·6	—	—	—	4740·0	+ 412·0
	80	7·4	2·0	—	2·0	—	—	5·4	2·0	—	—	—	4892·0	+ 148·0
Ornithoptera urvilliana, GUÉR.	0	7·0	2·0	—	—	—	—	5·0	2·0	—	—	—	4902·0	—
	45	5·5	2·3	—	0·0	—	—	3·2	2·3	—	—	—	5000·0	+ 98·0
	80	0·9	7·0	—	1·0	—	—	—	0·9	6·1	—	—	6056·0	+1103·0
	84	—	5·0	5·0	1·0	—	—	—	—	—	5·0	—	6877·0	+ 821·0
	88	—	5·0	7·0	1·4	—	—	—	—	—	5·0	2·0	7086·0	+ 104·0
Ornithoptera poseidon, DBLE.	0	7·3	27·0	—	1·2	—	—	—	7·3	19·7	—	—	5953·0	—
	45	7·3	27·0	—	2·0	—	—	—	7·3	19·7	—	—	5953·0	—
	75	—	4·0	7·0	—	—	—	—	—	—	4·0	3·0	7190·0	+1237·0
	80	—	3·0	8·0	—	—	—	—	—	—	3·0	5·0	7331·0	+ 141·0
Ornithoptera crœsus, WALL.	0	—	19·0	8·8	2·0	—	—	—	—	10·2	8·8	—	6486·0	—
	45	—	19·0	8·0	2·0	—	—	—	—	11·0	8·0	—	6456·0	- 30·0
	70	—	19·0	6·7	0·5	—	—	—	—	12·3	6·7	—	6406·0	- 50·0
	80	1·0	19·0	3·7	—	1·0	—	—	—	15·3	2·7	—	6259·0	-147·0
Hind wing	80	—	27·0	2·8	—	—	—	—	—	24·2	2·8	—	6225·0	- 34·0

* At 0° the wing is normal, consequently in these cases the interfering surfaces are normal at 90°.

length at grazing incidence is in fact appreciably shorter than it was at normal incidence.

Sections of these scales have been cut, and there can be no doubt that the periodic structure should give a change of colour similar to that of the preceding insects. It can only be supposed that certain additional factors complicate the case. In *M. menelaus,* indeed, the surface layer of blue scales must give colours due to diffraction as well as interference (see Plate 1, fig. 1*a*), and, in the lower scales of this and similar insects, the strips of chitin, which form the periodic structure, would, at oblique incidence, act as a grating, superposing diffraction effects upon those due to interference.*

The preceding measurements leave no doubt that there are two types of iridescent insects. In one of these the colour moves towards the violet as the angle of incidence increases, in the other towards the red. The latter case corresponds to insects having a periodic structure at right angles to the scale surface; the former to insects in which a periodic structure, if it exists, must be parallel to the scale surface. But there is another distinction between the two types of scales, which appears to illustrate the orientation in space of their respective colour-producing structures. If the scales are examined under a low power and a very oblique beam of illumination, those with a structure at right angles to their surface show no colour, so long as the beam is parallel with the plates, but if the stage is revolved, and the beam begins to cut the plates, colours appear. On the other hand, scales in which the plates lie parallel to the surface, show colours in almost any position. The foregoing evidence proves almost conclusively that, in the first case, the periodic structure is the true cause of colour, especially as it can be shown that this structure is approximately of the most effective magnitude for colour-production.

Now, the most favourable thickness for films is the half wave-length of the mean ray of white light, or some multiple of it. Allowing for the difference of the speed of light in the two substances, this would be 0·17 μ† for chitin and 0·25 μ for air, or a mean distance of about 0·2 μ. A number of measurements were made of the distance between the centre of one plate of chitin and that of the next, and it was found to vary between 0·5 μ and 1·0 μ, being usually about 0·75 μ. Now, in the case of *O. poseidon,* in which this distance is a little less than 0·6 μ, suppose the air-space, which always appears smaller than it really is (see p. 36), to be one half wave-length (0·25 μ), this would leave a thickness for the chitin plates of 0·35 μ, or exactly two half wave-lengths. If the chitin plates were double, both films would be of the most efficient thickness. That these are double is often suggested by the line of cleavage *c*, seen down the centre of each plate (fig. 4*a*, Plate 3), when some sections are mounted in a medium of low refractive index. The thickness of the

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* Some idea of the complex nature of the colours that can be produced by such a structure may be seen from the Appendix.

† $\mu = 1/1000$ mm.

plates in the other cases is of about the same order, and, for convenience, all the scale sections have been drawn to the scale $\mu = 2$ mm., *i.e.*, a magnification of about 2000. The beetle sections are mostly drawn to the scale $\mu = 1$ mm.

To return for a moment to the type of scales, which have a transparent layer parallel to the surface, and which are invariably iridescent (*e.g.*, *Papilio ulysses*, Plate 1, fig. 5). What evidence* is there of a periodic structure, which, if it exists, must be parallel to the surface? In the first and most important place, reference to p. 41 and Plate 1, fig. 11, will show that in oblique sections there is a laminated structure. Very faint lines can be made out at *mm* in fig. 11, which come into focus on raising or lowering the objective. Secondly, the behaviour of scales, when immersed in viscous fluids, is very striking. Collodion or oil can be employed, but great caution must be maintained when using scales with pronounced striæ for this experiment. This is because the oil flows down the channels formed between two striæ, filling them, and so causing the dark shadows thrown by the striæ to disappear. The whole scale grows transparent, and thus the appearance of air being driven from a tube is very closely simulated. BIEDERMANN quotes such an experiment as evidence for the existence of thin films, but, provided the scale is deeply striated, the appearance is the same whether it is iridescent or not. The behaviour, however, of scales like those of *Papilio ulysses*, which are comparatively flat, is very striking, and should be compared with those of *Morpho menelaus*. The moment the oil touches the edge of the latter scale, it rushes instantaneously between the upright plates of chitin, and at the same time the iridescence disappears. In the case of a scale of *P. ulysses*, on the other hand, if it is observed simultaneously by transmitted and reflected illumination, the fluid is seen first to touch the scale and then to overflow it. The bright blue reflection is thereby turned to a brilliant green, and the scale becomes slightly translucent. After a brief interval, the fluid appears to creep inwards from one edge, gradually spreading over the entire scale. In the area where this secondary penetration has taken place there is no iridescent green colour, and the scale itself has become much more translucent.

There is, however, one difficulty, which cannot be passed over without careful consideration. If the colours of the scales are due to "thin films" parallel to the surface, and not to selective reflection, is there sufficient space available within the layer of chitin to contain a suitable structure? Should the structure consist of two layers of chitin and air, it cannot be thinner than $0{\cdot}8\ \mu$, and MALLOCK is of the opinion that three or four chitin plates would be required to produce the saturated colours seen. This would demand a thickness of $1{\cdot}0\ \mu$ to $1{\cdot}4\ \mu$, but it must be remembered that the air-spaces may be very small. Thus, suppose the chitin plates were so close together that they were practically touching, and yet not in optical contact, then the

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* Though the spectra of iridescent insects do not usually show characteristic diffraction bands, a darkening in certain regions is frequently seen, and in *Papilio paris* F. J. KEELEY ('Philadelphia, Pa., Proc. Acad. Nat. Sci.,' p. 112, Feb., 1911) describes a "black band at wave length 0·588 micron."

colours produced would be quite saturated, for such a structure would simply give the colours due to three half wave-length plates. The available thickness has been measured in a number of scales, and a glance at the figures in Plate 1, which are drawn to the scale $\mu = 2$ mm., will show that the higher value mentioned is never reached. In most cases the thickness of transparent chitin is usually about 0·75 μ. This would only allow for two chitin plates in an air-chitin structure, but it would give four chitin plates if they were in close juxtaposition. This number should be more than sufficient, because, for reasons which will be discussed on p. 28, it will be seen that single films produce considerably more colour than might be supposed. In the case of beetles the difficulties are much greater, for there is reason to believe that the available thickness of chitin is somewhere between one and two half wave-lengths.

LORD RAYLEIGH* has criticised these measurements, because they are not easy to make, and because they may be disturbed by refraction effects, causing magnification. Truly, the measurements are not easy to make, but a certain degree of accuracy can be obtained by taking the mean of the "outside" and "inside" measurements made with a Ramsden screw micrometer. Further, these measurements can be checked by preparing a very long, thin, tapering wedge of paper, constructed so that an increase of 1 mm. in width corresponds to a length of 5 cm. If the length be graduated in millimetres, the size of the cuticle may be estimated by observing it in the camera lucida under a known magnification, and noting the exact point at which the edges of the cuticle coincide with the wedge.

To serve as a further check, these measurements were repeated on sections mounted in fluids, the refractive indices of which varied from 1·3–1·7. A control was also applied by measuring the spaces of several gratings, the rulings of which varied from 2·0–0·25 μ, and it was found possible to make these measurements with an error of not more than 3 per cent.† All these methods gave concordant results.

Before leaving the subject of thin films it would be well to mention one or two cases in which it seems probable that the colour is produced by one or, at most, two pairs of interfering surfaces. It will be shown (p. 28) that a single film can give a fairly saturated colour, and it is quite reasonable to suppose that the pale pinks and greens of many scaleless wings in Odonata and other insects are due to the wing membranes themselves. Moreover, the colour of some very pale insects like *Salamis parhassus*, DRURY (see p. 44, Plate 1, fig. 15) may be due to a similar cause.

There is, however, another instance where bright colours are produced by two surfaces. Anyone who has examined wings under a microscope must have noticed how occasionally a black scale, having become detached, has been turned over upon its face, exposing a brightly coloured reverse. Plate 1, fig. 10 shows a section from one of the black scales of the day-flying moth *Urania fulgens*, WALK. The lower

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* LORD RAYLEIGH, *loc. cit.* (see p. 3).

† My thanks are due to Mr. T. SMITH for most kindly making some of these measurements at the National Physical Laboratory.

membrane; *b*, in this and similar scales is almost, if not quite, devoid of pigment. It clearly consists of a single film, not more than 0·5 μ thick, so that when the scales were reversed, by gumming their upper sides on a piece of stiff paper, they were found, as was expected, to be iridescent. Their appearance is, however, entirely different from that of ordinary iridescent scales, for under the microscope a single scale shows as many changing colours as a soap-bubble. Moreover, the colours change rapidly with slight variations in the angle of the incident light. They strongly suggest the colours of a thin film of slightly varying thickness.

The Scarlet Tiger, *Callimorpha dominula*, LINN., and no doubt other insects, possess a brightly iridescent pellicle formed by the dry ecdysial fluid. This is best seen when the imago is ready to emerge, and may be found covering the unexpanded wings of the pupa. It is exceedingly thin, transparent, and slightly wrinkled, looking very much like the many-coloured films formed by dropping collodion, dissolved in amyl acetate, upon water.

4. *Blue Due to Scattering by Small Particles.*

According to LORD RAYLEIGH, if white light penetrates a heterogeneous system composed of bodies embedded in a medium, the refractive index of which is different from that of the bodies, the light scattered will be blue, provided the diameter of the said bodies is small compared with the wave-length of light. The light is blue, because such a system favours the scattering of the short blue waves at the expense of the longer red ones, which pass unhindered. It has already been mentioned that BAER, BIEDERMANN and other writers consider that blue due to scattering by small particles contributes to the phenomena of iridescence. It has indeed been shown[*] that the blue feathers of certain birds (Cotinga)[†] are composed of pale yellow keratin interpenetrated by tiny air-canals ("*Porenkanälen*"). Though these canals are visible, it is claimed that their diameters are nevertheless small enough to enable them to scatter blue light, so long as air is not excluded. A polygonal structure of prismatic rods[‡] has also been described in certain copepoda (Sapphirina)[§] and other animals, which is said to produce an analogous colour. The blue of the eyes[||], the blue skin of birds[¶] (guinea fowl) and the artificial blue of tattooing in Indian ink are all due to this cause. Moreover, the green colour of many frogs, lizards and other reptiles is due to the addition of a yellow pigment.

Although it seems unlikely that anything so dense can exist in Nature as LIPPMANN'S silver films, it must not be forgotten, when seeking for possible

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[*] HAECKER and MEYER, 'Zool. Jahrb.,' Jena, vol. 15, p. 267 (1902).

[†] A South American bird with vivid blue and purple plumage.

[‡] AMBRONN, H., 'Mitt. Zool. Stat. Neapel,' Berlin, vol. 9, p. 479 (1890).

[§] According to KEELEY (*loc. cit.*, see p. 20), the gem-like colours of this crustacean are caused by diffraction. The shell is said to be covered with fine markings similar to those on *Pleurosigma angulatum.*

[||] BANCROFT, W., "The Colors of Colloids," VI., 'J. Phys. Chem.,' vol. 23, p. 356 (May, 1919).

[¶] MANDOUL, H., 'Ann. Sci. Nat. (Zool.),' Paris, vol. 18, p. 225 (1903).

explanations of iridescence, that matter in an exceedingly fine state of division may probably cause the most vivid colours. R. W. WOOD* described films of metal deposited in this state on glass, by means of sodium vapour, etc. He at first attributed their colour to "optical resonance," analogous to the electrical resonance exhibited by strips of tin-foil mounted on a glass plate; but, owing to later investigations,† he was forced to abandon this hypothesis, and he now suggests that the cavities or pits between the octahedral crystals of sodium "trap the radiation in some way and cause almost complete absorption for certain values of λ." It seems that Prof. WOOD considered that these investigations had some bearing on the iridescence of insects, for he says:—"There appears to be a large number of cases in which brilliant colours are shown, which cannot be explained by any of the common laws of optics with which we are familiar. . . . . . So far as I am aware, no very satisfactory explanation has ever been given of the colours of certain feathers and butterflies, and I strongly suspect that there is some action of absorbing matter in a state of very fine division, upon light waves, which is not yet completely understood."

KOSSONOGOFF‡ has advanced a theory of "optical resonance" in which he assumes that *all* the colours of Lepidoptera are due to the selective reflection of minute granules said to exist between the striæ of every scale. He appears to have measured the size of these granules, maintaining that the wave-length of the coloured light reflected from the scales is a function of their diameter. Apart from the fact that many wing pigments can actually be extracted,§ he admits that he was unable to measure the diameter of single granules, but was obliged to assume that the size of the granules was uniform and equal to the distance between them. It is hardly necessary to add that many scales are perfectly transparent, and devoid of all granular matter.

BIEDERMANN describes a structure in the wing-cases of many beetles analogous to the prismatic formation in Sapphirina. He finds the following structures in all beetles:—

(1) A thin cuticle, on the surface of which is a network ("*Wabenwerk*,") corresponding to the ends of (2) a layer of parallel rods or columns ("*Stäbchenschicht*") set at right angles to the surface of the elytron, and seen through the cuticle. Below this again lie (3) several layers of pigmented chitin ("*innere Schicht*").

Unfortunately, BIEDERMANN shows no sections, and only a schematic diagram drawn in perspective. There seems, however, to be no doubt that he considered

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* WOOD, R. W. 'Physical Optics,' p. 635 (1919).

† WOOD, R. W., *loc. cit.* (see p. 1).

‡ KOSSONOGOFF, J., 'Physik. Zs., Leipzig,' vol. 4, p. 208 (1903).

§ HOPKINS, F. G., *loc. cit.* (see p. 8); also URECH, 'Zool. Anzeig.,' vol. 15, p. 281 (1892); and 'Zs. f. wiss. Zool.,' vol. 57, p. 306 (1894); also PERRY COSTE, F. H., 'Entom.,' vol. 23, p. 128 (1890), *ibid.*, vol. 24, pp. 9 etc. (1891); also TUTT, J. W., Introduction to 'British Noctuæ and their Varieties,' vol. 2.

this rod-like structure to be present in all the beetles he describes, as is evident from such passages as the following :—

> "*Die sogenannte 'Stäbchenschicht' . . . . deren Vorhandensein, wiewohl in gradweise sehr verschiedener Entwickelung, bei schillernden Käfern allgemein verbreitet zu sein scheint.*"*

Moreover, it is quite clear that he believes this peculiar structure, with the addition of the surface cuticle, to contribute most of the colour, as is evident from the passage quoted on p. 27. But there are several objections to this. In the first place, if the lower layers are really connected with colour-production, it is impossible to explain why the colour vanishes on shaving or scratching the wing surface of most beetles. Secondly, sections from the wings of a number of beetles, among them several investigated by BIEDERMANN, are figured and described later, but excepting in certain peculiar Cetoniids, no trace of any structure corresponding to the "*Stäbchenschicht*" could be discovered. It seems possible that BIEDERMANN may have mistaken the net-like pattern ("*Wabenwerk*"), nearly always to be seen on the wing-cases, for the ends of the rods or "*Stäbchen*," and referred to the presence of a "*Stäbchenschicht*," which only existed in a few exceptions.† These include *Heterorrhina elegans*, FABR., as well as *H. africana*, DRURY,‡ which differ from ordinary beetles in their structure, and in the fact that their colour remains after removal of the surface cuticle. Moreover, all sections cut tangentially to the surface show the characteristic colour, even when mounted in Canada balsam, if they are examined by reflected light. These rods, which contain yellow pigment, may possibly scatter blue light, as has been suggested in the case of many similar structures. To do this, the rods should be small when compared with the wave-length of light, that is to say, not larger than the more complex molecules, and it is doubtful, in view of the short range of wave-length of visible light, whether there would be a corresponding effect, when the rods are comparable in size to a wave-length as in this case.

There is one interesting observation that can conveniently be dealt with at this point. Though at first sight it is suggestive of a case in which at least some of the colour might be attributed to the scattering of small particles, this cannot well be so. Moreover, it is neither an argument for interference, nor yet for surface colour, but appears equally difficult to explain on any hypothesis. One of the principal pieces of evidence relied upon by those who support the theory of "thin films," as well as by

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* BIEDERMANN, W., 'Festschrift zum siebzigsten Geburtstage von Haeckel,' Jena, p. 243, 1904.

† Dr. HUGH SCOTT informs me that there are other Cetoniidæ which show the same peculiar enamel-like surface, and which no doubt possess the same structure.

‡ This insect is probably the same as *Smaragdisthes africana*, a green African beetle, mentioned by BIEDERMANN, which remains coloured after the surface has been scraped.

those who support the theory of selective reflection, is that the light transmitted through the coloured objects must be complementary to the light reflected. Thus MICHELSON[*] says, "in cases which could be investigated, unfortunately rather few, the transmitted light was complementary to that reflected." MALLOCK[†] says, "in cases where the structure is transparent, it transmits the complementary colour with nearly the same intensity as the colour reflected." Undoubtedly, if the effect were due to some substance such as an aniline dye, the colour of the transmitted light would be more vivid than if it were due to interference. It is true that in many scales the colour transmitted is very bright, but in others, though the colour reflected is no less intense, and the scale almost transparent, yet the light transmitted is either uncoloured or it is tinged with the *same* colour as is reflected. Thus the pink scales of *Salamis parhassus*, DRURY, the purple of *Precis œnone*, LINN., and the blue of *Hypolimnas salmacis*, DRURY, ♂, are all transparent and colourless by transmitted light; the metallic green scales of *Batesia prola*, DBLE., are grey, owing probably to air contained between the membranes, and the deep purple scales of *H. bolina*, LINN., ♂, are bluish grey by transmitted light.

It cannot be objected that the reflected light is so weak that the transmitted colour, if weaker, would be imperceptible, because the reflected colour of *H. bolina* is very saturated, and in some insects, *e.g.*, *Jalmenus evagoras*, DONOVAN, the reflected colours are paler than the colours transmitted. The transparent surface scales of *Morpho achilles*, LINN., and of some similar species, are still more remarkable. In these scales, not only is the reflected colour blue, but the transmitted colour is blue also, and, if anything, it is deeper and more saturated than the colour reflected. These scales are transparent and very thin, not more than 0·5 μ (see Plate 1, fig. 12*a*). If they are observed with a 2/3 inch objective (Zeiss AA), or a lower power, they are a bright blue, provided the condenser is racked down. On raising the condenser towards the object, the colour fades and disappears entirely, when the illumination becomes critical. With an objective of 1/6 inch (Zeiss DD) or higher magnification, no colour is visible in any position of the condenser. The colour appears to be intimately connected with the striæ, which are easily broken away, leaving the transparent and colourless basal membrane. Though the diameter of these striæ is small, they cannot appear blue for the same reason as the sea and sky, because if the blue rays are reflected in greater proportion than the red ones, the scales should appear a dull red by transmitted light. Curiously enough, BIEDERMANN[‡] mentions that the scales of *M. peleides*, a similar insect, are blue, but the strangeness of the phenomenon seems to have escaped him. At the time that these observations were

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[*] MICHELSON, A. A., *loc. cit.* (see p. 3).

[†] MALLOCK, A., *loc. cit.* (see p. 4).

[‡] BIEDERMANN, W., 'Handbuch der vergleich. Physiologie,' p. 1939. Edited by HANS WINTERSTEIN, Jena.

made, they were communicated to 'Nature,'* in the hope that someone would be able to suggest a possible explanation, but up till now none has appeared.

5. *Selective Metallic Reflection.*

The evidence advanced by WALTER and MICHELSON in support of this theory has already been considered, together with LORD RAYLEIGH'S ingenious hypothesis which admits of an explanation in terms of "thin plates," and which yet meets MICHELSON'S objections. One of the principal difficulties connected with the surface colour theory was pointed out by MALLOCK, who, as has been mentioned, showed that all the iridescent structures he examined lost their colour when subjected to moderate pressures, from which he concluded that the structure was of a mechanical rather than of a molecular nature.

I have repeated some of these experiments, and am able to confirm most of the results, but, with the wing-cases of all scaleless beetles and certain iridescent dragonflies, bees, etc., I found that considerable pressures had no effect.† In fact, the lenses invariably fractured without any change being seen in the colour. It may be objected that the chitin of beetles' wing-cases is so thick, that pressures would be useless with them which were effective with scales. Exactly similar results were, however, obtained with beetles having thin elytra, and with the thin surface layer of wing-cases, which is scarcely thicker than many scales.

Moreover, if there were any alternating structures of which air formed one of the plates, it should be possible to change or diminish the colour by replacing the air with a refractive fluid. Nevertheless, all attempts by LORD RAYLEIGH, Prof. POULTON, and myself to drive out the air entirely failed. This was the case even when small pieces of wing were used under a pressure of 0·5 mm. of mercury, to facilitate penetration. Special efforts were made by applying both this test and the pressure test, to discover whether there is a periodic structure in *Scutellera nobilis*, FABR., because the ease with which its surface cuticle frills (Plate 2, fig. 10) suggests such a structure.

The thin elytra of *Lytta vesicatoria*, LINN., were tested in the same way, because BIEDERMANN considers they contain a thin film of air, since the bright green colour slowly becomes a dull bronze after the wing has lain for some time in alcohol. Transverse sections of the wing-case, however (Plate 2, fig. 8), show no indication of such a structure, and it seems probable that the loss of colour is due to saturation with a refractive fluid, which causes the wing to become translucent, thereby losing the effect of the screen of melanic pigment, which, as in *E. tenuicollis* (p. 49), always intensifies the colour. BIEDERMANN appears to be of the opinion that *L. vesicatoria*

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* ONSLOW, H., 'Nature,' vol. 103, p. 84 (April 3rd, 1919).

† MANDOUL, H., *loc. cit.* (see p. 22), describes experiments with peacocks' feathers, which were said to retain their colour when hammered on an anvil. I have found these feathers to differ from others, since hammering, etc., only changes green into violet, this colour remaining until the surface seems to peel off.

and *Anoplognathus aureus*, WATERHOUSE, owe their colour to thin films of air, but in the case of all the other beetles examined he undoubtedly believes the colour to be due to thin films of chitin. Moreover, BIEDERMANN, curiously enough, seems to consider that it is the chitinous surface cuticle which produces much, if not all, of the colour, as is seen from the following passages :—

> "*Es war bisher nur von dem alleräussersten sehr dünnen, durchsichtigen und farblosen Oberflächenhäutchen* (*der Cuticula*) *die Rede, welches optisch als dünnes Blättchen die wesentlichste Ursache der glänzenden Interferenzfarben bei Käfern und andern schuppenlosen Insekten darstellt.*"

Or, again, speaking of the Rose Beetle :—

> "*Ich folgere daraus, dass . . . die 'Stäbchenschicht,' hier aber vor allem die 'Cuticula,' für die Färbung verantwortlich zu machen ist.*"*

This cannot, of course, be the case, for if it were, the colour would disappear as it does when fluids come into optical contact with the scales. There must, therefore, either be some protective layer which prevents this contact, or the colours must be due to selective metallic reflection.

Thus neither of these difficulties is met with in the case of beetles' wings, which retain their colour under all circumstances. Moreover—and this seems one of the strongest arguments against interference in the wing-cases of beetles—there is a very serious lack of space in which to place a periodic structure. Indeed, the space available in the case of beetles, especially when allowance has been made for a surface cuticle, is much less than in any scale examined. In the case of a dye, on the other hand, a film 0·1 μ or less, would be quite sufficient, though it would probably be invisible, even in oblique sections.

The question, however, whether a single film can or cannot produce colours of the saturation seen is extremely important, because, as will appear later, the layer of chitin is half a wave-length in thickness, or a little over. Now, in spite of the assertion by MALLOCK† that at least three or four films of chitin are necessary, the colour of a single film, such as sometimes peels from a sheet of mica, or even a soap film, when seen in a good light and against a black background, is very saturated. That it is not much paler than the metallic wings of many beetles is illustrated by the following experiment. To obtain some idea of the brilliance of single films, colour-measurements were made of a soap film,‡ of varying thickness, which were then compared with the colours of a number of beetles' wing-cases, measured under the same conditions. Artificial light was used and a mirror was

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* BIEDERMANN, W., *loc. cit.* (see p. 24).

† MALLOCK, A., *loc. cit.* (see p. 4).

‡ Prof. C. V. BOYS' instrument, which can be purchased under the name of the "Rainbow Cup," was used as a simple means of obtaining a flat film of definite uniform thickness. The colours of the first order of Newton's rings are rather difficult to measure, owing to their movement and rapid change, but the sequence of the colours of the thinner films of the later orders can be followed step by step, as they wax and wane, with the greatest accuracy.

substituted for the standard background of the "tintometer" with which the colour-measurements were made. The light from the mirror was first rendered the same as that reflected from a soap film, just too thick to show any colours, by adding the requisite number of neutral tint units. The following table shows the colour of a single soap film of varying thickness :—

Soap film.		Standard glasses.			Visual colours.					
Colour.	Thickness in μ.	Blue.	Yellow.	Red.	Violet.	Blue.	Green.	Yellow.	Orange.	Red.
Pale pink . . .	1·0	—	—	4·0	—	—	—	—	—	4·0
Pale green . . .	0·9	4·0	5·0	—	—	—	4·0	1·0	—	—
Pink	0·8	—	—	6·0	—	—	—	—	—	6·0
Green	0·7	6·0	8·0	—	—	—	6·0	2·0	—	—
Bright pink . .	0·6	0·6	—	8·0	0·6	—	—	—	—	7·4
Yellow	0·55	—	8·0	1·0	—	—	—	7·0	1·0	—
Bright green . .	0·5	8·0	12·0	—	—	—	8·0	4·0	—	—
Bright blue . .	0·45	14·0	4·0	—	—	10·0	4·0	—	—	—
Magenta . . .	0·4	6·0	—	16·0	6·0	—	—	—	—	10·0
Red	0·375	2·0	—	17·0	2·0	—	—	—	—	15·0
Orange to yellow	0·35	— —	2·0 to 18·3	11·0 to 3·0	— —	— —	— —	0·0 to 15·3	2·0 to 3·0	9·0 to 0·0
Steel to deep blue	0·25	0·7 to 11·0	3·0 to 1·0	— —	— —	0·0 to 10·0	0·7 to 1·0	2·3 to 0·0	— —	— —
Purple to deep magenta.	0·2	11·0 to 9·0	— —	1·0 to 23·0	1·0 to 9·0	10·0 to 0·0	— —	— —	— —	0·0 to 14·0

Owing to the fact that for convenience the measurements were carried out by artificial light, and with a mirror in place of the standard background, these readings are only relative.

The colour readings of the beetles' wing-cases, made under the same conditions as the previous measurements, were as follows :—

Name of insect.	Standard glasses.			Visual colours.					
	Blue.	Yellow.	Red.	Black.	Blue.	Green.	Yellow.	Orange.	Red.
Plusiotis resplendens, BOUCARD	—	6·0	2·5	—	—	—	3·5	2·5	—
Sternocera diardi, GORY . .	13·0	20·0	—	—	—	13·0	7·0	—	—
Cetonia aurata, LINN. . . .	10·0	20·0	1·0	1·0	—	9·0	10·0	—	—
Popillia cupricollis, HOPE—									
(Thorax)	4·0	20·0	12·0	4·0	—	—	8·0	8·0	—
(Elytron)	7·0	10·0	20·0	7·0	—	—	—	3·0	10·0
Anomala dussumieri, BLANCHARD	10·0	20·0	3·0	3·0	—	7·0	10·0	—	—
Heterorrhina africana, FABR.	8·0	35·0	—	—	—	8·0	27·0	—	—
Callistopopillia iris, CANDÈZE	11·0	23·0	—	—	—	11·0	12·0	—	—
Papilio arjuna, HORSF. . .	20·0	23·0	—	—	—	20·0	3·0	—	—
Ornithoptera urvilliana, GUÉR.	20·0	17·0	15·0	15·0	3·0	2·0	—	—	—

It can be seen that the paler colours in a soap film about 1 μ thick measure 4 or 5 units of the tintometer scale, and the thin films showing the brightest colours 10 to 15 units. The values for the beetles, measured under the same conditions, are also seen to be about 10 to 15 units, and, moreover, in the case of beetles some neutral tint or black units were occasionally required to equalise the colours; that is to say, the amount of light reflected from the beetles was sometimes less than in the case of the soap films. A reading of a bright butterfly's wing (*P. arjuna*), which measures 20 units, is included for comparison. The pale blue insect, *O. urvilliana*, which requires 15 units of black, is an example of the other extreme.

The colour values of films of two aniline dyes have been shown below, in order to give an idea of the depth and change of colour, and the rapid falling off of the saturation with obliquity.

Dye.	Angle in °.	Standard glasses.			Visual colours.					
		Blue.	Yellow.	Red.	Violet.	Blue.	Green.	Yellow.	Orange.	Red.
Basic fuchsin (2 per cent. solution)	22	0·6	4·6	—	—	—	0·6	4·0	—	—
	32	1·0	4·0	—	—	—	1·0	3·0	—	—
	45	1·0	3·0	—	—	—	1·0	2·0	—	—
	60	0·9	1·7	—	—	—	0·9	0·8	—	—
+ Cedar-wood oil . .	45	6·0	1·9	—	—	—	1·9	4·1	—	—
Brilliant green (5 per cent. solution)	0	—	1·7	10·3	—	—	—	—	1·7	8·6
	30	—	1·7	9·7	—	—	—	—	1·7	8·0
	50	—	1·1	9·1	—	—	—	—	1·1	8·0
	60	—	2·4	6·6	—	—	—	—	2·4	4·2
	70	—	1·5	2·9	—	—	—	—	1·5	1·4
+ Cedar-wood oil . .	50	7·0	10·0	—	—	—	7·0	3·0	—	—

The films were prepared by pouring hot solutions on to glass plates, and the colours were measured from the glass side. On the whole, the colours are less saturated than those of thin soap films. In the case of fuchsin, the addition of a film of oil slightly increases the saturation, probably because it reflects to one side some of the white light from the surface. In the case of brilliant green the effect of the oil film is most striking, for it undoubtedly causes the reflected red to become a deep complementary green.* The transmitted colour is, of course, exceedingly saturated

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* The surface colour of an iridescent substance varies greatly with the index of refraction of the medium in contact with it. This is because there are great differences in the relative indices of refraction on either side of the absorption maximum, causing relatively large changes in the contributions to the total reflected light in different parts of the spectrum. It follows that the rays which are chiefly reflected must be those situated in that part of the spectrum where the difference in the refractive indices of the two substances is greatest. For instance, fuchsin is yellowish-green in contact with air, but pure blue in contact with a diamond. In the above case of brilliant green the change is more striking, but the

compared with the reflected light, which, as LORD RAYLEIGH has said, is always characteristic of surface colours. In this case the transmission colour of the fuchsin was about: 1·0 (black), 4·5 (violet), and 14·5 (red), or at least twice as saturated as the reflected colour at any angle.

Now to return to the question whether the colour of scaleless beetles is a surface colour or due to interference. In spite of the intensity of the colours of single films, it is obviously of primary importance to find out at exactly what depth the colour-producing layer of wing-cases is situated, for it is conceivable that it might lie in one of the deeper layers of chitin below the surface cuticle. For this purpose, the following ingenious experiment was suggested by Dr. KEILIN. A portion of the golden wing-case of *Plusiotis resplendens*, BOUCARD, is polished with carborundum. At first no change takes place, but at a certain moment the colour suddenly alters from gold to a bright magenta, and on further polishing, the magenta soon disappears, giving place to the black of the underlying chitin. Sections were cut from a small right-angled triangle of the wing-case, in which all stages from black, through magenta, to gold occurred. The exact position of each section along the perpendicular of the triangle could be roughly estimated from the length of the section, since the angles of the triangle were previously measured. Plate 2, fig. 6, shows a composite section, derived from three drawings, of which I is the unpolished wing-case, II the magenta layer, and III the black chitin (*cf.* fig. 8, Plate 3). Examination of these sections suggests that the colour-producing layer is situated along the dark and rather uneven line which is always seen lying between the cuticle and the lower layers of chitin. In all sections in which the polishing was carried deeper no colour remained. The only part that can be polished away without affecting the colour is thus the surface cuticle. As the whole distance from the surface of the wing-case to the bottom of the dark line scarcely measures 0·5 μ, there is little or nothing left when the width of the cuticle has been subtracted.

In order to check the above measurement, other means were adopted. On looking at the polished surface of the wing, a dark elliptical area will be seen, where the black underlying chitin has been exposed. Examination under a microscope reveals that there is a distinct edge to the coloured area, orange on the inner side, changing to magenta and gold. The depth of the colour-producing layer may be calculated, if R and r are the mean radii of curvature of the wing-case, D and d the diameters of the dark ellipse, and T the width of the edge of the metallic layer exposed by polishing. For if the laminæ are nearly the same thickness at the plane of section, the value of the depth required, x, may be determined from the equation

$$x = (\mathrm{D}/2\mathrm{R}) \times \mathrm{T}.^{*}$$

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cause is doubtless the same. (*Cf.* BANCROFT, W., "The Colors of Colloids," VIII, 'J. Phys. Chem.,' vol. 23, p. 448, October, 1919.)

[*] Dr. E. H. GRIFFITHS has most kindly assisted me with these measurements.

From the above data, two values may be calculated for x, which agree fairly well. The average value in several experiments was $0{\cdot}53\,\mu$, which is in close agreement with the thickness of the surface cuticle measured under the microscope ($0{\cdot}5\,\mu$).

Special precautions must be observed in carrying out the polishing. A paste of the finest carborundum must be used, made with cedar-wood oil, which is spread upon a piece of soft leather tied to a small metal wheel driven by an electric motor. The wing-case must be glued to a suitable handle or support, so that it can be fixed easily at right angles to the axis of the wheel. If these precautions are not taken, the area polished will not be flat but curved, and, consequently, the exposed edge of the film will be far too wide. Even with care, probably no great degree of accuracy can be obtained, but it is enough that the two methods give sufficiently concordant results to show that there is only room for a one half wave-length plate.

There are, further, several details, best seen while the wing-case is being polished by hand under the microscope, which offer independent evidence in favour of the surface colour theory and against that of interference. The results obtained vary in different cases, and it is sometimes advisable to examine the polished wing-cases under some fluid, which cuts off the white light often reflected from the surface, so that the colours can be seen better. For instance, in bugs, like *Scutellera nobilis*, FABR., the colour disappears almost instantaneously, and no change to magenta is observed. In many beetles, the interval that elapses before any change of colour takes place is much longer, and varies, even in different portions of the same insect. This delay probably corresponds to the variations found in the thickness of the cuticle. Blue beetles and green beetles also show a change of colour, not to magenta, but rather to crimson or scarlet. The green Rose Beetle, for instance, *Cetonia aurata*, becomes a fiery red.

The way in which the colours change to red is so peculiar that it is worth while describing it briefly. When, for instance, the golden beetle, *P. resplendens*, is polished, nothing is at first seen but the scratches and grooves cut by the polishing crystals, as if on a sheet of metal, and, when the change to magenta does take place, it is abrupt and strongly impresses the observer with the difficulty of attributing the phenomenon to interference. Plate 3, fig. 8, in which I corresponds to the gold, II to the magenta, and III to the brown areas, shows an attempt to reproduce this change of colour, so suggestive of metallic films. The result is not altogether satisfactory, owing to the difficulty of reproducing metallic effects. In the original wing-case, the area *s*, between the gold and the magenta, has a peculiar bluish-silver high light impossible to reproduce, which appears to be due to the magenta shining through the gold film where this is very thin.

This effect was to some extent reproduced by polishing a film of gold, $1\,\mu$ thick, which had been deposited electrolytically on strips of bright copper.* The magenta was represented by a tint of copper, and there was an intervening strip, which had

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* Dr. E. H. GRIFFITHS very kindly prepared these strips.

much the same silvery appearance described above. An even more similar effect could be obtained by heating a strip of copper in the steam oven, till coloured films of oxide were formed. In connection with these films of oxide, it is worth mentioning that MALLOCK* has suggested, as a result of polishing experiments, that the colours of films of steel oxide are not due to interference in the manner usually supposed. Both the above methods of producing colours recall to mind Nobili's rings.

In the case of these beetles, it may be objected that the colour of a thin film *would* change, if its thickness was reduced by polishing in the above way. The change, however, would be gradual, and not abrupt, as in this case. Moreover, the sequence of colours would be different from that which actually occurs, *i.e.*, green, blue, or golden, to crimson, magenta, or scarlet.

Thus it is seen that the case for surface colours or selective metallic reflection appears to be fairly strong. To recapitulate, the principal objections to attributing the colours of scales to this theory do not apply to the wing-cases of scaleless beetles. These objections are: (1) the colours of scaleless beetles do not disappear under pressure; (2) the reflected colours do not disappear on immersion in highly refractive fluids; (3) the transmitted colours, so far as these can be seen in the thin surface layer, also persist; (4) the colour-producing layer appears to be so near the surface that no room remains for a suitable structure; and (5) the changes of colour seen on reducing the thickness of the metallic layer by polishing are abrupt, and in other respects quite unlike the colours of thin films.

It must be remembered that single films have been shown to be very bright, but, if insect colours are due to such films, it is essential to suppose that they are of extraordinarily uniform thickness throughout, so that the colour may be the same all over. Moreover, the thickness in all specimens of the same species must be exactly the same, for the difference of a fraction of a wave-length would cause a considerable alteration of colour, and it seems very difficult to imagine an organic film complying with these conditions. One of the only difficulties that remain was pointed out by LORD RAYLEIGH. In his experience, "surface colour is always less saturated than transmission colour. The reverse is the case with beetles." LORD RAYLEIGH has also pointed out that the variety of colouring in different parts, but at the same angle, as seen in *Chrysochroa fulminans*, FABR., and many Scutelleridæ, makes large demands upon the surface colour theory, but a moderate change of structure is all that would be required by interference. To these difficulties it can only be replied, in the first place, that the treatment used in separating the surface layer, or "*Emailschicht*," as it was called by BIEDERMANN, from the rest of the wing-case, is very violent, and may modify the appearance of the transmission colours. To the second objection, it may be pointed out that the very slight modification due to polishing, whatever this may be, can change the colour from gold or green to red, so that some similar modification may cause the

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* MALLOCK, A., 'Roy. Soc. Proc.,' A, vol. 94, p. 561 (April, 1919).

diversity of colouring noticed on the surface. In fact, the colours may be due to several organic films, giving different surface colours, though what the nature of these films may be it is difficult to say. The only thing like them that is known is a thick layer of chitin in certain Tortoise Beetles (see p. 65), which appears a shining gold, when moistened, at whatever depth the surface is exposed. A slight modification of this chitin might easily produce a red or a green colour instead of gold.

Finally, on morphological grounds, it is easier to conceive of the development of a layer of "*Schillerstoff*" than a periodic structure. Schulze* has shown that the surface layer of the Stag Beetle (*Lucanus cervus*, LINN.) is not formed gradually from the hypodermal cells, as in the case of skin or scales, but is due to a fluid secreted from special glandular cells, which is ejected upon the surface of the wing at a late period in pupal development, where it rapidly hardens. This beetle is not iridescent, but presumably iridescent cuticles would be formed in the same way. It is difficult to see how a periodic structure can arise in a homogeneous medium after it has been excreted, except perhaps by a process analogous to crystallisation. I was myself strongly opposed to the surface colour theory, but the force of evidence has made me accept the fact that in the case of scaleless beetles it is a more probable solution than the only other alternative, a single film.

IV.—DESCRIPTION OF SECTIONS MADE FROM CERTAIN IRIDESCENT STRUCTURES.

(a) *Material and Methods.*

Many methods have been described for cutting chitinous structures, but no details could be found of a procedure specially devised for cutting scales. Very great difficulty was at first encountered in obtaining sections of suitable thickness, *i.e.*, 1μ to 2μ. The method eventually adopted certainly contains nothing new, but a brief account of the exact technique followed may be found serviceable, since success in cutting such difficult objects depends on strict adherence to details.

It was at first thought it would be impossible to obtain sections without some preliminary softening treatment, at any rate in the case of insects that were not freshly killed. With a few exceptions, however, it was found possible to cut even serial sections of wings of insects that had been preserved for many years. Softening was sometimes of service, with thick wing-cases, and both sodium hypochlorite and other means were employed. This treatment did not diminish the iridescence of wings, so that in all probability their structure remained unaltered. For objects that required depigmenting, hypochlorite was useful, but for softening only, a mixture of equal parts of strong hydrochloric acid, glycerol and alcohol was employed, maceration being carried out at 38° C. In cases where it is desired to

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* SCHULZE, P., 'Verhandl. d. Deutsch. Zool. Ges.,' p. 165 (1913).

remove the surface layer, or "*Emailschicht*," treatment with dilute nitric acid or 15 per cent. caustic soda was sometimes used. In some beetles, *e.g.*, *Anoplognathus aureus*, this treatment will destroy the iridescence, so that it was found convenient to paint the surface with a solution of paraffin, which could be removed from the back by some solvent. Some insects and pupæ were treated with a strong solution of soap in 70 per cent. alcohol for several days or longer, but this method* was only of use with the softer chitin of the body. When it was desired to obtain sections of the entire wing, suitable pieces were cut, passed into alcohol, and then infiltrated with collodion. They were then embedded in blocks of 6 per cent. collodion, hardened in chloroform, passed through benzol, and benzol saturated with paraffin at 40° C.; next they were passed through three successive baths of pure paraffin with melting points of 40°, 45°, and 50° C. respectively, and finally they were embedded in paraffin with m.p. 55° C. It is very important that great attention should be paid to the period that the blocks remain in paraffin. By prolonging the time, especially at the higher temperatures, any desired degree of hardness could be obtained. The quality of the sections depended entirely on making the embedding medium as nearly as possible the same consistency as the object embedded, but care must be taken not to allow the collodion to become too brittle to cut. The infiltration with paraffin can be more rapidly carried out by the cautious use of a vacuum, which enables softer blocks of collodion to be obtained. This procedure, however, was apt to aggravate the principal difficulty, which is due to a bubble of vapour from the solvent forming between the two membranes of the wing, making it become cylindrical, with a cavity in the centre of the block. The blocks were finally cut on a Cambridge rocking microtome, the blade of the knife being packed with strips of sheet lead to avoid vibration.

When it was desired to obtain sections of the scales only, and especially when it was necessary to avoid confusing the scales on the upper surface of the wing with those on the lower, the following method was adopted, and on the whole it produced the thinnest and most uniform sections. In order to detach the scales from the wing, a layer of collodion was poured into a watch-glass, and a piece of wing drained from collodion was floated upon the surface, the scales required being downward. The watch-glass was then placed in the chloroform until the surface had hardened. The wing, fixed to the surface of the collodion, can be removed by seizing a nervure in the forceps and carefully peeling it off, so that if the period of hardening was correct, it will leave all the scales embedded in the collodion, looking like a child's "transfer." The scales are then cautiously moistened with a drop of ether, and a fresh layer of collodion poured on, forming as it were a sandwich, which can be finally hardened and infiltrated in paraffin as above. It is essential that the union between the two layers should be perfect, but the greatest

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* Prof. C. H. O'DONOGHUE kindly supplied me with the details of this method.

caution is necessary in order to prevent the solvent action of the ether in the fresh collodion solution from loosening the scales and allowing them to float away.

The sections were found to ribbon well, so that they could be mounted in the usual way, but considerable difficulty was encountered in staining the chitin. A number of methods were tried, including several stains especially recommended, such as BETHE'S[*] aniline hydrochloride stain and HOFFMANN'S[†] pyroligneous acid stain, but none of them was effectual, even when the treatment was prolonged for a considerable period. With the most satisfactory stains it was found necessary to immerse sections from 12 to 24 hours, so that is was impossible to keep them properly fixed to the slide unless coated by a film of collodion. The three following stains were found the most efficient in the order mentioned: carbol gentian violet (five times the usual strength), HEIDENHAIN'S hæmatoxylin, and carbol fuchsin. Of the other stains tried, picro-indigo-carmine (RAMÓN Y CAJAL) and MANN'S stain were found excellent for the chitin of the body. After staining, the slides can be mounted in balsam, but if unstained, AMANN'S "lacto-phenol"[‡] is preferable, owing to its low refractive index. Highly refractive media such as STEPHENSON'S biniodide of mercury and iodide of potassium dissolved in glycerol were also found very useful for showing the structure of unstained pigmentless scales.

(b) *Scales showing a Periodic Structure at Right Angles to the Surface.*

1. *Morpho menelaus*, LINN. ♂ (South America).

Two layers of scales combine to form the brilliant greenish blue of these butterflies. Each layer is characteristic of a group of insects, and the scales of the lower layer were the first in which the typical periodic structure, here described, was seen. No passage in the literature could be found describing the structure of iridescent scales. BIEDERMANN[§] soaked portions of wings for 24 hours in dilute alkali. When the lustre had gone, the scale became transparent and curled round its long axis. If the profile of the scale is examined, it is found that this upper layer is formed of a "double, crystal-clear skin, which can be easily made out in longitudinal section. It is seen to be divided into two parts by a dark line which runs down the centre."

A cross-section of one of the lower scales of *M. menelaus* is shown in Plate 1, fig. 1*b*. Comparison with Plate 1, fig. 21, will show that these scales resemble the ordinary non-iridescent scales, except that the black striæ, *c*, are in the iridescent scale prolonged into transparent colourless strips or plates of chitin, *a*. Fig. 2 on the next page is a diagrammatic representation of a small portion of an iridescent

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[*] BETHE, 'Zool. Jahrb.,' vol. 8, p. 544 (1895).

[†] HOFFMANN, 'Zs. Wiss. Zool.,' vol. 89, p. 684 (1903).

[‡] LANGERON, M., 'C. R. Soc. Biol.,' vol. 58, p. 750 (1905).

[§] BIEDERMANN, W., *loc. cit.* (see p. 24).

scale, showing four of these chitin plates much enlarged; a comparison between this and fig. 1*b*, Plate 1, should make the structure quite clear. The lettering is the same on both. The lower membrane, *b*, fig. 1*b*, is attached to the striæ, *c*, by strips of pigmented chitin, *d*, the "*Brücke*" of SPULER.* Similar bands run at right angles to these, so that the body of the scale is divided into small compartments. These bands, *d*, are clearly seen in the longitudinal section of the same scale (fig. 1*c*, Plate 1). Each transparent chitin plate, *a*, is separated from the next by an air-film (*af*, fig. 2), which acts of course as an additional thin plate. In unstained sections, especially if they are thick, it is very difficult to make out this space. If, however, the section stained be thin enough, the division is clearly seen. Further, if the section is distorted by cutting, the plates may be bent to right or left, leaving a considerable gap, and occasionally the pressure of the knife causes the scale to be bent about its axis, so that the chitin plates open out like the sticks of a fan.

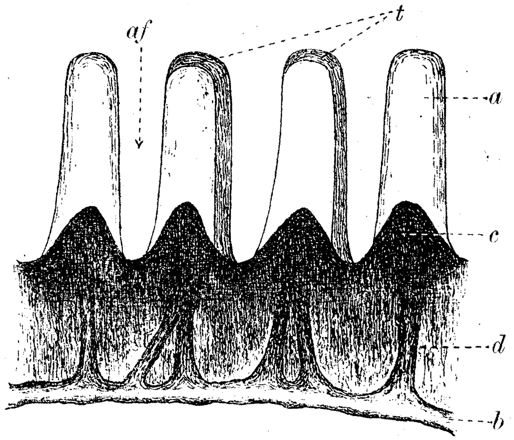

FIG. 2.—Diagram showing perpendicular chitin plates of an iridescent scale, much enlarged. *af*, air-films, other letters same as in fig. 1*b*, Plate 1.

Prolonged staining, especially when hot, often causes swelling and loosening of the structure. Even in the same insect, the thickness of the plates, relative to the space between them, varies considerably. This is partly accounted for by variations in the thickness of the sections. As a rule, sections are about 2 μ thick, and in these the chitin plates must appear in perspective, because the sides of the plates are not always parallel to the optical axis. If the side of the plate is seen either to the right or the left of the end, as the shaded portions, *t* in fig. 2, the plates appear broader and the air-spaces thinner than would otherwise have been the case.

The mean distance between the centres of the plates of *M. menelaus* is found to be from 0·75 μ to 0·8 μ. As a rule, the air film between two plates is slightly less than their own thickness. These spaces are apparently thicker than 0·25 μ, being probably about 0·4 μ, or twice the half wave-length of one of the shorter violet rays. The chitin plates must, therefore, be a little over 0·34 μ, which is equal to two half wave-lengths of the mean ray in chitin. Small variations in thickness only affect the colour of the light reflected. If 0·25 μ causes interference in the middle of the spectrum, a slightly greater or less thickness would cause interference towards the red or the violet end respectively.

Like all other iridescent scales, those that have the above structure lose their colour on pressure. Since the pressure is, in this case, applied to the ends of the chitin

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* SPULER, A., *loc. cit.* (see p. 7).

plates, loss of colour must be due to a complete disintegration of the structure, rather than to any alteration of the spacing between the plates, as may probably be the case with insects like *P. ulysses.*

The scales of the surface layer (Plate 1, fig. 1*a*) are very thin and transparent, and cannot be seen clearly unless stained. They are very like the peculiar scales of *Morpho achilles*, LINN., which are blue both by reflected and transmitted light. They are composed of a very thin membrane, *b*, which at first appears to be single, but there is often evidence of a double layer, which no doubt exists. The striæ are composed of thin plates of chitin, *a*, at right angles to these membranes, but situated so far from each other that the intervening air space cannot be the cause of any colour. No doubt all these membranes, which are about two half wave-lengths in thickness, could cause a certain amount of colour by interference, but if the colour is produced in this way, there is no explanation why the scales should, like those of *Morpho achilles*, appear blue, both by transmitted and by reflected light. All these vertical plates of chitin in both types of scale would form "gratings," thus giving faint spectra at oblique angles.

Morpho cypris, WESTW., ♂ (South America).—The scales of this insect are exactly similar to those shown in Plate 1, fig. 1*b*, and the upper transparent scales of *M. menelaus* are absent. The white spots of *M. cypris*, which are slightly iridescent, are due to the same shaped scales as occur in the rest of the wing, but they are totally devoid of any brown or black pigment. The absence of this absorbing screen causes the spots to appear white and the iridescence to be greatly reduced.

Morpho sulkowskyi, KOLL., ♂.—All the scales of this insect resemble those in the white spots of the preceding one, because they are devoid of pigment and appear as in Plate 1, fig. 2. It is perhaps the lack of absorbing pigment which gives to this insect its peculiar scintillating appearance. The iridescent scales of *Hypolimnas bolina*, LINN., ♂, from Ceylon, appear to be very similar to those of the last insect.

2. *Chlorippe laurentia*, GODART, ♂ (South America).

The peculiarity of this insect is that the portion of the wing surrounding the iridescent green patches is brown at normal incidence, but turns blue and then green as the angle increases (see p. 17). It was thought that sections from the two portions of the wing might yield instructive information. A section from the central green part (Plate 1, fig. 3*a*) shows a periodic structure of the typical sort, except that the chitin plates, *a*, are very thin and close together, their centres being about $0{\cdot}6\,\mu$ apart. If the air film is a half wave-length thick, two half wave-lengths remain for each of the plates, provided they are not double.

A section from the peripheral blue area (Plate 1, fig. 3*b*) shows a very striking contrast. The chitin pillars, *a*, instead of being over $2\,\mu$ in height, are less than $1\,\mu$, becoming, in fact, merely bosses of chitin at the extreme edge of the blue border. The change of colour is no doubt correlated with this variation in height, for it is clear that the number of plates traversed by a ray of light at any angle depends upon the height of the plates, as well as upon the inclination of the ray; and the greater the number of interfering surfaces, the greater will be the saturation of the resulting colour. This is indeed the case, for at normal incidence the central portion is bronze green, the periphery brown, whereas, when the incidence increases, more and more plates are cut by the oblique rays, and the central portion changing to a vivid green, seems to spread outwards, because the periphery containing the shorter pillars becomes an iridescent blue.

3. *Hebomoia glaucippe*, LINN.

The orange bands on the fore wings of this Indian Pierid do not at first sight appear iridescent, but in a suitable light a faint violet flush is revealed. A section of one of these scales is shown in Plate 3, fig. 6. The yellow colour is due to granular masses of deep orange pigment, *p*, which entirely fill the interior of the scale. The faint flush is no doubt due to the chitinous plates, *a*, which are seen to be unusually far apart (0·8 μ), and the air-spaces, *s*, are probably too wide to be the cause of much colour. The small amount of colour due to the plates themselves is very suggestive of the important part played by the air-films of brilliant insects like *C. laurentia* (Plate 1, figs. 3*a* and 3*b*). A number of other tropical Pierids have a similar flush, sometimes extending over most of the wing surface, as in *Colias edusina*, FELDER, *Catopsilia argante*, F., and *Catopsilia hersilia*, CRAMER, except on the margins of the wings, where the scales have a different structure.

4. *Teracolus phlegyas*, BUTL., ♂ (Africa).

The purple shimmer over the bright red scales of some Pierids is well known. It is a combination typical of a large number of insects, all of which probably owe their iridescence to a similar cause. A section of a scale from the magenta stripe on the fore wing of *T. phlegyas* is seen in Plate 3, fig. 5, where the granular pigment, *p*, fills the body of the scale. The plates are about 0·75 μ apart, which allows three half wave-lengths for each chitin film, if one half wave-length is occupied by the air-space.

5. *Callitæra esmeralda*, DBLE. (South America).

The magenta red spots on the otherwise clear scaleless hind wings of this insect are another very striking example of a similar nature to the above. The pigment, as can be seen from Plate 3, fig. 4, contributes little to the colour, as it is a dull reddish brown, whereas the iridescent colours are vivid magenta. When the scales are observed in a medium of low refractive index (fig. 4*a*), the rather peculiar appearance of the chitin plates, *a*, is enhanced. The tops of the plates appear square, instead of having rounded corners, as is usual, and in the centre of each plate is an obvious line or cleft, *c*. It seems as if the plates were divided into two, and sometimes the division is marked at the base by a trace of pigment, but it is difficult to say whether there is an air-film present or not. If there is, it must be exceedingly thin, because the chitin films must be almost in optical contact. The structure of these plates is only what might be expected on morphological grounds, for it is clear that these plates are prolongations of the normal striæ, which in section are, as a rule, more or less acute-angled triangles (*cf.* Plate 3, fig. 3*b*). The sides of these triangles have here reached the limiting position in which they have become parallel, the narrow cleft between them representing the angular space which they formerly enclosed. Plate 3, fig. 4*b* shows another section of the same scale made close to the root, from which it is seen that the chitinous pillars, though somewhat irregular, extend the entire length of the scale. Near the root there is a lumen, *m*, where the pigment is very scarce, and the basal membrane is tightly attached to the rest of the scale. Fig. 4*c* shows a section of the scale through the root, just above its point of insertion in the wing. Here there are no chitin plates whatever, but only a thin membrane, *n*, on the surface, and a core or medulla, *o*. The centres of the chitin plates are $0{\cdot}82\,\mu$ apart, which allows three half wave-lengths for the chitin, if the air-film is one half wave-length thick.

6. *Ornithoptera urvilliana*, GUÉR., ♂ (Australia).

This insect, which is a pale powder blue, is the first of a group of three *Ornithoptera* of different colours. It was thought that a study of their scales might prove instructive. Plate 1, fig. 4, shows a section of *O. urvilliana*, of which the chitinous plates are very thick. The mean distance between their centres is nearly $1{\cdot}0\,\mu$, which accounts for the paleness of the colour. The depth of the scales varies very greatly, being sometimes double that shown in the figure. They are devoid of pigment, the colour being entirely structural, but, on the underside of the insect, which is a very pale green, the scales show traces of yellow pigment.

Heliconius doris, LINN., ♂ (S. America).—The pale blue digitation on the hind wings of this insect is of a very similar colour to that of the last, and sections show that the structure is identical, all pigment being absent. The red-rayed variety of this insect is entirely due to a red granular pigment. The colour of the green-rayed form, var. *viridis*, STAUDINGER, of which no material could be obtained, is doubtless due to a combination of a yellow pigment and a blue structural colour, as in the next example.

7. *Ornithoptera poseidon*, DBLE., ♂ (Australia).

A section of one of the scales of this green insect is shown in Plate 3, fig. 2*a*. It is seen to be coloured throughout with a diffused yellow pigment, even including the chitin plates themselves, almost as if they had been stained with picric acid, and it is evident that the plates *a*, which are very thin and close together, give a blue colour as in *O. urvilliana*. This combined with the yellow pigment, produces the emerald green colour seen. The centres of the chitin plates are as close together as in any insect examined, and a number of measurements give an average value of about 0·6μ. This allows of one half wave-length for the air-film, and two half wave-lengths for each chitin plate.

On the underside of the hind wings, near the anal angle, there are two yellow spots, showing no iridescence, from which sections were made. One of these is represented in Plate 3, fig. 2*b*, showing, as was expected, that the scales have no plates of chitin, but that the same yellow pigment is present. This is in itself strong evidence that the blue colour in *O. urvilliana* is caused by the structure to which it has been attributed. The striæ of the scales in these yellow spots are represented by a coarse comb-like structure *a*. The scales are often hollow, and the usual chitinous bands joining the upper to the lower membrane are represented by a delicate network *d*.

8. *Ornithoptera crœsus*, WALL, ♂ (Australia).

It was expected that sections of this insect, which is in colour a red gold, would be much like those of the yellow spots just described, but as was previously mentioned, the insect shows several anomalies (p. 17). In the first place, unlike the yellow spots, the wings are slightly iridescent, that is to say, they are reddish gold at normal incidence, but greenish yellow at grazing incidence. Now this is exactly the opposite of what would be expected of insects possessing a structure at right angles to their scale surface. The cause was not at once apparent, even when sections of the scales had been cut. At first they were thought to be exactly the same as those of *O. poseidon*, but this was only the case upon the underside where the scales are a pale green even at normal incidence. There are, however, several matt yellow patches on the hind wings, which remain the same colour at all angles. The striæ of these scales are tooth-shaped (see Plate 3, fig. 3*b*), though not quite so coarse and comb-like as those on the corresponding patches of *O. poseidon*. No colour, except that due to pigment, can be produced by structures of this description, but careful examination reveals the fact that the transition to other portions of the wing is not so abrupt as was thought. Indeed, scales may be found in which the triangular striæ are so acute and compressed that they become approximately parallel-sided plates. Moreover, with the best apochromatic objectives, and in thin sections, it can be seen that in most scales the pillars appear to have pointed or acute-angled tops, as shown in Plate 3, fig. 3*a*, instead of square or round ones. Owing to the thickness of the sections and other difficulties, the above figure rather exaggerates this appearance. In addition, the plates are not quite as tall as in *O. poseidon*, and they are placed rather further apart.

The explanation of the colour changes is probably as follows. If the upper portion of each plate is an acute-angled triangle, part of it will be unable to act as a thin film, since it will be too thin; and moreover, since the ends of the plates are pointed and not flat, no rays will be reflected from them, so as to interfere with those coming from a lower plane (see explanation of "laminary" gratings in the Appendix, p. 66). The lower portion of the plates, where the sides are parallel, may however give rise to interference. The result of this is the same as if the plates were very short, as in the periphery of the green spots of *C. laurentia* (p. 37 and fig. 3*b*, Plate 1). Now, as will be remembered, these plates are so short that rays normal to the surface cut too few to give any colour. Similarly, in *O. crœsus*, at normal incidence, the bases of only a few plates are cut, and therefore the colour remains a bright orange, due only to the pigment. At moderate angles a greater number of the plates are cut, and consequently a desaturated purple or blue is produced, which combines with the complementary orange rays to give white. Thus the orange colour becomes less red and more yellow. As the angle increases still further, the blue becomes more saturated, as well as less violet, and combines with the yellow rays to form green. In this way the colour appears to be moving from the orange towards the blue. In reality an orange colour due to pigment is being changed into green by an increasing admixture of blue, the latter being caused by a structure of such a kind that it can produce no colour at normal incidence.

(c) *Scales in which any Periodic Structure must be parallel to the Surface.*

9. *Papilio ulysses*, LINN., ♂ (East Indies).

A number of iridescent insects which do not show a periodic structure at right angles to the surface, have scales somewhat similar in appearance to those of *P. ulysses*, that is to say, they show, on their surface a layer of transparent chitin, *c*, of varying thickness and form (Plate 1, fig. 5). The striæ are some distance apart and they are crossed at right angles by similar equidistant ridges, dividing the surface into over 100 concave rectangular fields. Sections show that these striæ are formed by the scale itself being raised up into waves, as at *a*, Plate 1, fig. 5. Longitudinal sections are indistinguishable from transverse sections, so that the striæ in this direction are evidently formed in exactly the same way. The lower part of the scale, *b*, is heavily pigmented, and though it appears single, it is in reality double. This will be seen clearly from the longitudinal section of the scale root shown in Plate 1, fig. 6. In this, *r* is the root, and *ww* the wing membranes. The surface membrane of the scale which begins from the top of the root is shown at b_1. The lower membrane is shown at b_2, and they fuse at *t*, becoming indistinguishable. Even with carefully stained sections, prolonged scrutiny with a 2 mm. Zeiss apochromatic objective N.A. 1·4, and oblique illumination, failed to show any signs of stratification* in the

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* LANGERON, M. ('Précis de Microscopie,' Masson, Paris), gives the usual limit of resolution as less than 0·24μ, and with oblique illumination 0·12μ. With the above objective and no colour screen the

transparent layer of chitin, *c*, in fig. 5. If present, therefore, it must be just below the resolving power of the objective. The thickness of this transparent layer is not very great, varying from about $0 \cdot 75\mu$ to $1 \cdot 0\mu$, which would be equivalent to five half wave-lengths. Attempts were made to cut oblique sections in order to reveal this structure, if it existed. Sections $1 \cdot 0\mu$ in thickness, but cut at an angle of 70° should cause a structure just below the resolving power of objectives to become visible, but the technical difficulties of staining such sections, and getting them to remain "edge-on" is very great. However, even when lying on their sides, the obliquely cut edge of the transparent chitin projects some distance beyond the pigmented portion of the scale, as shown in Plate 1, fig. 11, where *a* is the apex of the striæ, and *r* the reticulation of the scale seen in plan. By slightly raising and lowering the objective, several edges of chitin can be made out at *mm*, generally three, sometimes four. The appearance is such that it is very difficult indeed to believe that these do not represent discrete layers of chitin, especially as this is not the only evidence; various additional reasons, including the behaviour of the scales in viscous fluids, have already been discussed at some length in a previous section (see p. 20).

Papilio arjuna, HORSF., ♀, and *P. crino*, FABR., ♀, as is the case with many other Papilionidæ, have iridescent scales, similar in structure to those of *P. ulysses*. In the two first mentioned the scales are green, which may be because the surface layer of chitin contains a small amount of diffused yellow pigment, like *O. poseidon*.

10. *Jamides bochus*, CRAMER, ♂ (Oriental).

Sections of the scales of this insect are shown in Plate 1, fig. 7. The chitin layer, *a*, is slightly undulating, and the structure is not unlike the lower layer of scales in *M. achilles* (Plate 1, fig. 12*c*). The scales of several tropical American *Thecla* which were examined showed an absolutely similar structure, except that in some cases the chitin layer appeared considerably thinner.

11. *Amblypodia eumolphus*, CRAMER, ♂ (India).

Sections of the green scales of this insect are shown in Plate 1, fig. 8. The scale is composed of several layers, the first of which, *a*, is transparent, the rest more or less pigmented. The central portion, *c*, is heavily pigmented, the lowest membrane, *b*, is much paler, and there are indications of another layer, *d*, which is slightly pigmented. It is uncertain whether the lower layers of chitin, *b* and *c*, contribute to the production of colour or not. At considerable distances from one another, there are small bosses, *s*, which are obviously undeveloped striæ.

100,000 line band of Grayson's test-plate is easily resolved ($0 \cdot 25\mu$). With a suitable screen, etc., the 120,000 line band was resolved ($0 \cdot 21\mu$)., though MALLOCK (*loc. cit.*, p. 4) and many text-books give $0 \cdot 25\mu$ as beyond the resolving power of the microscope.

12. *Urania fulgens*, Walk. (Madagascar).

The iridescent colours of these well known diurnal moths vary from the deepest emerald green to a pale blue. The deep green scales have a pigmented basal membrane, *b* (Plate 1, fig. 9), which serves as an absorbing screen. The paler the reflected colour the less pigment in this membrane, the palest blue scales being without pigment. On staining, however, this membrane takes more stain than the upper membrane, as may be seen from the section which has been treated with iron hæmatoxylin. The striæ, *s*, are exceedingly thin, and placed at a considerable distance from each other, so that the air-spaces between them can hardly function as thin films.

Besides the black pigment in many of the scales, there is in this insect an additional screen of plain black scales, one of which is shown in Plate 1, fig. 10. The striæ, *s*, are heavily pigmented, and the basal membrane, *b*, is entirely without pigment, so that it produces the colours of thin films, as has already been described (see p. 21).

13. *Morpho achilles*, Linn., ♂ (South America).

The surface scales of this insect are very similar to those of *M. menelaus*, and, being heavily striated as well as transparent, they give rise to diffraction colours. They differ slightly, however, in that the striæ, *a*, are double (see Plate 1, fig. 12*a*). The chitin is transparent, so that the section is only clearly seen when stained. Fig. 12*b* shows a plan of a section of a similar scale in which the double nature of the striæ is seen very clearly. The lower layer of scales (fig. 12*c*) gives the most colour, since they are heavily pigmented. A somewhat thick layer of undulating chitin lies over the pigmented striæ. A portion of it has become stripped off, and is shown at *c*. If a periodic structure produces the colour in this case, it must be situated somewhere in this layer.

14. *Hypolimnas salmacis*, Drury, ♂ (Africa).

The lower scales of this insect are not iridescent, but only act as a screen for the upper layer. In plan the latter appear to be covered with protuberances or rows of beads, which in cross-section appear as in Plate 1, fig. 13. The basal membrane, *b*, appears double when stained, and the round knob-like striæ, *a*, are sometimes more acute than is shown. There is some evidence to suggest that the chitin has been deposited in layers, because the structure of the striæ, *a*, somewhat resembles a tunicate bulb like the onion. The iridescent scales of *Precis œnone*, Linn., though probably somewhat thinner, appear very similar in section to the above.

15. *Zesius chrysomallus*, Hübn., ♀ (Ceylon).

The brilliant colours of this insect seem merely to be due to the form of scale shown in Plate 1, fig. 14. There is apparently no structure displayed by this insect capable of producing colour. The striæ are well defined, but are obviously an insufficient cause. These scales serve as another instance of the almost infinite variety in the colour and structure that is so constantly met with.

The iridescent hues of *Jalmenus evagoras*, DONOVAN (Brisbane), are due to an almost identical type of scale, and in neither case is there any sign of a periodic structure that could adequately account for the colours.

(d) *Scales which show no Colour-producing Structure.*

The following examples have been treated together, on account of the very puzzling forms assumed by their scales. In some cases it is quite impossible to determine where the colour-producing layer may be. As a rule, though the scales themselves are exceedingly brilliant, the structures they reveal might almost be those of the non-iridescent scales of the same insect.

16. *Salamis parhassus*, DRURY (Africa).

This insect shows a soft, rose-pink iridescence of about the intensity of the first orders of NEWTON'S rings, and it is possible that this colour is caused by the two pairs of interfering surfaces formed by the membranes composing the scales, which, as may be seen from Plate 1, fig. 15, are very thin. It is curious, however, that the colour should be as uniform as it is, because such membranes must vary considerably in thickness. The scales are also devoid of pigment, so that diffraction effects contribute to the colour. The scales are no doubt of the form shown in fig. 15*a*, in which *a* are the striæ and *b* probably the basal membrane, but the upper membrane often gets stripped away, giving the scales the appearance shown in fig. 15*b*. When the sections are made through the points of the scale, the striæ invariably give it a star-shaped appearance (fig. 15*c*).

17. *Papilio parinda*, MOORE, ♂ (Ceylon).

At first sight the faint silvery patches of this insect scarcely seem iridescent, but a careful scrutiny shows that they are faintly blue like the surface scales of *M. achilles*, except that no colour is visible by transmitted light, owing, no doubt, to the large amount of air contained in the scales. A section is shown (Plate 1, fig. 16), but it is even more difficult than in the last case to discover any possible cause of colour, for none of the membranes appear thin enough for the purpose. Possibly an ultra-microscopic periodic structure may exist, giving a colour which is very faint, owing to the irregularity of the different thicknesses of the strata. LORD RAYLEIGH has suggested that the appearance of certain crystals, which show a silvery lustre, is due to a phenomenon similar to the periodic "twinning" of crystals of chlorate of potash, but of a more irregular nature.

18. *Lycæna icarus*, POD., ♂ (Europe).

The Common Blue is the most abundant iridescent British butterfly or moth.

Its scales, a section of one of which is shown in Plate 1, fig. 17, reveal when stained a line of juncture in the centre, and no doubt the lower membrane is double. The striæ are of triangular form, appearing to be quite solid instead of hollow, as is usually the case. They give no clue as to the origin of their brilliant colours, which may, however, arise from a structure somewhat similar to that present in *P. ulysses* (Plate 1, fig. 5).

19. *Thecla rubi*, LINN. (Europe).

The green of the underside of this British butterfly is iridescent, though it might be mistaken for pigment. Examined by transmitted light, the scales have the appearance shown in Plate 1, fig. 23. The whole surface is covered by a reticulation which divides it into small irregular polygonal areas, some of which, *b*, are darker than others. If now the transmitted light be partly cut off, and the scale examined by reflected light, it will appear as if covered with green spangles which correspond to these areas. Moreover, it will be seen that the darkest areas, by transmitted light, correspond to those that are the brightest green by reflected light. The cause of this reticulation and the colour of the scales has given rise to a lengthy discussion,* but the explanation is very simple, as may be seen by examining the cross-section given in Plate 1, fig. 18. The fine striation is formed by little round bosses, *a*, under which runs a faint indication of a cuticle, but as the whole scale is pigmented, this is very difficult to distinguish. The reticulation is due to the fact that the scale is looped up, as at *b*, so as to become very thin, and consequently a white line appears by transmitted light. In between two such thin places the scale is much thicker. This causes the density of certain polygonal areas, as well as their bright colour by reflected light, because an increase in the pigment of the absorbing layer prevents the dilution of the green colour by reflected white light. A section through two points of a scale is shown at *c*; they are oval-shaped and only striated on the upper surface.

The formation of these iridescent scales was also studied during various stages of pupal development. For this purpose the wings were dissected out of pupæ some time before emergence, fixed in CARNOY'S fluid, cut in the usual way, and stained with picro-indigo-carmine, or MANN'S stain. At first the scales develop no pigment, and it is not very easy to differentiate the green scales from the others. As soon as any pigment appears it is quite easy to identify the iridescent scales, because of their light brown colour. However, no material difference could be seen between the immature scales and those of the fully developed insect. It appears, however, that the variations in thickness of the scale, which produce the spangled appearance and the reticulation, do not develop till the very last stages before emergence, and possibly not until the wings are expanding to dry. A comparison

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* 'Ent. Record,' vol. 6, p. 35 (1895).

was moreover made between the mother cells, which respectively produce the ordinary and the iridescent scales, but no obvious differences could be discerned, though it must be admitted that the examination was not exhaustively carried out from the earliest stages.

20. *Thecla telemus*, CRAMER, ♀ (South America).

This tropical *Thecla* is green and red on the under side, and peacock blue on the upper side. Plate 1, fig. 19, is a section through a blue scale. The structure is clearly not unlike that of *T. rubi.* The cuticle, *a*, is thicker and sharply defined, and the striæ, which are of quite a different shape, are divided from one another by the pale vertical band, *c*; there is also a basal membrane, *b*.

21. *Dynamine mylitta*, CRAMER, ♂ (South America).

The iridescent green scales of this insect have a metallic sheen, like steel. In many insects this seems to be associated with a pigmented structure similar to that shown in Plate 1, fig. 20. The striæ, *a*, contain a small amount of pigment, and are placed at some distance apart. The lower membrane, which becomes much distorted by cutting, shows evidences of being broken up into several layers, *b*, but it is difficult to make out any regular periodicity even in thin sections. These irregular layers may be the cause of colour, though they are certainly heavily pigmented. There is no trace of a cuticle to be seen in the striæ, and it is only occasionally that signs of frilling are shown in the basal membrane as clearly as in this section.

22. *Batesia prola*, DBLE. (South America).

The appearance of this insect is duller than that of the preceding one. The colour is steel-blue. The central area of the wing is bright, but it fades gradually towards the edge, where the iridescence gives way to ordinary black scales. Sections were made along a strip, which showed these various changes of colour. Plate 2, fig. 1*a*, is a section taken from the brightest portion. There is very little pigment, the striæ, *a*, are tall, and are placed widely apart. There are no signs of a cuticle, or other colour-giving structure. Plate 2, fig. 1*b*, shows a section made through a rather duller area. It can be clearly seen that the amount of pigment has become increased, and a connective membrane, *m*, has arisen between the striæ. There are also traces of a band of chitin joining the upper to the lower portion. Plate 2, fig. 1*c*, is made through a part of the wing in which there was little or no iridescence. The striæ, *a*, which are more triangular in shape, are very heavily pigmented, as is the membrane between them. Even the basal membrane has developed a good deal of pigment, and though there is nothing to show what produces the colour, there seems to be no doubt that progressive pigmentation can gradually reduce the iridescence until it vanishes.

23. *Euplœa deione*, WESTW. (India).

This butterfly is representative of the very large class of bottle-green, purple and blue iridescent insects, the colour of which is usually not very bright but velvety, and sometimes scarcely perceptible. In this type of iridescence can be included the British day-flying moths, *Callimorpha dominula*, LINN., and some burnets, also the butterflies like *Apatura iris*, LINN., etc. *E. deione* resembles this last insect in that specimens from many localities are a velvety blue, which is only visible when looking from the base of the wing to the apex. A section of one of these scales is shown in Plate 1, fig. 21. It is heavily pigmented with dense black pigment throughout. Generally, no cuticle is to be seen in the striæ, *c*, even when the scales have been bleached with chlorine. The lower membrane, *b*, is, as usual, attached to the upper by means of bands of chitin, *d*. No cuticle or other structure could be detected, even on restaining bleached sections. In fact, with insects like *C. dominula*, in which the scales on the lower surface are similar to those on the upper (except for the absence of any coloured sheen), there is no means of telling the two layers apart when seen in section, unless one of them has been previously very carefully marked.

24. *Dione juno*, CRAMER (Central and South America).

This insect is representative of another large group which have golden or silver patches and spots, such as occur in many of the British species of *Plusia*. In the case of this insect there is a pattern on the underside of the wings which is like gold foil. It has been suggested by BIEDERMANN that a large air content, combined with a suitable folding of the scale, is sufficient to cause an effect like silver, but, as was pointed out on p. 8, this would only give a brilliant white appearance, like the hairs of white animals, not a metallic glitter, unless the air-spaces were not more than the diameter of several air molecules in thickness.

The air-spaces, *h*, are seen in Plate 1, fig. 22, a section of one of the metallic scales of *D. juno*. There is practically no yellow pigment present, and unfortunately there is no suggestion as to what causes the colour. Indeed, in shape and structure there is nothing to differentiate the golden scales from the slightly pigmented brown scales on either side. Moreover, this type of scale is similar to that seen in most dull-coloured insects, and is therefore hollow and without space to contain a periodic structure, which, if very irregular, might cause total reflection to take place, as in the silvery crystals mentioned by LORD RAYLEIGH (p. 44).

(e) *Iridescent Scaleless Beetles, etc.*

The cause of the colour of most scaleless iridescent beetles, which appears to be selective metallic reflection, was fully discussed on p. 26 *et seq.*

25. *Cetonia aurata*, LINN. (Europe).

The common green Rose Beetle has been considered by BIEDERMANN in some detail, both in the pupal as well as in the adult stage. He separated the "*Emailschicht*" from the other chitinous structures by maceration in dilute caustic soda, or 5 per cent. nitric acid. It is a very thin shell of chitin, almost free from pigment and iridescent on both sides, although the transmission colour was very feeble. A section through this "*Emailschicht*" is shown in Plate 2, fig. 2, but nothing can be seen of the "*Stäbchenschicht*" described by BIEDERMANN (p. 24). The surface cuticle, which is about 0·5 μ thick, lies on a homogenous layer of chitin, containing diffused yellow pigment. The chitin must be very brittle, as the vertical fractures seen at intervals throughout the sections are caused by cutting. Like other iridescent beetles, there is nothing in these sections to differentiate them from any ordinary non-iridescent species (*cf.* Plate 2, fig. 13*a*). If the thorax of *C. aurata* or of *Ceroglossus gloriosus*, GERST., is macerated in hydrochloric acid, glycerol, and alcohol at 38° C., it turns a deep red. Sections are in all essentials like Plate 2, fig. 2, except that the thickness of the "*Emailschicht*" varies.

As a rule, red seems to be a very rare colour among metallic beetles; but, curiously enough, bright red specimens of both golden and green insects have occasionally been found. These were often given new specific names before their true nature was realised.

26. *Sternocera diardi*, GORY (India).

This deep green Buprestid, closely resembling *S. sternicornis*, is representative of a very large class of insects. They are usually a dark green, and so heavily pigmented that in unbleached sections no structure can be made out, not even the surface cuticle. Plate 2, fig. 3, shows a section of a wing-case which has been bleached with chlorine. The surface cuticle, which now appears, seems to be rather thick, notwithstanding the fact that the colour disappears fairly soon, if the beetle is polished with carborundum. Sections of other Buprestids show a very similar structure when treated in the same way, except that the surface cuticle sometimes tears away, though remaining a single layer. If it were not for the fact that the colour disappears with very varying rapidity on polishing such wing-cases as these, it would seem as if the layer which produces the metallic colour must lie on the surface, for, as in the dragon-fly, *Neurobasis chinensis*, LINN. (p. 53), the chitin is so heavily pigmented that if the colour-producing layer were more deeply seated, nothing would be seen, because of the intervening black pigment.

27. *Lytta vesicatoria*, LINN. (Europe).

This green beetle of the family Meloidæ has wing-cases which are very thin, and which, therefore, give little difficulty in cutting. The colour was supposed by BIEDERMANN to be due to a thin film of air. This possibility was discussed on p. 26, and no traces of such an air-space are visible in sections like fig. 8, Plate 2. It is true that the surface cuticle, *c*, has become detached, but this only happens occasionally, for as a rule it lies closely adhering to the lower layer of chitin. When the cuticle is detached, a portion of it is often seen still adhering to the lower layer, as at *c'*.

Epicauta tenuicollis, PALL., from India, is a very similar insect of the same family, and it is too heavily pigmented to show any structure when not bleached, but after treatment, sections closely resemble those of *L. vesicatoria*. *E. tenuicollis* shows no loss of colour when immersed in alcohol, on account of its more opaque backing of black chitin.

28. *Ceroglossus gloriosus*, GERST. (Chile).

This Carabid has deeply ribbed red elytra with a greenish blue iridescence and a deep green thorax. Sections of the macerated thorax are essentially like those of the elytra of *C. aurata* (Plate 2, fig. 2). Here the red colour is due to a pigment which dissolves in caustic soda giving a brown solution. A section of an elytron so treated is shown (Plate 2, fig. 4). It has the usual surface cuticle, *c*, and the underlying chitin has a coarse, foliate structure, *s*, the layers of which are obviously too thick and too far apart to cause any colour.

29. *Anoplognathus aureus*, WATERHOUSE (Australia).

The colour of this beetle, a burnished gold, was ascribed by BIEDERMANN to three layers of air between chitinous films, which he was able to separate from each other with a sharp scalpel. He describes how the colour disappears on maceration, except in patches, and how these patches are found to be the seat of air-bubbles when viewed by transmitted light. It is true that the colour rapidly disappears, on maceration, but no air-bubbles could be seen in the parts that remained metallic. Moreover, the colour cannot be due to air, or it would disappear when pieces were placed in a refractive fluid *in vacuo*. Plate 2, fig. 7, shows a section through the wing-case, the surface cuticle of which, *c*, appears extraordinarily bright, and is considerably thicker than usual. The three layers described by BIEDERMANN are seen at *e*, *f*, and *g*, but no regular air-spaces can be made out between them. It is interesting to notice that sections made through the wing-cases after prolonged maceration, which deprives them of all colour, show no discernible difference from untreated sections. The thickness of the cuticle appears to be immaterial, as well as the existence of the underlying layers of chitin, for the abdomen, which is as metallic as the wing-cases, gives sections as in Plate 2, fig. 5. In all sections of the wing-cases of scaleless beetles, diffraction fringes are apt to appear, but this is especially the case in *A. aureus* and other golden beetles with translucent chitin. One of these diffraction fringes, which looks like a most definite stratification, is shown at *df*, in fig. 5, and it is sometimes very difficult to believe that these have no significance.

30. *Plusiotis resplendens*, BOUCARD.

This golden beetle closely resembles the last, and has only been figured and described because it was extensively used for the polishing experiments, which have already been detailed (p. 31). The section shown in fig. 6, Plate 2, is a composite one, being made up of three portions. The first (I) shows the unpolished cuticle, *c*; the second (II) shows the metallic magenta film with *l*, one of the small black objects often seen on this film, which may be fragments of carborundum. The dark line marking this film seems to lie between the surface cuticle and the adjacent layer of chitin; it also seems to mark the lowest limit of the colour-producing layer. The last section (III) shows the underlying deep brown chitin. These three sections correspond to the three areas similarly numbered in the coloured figure 8, Plate 3.

31. *Scutellera nobilis*, FABR. (India), Hemiptera.

A number of tropical Scutelleridæ show the brightest and most varied colours, portions of a small area of the scutellum being red, green, and purple at the same angle. The colours are also very changeable, and can be made to vary in specimens preserved in alcohol by the mere traces of grease that come from the fingers in handling. A section of the scutellum of the above insect is shown in Plate 2, fig. 10. There is a surface cuticle, *c*, on a deep layer of chitin, which if partially depigmented by sodium hypochlorite, shows a roughly striated structure. It is impossible that this structure can take any part in the production of colour, as is the case with the two following examples, because *S. nobilis* and similar bugs are peculiar for the rapidity with which all colour disappears at the first attempt to polish them. The cuticle is liable to frill with great ease, as is shown in the figure. In fact, it seemed so possible that, in spite of its thinness, this film might be divided into layers of air and chitin, that renewed attempts were made to alter the colour by pressure and by placing *in vacuo*, but without success. Thus it appears that chitin may frill in this way, though the layers were previously in optical contact. If the colour is due to selective metallic reflection, it is destroyed so easily by polishing that it seems possible the colour-producing layer is on the surface instead of under a protecting cuticle.

Among similar bugs examined was *Chrysocoris stockerus*, LINN. (India), the structure of which was exactly the same.

32. *Heterorrhina africana*,* DRURY (West Africa).

This beetle is characteristic of certain Cetoniidæ, which have a deep-seated colour like enamel, and a peculiar luminous shadow on the thorax and wing-cases, which shifts its position according to the angle at which the specimen is held. This appearance is quite indescribable, though it can be recognised instantly on

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* See the last note on p. 24. This is undoubtedly synonymous with the insect BIEDERMANN called *Smaragdisthes africana*.

seeing a specimen. The colour is usually green, often with a considerable addition of red. The intensity of this colour rapidly changes with obliquity, until at grazing incidence the insect may be scarlet. This change towards the red is the reverse of that in other scaleless beetles, the colour of which moves towards the violet, as would be expected. As was mentioned on p. 24, these insects also differ from all the others described, in that the colour does not disappear on removing the surface strata, and, moreover, sections (Plate 2, fig. 11*b*) made in the plane $a-b$ of fig. 11*a* throughout the entire thickness of the rod-like layer show the same colour as the intact wing-cases, even when they are mounted in Canada balsam. These sections are blue and green by reflected light, yellow by transmitted light. The striations or rods, *s*, are columnar in transverse sections (fig. 11*a*). In tangential sections, which appear yellow both by transmitted and reflected light, these rods appear like small pores (fig. 11*b*). The striations, which are evenly spaced, seem to be separated from each other by material of a different nature. They are about $0{\cdot}75\,\mu$ apart, their diameter being rather less, and, when examined under crossed nicols, they appear to be doubly refractive. As was previously said, although these bodies are not small when compared with light waves, but comparable to them, no explanation of this colour can be suggested, except that they may scatter blue light in the same way as the other structures mentioned on p. 22, such as the "*Porencanälen*" of HÄCKER and MEYER, most of which are about the same size. The colour in different specimens of *H. africana* is very variable, and changes from yellowish-green, with red iridescence, through emerald green, to the deepest blue. The change of colour seems to be correlated with the amount of pigment, the pale green varieties with bright red iridescence having least, the dark blue, sometimes almost black, having most. The red colour is probably not caused by the same structure as the green, because, if the surface is carefully polished away, and the wing-case placed in a fluid in such a position that it appears red, the part that has been polished will be a pure green.

33. *Heterorrhina elegans*, FABR.

This is the only other beetle that could be obtained with exactly the same appearance as the last insect. It varies in colour from green to blue, and sometimes there are traces of red. A section of the wing is shown in Plate 2, fig. 12, at a smaller magnification. It resembles *H. africana* in that the surface layer, *c*, can be removed without affecting the green colour, and that all sections in the plane $a-b$ appear coloured by reflected light. The thickness of the "*Emailschicht*" appears considerably greater, and the striations may be slightly closer together than in the last example ($0{\cdot}75\,\mu$). In many sections there appear to be more than one set of striations. Most of the striations, s_1, are perpendicular, but a second series, s_2, are inclined at an appreciable angle, and, from the change of focus necessary to see them clearly, appear to be situated in a lower plane. As in the previous example, the chitin appears to be doubly refractive, a phenomenon which recalls the dichroic colours of certain doubly refractive crystals.

34. *Anomala dussumieri*, BLANCHARD (India).

This Rutelid beetle is interesting, because though it has not the same enamel-like appearance as the two preceding examples, and although it is much duller, it still has the peculiar mobile shadow on the thorax and wing-cases. That this was probably not due to the same cause was apparent, since the colour disappeared as soon as the surface cuticle was removed by polishing. The real cause, however, is at once seen on examining a slightly depigmented section (Plate 2, fig. 9). The whole surface is covered with small hemispherical bosses, *b*, which are sunk almost level with the surface. The surface cuticle, *c*, can be seen following the circumference of these protuberances, and the surface of the wing itself may be seen between the bosses at *e*.

No doubt only a limited number of these bosses can catch and reflect the light in any given position, and this causes the peculiar shadow. Except for this raised structure, which is well seen in a collodion film, there is no difference from beetles of the type of *C. aurata*.

(f) *Iridescent Scale-bearing Beetles.*

The question of the cause of colour in the varied scales of these beetles has been discussed fully on p. 12.

35. *Eupholus magnificus*, KIRSCH.

The scales of this insect are characteristic of the large number of iridescent weevils which do not show any stratification when seen in section. Sections were cut of scales from a number of weevils, including *Entimus imperialis*, FORSTER, as well as two British species, namely *Phyllobius maculicornis*, GERM., and *Ph. glaucus*, SCOP. (= *calcaratus*, FABR.). Most scales have a slight undulation on the upper surface, forming a coarse striation. The section shown in Plate 2, fig. 16, which was mounted in aqueous glycerol is of a typical scale from *E. magnificus*. It is cut parallel to the long axis, so that the coarse striation does not show. There is a cuticle and a number of small granular masses, *g*, probably portions of the spongy cellular tissue, which had not become completely impregnated with the mounting fluid. The small circles, *b*, are air-bubbles.

A transverse section of the dull brown non-iridescent wing-case of a bright green weevil, possibly *Entimus nobilis*, OLIV., is shown in Plate 2, fig. 13*a*. The alternate layers are striated, as appears in fig. 13*b*, where the strata *a* and *b* are seen in plan.

36. *Hypomeces squamosus*, FABR., var. *durulentus*, HERBST. (Siam).

This pale pink variety comes from a species which as a rule exhibits very great variation of colour. It has been selected because it shows the internal striations better than any other insect. Unfortunately, it could not be compared with a type specimen, as no material was available for sections. Plate 2, fig. 15*a*, shows a portion of a scale in plan. There is a cuticle, *c*, and a faint striation on the surface. The whole body of the scale is covered with innumerable criss-cross striations, which give the effect of the strings of a number of superimposed tennis-rackets. In cross-section, figs. 15*b* and *c*, these striations are equally clearly shown in the body of the scale, and the space between the lines is very variable, being from $1{\cdot}0\mu$ to $0{\cdot}3\mu$. The undulation seen in the cuticle produces the coarse striation on the surface. As a rule the scales are slightly convex, and closely resemble the pilgrim's scallop shell.

Plate 2, fig. 15*b* shows a section mounted in glycerol made through the root of one of the same scales. At this point many of the scales are almost mushroom shaped, owing to the fact that the root, *b*, instead of being at the base of the scale, is affixed some way towards the middle. The relation of the striation to the colour has been discussed (p. 12), and reasons have been given for the belief that the colour, though it may be associated with diffraction, is produced partly by interference.

(g) *Other Iridescent Insects, Hairs, Feathers, etc.*

A few other iridescent insects were chosen at random, and sections were made from the wings and other portions of certain Hymenoptera, Hemiptera, Odonata, etc. Most of the sections closely resembled the type of wing-case found in scaleless beetles like *C. aurata*, and a few examples are given.

37. *Chrysis ignita*, LINN. (Europe), Hymenoptera.

Plate 2, fig. 19, shows a section from the rough green thorax of this brilliant little parasitic wasp. There is a heavy layer of pigment, *p*, extending to the surface of the cuticle, *c*, which is not, however, entirely obscured. The underlying chitin is closely striated. This cannot, however, have anything to do with the production of colour.

38. *Neurobasis chinensis*, LINN., Calopterygidæ.

The emerald green wings of this dragon-fly appear as if made of metal foil, and are divided by veins into fairly big rectangular concave fields. This surface structure was found to give no colour when tested on a collodion film. The colour is not altered by any pressure that can be exerted by a convex lens, and sections of the untreated wing showed nothing but a narrow strip of chitin, so heavily pigmented that no structure of any sort was discernible. It is difficult to see in these circumstances how anything short of a layer of metallic substance situated on the surface could cause the colour. For if a layer were situated even at a short depth below the surface it would be entirely obscured by the black pigment, which is so thickly deposited that even the cuticle is quite invisible in thin sections. A portion of this wing which has been depigmented with chlorine, is shown in Plate 2, fig. 20. The surface cuticle, *c*, now becomes quite visible, but there is no other structure except the layer of medullary substance, *m*. Very similar in appearance are the iridescent wings of some of the Carpenter Bees (*Xylocopa*).

39. Pentatomid ? Sp. Hemiptera.

This was an immature stage of a Pentatomid bug, possibly of *Pycanum rubens*, the wings of which are described below. In alcohol all the chitin is a dull bottle-green; when dry, a deep blue, except for a dark red line on the dorsal surface. Sections were made through this line, and Plate 2, fig. 18, shows the point of junction, *p*, between it and the iridescent chitin. The latter has a cuticle, *c*, beneath which the pigment is quite opaque. The red portion is raised into curious cone-shaped papillæ, *b*, which contain much less pigment than is shown in the illustration. The red colour is due to the fact that the underlying tissues, which are pigmented red, show through the transparent chitinous layer.

40. *Pycanum rubens*, FABR. (Malay), Hemiptera.

When alive, the head, pronotum, scutellum, and horny parts of this bug are said to be a vivid apple-green, and in specimens preserved in alcohol this colour persists. On drying, the green completely vanishes, leaving a dull purple-brown. A number of other insects behave like this, as, for example, the Cetoniid, *Stephanocrates thomasi*, KOLBE, upon which a touch of a wet brush will cause a vivid green spot.

On wetting *P. rubens* the colour returns, and is gradually seen to vanish again as it slowly dries. The effect of a number of other organic fluids was tried, such as benzol, ligroin, etc., but they only converted the purple iridescence into a faint blue-violet. The effect of other fluids such as chloroform, ether, etc., was rather obscure until the water-content of these fluids was examined. It was then seen that the development of colour depended upon this factor. If absolute alcohol, prepared by distillation over metallic calcium, is used, no green colour is produced, but on the addition of even minute traces of moisture the apple-green rapidly develops. From these experiments it was concluded that on wetting, either (1) two or more films of chitin, which could not themselves cause interference, became separated by a thin film of water, causing a brilliant colour; or (2) a membrane or membranes, of chitin, too thin, too irregular, or too opaque to cause colour when dry, can absorb water and swell, so as to oppose when wet a homogeneous thin film to the passage of light. If either of these suppositions were true, pressure under a convex lens should cause distortion or compression of the aqueous layer and consequently loss of colour. When this experiment was tried, it was found that quite moderate pressures caused the green colour to disappear and to be replaced by a dull yellow bronze. However, if the wing was kept moist, the colour instantly and completely returned on removing the pressure. The fact that water is specific in its action, and that no other fluid will serve the same purpose, suggests that there is a film which, like gelatin, can only absorb water. Acids also appear to restore the green colour, rendering it fairly permanent, presumably because they are more easily absorbed. If this is the true explanation, it is perhaps curious that there should be no traces of this membrane in cross-sections. Plate 3, fig. 1, is a transverse section through the horny part of the fore wing, not far from its membranous tip, mounted in Canada balsam. Careful comparisons between sections mounted in aqueous media and others mounted in anhydrous media with exactly the same refractive index,* such as absolute glycerol, show no appreciable difference. In the figure this cuticle is shown at *c*, where it has become detached. Under the cuticle lies a clear yellow layer of chitin, *d*, and below this again a broad layer, covered with striæ, *r*. These can have no effect on the colour, because they are situated too deeply. It should be mentioned that special attention was at first paid to these wings, owing to the fact that by transmitted light they showed such a deep red colour complementary to that reflected, and it was not until the sections were examined that it was seen that below the layer of clear chitin, *e*, there was a double layer of crimson pigment, *p*, separated by a pale yellow layer of chitin, *f*. The pigment is granular and presents a very striking appearance, although its significance is not clear. Below the pigment is another layer of transparent chitin, and below this again a yellow layer, *h*, the exterior surface of which is covered by small papillæ, *s*. In the right-hand corner of the section this membrane has been flattened, so that the papillæ are seen in plan.

41. *Thlaspidomorpha balyi*, BOHEMAN (Ceylon). Coleoptera.

This is one of the Cassidinæ, or "Tortoise Beetles," so called because the margin of the wing-cases is explanate and projects somewhat like the shell of that animal. In this insect the wing-cases are a brilliant metallic gold, with several distinct black spots. These beetles are of special interest, because, like *Pycanum rubens*, those that are iridescent while alive rapidly lose their colour and become dull brown on drying. The iridescence, which is generally golden, but sometimes shows traces of red, usually returns on soaking in water. After prolonged drying, however, some species remain dull or only slightly iridescent.†

Though somewhat similar to the Pentatomid described, these beetles show remarkable differences. In the first place, an attempt was made to destroy the colour by pressure. A small thin piece of wing-case was taken from fresh alcohol material, but

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* For the determination of the refractive indices of these media, which enabled the comparison to be exact, I am indebted to Mr. T. SMITH, of the National Physical Laboratory.

† MAULIK, S., 'Fauna of British India, Coleoptera, Hispinæ and Cassidinæ,' July, 1919, p. 70.

so long as it was moist, no pressure that could be exerted had the slightest effect on the colour. It was at first thought that this similarity to beetles that always remain golden might be due to the thickness of the wing-case. A moist wing was, therefore, polished, to see whether the effect would be like that observed in *Plusiotis resplendens* (see p. 31). No matter at what depth the surface was exposed, so long as the wing was kept moist, the colour, strange to say, did not vanish. In fact, a piece of wing-case was polished until its end was ground to the form of a sharp chisel, exposing the entire thickness of the chitin. As soon as this was moistened with any fluid it became intensely metallic and golden. This piece was mounted in glycerol and examined microscopically, when it was seen that not only was the surface golden, but any cracks in other planes were metallic also, as if carved out of solid gold. Clearly it is a property of the whole mass of the chitin that is here being dealt with. The chitin is stained with a diffuse yellow pigment, and its nature is such that if the surface is polished and moist, it reflects an intense metallic surface colour, much in the same way that the dull brown pebbles glisten with brilliant colours when a wave from the rising tide washes the beach. When moist, the surface cuticle acts as a protection, maintaining the iridescence; when dry, it prevents the access of moisture. This is the reason why the wing-cases require to soak an appreciable time before they regain their iridescence. Moreover, fluids like xylol and ether, which do not restore the iridescence, must be unable to penetrate the cuticle, which, like gelatin, requires an aqueous medium. This type of iridescence is of great interest, because it suggests that chitin may, under certain conditions, appear metallic, so that it is easy to see how scaleless beetles may have iridescent films of chitin.

Sections were made through the metallic part of the wing of *Th. balyi*, *Aspidomorpha dorsata*, FABR. (Java), and three or four similar Cassidine beetles. As might be expected, very little difference in the structure is seen between these sections and those of *Cetonia aurata* (Plate 2, fig. 2). In *Th. balyi* the edge of the wing-cases is explanate, colourless, and not iridescent. Two of the black spots are on the projecting edge, and Plate 2, fig. 17, shows a section through the margin of one of the spots. The chitin grows in concentric rings, *h*, and the spot is due to a deposit of black pigment, *pp*, on both sides of the wing-case. There is a cuticle, *c*, which is clearly visible in the pigmented area, but which tends to become invisible in the pigmentless parts. The black spots generally show a trace of iridescence.

42. *Amblyomma hebræum*, KOCH.

This tick, which carries "heart-water," a disease affecting cattle, goats, and sheep in Africa, was kindly given to me by Prof. NUTTALL,[*] who has drawn attention to the change of colour in this parasite, after it has fed for some time upon its host. Moreover, he has shown that in alcohol (70 per cent.) the pale ochre colour of the dried tick disappears, and is replaced by the most brilliant green and coppery red

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[*] NUTTALL, G., 'Parasitology,' vol. 12, p. 1, Plates 1 and 2.

metallic colours. When the ticks are dry, the pale ochre of the scutum is picked out with a black pattern. The effect of aqueous solutions is much the same in this as in the preceding case. If the organic fluids* are quite free from water, the ochreous areas have a beautiful silvery appearance, like freshly cut aluminium, with often the very faintest pink flush.

On the addition of water, the silvery colour is reduced, and a bright metallic green makes its appearance, but the pigmented parts do not become metallic. If, instead of dry specimens, material is taken from aqueous alcohol for these experiments, the colours remain metallic in all fluids, or only become very slowly dehydrated.

On allowing a wet specimen to dry, the impression is very strongly given that in the ochreous portions the fluid is leaving a spongy structure, or one that contains air. A section through the scutum is shown in Plate 3, fig. 7. It is made at a point where the black and pale patterns meet, but the pigment of the former is not dark enough in the drawing. The surface cuticle is shown at *c*. All the chitin appears to be interpenetrated by tiny hair-like canals, *h*, which are occasionally filled with air, when they seem quite black. It appears as if the white light reflected from this air effectually prevents any iridescence, but, when these canals are filled with aqueous solutions, to which the cuticle is pervious, fairly saturated colours are seen. The surface, as in several similar examples, appears impervious to anhydrous organic solvents, such as xylol, in which the chitin appears almost silver.

Among other structures which show somewhat similar phenomena are the brilliant coloured eyes of many Diptera, such as the green and golden eyes of the genus *Chrysops*. These are undoubtedly iridescent, but lose their colour on drying. (The phenomenon is no doubt quite different from the so-called "pseudo pupil" effect, the fiery colours seen by artificial light in the eyes of some nocturnal moths, such as *Boarmia abietaria*, HÜBN.) Sections were made through the green eyes of *Chrysops*, and were examined in various media, but, as no special structure could be seen, a figure is not given. Pressure experiments are rather difficult to carry out, but, as far as can be seen from trying a portion of the exterior cuticle, the colour is permanently destroyed on compression.

43. *Chrysochloris aurea.*

Among mammals, iridescence is very rare, but there are a few notable exceptions. For instance, the Cape Mole, a small South African insectivore, has the most beautiful iridescent fur. The most conspicuous colours are red and green, though the whole range of the spectrum is included. As a rule, it is only the "bristle" or "contour" hairs which show this brilliant iridescence. *Chrysochloris aurea* shows these prismatic colours while alive, and, in a spirit specimen, they persist with the most

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* In some fluids, as, for instance, chloroform, the colours were metallic, but only ordinary laboratory samples were available, and were no doubt moist.

striking brilliance. Hairs mounted in alcohol show their colours well under the microscope, but they are normally pigmented, and there is nothing in their structure to differentiate them from ordinary mammalian hairs. The usual imbrications of the hair scales were looked for, to discover whether these were close enough to form a diffraction "grating." In most hairs they are not very clearly defined, but in some cases they are visible over a short length, and appear as shown at *s*, in Plate 2, fig. 14. There were about 100 imbrications to the millimetre, but since it was found that on allowing the hairs to dry, every trace of the colour disappeared until the fluid was replaced, it seemed hardly possible that these imbrications could cause the colours.

As it seemed unlikely the colours could be due to an external grating, sections were cut and stained with picric acid. The result was most disappointing, because no internal structure of any kind could be found. No figure is given of these sections, because they differ in no way from similar sections of non-iridescent hairs.

There are also certain small Russian Desmans with aquatic habits, which are said to be iridescent. *Myogale moschata*, the Musk Shrew of the Volga, is, for instance, said to be highly iridescent, but no specimen could be obtained.

44. *Aphrodite aculeata.*

This is the common "Sea-Mouse." It is, of course, not a mammal, but one of the free swimming marine Bristle Worms, Polychætes. Many of the bristles arising from the upper divisions of the foot-stumps are long and beautifully iridescent, so that they look like spun glass shining with all the colours of the rainbow. The colours of the living specimen are maintained in spirit, but, on drying, they vanish like those of the Cape Mole. Under the microscope, the bristles of *A. aculeata* are transparent, of a pale yellow, and perfectly smooth and regular from end to end, without a structure of any sort. As in the case of the Cape Mole, transverse sections were cut and stained. The oval bristles appear to have a thin cuticle, within which is a clear substance, that seems to be pitted with excessively fine pores, but there is little to suggest the real cause of the colour. These bristles and the hairs of the Cape Mole both require further investigation, which will shortly be carried out.

45. *Barbules of a Green Widgeon Feather.*

An extensive study was not made of iridescent birds' feathers. It is clear that the colour cannot be due to a surface cuticle, as assumed by MANDOUL,[*] for the reason that it is much too thick. Many feathers lose their colour under pressure,[†] as was first observed by GADOW,[‡] and later by MALLOCK,[§] but they return slightly when

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[*] MANDOUL, H., 'Ann. Sci. Nat. (Zool.),' Paris, vol. 18, p. 250 (1903).

[†] See note on p. 26.

[‡] GADOW, HANS, 'Rouen, Bul. Soc. Amis Sci. Nat.,' 1re Semestre, 1883.

[§] MALLOCK, A., *loc. cit.* (see p. 4).

the pressure is released. According to BIEDERMANN,[*] the colour is also changed very slowly by immersion in alcohol. He consequently concludes that the iridescence is due partly to films of air, and partly to films of keratin. The change in alcohol may, however, be caused by gradual dehydration and shrinkage of the keratin. GADOW considers the cuticle is often too thick to cause colour, but he believes that in many cases the barbules themselves act as prisms, giving colour by dispersion. This is not possible in many iridescent feathers like the above, for they contain too large a quantity of black pigment. Sections were made through several feathers, among them those of a bright green humming-bird. The sections were stained in picric acid, which usually revealed a cuticle, the amount of pigment in which depended upon the thickness of the section. Plate 2, fig. 21, represents a section through four barbules of the iridescent green portion of a widgeon's feather. The oval-shaped section of the barbule was cut near the tip, the other three were cut lower down, close to where they are joined to the central barb. They show a cuticle, *c*, and are all heavily pigmented with black pigment, which is sometimes granular, as at *p*, and sometimes diffused. Sections were also made from an adjacent portion of the same feather, which was dull black, but, after staining in picric acid, no distinction could be made between the two. From the appearance of these sections, it would seem that the colour-producing structure was more nearly allied to that of scaleless beetles than any other described, but, owing to the fact that the colour disappears or changes on pressure, it is more likely that it depends in some way "on the interference of thin plates."[†] It is, however, hoped that a further investigation will be made of feathers and certain other iridescent structures.

A brief examination was made of a few miscellaneous objects which show iridescence. In the vegetable kingdom the phenomenon is very rare, and has been noticed in some seeds such as those of the Peony, where it is said to be due to a pigment which dissolves in alcohol, giving a brown fluid with a blue fluorescence.[‡] Pteridophytes of the genus *Selaginella* sometimes show strong iridescent colours. Two species were investigated by KNY,[§] who came to the conclusion that the colour was due to the surface cuticle, although he admits that this is only a little less than 1·0 μ thick.

Sections were cut of *S. Willdenowii*, BAK., which has a very beautiful purple iridescence that is destroyed by alcohol and other dehydrating reagents. The cuticle seems to be no thinner than usual, and is certainly too thick to cause the colour. This did not disappear on pressure, and may therefore be surface colour.

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[*] BIEDERMANN, W., *loc. cit.* (see p. 24).

[†] KEELEY, H. J., *loc. cit.* (see p. 20) describes the spectra of feathers as containing bright bands like those of the opal, and believes they owe their colour to a structure analogous to the twinning of potassium chlorate crystals.

[‡] FRANK, B., 'Bot. Zeitung,' vol. 25, No. 51, p. 405 (1867).

[§] KNY, L., 'Bot. Zeitung,' vol. 29, No. 12, p. 185 (1871).

V. SUMMARY AND CONCLUSIONS.

All explanations of iridescence depend on (1) diffraction, (2) interference, (3) the scattering of light by small particles, and (4) selective metallic reflection.

The earlier writers appealed to all four explanations, but recently there has been a tendency to ascribe all cases to the last cause only. Thus WALTER, on account of the behaviour of polarized light when reflected from iridescent objects, attributed the colours to a hypothetical metallic substance called "*Schillerstoff*" which is "in solution in the chitin."

MICHELSON, basing his opinion on "the rigorous optical tests of the phase difference and the amplitude ratio," takes the same view.

BIEDERMANN has nevertheless rejected this explanation in favour of interference. His principal objection is that the disappearance of all transmission colours, on placing scales in a refractive fluid, is quite incompatible with surface colour. He believes that in scales, the interference is mainly caused by films of air, since the colour vanishes as soon as the air is replaced by a refractive fluid. In beetles' wing-cases, on the contrary, he believes that the interference is caused by thin films of chitin, since immersion in refractive fluids causes no loss of colour.

MALLOCK supports the theory of interference, claiming that there is a periodic structure. This is partly because the colours of scales vanish in refractive fluids, but chiefly because a pressure, insufficient to destroy the molecular structure, can by altering the spacing between the plates, cause the colours to disappear.

Recently the late LORD RAYLEIGH reviewed all the evidence, and considered it, on the whole, favourable to interference. He admits the force of MICHELSON'S arguments, but shows how by assuming that the plates of chitin have a definite structure, they may give strong interference colours, and yet reflect polarized light in the manner of metallic films. He is confirmed in his opinion by the weakness of the transmission colours, which in the case of surface colours, should always be stronger than those reflected.

The fact that many of these discussions are so theoretical suggested the present work, which mainly consists in an examination of the minute structure of a number of iridescent objects. It was hoped that this might supply evidence which would help to decide the true explanation. As was expected, the enormous diversity of form makes any general theory quite impossible. It is, therefore, essential that any type of structure should be considered on its own merits, and for this purpose many microscopical sections are described and figured. Unfortunately, owing to their number, they have not been dealt with exhaustively. An attempt has rather been made to show how complicated and contradictory is the evidence. Any explanation that has been advanced has only been given with the greatest diffidence, not necessarily as true, but rather as a tentative suggestion, sometimes only as a note of interrogation. Indeed, in more than one case, it has only been possible to record the facts.

In order to correlate the observations and experiments made in the course of this work, with those of other investigators, an attempt has been made to analyse roughly all the factors which determine the colours of insects.

The fundamental colour must depend upon one or more of the four causes of iridescence first mentioned, to which should be added that of pigmentation. A very small physical change, however, in any one of the conditions may effect a profound alteration in the colour. But there are in addition certain modifying factors, such as the shape and position of the scales, the sculpture and quality of their surface, etc. These being much less sensitive to small changes, give the insects their peculiar shade, quality and lustre, and thus tend to keep constant the colour of the scales on the same insect, as well as the characteristic appearance of all the insects in the same species.

Diffraction.

A method is described of taking impressions on colourless collodion films, by which the effect of any surface pattern can be analysed and isolated from colours produced in any other way. These replica films show that the upper surfaces of most scales give good "gratings." No pigmented scale gives diffraction colours by reflected light, but striated, transparent scales are found, which give faint but very characteristic colours of this nature.

The only recent author to attribute any colours to diffraction is MICHELSON, who considers that the scales of weevils are an exception to the surface colour theory. He bases his opinion on the agreement between the calculated and the observed values for the "grating" space, and he postulates that the bars of the "grating" have an asymmetric saw-tooth shape, concentrating all the light in one spectrum. The most obvious objection to this theory is that no ordinary grating could give the strong complementary transmission colours, or the monochromatic colours often seen at all angles. It has, however, been suggested that "gratings" with a large number of rulings, and especially "laminary" gratings, might be designed which could produce these effects. There are many other difficulties, but the chief point to be observed is that a microscopical examination of some of the palest insects reveals a distinct stratification which suggests that fine laminæ extend throughout the scale. Probably the more brilliant scales contain analogous strata, which may be too fine to be seen. Thus it appears that even if some colour is caused by diffraction, interference must also take place. If the spacing between these strata were in some cases very irregular, it would account for the pale colours which are otherwise difficult to explain by diffraction.

Interference.

The opinions of RAYLEIGH, MALLOCK, and BIEDERMANN, already mentioned, are in favour of the interference theory; in the case of Lepidoptera this view is enormously strengthened by the discovery of a regular periodic structure, of the correct magnitude, in certain iridescent scales. The structure is formed by plates of transparent chitin, which are the prolongation of the pigmented, triangular striæ to be seen on most scales. The plates are separated from each other by thin films of air. The thickness of both the chitin and air-films varies from one to three half wave-lengths. The plates are at right angles to the surface of the scale, and consequently the change of colour with obliquity should be towards the red, and not, as is always said, towards the blue. A number of colour measurements show that the wave-length increases with the obliquity; whereas in those iridescent scales in which any periodic structure must be parallel to the surface, the wave-length shortens.

There seems to be no doubt that those iridescent scales, which show a transparent surface layer of clear chitin, also possess a periodic structure, but in this case it is parallel to the surface. Although the available thickness of chitin is sometimes hardly sufficient for more than three to four half wave-lengths, the appearance of oblique sections suggests several superimposed films. This appearance, as well as the behaviour of scales in viscous fluids, is so characteristic of a periodic structure, that its existence cannot be doubted. The air-films may of course be so thin as to be negligible, and thus need not be taken into account in calculating the available space. Certain black scales are also described, in which the lower membrane consists of a single transparent film. They give fairly bright and varied colours like those of a soap bubble.

Blue due to Scattering of Light by Small Particles.

KOSSONOGOFF has suggested that *all* Lepidoptera owe their colours to "optical resonance," but his theory does not deserve serious attention. However, no possible cause of colour should be neglected in the search for the true explanation, and it must not be forgotten that, in addition to "optical resonance," there are other phenomena such as LIPPMANN'S films, and the coloured sodium films of Prof. WOOD. Systems which selectively reflect the short blue waves can undoubtedly produce very bright colours, as in the case of certain feathers and some small marine animals. BIEDERMANN describes a structure called the "*Stäbchenschicht*," which he declares is present in the wing-cases of most iridescent beetles, and which, with the assistance of the surface cuticle, produces all their colour. Except in the case of certain Cetoniids, however, no such layer could be found. Moreover, the surface cuticle is not responsible for much colour, or its disappearance would be noticed when the wing-cases are placed in a highly refractive fluid.

The peculiar colour of the Cetoniids mentioned is probably caused by a layer of rod-like structures at right angles to the wing surface. Any section tangential to the surface of the wing-case which exposes the ends of these rods is intensely coloured by reflected light, even when in Canada balsam. By transmitted light, or in transverse section, this columnar layer is yellow. The fact that the chitin is doubly refractive recalls the colours of similar crystals (*e.g.*, tourmaline).

Selective Metallic Reflection.

In beetles, the available depth of chitin is especially limited. If the colours are due to interference, part of the surface layer must be occupied by a protective skin, and hence there is only available a thickness of one half wave-length. It is therefore important to know the maximum saturation that can be produced by a single film.

Colour measurements of a soap film, and of some films of aniline dyes, were compared with those of several beetles under identically similar conditions, and they were all found to be about equally saturated. This makes it important to determine accurately the depth of the colour-producing layer. The result of several estimations gives an average depth of 0·53 μ, which agrees with the microscopical measurements. Thus, if the layer is situated along the dark line between the cuticle and the underlying chitin, as appears from sections of polished areas, there can be room for nothing but a film of "*Schillerstoff*." Moreover, the successive changes of colour seen on polishing these wing-cases, strongly suggest several metallic films, and could hardly be explained by the interference of thin plates (see Plate 3, fig. 8). It is possible that such iridescent, organic films are a modification of chitin, because the chitinous wing-cases of many Tortoise Beetles have the property of reflecting a highly metallic golden colour, no matter at what depth the surface is exposed.

The descriptions of the sections of scales that are given appear to be the first published, though the scales of iridescent scale-bearing beetles and the wings of scaleless beetles have both been described.

(1) The first group to be considered represents scales with a peculiar periodic structure at right angles to their surface. There are several modifications of the chitinous plates of this structure which greatly affect the colour, such as—

(*a*) The width of the plates and that of the intervening air-films. There is some indication that the air-films produce more colour than the chitin plates, *e.g.*, *Hebomoia glaucippe*, etc. (see Plate 3, fig. 6).

(*b*) The height of the chitin plates, and consequently the obliquity of the light, strongly affects the colour. In certain insects there are areas where the plates are so short as to appear in section like beads. No colour is produced at normal incidence, but a sufficient number of interfering surfaces are cut at oblique angles to produce a deep blue colour, as in the case of *Chlorippe laurentia* (Plate 1, figs. 3*a* and 3*b*). The shape of the plates also affects the colour. Thus, with change of obliquity, the colour of *Ornithoptera crœsus* (see Plate 3, fig. 3*a*) appears to be moving from orange towards green; whereas in reality it is an orange pigment being gradually changed to green by an increasing admixture of blue. This blue is caused by a structure which, though it cannot give any colour at normal incidence, produces a deep blue at grazing incidence.

(*c*) Combinations between periodic structures and pigmentary colours are quite common. The pigment may be (i) granular, and situated within the envelope of the scale, as in *Teracolus phlegyas* (see Plate 3, fig. 5), where a red pigment combines with the structural violet to form magenta; or (ii) diffused throughout the scale walls and chitin pillars, as in *Ornithoptera poseidon*, the emerald green of which is due to a periodic structure containing a diffuse yellow pigment (see Plate 3, fig. 2*a*).

(2) There is a large group of scales in which the colour is produced by layers of transparent chitin parallel to their surface, *e.g.*, *Papilio ulysses* (Plate 1, fig. 5). These films cannot be resolved by any objective, nevertheless their appearance in oblique sections, and while being immersed in viscous fluids, strongly indicates a periodic structure.

(3) There is also a large heterogeneous group of scales, the structure of which gives no clue to the cause of colour. There are several types:—

(*a*) A very large class of dark blue, violet, and green iridescent insects have scales indistinguishable from those that have no sheen. The dense black pigment extends to the surface, and there is practically no structure, even when they are bleached, *e.g.*, *Euplœa deione* (Plate 1, fig. 21).

(*b*) There is a second group of iridescent insects, the structure of whose scales shows no indication of the cause of their colour. Their striæ are sometimes solid, as in the "Common Blue," *Lycæna icarus* (Plate 1, fig. 17), and sometimes filled with air, like those of *Papilio parinda* (Plate 1, fig. 16). There are yet other scales having very thin walls, which may produce, by interference and diffraction, pale colours such as are seen in *Salamis parhassus* (Plate 1, fig. 15).

(*c*) The metallic silver and gold scales common in certain *Plusia* are often transparent, and have a structure similar to that of the adjacent pigmented scales, and yet so much light is reflected that it is difficult to believe that there is no regular periodic structure, *e.g.*, *Dione juno* (Plate 1, fig. 22).

(*d*) Certain other scales are characterised by their peculiar steel-like iridescence. There is no typical structure, and in places the colours may be bright, but the intensity fades, as in *Batesia prola* (Plate 2, figs. 1*a*, 1*b*, 1*c*), in direct proportion to the amount of pigment present.

(4) The wing-cases of nearly all scaleless iridescent beetles, as well as many other scaleless objects, form a group whose colour seems due to selective metallic reflection. They have a very simple structure, *e.g.*, *Cetonia aurata* (Plate 2, fig. 2), there being merely a surface cuticle (about 0·5 μ thick) resting upon one or more layers of chitin. A stratified structure is shown to exist in the scales of some pale iridescent weevils, and it is probably present in many others, causing colour by interference as well as by diffraction.

(5) In addition to these structures, iridescent wings of certain dragon-flies, *Neurobasis chinensis* (Plate 2, fig. 20) and bees, etc., have been examined. The colour does not disappear on pressure, and may be due to surface colour, as in the case of scaleless beetles.

(6) Certain bugs and beetles, like *Pycanum rubens* (Plate 3, fig. 1), are iridescent

when alive and dull when dry or under pressure, but regain their colour on becoming moist. Organic fluids, when the samples are quite free from water, have no effect, which seems to indicate that the colour is caused by the absorption of water by a membrane, which though too thin or irregular to give colours when dry, swells and causes interference when wet. The brilliant eyes of certain genera of Diptera, *e.g.*, Chrysops, are probably of a similar structure.

(7) The golden iridescence of the "Tortoise Beetles," which fades on drying, at first appears analogous to the above, but the chitin is such that a film of moisture can give it a brilliant metallic golden colour at no matter what depth the surface is exposed. The surface cuticle appears to protect the underlying chitin while alive, keeping it moist; when dry it prevents the access of water, causing a delay before the colour returns completely. Any fluid can supply the surface film, but only aqueous ones appear able to penetrate the cuticle (Plate 2, fig. 17).

(8) Iridescent feathers show no peculiar structure. There is usually a clear cuticle, but as the colour often goes on pressure, it may be caused by interference (Plate 2, fig. 21). Some other iridescent objects are described, such as the Pteridophyte *Selaginella Willdenowii*, BAK., also the iridescent hairs of the Cape Mole (Plate 2, fig. 14) and the bristles of the "Sea-Mouse"; but the cause of their colour is doubtful and requires further investigation.

I am indebted to a very large number of my friends for advice and assistance, but principally to the late LORD RAYLEIGH, who helped me in a variety of ways, by his letters, specimens, and suggestions. Though he was aware of my principal results, his death has robbed this paper of the incalculable advantage of the criticism he had most generously promised. It was my hope that he would have embodied this in the form of an introduction, containing most of the discussion of the physical theories which I have now been forced to deal with, inadequately though it be, in the first part of the paper.

Assistance and advice of the utmost value in connection with the physical problems have been given to me by Mr. T. SMITH, who has helped me in ways too many to mention. My deepest thanks are also due to Dr. E. H. GRIFFITHS, Mr. W. C. DAMPIER WHETHAM, Sir RICHARD GLAZEBROOK, and Mr. T. G. BEDFORD. For help and advice in the preparation of the paper I owe my thanks to the present LORD RAYLEIGH, Prof. HOPKINS, and the late Prof. DONCASTER.

For much encouragement and advice throughout the work, but particularly in the biological section, I am indebted to Dr. D. KEILIN, who has given me his unstinted help. Dr. HUGH SCOTT has helped me in naming the insects, as well as in procuring material, and I am also most grateful to Mr. C. FORSTER COOPER for putting at my disposal many of the valuable specimens of the Cambridge University Museum of Zoology. For numerous specimens I have to thank Mr. BALFOUR BROWNE, Prof. NUTTALL, Prof. PUNNETT, LORD ROTHSCHILD, and Mr. N. D. F. PEARCE. Dr. K. JORDAN, Mr. G. J. ARROW, and Mr. W. H. T. TAMS have all assisted me in naming

many of the insects. In the case of the butterflies most of the names were determined by Mr. W. F. H. Rosenberg.

The Plates were lithographed by Mr. W. West, to whose skill and care any success is due.

APPENDIX.

On Some Effects it is Possible to Produce with Different Forms of Gratings.

When discussing the question whether the colours of weevils are produced by diffraction, as is maintained by Michelson, it was pointed out that no spectra are formed by a grating unless the light is broken up into beams; for instance, no colours are shown by a grating under a cloudless sky. Moreover, the complementary transmission colours seen in these scales could not be produced by an ordinary grating consisting of alternate transparent and opaque strips. Mr. T. Smith has, however, written to me, making the following suggestion as to the colours it is possible to produce with certain types of "laminary" gratings:—

"If it is assumed that a grating is constructed of transparent laminæ, which give it a ribbed or corrugated external surface, so that a section presents a battlemented appearance, as is shown in fig. 3, quite a number of effects may be superposed, and, by suitably varying the thicknesses of different parts, almost any desired relation of the colours shown by transmitted and reflected light can be obtained."

"Thus, with normal transmitted light, interference would take place between the rays which have pursued such different paths as ABC and DEF, resulting in a colour of wave-length λ, where $m\lambda = (\mu - 1)\,\mathrm{DE}$, μ being the refractive index, and m an integer, usually unity. Reflected rays, on the other hand, may follow four different types of paths, and the differences of path length will be $2\mathrm{DE}$, $2\mathrm{DE}+2\mu\mathrm{EF}$, $2\mu\mathrm{AC}$, and the differences between any two of these. By assigning different values to DE and EF, considerable changes should take place in the colour seen. At oblique incidence, the corrugated structure would act as a grating, and diffraction effects would be superposed on those due to interference. At very oblique incidence, the sides of the corrugations may introduce yet further effects (as at O, fig. 3), which would become increasingly important as grazing incidence was approached."

"The conclusion to be drawn is that, if other evidence does not render the existence of such a structure very improbable, the absence of the ordinary relation between the colours seen by transmitted and reflected light is not conclusive evidence that a periodic structure, capable of giving rise to such colour effects, is not present."

In discussing whether the colour effects are due to diffraction or interference, it is important to notice that, in several of the above-mentioned cases, as, for instance, when the path difference is $2\mu\,\mathrm{AC}$, or, for rays inclined at an angle θ, $2\mu\,\mathrm{AC}\cos\theta$, the grating is acting as an ordinary thin plate (as at R and S, fig. 3), and these effects would at least be as important as the diffraction effects.

Certain other interesting phenomena will be seen with such a grating. In the first place, some of the colours of the lateral spectra should be brighter than usual. This is because the central image is coloured, owing to the retardation 2DE. Since the energy of light waves cannot be destroyed by interference, the light which fails to appear in this central image must reappear somewhere else. Thus, suppose the retardation of rays from any two adjacent elements, for a given angle, θ, is the same as the retardation due to the laminæ, then these disturbances would destroy one another; but the rays passing through the laminæ will have, in addition to their retardation due to the angle θ, an equal retardation due to the thickness of the laminæ. This would cause the rays to arrive in a condition to reinforce one another, and the particular colour which was absent from the central image would appear in the lateral spectra.

Thus suppose the depth of the battlemented structure is such that when light is incident normally, the beam reflected normally has all light of wave-length λ completely removed by interference, as would occur if in the diagram (fig. 4) $SW = \lambda/4$. The interference is complete for this wave-length, and almost complete for any wave-length differing slightly from λ.

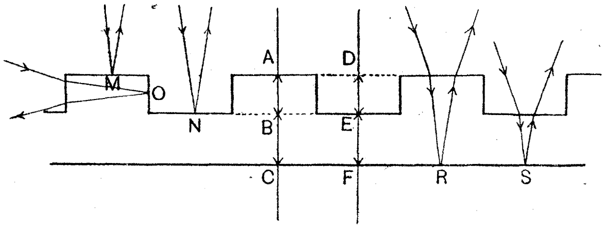


FIG. 3.

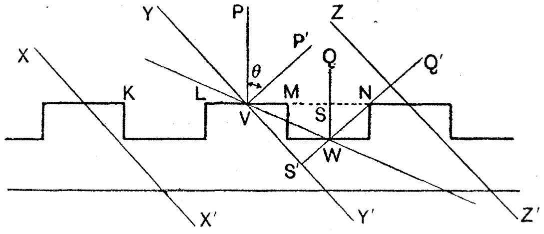


FIG. 4.

For some values of λ the waves coming from the laminæ might destroy those coming from the thin spaces, so that this colour would be absent from the central image as well as the lateral spectra—an important method of producing, by diffraction, colours embracing a limited region of the spectrum. Similar effects may be obtained with some of Prof. R. W. WOOD's "échelette" gratings as well as by what are termed "mixed films," formed by a froth of egg albumen squeezed between two glass plates, both of which systems are special cases of "laminary" gratings (see 'Physical Optics,' p. 252, by R. W. WOOD, 1919).

Still further complications may be introduced by making the laminæ prism or saw-tooth shaped. When the angles of these prisms are such as to refract the incident rays in the same direction as the diffracted rays, all the light will be concentrated in a single spectrum. Naturally, the same effect would be produced by grooves, if they had flat sides which could reflect the light in the same direction as the teeth.

The above effects will appear clearer from a consideration of the following example suggested by Mr. T. SMITH. "Let λ' be the wave-length of light almost absent from the normal reflection, that completely removed being of wave-length λ, where the difference between λ and λ' is necessarily small. Suppose that with an ordinary grating of the same period as that of the structure to be considered the first order light of this wave-length is diffracted in a direction making an angle, θ, with the normal. Then the grating interval is $\lambda' \sin\theta$. The assumption that λ and λ' are nearly equal will be fulfilled if $2\lambda' = \lambda(1+\cos\theta)$ making half the grating interval $\lambda/4 \tan\theta/2$. Referring to fig. 4. $SW = \lambda/4$, $VS = \lambda/4 \tan\theta/2$, where V is the centre of a crest, and W the centre of a hollow. The angle SVW is thus equal to $\theta/2$. Make the angle WVS′ equal to SVW, so that SVS′ is θ. Then VS′ is parallel to a wave front of the diffracted light of wave-length λ', and since $SW = S'W$ the light from the crest LM lies in the same front YY′ as that from the hollow containing W. Neighbouring crests and hollows give the parallel wave fronts XX′ and ZZ′, and each of the fronts is separated from its neighbour by the amount, grating interval $\times \sin\theta = \lambda'$. The substitution of the battlemented structure for the usual dark and light stripes thus produces no alteration in the direction in which the light is diffracted, but the intensity of the light is increased. For in the case of an ordinary grating, light is contributed from alternate elements such as KL and MN, the intervening space LM being dark; but with the battlemented grating each of these elements contributes to the total light, which is thereby increased in intensity. Similar considerations may be applied to any other case to show that what is apparently lost in one position is in reality only transferred elsewhere."

DESCRIPTION OF PLATES.

PLATE 1.

All figures, with the exception of 6 and 23, were drawn with a Zeiss oil immersion apochromat 2 mm., N.A., 1·4, and Comp. Oc. 27^e. A slight reduction was made in reproducing, so that the magnification is about 2000, *i.e.*, to the scale of $\mu = 2$ mm. Fig. 6 was drawn with the same objective and Comp. Oc. 5, and fig. 23 with a Zeiss DD objective (focal length 4·3 mm.), magnification about 140. Where not otherwise stated, the sections were mounted in Canada balsam.

Fig. 1.—*Morpho menelaus*, LINN., ♂. (See p. 35.)

1a. Upper scale, stained with carbol-gentian violet; *a*, striæ; *b*, basal membrane, which is probably double.

1b. Dark blue under-scale, stained with carbol-gentian violet; *a*, chitin plates, between which may be seen the air-films; *c*, striæ which are heavily pigmented; *d*, bands of pigmented chitin (the "*Brücke*" of Spuler) attaching the upper membrane to the lower; *b*, basal membrane.

1c. Longitudinal section of the above scale stained with carbol-fuchsin. All the other sections of scales are transverse; *a*, single plate of chitin seen from the side; *d*, bands of chitin running at right angles to those in the last figure; *b*, basal membrane.

Fig. 2.—*Morpho sulkowskyi*, KOLL., ♂. (See p. 37.) Unstained section, mounted in aqueous glycerol.

Fig. 3.—*Chlorippe laurentia*, GODART, ♂. (See p. 37.)

3a. Scale from the centre of green iridescent patch, stained with carbol-gentian violet; *a*, tall plates of chitin which give iridescent colours at all angles.

3b. Scale from the periphery of the green patch, which is colourless at normal incidence, but deep blue at grazing incidence; *a*, short plates or bosses of chitin, which are only tall enough to give colour at oblique angles.

Fig. 4.—*Ornithoptera urvilliana*, GUÉR., ♂. (See p. 39.) Unstained, mounted in aqueous glycerol. Compare this structure, which gives a pale powdery blue, with the structure and yellow colour of fig. 2a, Plate 3, a scale of *O. poseidon*, which is emerald green.

Fig. 5.—*Papilio ulysses*, LINN., ♂. (See p. 41.) Stained with carbol-gentian violet; *a*, striæ, formed by undulations of the chitin; *b*, pigmented basal membrane, probably double (*cf.* fig. 6); *c*, transparent surface layer of chitin about 1μ thick, which shows no definite structure.

Fig. 6.—*Papilio ulysses*, LINN., ♂. Longitudinal section of scale-root attached to the wing membrane, unstained; *b*1, *b*2, two halves of the pigmented layer *b* of fig. 5, which join at *t*; *ww*, wing membranes; *r*, scale-root.

Fig. 7.—*Jamides bochus*, CRAMER, ♂. (See p. 42.) Transverse section of iridescent scale, unstained; *a*, undulations in the superficial layer of transparent chitin, corresponding to the pigmented striæ below.

Fig. 8.—*Amblypodia eumolphus*, CRAMER, ♂. (See p. 42.) Iridescent green scale, unstained; *a*, transparent superficial layer of chitin; *b*, basal membrane; *c*, heavily pigmented central portion; *d*, second layer of chitin, slightly pigmented, and possibly involved in the production of colour, as well as the superficial layer; *s*, rudimentary knobs or striæ.

Fig. 9.—*Urania fulgens*, WALK. (See p. 43.) Section of pale blue scale, stained with iron hæmatoxylin; *a*, transparent surface layer of chitin; *b*, lower layer of chitin, probably double, which takes the stain much more easily than *a*. In the dark green scales of the same insect, the layer *b* contains a natural brown pigment, the amount of which varies with the intensity of the reflected colour; *s*, thin striæ.

Fig. 10.—*Urania fulgens*, WALK. (See p. 43.) Section of black under-scale, stained with iron hæmatoxylin; *b*, transparent basal membrane, which gives the varied iridescent colours of a single thin film; *s*, heavily pigmented striæ.

Fig. 11.—*Papilio ulysses*, LINN., ♂. (See p. 20.) Transverse section, cut diagonally at an angle of 60°. (*Cf.* fig. 5, cut normally.) Stained with carbol-gentian violet. The section is lying on its cut face; *a*, represents the wave-like striæ; *mm*, layers of chitin, which successively come into focus on lowering the objective; *r*, pigmented portion of the striæ.

Fig. 12.—*Morpho achilles*, LINN., ♂. (See p. 43.)

12a. Section of upper scale which appears pale blue both by transmitted and reflected light, stained with carbol-fuchsin; *a*, striæ which are double; *b*, basal membrane, which is also double, and has here become separated.

12b. Plan of the last scale, stained with carbol-gentian violet, obtained by the section having turned over upon its face. The double nature of the striæ, *a*, is well seen.

12c. Section of dark blue under-scale, stained with carbol-gentian violet; *a*, heavily pigmented striæ; *c*, transparent surface layer of chitin, which has here become separated from the scale.

Fig. 13.—*Hypolimnas salmacis*, DRURY, ♂. (See p. 43.) *a*, striæ showing a structure somewhat like a tunicate bulb; *b*, basal membrane.

Fig. 14.—*Zesius chrysomallus*, HÜBN. (See p. 43.) Transverse section of iridescent scale. Unstained, mounted in STEPHENSON'S highly refractive mercury biniodide medium.

Fig. 15.—*Salamis parhassus*, DRURY. (See p. 44.)

15a. Unstained section of pale pink scale, mounted in STEPHENSON'S medium; *a*, upper membrane; *b*, lower membrane.

15b. Lower membrane, which frequently becomes separated from the upper portion.

15c. Section through the scale tips, showing the striæ *a*.

Fig. 16.—*Papilio parinda*, MOORE, ♂. (See p. 44.) Section of pale blue scale, unstained, mounted in aqueous glycerol.

Fig. 17.—*Lycæna icarus*, POD. (The Common Blue). (See p. 44.) Section of iridescent surface scale. Stained with iron hæmatoxylin, which reveals a basal membrane.

Fig. 18.—*Thecla rubi*, LINN. (The Green Hairstreak). (See p. 45.) Transverse unstained section of scale, shown in fig. 23, in which the pale reticulation corresponds to the points *b*, where the scale is looped up and therefore thin; *a*, small knob-like striæ with an indefinite cuticle stained with a natural reddish brown pigment; *c*, section through scale tips.

Fig. 19.—*Thecla telemus*, CRAMER, ♀. (See p. 46.) Unstained section of blue upper scale; *a*, striæ with pigmented cuticle; *b*, basal membrane; *c*, pale bands of chitin joining the upper to the lower membrane.

Fig. 20.—*Dynamine mylitta*, CRAMER, ♂. (See p. 46.) Unstained section through metallic scale; *a*, slightly pigmented striæ; *b*, broad foliated basal membrane.

Fig. 21.—*Euploea deione*, WESTW. (See p. 47.) Unstained section, partly bleached with chlorine, of typical dark purple or green scale, which shows nothing but a faint cuticle in some well bleached sections, and apparently does not differ from the adjacent scales which are not iridescent; *b*, basal

membrane; *c*, pigmented striæ, sometimes showing faint cuticle; *d*, pigmented bands of chitin.

Fig. 22.—*Dione juno*, CRAMER. (See p. 47.) Unstained section, mounted in glycerol, of metallic golden scale, the structure of which does not differ from the adjacent dull brown scales; *h*, air spaces, probably too large to cause metallic reflection.

Fig. 23.—*Thecla rubi*, LINN. (The Green Hairstreak). (See p. 45.) Iridescent green under-scale showing fine striation, and the reticulation caused by the polygonal areas *b*. The reticulation corresponds to the thin places *b*, of fig. 18, and where the polygonal areas are thickest, and therefore darkest, they reflect the deepest green colour. The scale is coloured with a reddish pigment, except towards the root *a*, where it is very pale.

PLATE 2.

All figures except 14 were drawn with 2 mm. Zeiss apochromat., N.A. 1·4, and Comp. Ocs., figs. 1 and 20 being reproduced to the scale, $\mu = 2$ mm., *i.e.*, 2000 diameters; figs. 3, 12, 15a, 15b and 17 to the scale, $\mu = 0·5$ mm., *i.e.*, 500 diameters; and all the other figures to the scale, $\mu = 1$ mm., *i.e.*, 1000 diameters. Fig. 14 was drawn with Zeiss A.A. objective, and Oc. 10, *i.e.*, 100 diameters.

Fig. 1.—*Batesia prola*, DBLE. (See p. 46.)

1a. Bright iridescent scale, very slightly pigmented, showing simple striæ *a*, unstained.

1b. Dark scale, somewhat iridescent, unstained; *a*, striæ showing increased pigmentation; *m*, pigmented membrane joining the striæ.

1c. Heavily pigmented scale, showing little or no iridescence; *a*, pigmented striæ, which have become almost triangular.

Fig. 2.—*Cetonia aurata*, LINN. (See p. 48.) Depigmented and unstained transverse section of surface layer or "*Emailschicht*"; *c*, thin surface cuticle; *b*, fractures during cutting, owing to brittle nature of the section.

Fig. 3.—*Sternocera diardi*, GORY. (See p. 48.) Depigmented transverse section of wing-case, unstained, revealing thick surface cuticle. No structure is seen without bleaching.

Fig. 4.—*Ceroglossus gloriosus*, GERST. (See p. 49.) Depigmented transverse section of wing-case, unstained, showing coarse foliated structure *s*, and cuticle *c*.

Fig. 5.—*Anoplognathus aureus*, WATERHOUSE. (See p. 49.) Unstained section of the belly; *c*, surface cuticle; *df*, diffraction fringe.

Fig. 6.—*Plusiotis resplendens*, BOUCARD. (See p. 50.) Composite section of polished wing-case; I, unpolished cuticle; II, metallic magenta area;

III, black underlying chitin; *c*, surface cuticle; *l*, black dots on a dark line, situated between the cuticle and the underlying chitin, *g*. This line is probably the limit of the colour-producing layer; *g*, irregular layer of black underlying chitin.

Fig. 7.—*Anoplognathus aureus*, WATERHOUSE. (See p. 49.) Unstained section of wing-case; *c*, bright and somewhat thick surface cuticle; *e*, *f*, and *g*, first, second, and third layers of chitin, described by BIEDERMANN, and said by him to be the cause of colour.

Fig. 8.—*Lytta vesicatoria*, LINN. (See p. 48.) Unstained section of thin wing-case; *c*, surface cuticle, which frequently becomes detached; *c'*, lower portion of the cuticle, showing that it is capable of being split in two.

Fig. 9.—*Anomala dussumieri*, BLANCHARD. (See p. 52.) Depigmented and unstained section of wing-case; *b*, small hemispherical processes, which give it a peculiar lustrous shadow; *c*, cuticle; *e*, surface of wing-case, which can be seen between the bosses.

Fig. 10.—*Scutellera nobilis*, FABR. (See p. 50.) Depigmented and unstained transverse section of scutellum; *c*, surface cuticle, which is seen to frill exceedingly easily; *s*, rough irregular striæ which have no influence on the colour.

Fig. 11.—*Heterorrhina africana*, DRURY. (See p. 51.)

11a. Depigmented and unstained transverse section of wing-case; *c*, surface cuticle; *s*, doubly refractive pillars of chitin; *a–b*, plane in which tangential sections like fig. 11b are made.

11b. Tangential section made in the plane *a–b* of fig. 11a, exposing the cut ends of the doubly refractive rods *s*; all such sections appear bright green by reflected light, even when mounted in aqueous media.

Fig. 12.—*Heterorrhina elegans*, FABR. (See p. 51.) Transverse, slightly depigmented section, drawn to half the magnification of the preceding figure; *c*, surface cuticle; s_1 and s_2, two layers of doubly refractive chitin rods. The second layer is in a plane slightly below the first; *a–b*, plane in which sections appear green by reflected light.

Fig. 13.—(?) *Entimus nobilis*, OLIV. (See p. 52.)

13a. Transverse section of brown non-iridescent wing-case, unstained, showing apparent resemblance to sections of iridescent wing-cases; *c*, surface cuticle; *s*, layers of striated chitin.

13b. *a* and *b*, two of the above layers seen in plan.

Fig. 14.—*Chrysochloris aurea* (The Cape Golden Mole). (See p. 57.) Iridescent bristle hair, unstained; *s*, fine imbricated scales, which are to be seen in many hairs, but which are hardly likely to be the cause of iridescence.

Fig. 15.—*Hypomeces squamosus*, FABR., var. *durulentus*, HERBST. (See p. 53.)

15a. Scale seen in plan, unstained, mounted in glycerol, showing closely striated appearance.

15b. Section through scale and wing-case, unstained, showing stratification; *c*, surface cuticle; *r*, scale-root.

15c. Transverse section through scale, stained with carbol-fuchsin. The series of strata lying at different depths, cross each other, and a faintly ribbed surface can be discerned at *c*.

Fig. 16.—*Eupholus magnificus*, KIRSCH. (See p. 52.) Transverse section of scale, unstained, mounted in Stephenson's medium; *c*, cuticle; *b*, air bubbles; *g*, portions of cellular structure, which have not become interpenetrated by the mounting fluid.

Fig. 17.—*Thlaspidomorpha balyi*, BOHEMAN. (See p. 55.) Unstained section through black spot of explanate wing-case; *c*, cuticle; *h*, concentric ring-like structure of chitin; *p p*, pigment of black spot.

Fig. 18.—Pentatomid, ? sp. (See p. 54.) Unstained section of immature stage, through red dorsal line; *c*, surface cuticle; *b*, transparent papillary structure; *p*, heavily pigmented iridescent portion.

Fig. 19.—*Chrysis ignita*, LINN. (See p. 53.) Unstained transverse section through green thorax; *c*, surface cuticle; *p*, pigmented layer; *s*, broad striated layer.

Fig. 20.—*Neurobasis chinensis*, LINN. (See p. 53.) Unstained, bleached, transverse section through wing; *c*, indistinct surface cuticle; *m*, layer of medullary substance.

Fig. 21.—Green Widgeon's Feather. (See p. 58.) Transverse section through barbules, stained with picric acid; *c*, surface cuticle; *p*, masses of black granular pigment.

PLATE 3.

With the exception of 8 and 9, all figures were drawn with Zeiss oil-immersion apochromat, 2 mm. N.A. 1·4. and Comp. Ocs. Fig. 1 was reproduced to the scale, $\mu = 1$ mm., *i.e.*, 1000 diameters; the sections (figs. 2–6) to the scale $\mu = 2$ mm., *i.e.*, 2000 diameters; and fig. 7 to the scale $\mu = 0·5$ mm., *i.e.* 500 diameters. Fig. 8 had a magnification of about 10 diameters; and fig. 9 was drawn with the Zeiss objective A.A., *i.e.*, about 50 diameters.

Fig. 1.—*Pycanum rubens*, FABR. (See p. 54.) Transverse section through horny part of the apple-green wing, unstained, mounted in Canada balsam; *c*, surface cuticle which has become slightly displaced; *d*, layer of structureless chitin; *r*, finely striated layer of chitin; *e*, stratified layer of clear chitin; *p*, granular masses of carmine pigment; *f*, core of clear yellow chitin; *h*, bottom layer of yellow chitin; *s s*, small papillæ which are, on the right, seen in plan; *g*, chitinous depression near root of hair.

Fig. 2.—*Ornithoptera poseidon*, Dble., ♂. (See p. 39.)

2a. Transverse section through bright green scale, unstained; *a*, plates of chitin filled with diffuse yellow pigment.

2b. Section of scale from non-iridescent yellow spot on the hind wing unstained; *a*, triangular striæ; *d*, connecting bands of chitin.

Fig. 3.—*Ornithoptera crœsus*, Wall., ♂. (See p. 40.)

3a. Section, unstained, through yellow iridescent scale, which becomes green a. grazing incidence; *a*, slightly pointed chitin plates.

3b. Section through non-iridescent yellow spot on hind wing, unstained.

Fig. 4.—*Callitæra esmeralda*, Dble. (See p. 38.)

4a. Section through scale from magenta eyes of hind wing, unstained, mounted in aqueous glycerol; *a*, chitin plates which have rather square tops; *b*, pale basal membrane; *c*, faint line marking cleft, which divides the chitin plates in two.

4b. Section through base of scale, still showing a few chitin plates, and a hollow core *m*.

4c. Section through stem of scale root; *n*, surface cuticle; *o*, central core.

Fig. 5.—*Teracolus phlegyas*, Butl. (See p. 38.) Unstained section through scale from magenta band on fore wings, mounted in aqueous glycerol; *a*, chitin plates; *b*, basal membrane; *c*, pigmented striæ; *p*, masses of granular pigment.

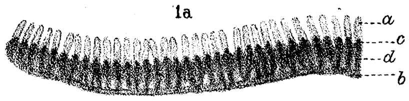
Fig. 6.—*Hebomoia glaucippe*, Linn. (See p. 38.) Section through yellow band with violet sheen on fore wings; *a*, chitin plates; *p*, granular pigment; *s*, wide air-spaces.

Fig. 7.—*Amblyomma hebræum*, Koch. (See p. 56.) Transverse section through scutum, unstained, showing masses of tiny hair-like canals, which here and there are black as at *h*, because still filled with air; *c*, surface cuticle.

Fig. 8.—*Plusiotis resplendens*, Boucard. (See p. 50.) Portion of wing-case, magnified about 20 diameters, which has been polished with carborundum paste; *s*, position of bluish silver high light, which could not be reproduced; I, unchanged golden film; II, iridescent magenta film; III, black underlying chitin.

Fig. 9.—Portion of collodion film with impression of wing of *Papilio agamemnon*, Linn. (See p. 10.) The surface structure of the scales may be clearly seen, and on the right are the small striated hairs, which are found on the green areas instead of scales.

1a



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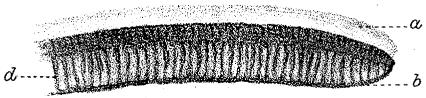

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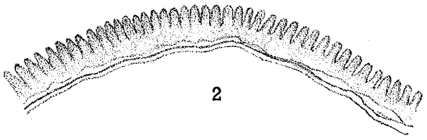

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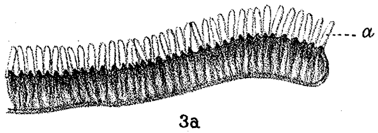

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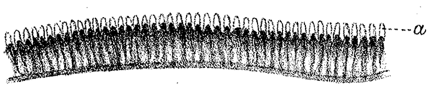

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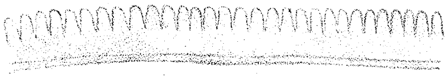

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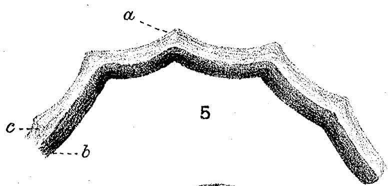

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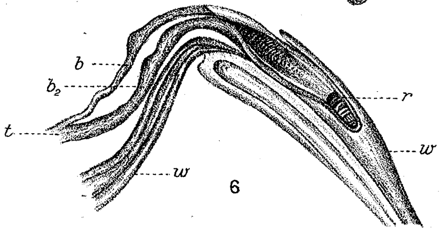

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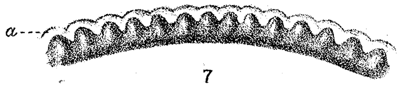

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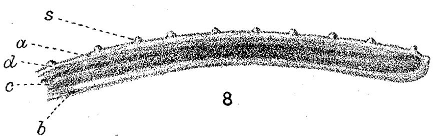

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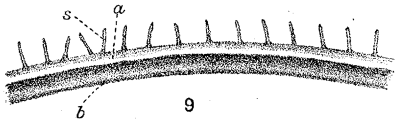

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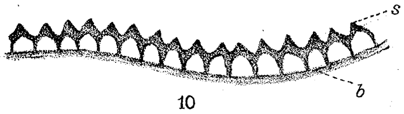

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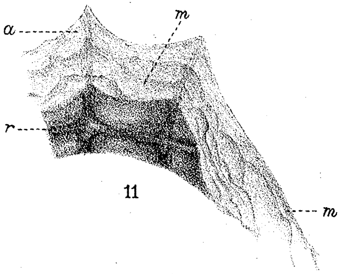

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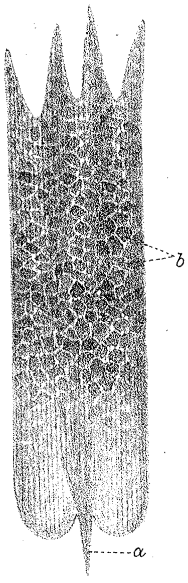

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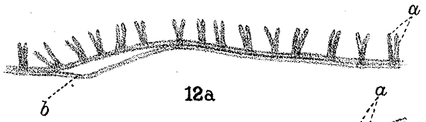

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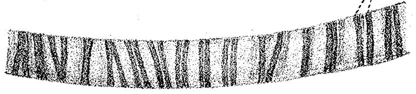

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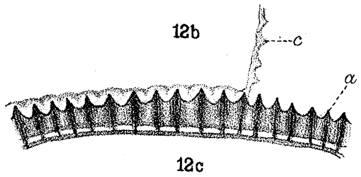

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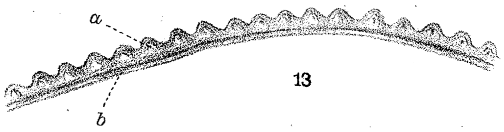

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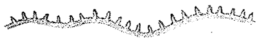

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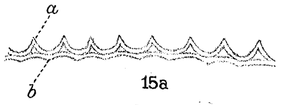

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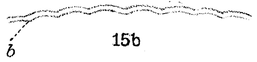

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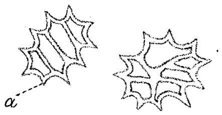

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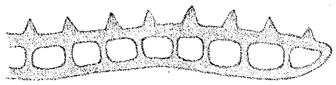

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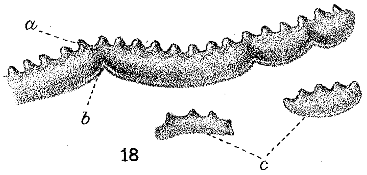

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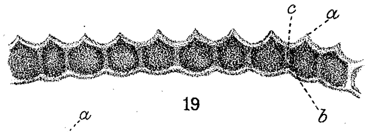

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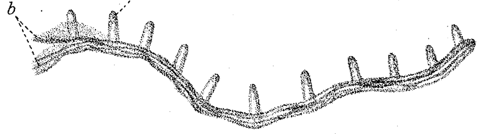

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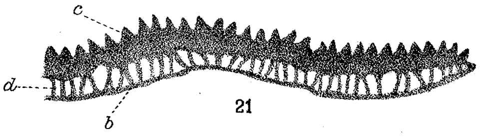

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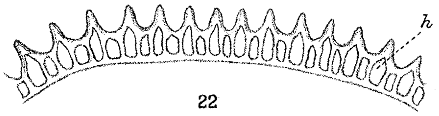

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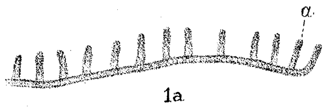

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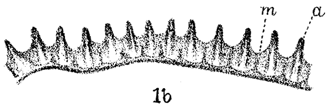

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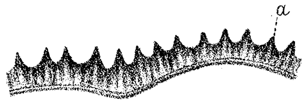

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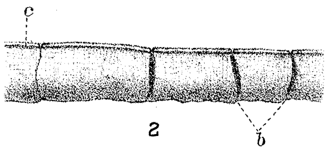

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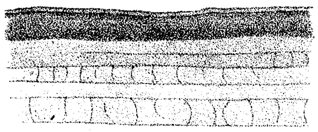

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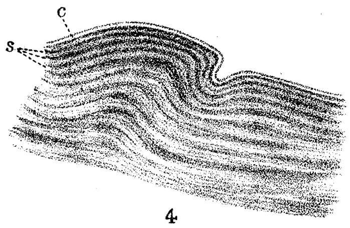

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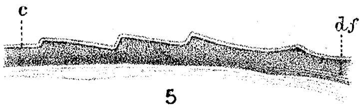

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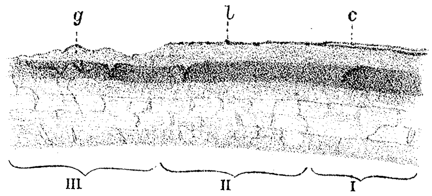

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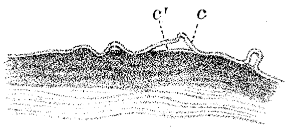

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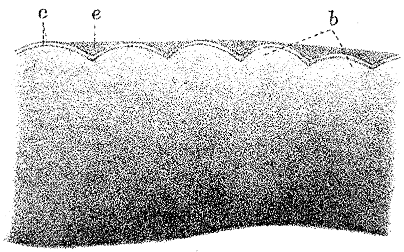

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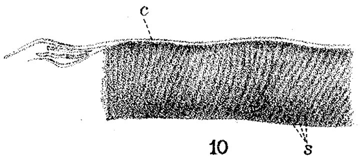

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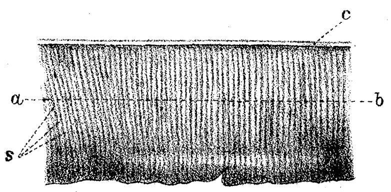

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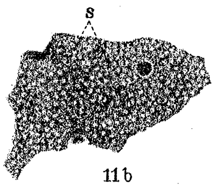

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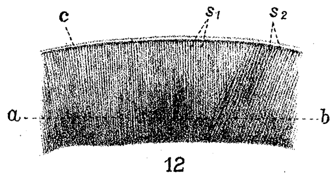

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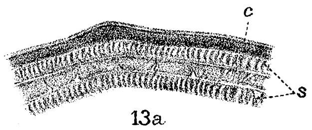

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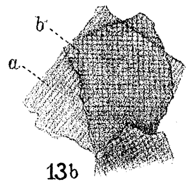

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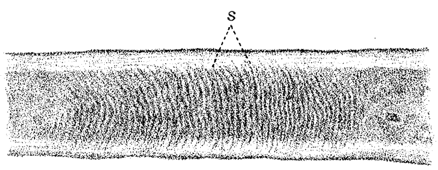

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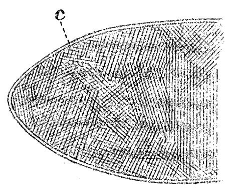

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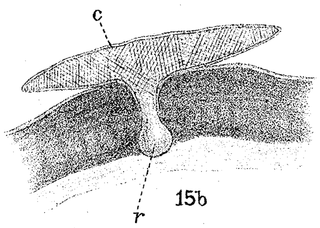

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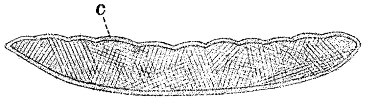

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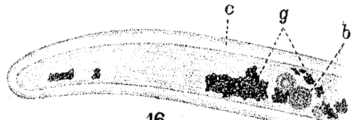

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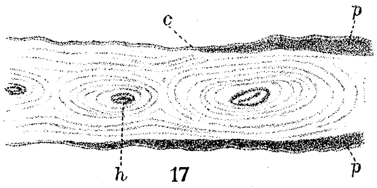

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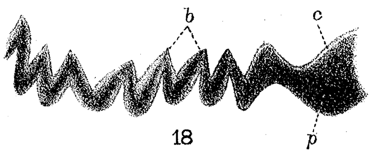

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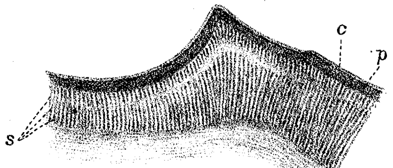

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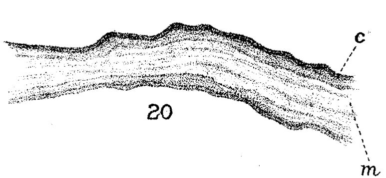

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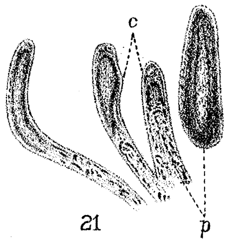

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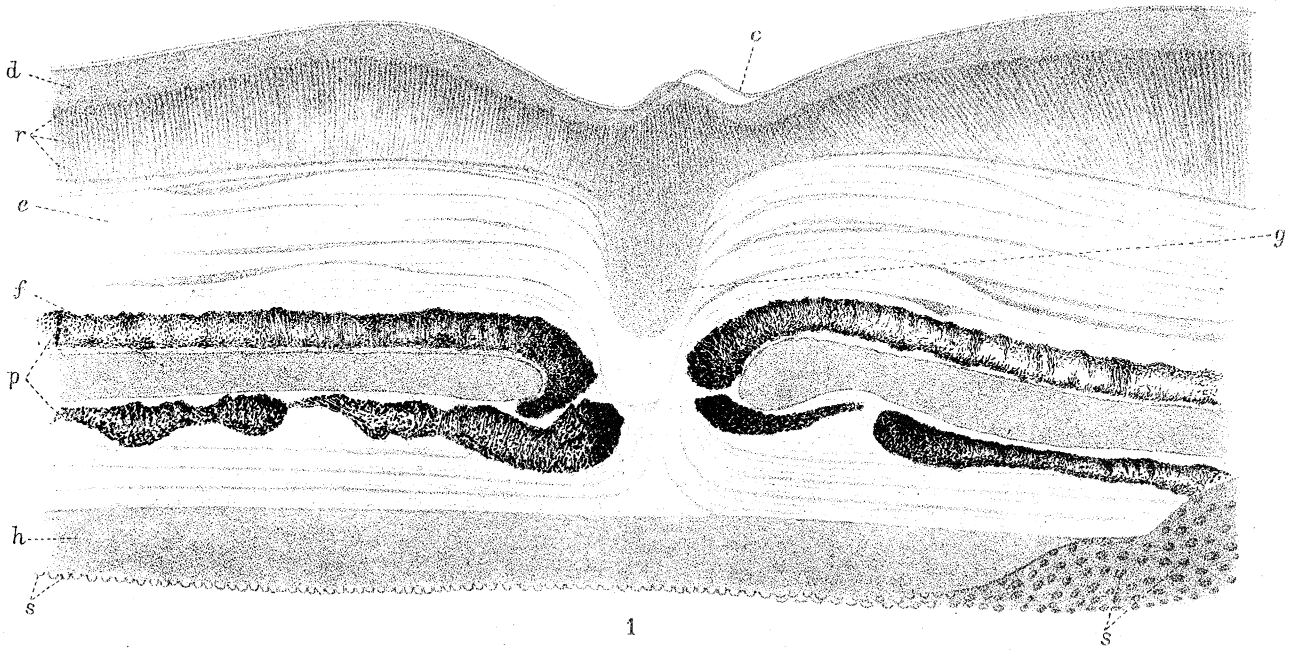

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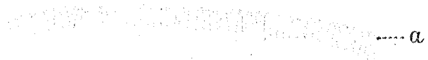

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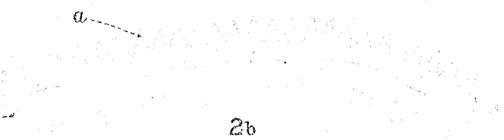

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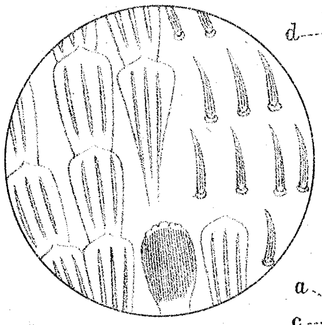

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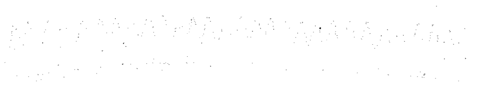

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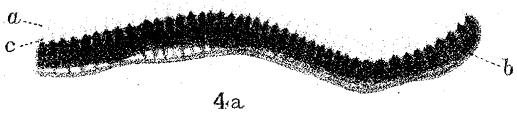

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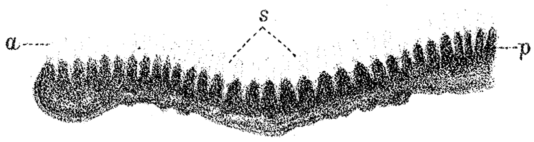

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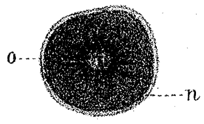

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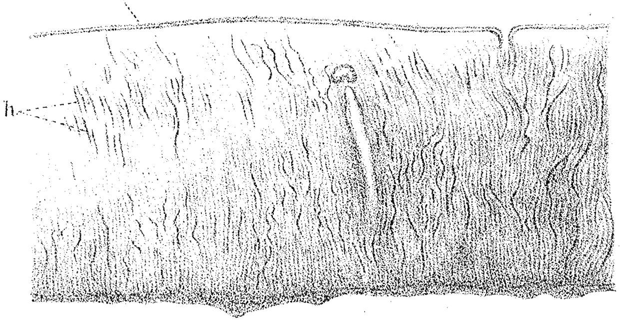

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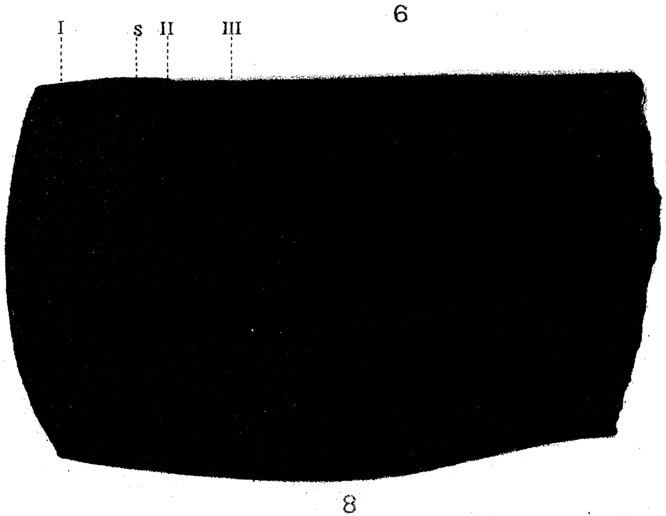

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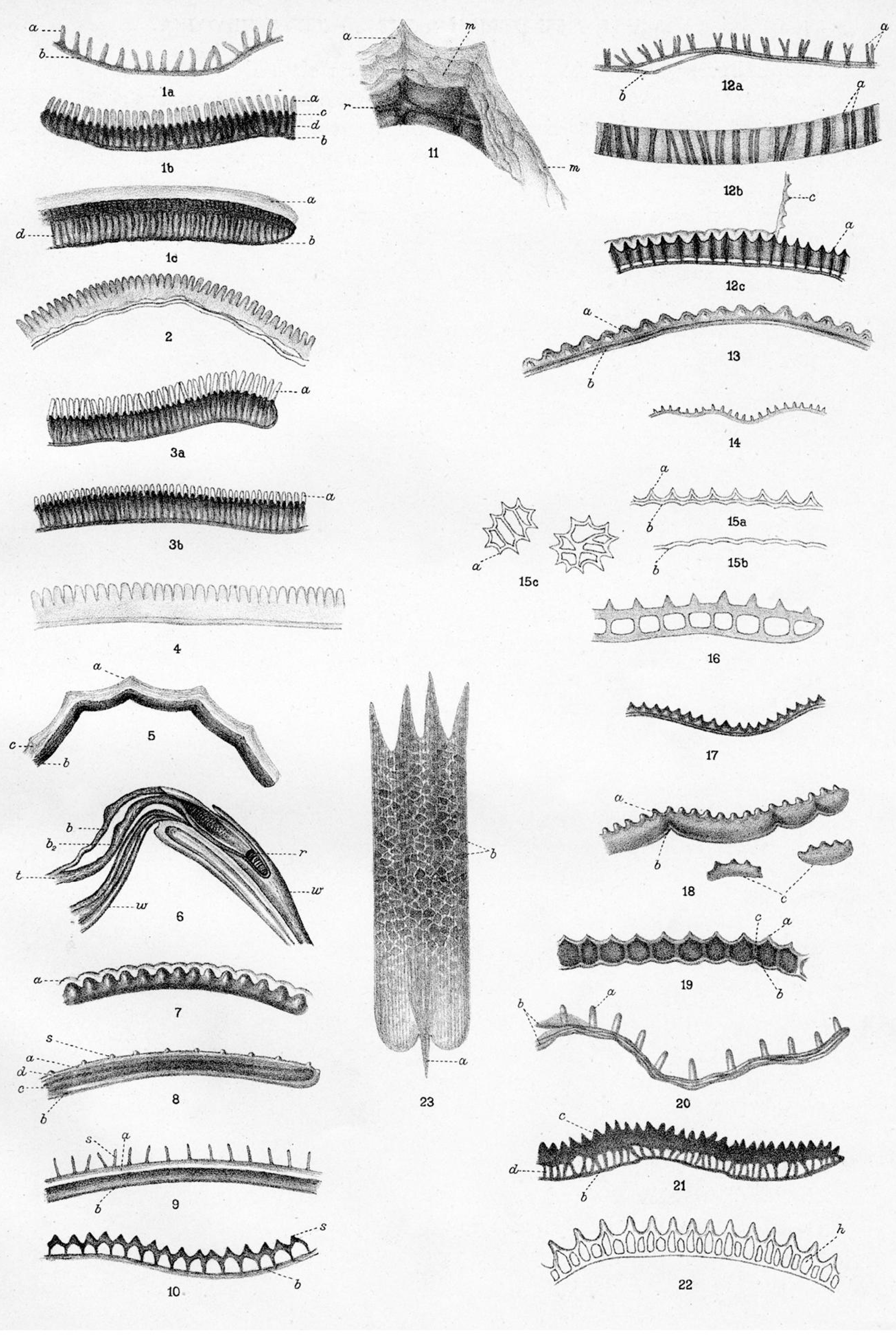


Plate 1.

All figures, with the exception of 6 and 23, were drawn with a Zeiss oil immersion apochromat 2 mm., N.A., 1·4, and Comp. Oc. 27ᵉ. A slight reduction was made in reproducing, so that the magnification is about 2000, *i.e.*, to the scale of $\mu = 2$ mm. Fig. 6 was drawn with the same objective and Comp. Oc. 5, and fig. 23 with a Zeiss DD objective (focal length 4·3 mm.), magnification about 140. Where not otherwise stated, the sections were mounted in Canada balsam.

Fig. 1.—*Morpho menelaus*, Linn., ♂. (See p. 35.)

- 1a. Upper scale, stained with carbol-gentian violet; *a*, striæ; *b*, basal membrane, which is probably double.
- 1b. Dark blue under-scale, stained with carbol-gentian violet; *a*, chitin plates, between which may be seen the air-films; *c*, striæ which are heavily pigmented; *d*, bands of pigmented chitin (the "*Brücke*" of Spuler) attaching the upper membrane to the lower; *b*, basal membrane.
- 1c. Longitudinal section of the above scale stained with carbol-fuchsin. All the other sections of scales are transverse; *a*, single plate of chitin seen from the side; *d*, bands of chitin running at right angles to those in the last figure; *b*, basal membrane.

Fig. 2.—*Morpho sulkowskyi*, Koll., ♂. (See p. 37.) Unstained section, mounted in aqueous glycerol.

Fig. 3.—*Chlorippe laurentia*, Godart, ♂. (See p. 37.)

- 3a. Scale from the centre of green iridescent patch, stained with carbol-gentian violet; *a*, tall plates of chitin which give iridescent colours at all angles.
- 3b. Scale from the periphery of the green patch, which is colourless at normal incidence, but deep blue at grazing incidence; *a*, short plates or bosses of chitin, which are only tall enough to give colour at oblique angles.

Fig. 4.—*Ornithoptera urvilliana*, Guér., ♂. (See p. 39.) Unstained, mounted in aqueous glycerol. Compare this structure, which gives a pale powdery blue, with the structure and yellow colour of fig. 2a, Plate 3, a scale of *O. poseidon*, which is emerald green.

Fig. 5.—*Papilio ulysses*, Linn., ♂. (See p. 41.) Stained with carbol-gentian violet; *a*, striæ, formed by undulations of the chitin; *b*, pigmented basal membrane, probably double (*cf.* fig. 6); *c*, transparent surface layer of chitin about 1μ thick, which shows no definite structure.

Fig. 6.—*Papilio ulysses*, Linn., ♂. Longitudinal section of scale-root attached to the wing membrane, unstained; *b*1, *b*2, two halves of the pigmented layer *b* of fig. 5, which join at *t*; *ww*, wing membranes; *r*, scale-root.

Fig. 7.—*Jamides bochus*, Cramer, ♂. (See p. 42.) Transverse section of iridescent scale, unstained; *a*, undulations in the superficial layer of transparent chitin, corresponding to the pigmented striæ below.

Fig. 8.—*Amblypodia eumolphus*, Cramer, ♂. (See p. 42.) Iridescent green scale, unstained; *a*, transparent superficial layer of chitin; *b*, basal membrane; *c*, heavily pigmented central portion; *d*, second layer of chitin, slightly pigmented, and possibly involved in the production of colour, as well as the superficial layer; *s*, rudimentary knobs or striæ.

Fig. 9.—*Urania fulgens*, Walk. (See p. 43.) Section of pale blue scale, stained with iron hæmatoxylin; *a*, transparent surface layer of chitin; *b*, lower layer of chitin, probably double, which takes the stain much more easily than *a*. In the dark green scales of the same insect, the layer *b* contains a natural brown pigment, the amount of which varies with the intensity of the reflected colour; *s*, thin striæ.

Fig. 10.—*Urania fulgens*, Walk. (See p. 43.) Section of black under-scale, stained with iron hæmatoxylin; *b*, transparent basal membrane, which gives the varied iridescent colours of a single thin film; *s*, heavily pigmented striæ.

Fig. 11.—*Papilio ulysses*, Linn., ♂. (See p. 20.) Transverse section, cut diagonally at an angle of 60°. (*Cf.* fig. 5, cut normally.) Stained with carbol-gentian violet. The section is lying on its cut face; *a*, represents the wave-like striæ; *mm*, layers of chitin, which successively come into focus on lowering the objective; *r*, pigmented portion of the striæ.

Fig. 12.—*Morpho achilles*, Linn., ♂. (See p. 43.)

- 12a. Section of upper scale which appears pale blue both by transmitted and reflected light, stained with carbol-fuchsin; *a*, striæ which are double; *b*, basal membrane, which is also double, and has here become separated.
- 12b. Plan of the last scale, stained with carbol-gentian violet, obtained by the section having turned over upon its face. The double nature of the striæ, *a*, is well seen.
- 12c. Section of dark blue under-scale, stained with carbol-gentian violet; *a*, heavily pigmented striæ; *c*, transparent surface layer of chitin, which has here become separated from the scale.

Fig. 13.—*Hypolimnas salmacis*, Drury, ♂. (See p. 43.) *a*, striæ showing a structure somewhat like a tunicate bulb; *b*, basal membrane.

Fig. 14.—*Zesius chrysomallus*, Hübn. (See p. 43.) Transverse section of iridescent scale. Unstained, mounted in Stephenson's highly refractive mercury biniodide medium.

Fig. 15.—*Salamis parhassus*, Drury. (See p. 44.)

- 15a. Unstained section of pale pink scale, mounted in Stephenson's medium; *a*, upper membrane; *b*, lower membrane.
- 15b. Lower membrane, which frequently becomes separated from the upper portion.
- 15c. Section through the scale tips, showing the striæ *a*.

Fig. 16.—*Papilio parinda*, Moore, ♂. (See p. 44.) Section of pale blue scale, unstained, mounted in aqueous glycerol.

Fig. 17.—*Lycæna icarus*, Pod. (The Common Blue). (See p. 44.) Section of iridescent surface scale. Stained with iron hæmatoxylin, which reveals a basal membrane.

Fig. 18.—*Thecla rubi*, Linn. (The Green Hairstreak). (See p. 45.) Transverse unstained section of scale, shown in fig. 23, in which the pale reticulation corresponds to the points *b*, where the scale is looped up and therefore thin; *a*, small knob-like striæ with an indefinite cuticle stained with a natural reddish brown pigment; *c*, section through scale tips.

Fig. 19.—*Thecla telemus*, Cramer, ♀. (See p. 46.) Unstained section of blue upper scale; *a*, striæ with pigmented cuticle; *b*, basal membrane; *c*, pale bands of chitin joining the upper to the lower membrane.

Fig. 20.—*Dynamine mylitta*, Cramer, ♂. (See p. 46.) Unstained section through metallic scale; *a*, slightly pigmented striæ; *b*, broad foliated basal membrane.

Fig. 21.—*Euploea deione*, Westw. (See p. 47.) Unstained section, partly bleached with chlorine, of typical dark purple or green scale, which shows nothing but a faint cuticle in some well bleached sections, and apparently does not differ from the adjacent scales which are not iridescent; *b*, basal membrane; *c*, pigmented striæ, sometimes showing faint cuticle; *d*, pigmented bands of chitin.

Fig. 22.—*Dione juno*, Cramer. (See p. 47.) Unstained section, mounted in glycerol, of metallic golden scale, the structure of which does not differ from the adjacent dull brown scales; *h*, air spaces, probably too large to cause metallic reflection.

Fig. 23.—*Thecla rubi*, Linn. (The Green Hairstreak). (See p. 45.) Iridescent green under-scale showing fine striation, and the reticulation caused by the polygonal areas *b*. The reticulation corresponds to the thin places *b*, of fig. 18, and where the polygonal areas are thickest, and therefore darkest, they reflect the deepest green colour. The scale is coloured with a reddish pigment, except towards the root *a*, where it is very pale.

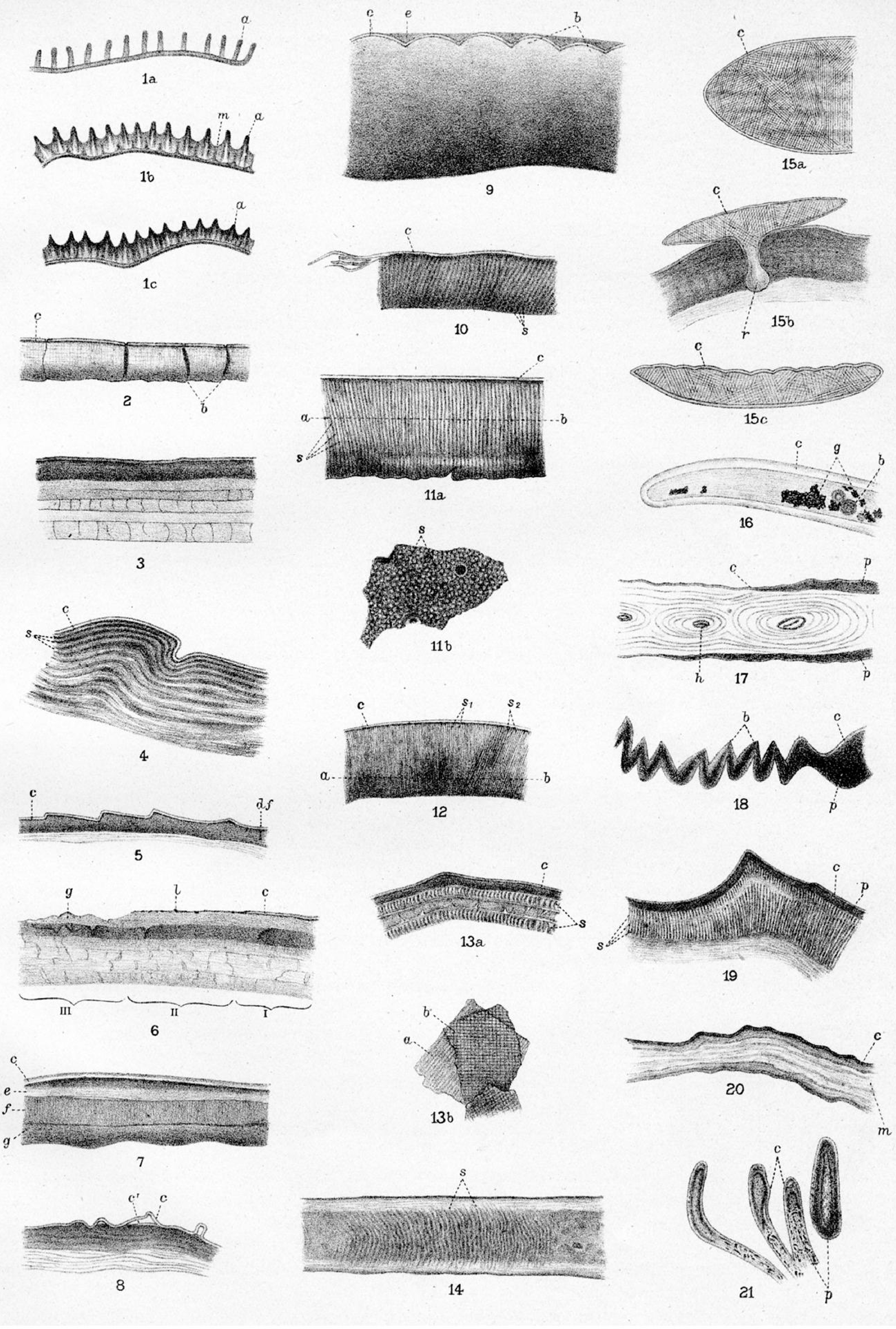


PLATE 2.

All figures except 14 were drawn with 2 mm. Zeiss apochromat., N.A. 1·4, and Comp. Ocs., figs. 1 and 20 being reproduced to the scale, $\mu = 2$ mm., *i.e.*, 2000 diameters; figs. 3, 12, 15a, 15b and 17 to the scale, $\mu = 0·5$ mm., *i.e.*, 500 diameters; and all the other figures to the scale, $\mu = 1$ mm., *i.e.*, 1000 diameters. Fig. 14 was drawn with Zeiss A.A. objective, and Oc. 10, *i.e.*, 100 diameters.

Fig. 1.—*Batesia prola*, Dble. (See p. 46.)
- 1a. Bright iridescent scale, very slightly pigmented, showing simple striæ *a*, unstained.
- 1b. Dark scale, somewhat iridescent, unstained; *a*, striæ showing increased pigmentation; *m*, pigmented membrane joining the striæ.
- 1c. Heavily pigmented scale, showing little or no iridescence; *a*, pigmented striæ, which have become almost triangular.

Fig. 2.—*Cetonia aurata*, Linn. (See p. 48.) Depigmented and unstained transverse section of surface layer or "*Emailschicht*"; *c*, thin surface cuticle; *b*, fractures during cutting, owing to brittle nature of the section.

Fig. 3.—*Sternocera diardi*, Gory. (See p. 48.) Depigmented transverse section of wing-case, unstained, revealing thick surface cuticle. No structure is seen without bleaching.

Fig. 4.—*Ceroglossus gloriosus*, Gerst. (See p. 49.) Depigmented transverse section of wing-case, unstained, showing coarse foliated structure *s*, and cuticle *c*.

Fig. 5.—*Anoplognathus aureus*, Waterhouse. (See p. 49.) Unstained section of the belly; *c*, surface cuticle; *df*, diffraction fringe.

Fig. 6.—*Plusiotis resplendens*, Boucard. (See p. 50.) Composite section of polished wing-case; I, unpolished cuticle; II, metallic magenta area; III, black underlying chitin; *c*, surface cuticle; *l*, black dots on a dark line, situated between the cuticle and the underlying chitin, *g*. This line is probably the limit of the colour-producing layer; *g*, irregular layer of black underlying chitin.

Fig. 7.—*Anoplognathus aureus*, Waterhouse. (See p. 49.) Unstained section of wing-case; *c*, bright and somewhat thick surface cuticle; *e*, *f*, and *g*, first, second, and third layers of chitin, described by Biedermann, and said by him to be the cause of colour.

Fig. 8.—*Lytta vesicatoria*, Linn. (See p. 48.) Unstained section of thin wing-case; *c*, surface cuticle, which frequently becomes detached; *c′*, lower portion of the cuticle, showing that it is capable of being split in two.

Fig. 9.—*Anomala dussumieri*, Blanchard. (See p. 52.) Depigmented and unstained section of wing-case; *b*, small hemispherical processes, which give it a peculiar lustrous shadow; *c*, cuticle; *e*, surface of wing-case, which can be seen between the bosses.

Fig. 10.—*Scutellera nobilis*, Fabr. (See p. 50.) Depigmented and unstained transverse section of scutellum; *c*, surface cuticle, which is seen to frill exceedingly easily; *s*, rough irregular striæ which have no influence on the colour.

Fig. 11.—*Heterorrhina africana*, Drury. (See p. 51.)
- 11a. Depigmented and unstained transverse section of wing-case; *c*, surface cuticle; *s*, doubly refractive pillars of chitin; *a*–*b*, plane in which tangential sections like fig. 11b are made.
- 11b. Tangential section made in the plane *a*–*b* of fig. 11a, exposing the cut ends of the doubly refractive rods *s*; all such sections appear bright green by reflected light, even when mounted in aqueous media.

Fig. 12.—*Heterorrhina elegans*, Fabr. (See p. 51.) Transverse, slightly depigmented section, drawn to half the magnification of the preceding figure; *c*, surface cuticle; s_1 and s_2, two layers of doubly refractive chitin rods. The second layer is in a plane slightly below the first; *a*–*b*, plane in which sections appear green by reflected light.

Fig. 13.—(?) *Entimus nobilis*, Oliv. (See p. 52.)
- 13a. Transverse section of brown non-iridescent wing-case, unstained, showing apparent resemblance to sections of iridescent wing-cases; *c*, surface cuticle; *s*, layers of striated chitin.
- 13b. *a* and *b*, two of the above layers seen in plan.

Fig. 14.—*Chrysochloris aurea* (The Cape Golden Mole). (See p. 57.) Iridescent bristle hair, unstained; *s*, fine imbricated scales, which are to be seen in many hairs, but which are hardly likely to be the cause of iridescence.

Fig. 15.—*Hypomeces squamosus*, Fabr., var. *durulentus*, Herbst. (See p. 53.)
- 15a. Scale seen in plan, unstained, mounted in glycerol, showing closely striated appearance.
- 15b. Section through scale and wing-case, unstained, showing stratification; *c*, surface cuticle; *r*, scale-root.
- 15c. Transverse section through scale, stained with carbol-fuchsin. The series of strata lying at different depths, cross each other, and a faintly ribbed surface can be discerned at *c*.

Fig. 16.—*Eupholus magnificus*, Kirsch. (See p. 52.) Transverse section of scale, unstained, mounted in Stephenson's medium; *c*, cuticle; *b*, air bubbles; *g*, portions of cellular structure, which have not become interpenetrated by the mounting fluid.

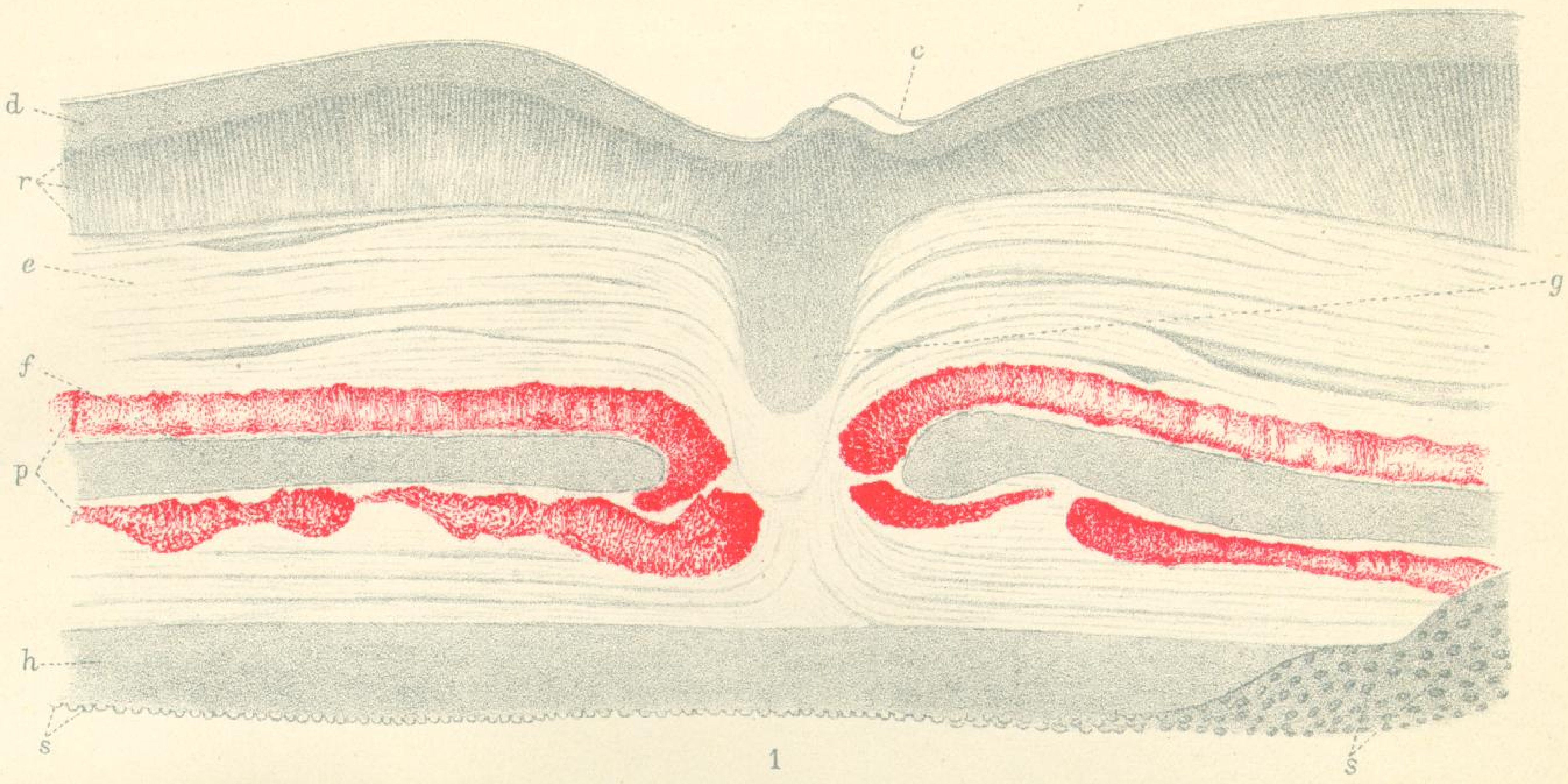
Fig. 17.—*Thlaspidomorpha balyi*, Boheman. (See p. 55.) Unstained section through black spot of explanate wing-case; *c*, cuticle; *h*, concentric ring-like structure of chitin; *p p*, pigment of black spot.

Fig. 18.—Pentatomid, ? sp. (See p. 54.) Unstained section of immature stage, through red dorsal line; *c*, surface cuticle; *b*, transparent papillary structure; *p*, heavily pigmented iridescent portion.

Fig. 19.—*Chrysis ignita*, Linn. (See p. 53.) Unstained transverse section through green thorax; *c*, surface cuticle; *p*, pigmented layer; *s*, broad striated layer.

Fig. 20.—*Neurobasis chinensis*, Linn. (See p. 53.) Unstained, bleached, transverse section through wing; *c*, indistinct surface cuticle; *m*, layer of medullary substance.

Fig. 21.—Green Widgeon's Feather. (See p. 58.) Transverse section through barbules, stained with picric acid; *c*, surface cuticle; *p*, masses of black granular pigment.



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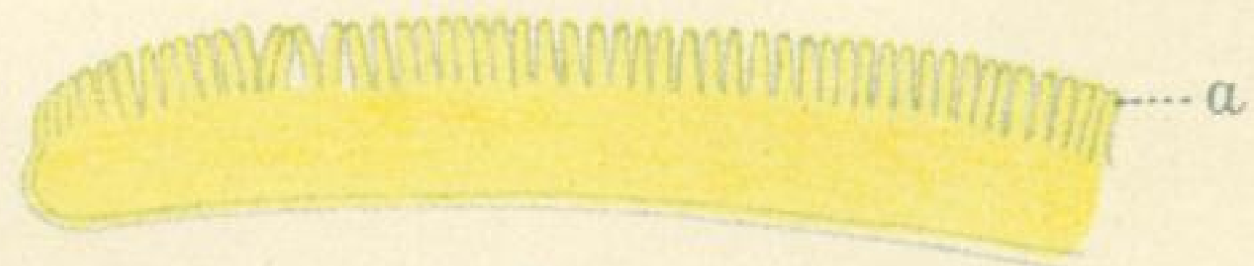

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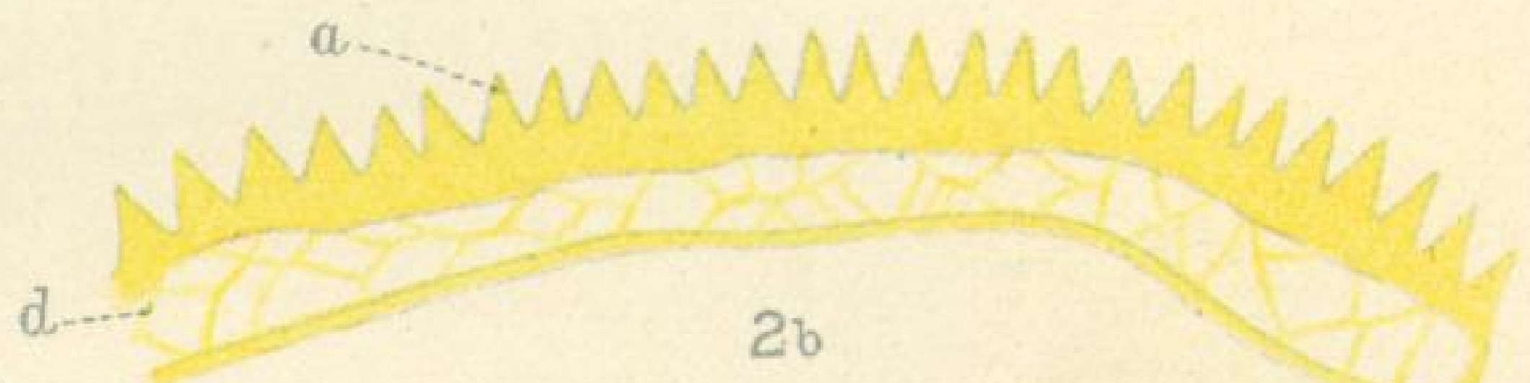

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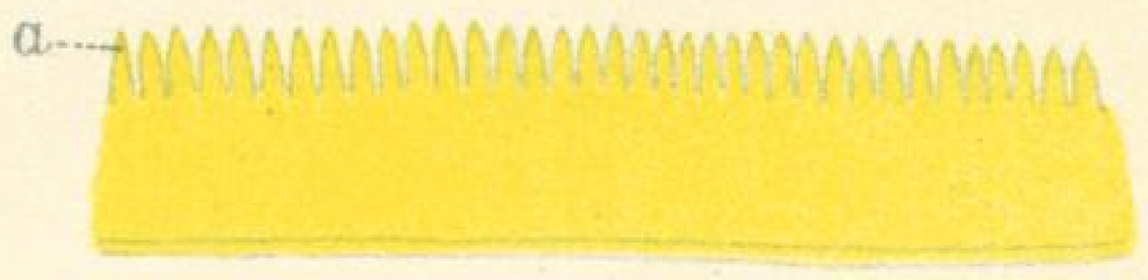

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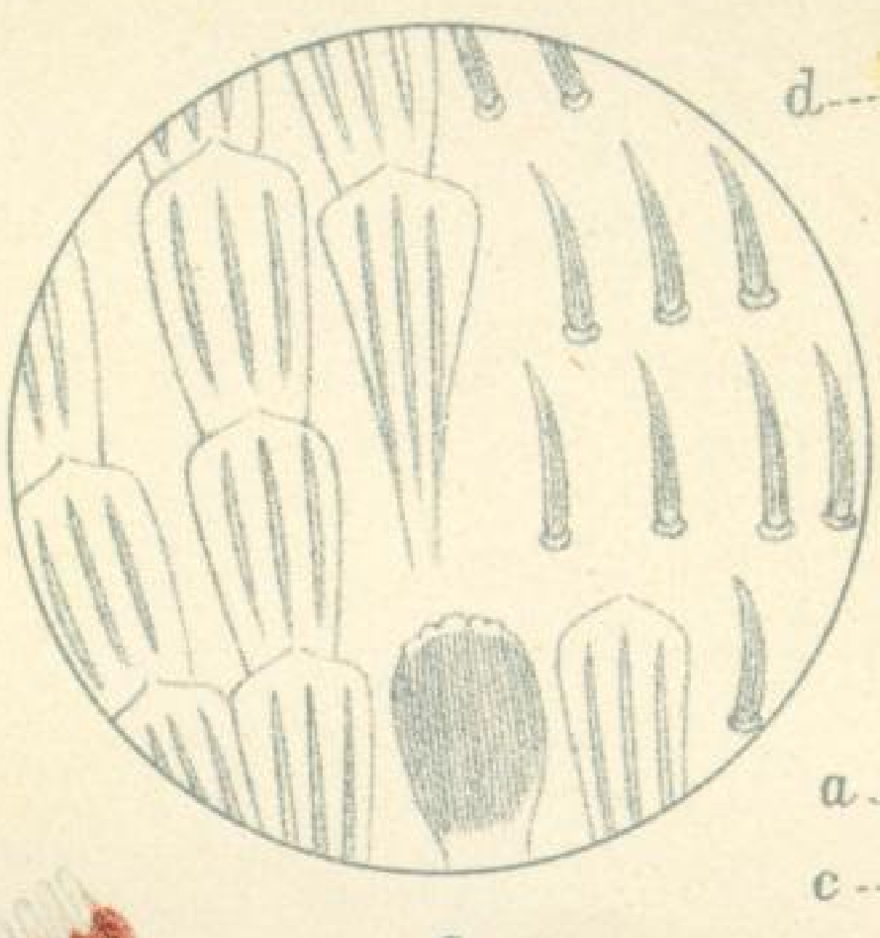

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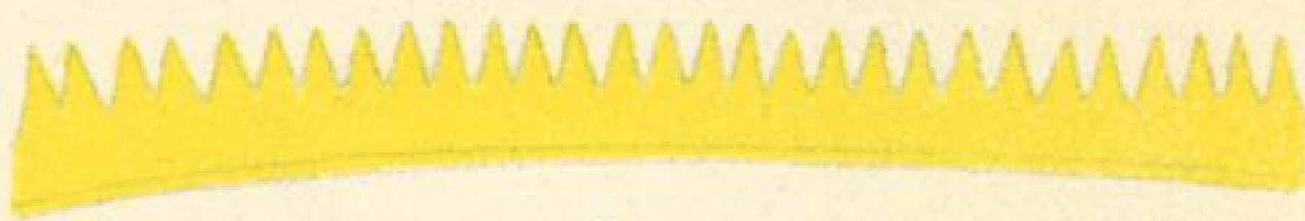

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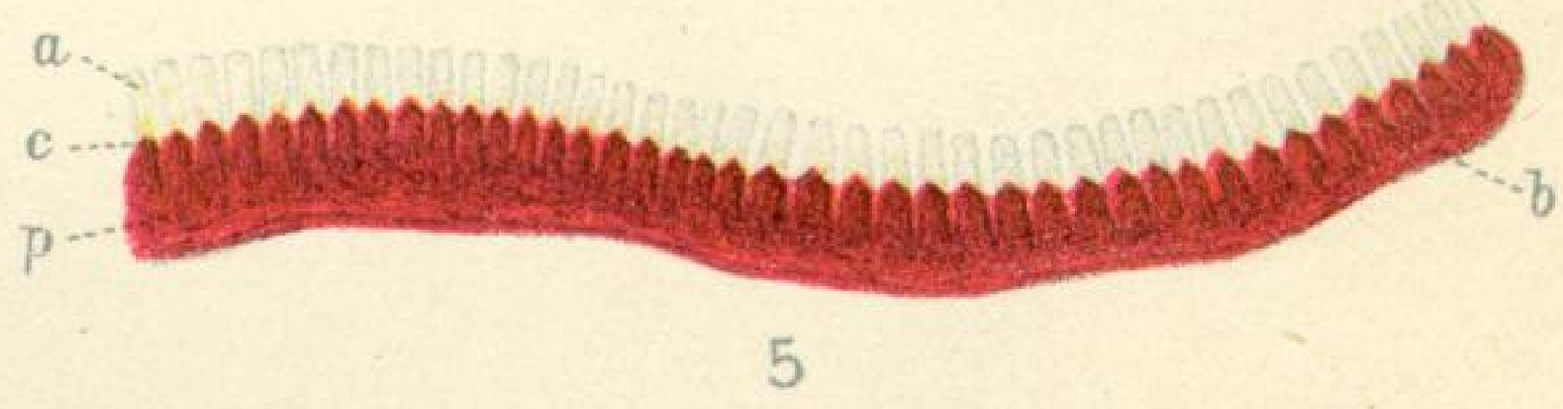

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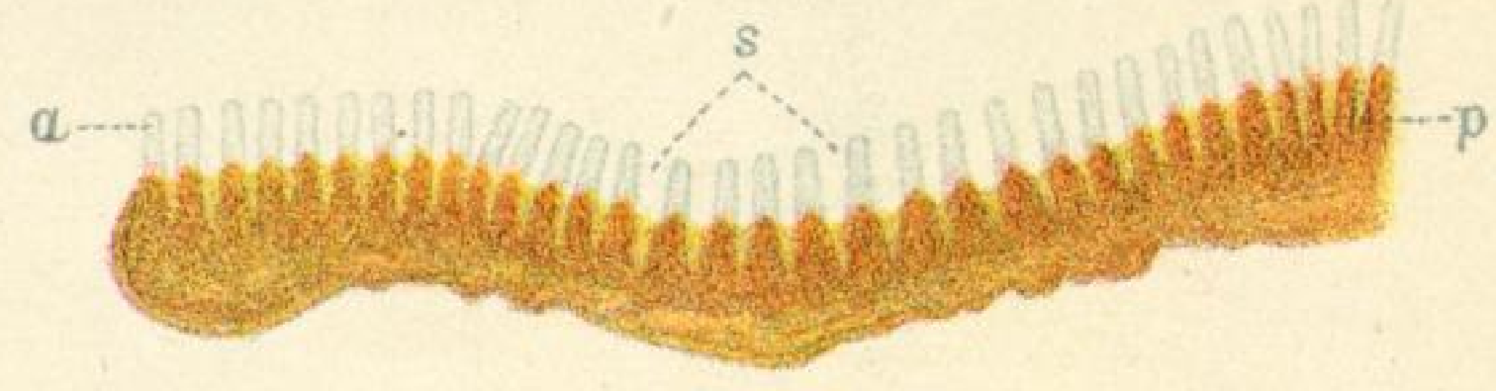

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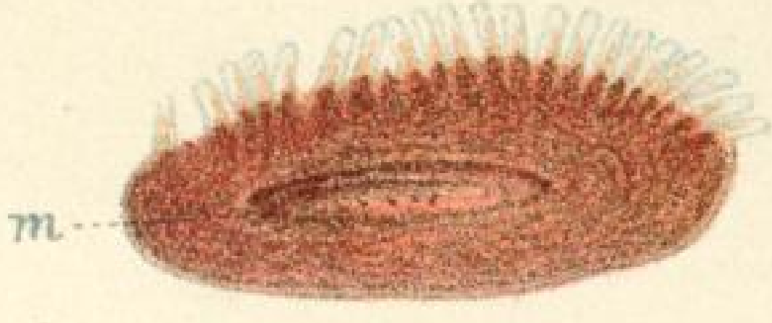

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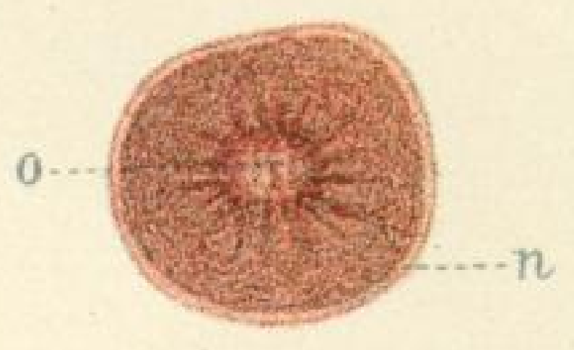

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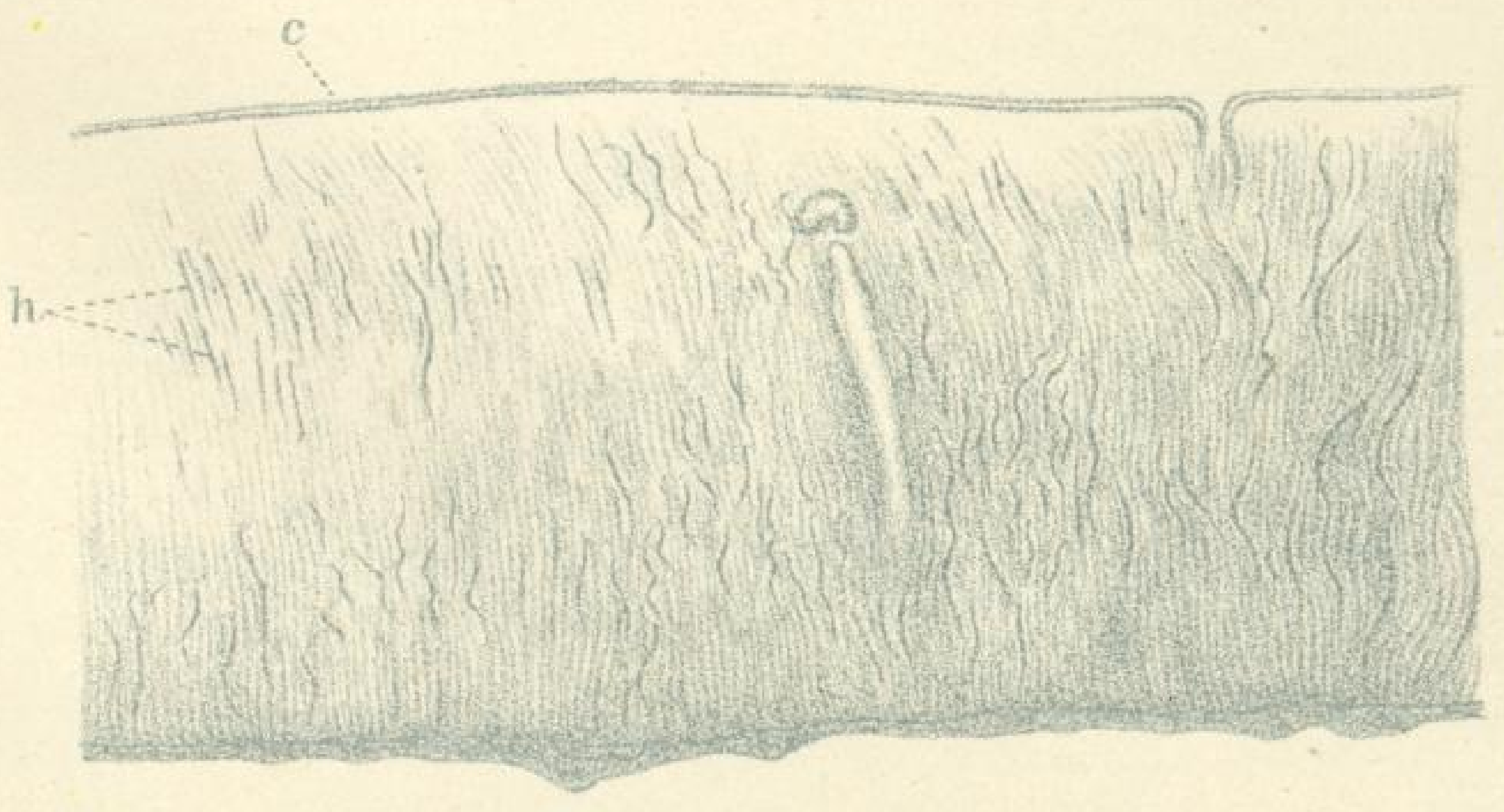

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Plate 3.

With the exception of 8 and 9, all figures were drawn with Zeiss oil-immersion apochromat, 2 mm. N.A. 1·4. and Comp. Ocs. Fig. 1 was reproduced to the scale, $\mu = 1$ mm., *i.e.*, 1000 diameters; the sections (figs. 2–6) to the scale $\mu = 2$ mm., *i.e.*, 2000 diameters; and fig. 7 to the scale $\mu = 0{\cdot}5$ mm., *i.e.* 500 diameters. Fig. 8 had a magnification of about 10 diameters; and fig. 9 was drawn with the Zeiss objective A.A., *i.e.*, about 50 diameters.

Fig. 1.—*Pycanum rubens*, FABR. (See p. 54.) Transverse section through horny part of the apple-green wing, unstained, mounted in Canada balsam; *c*, surface cuticle which has become slightly displaced; *d*, layer of structureless chitin; *r*, finely striated layer of chitin; *e*, stratified layer of clear chitin; *p*, granular masses of carmine pigment; *f*, core of clear yellow chitin; *h*, bottom layer of yellow chitin; *s s*, small papillæ which are, on the right, seen in plan; *g*, chitinous depression near root of hair.

Fig. 2.—*Ornithoptera poseidon*, DBLE., ♂. (See p. 39.)

2a. Transverse section through bright green scale, unstained; *a*, plates of chitin filled with diffuse yellow pigment.

2b. Section of scale from non-iridescent yellow spot on the hind wing unstained; *a*, triangular striæ; *d*, connecting bands of chitin.

Fig. 3.—*Ornithoptera crœsus*, WALL., ♂. (See p. 40.)

3a. Section, unstained, through yellow iridescent scale, which becomes green a grazing incidence; *a*, slightly pointed chitin plates.

3b. Section through non-iridescent yellow spot on hind wing, unstained.

Fig. 4.—*Callitæra esmeralda*, DBLE. (See p. 38.)

4a. Section through scale from magenta eyes of hind wing, unstained, mounted in aqueous glycerol; *a*, chitin plates which have rather square tops; *b*, pale basal membrane; *c*, faint line marking cleft, which divides the chitin plates in two.

4b. Section through base of scale, still showing a few chitin plates, and a hollow core *m*.

4c. Section through stem of scale root; *n*, surface cuticle; *o*, central core.

Fig. 5.—*Teracolus phlegyas*, BUTL. (See p. 38.) Unstained section through scale from magenta band on fore wings, mounted in aqueous glycerol; *a*, chitin plates; *b*, basal membrane; *c*, pigmented striæ; *p*, masses of granular pigment.

Fig. 6.—*Hebomoia glaucippe*, LINN. (See p. 38.) Section through yellow band with violet sheen on fore wings; *a*, chitin plates; *p*, granular pigment; *s*, wide air-spaces.

Fig. 7.—*Amblyomma hebræum*, KOCH. (See p. 56.) Transverse section through scutum, unstained, showing masses of tiny hair-like canals, which here and there are black as at *h*, because still filled with air; *c*, surface cuticle.

Fig. 8.—*Plusiotis resplendens*, BOUCARD. (See p. 50.) Portion of wing-case, magnified about 20 diameters, which has been polished with carborundum paste; *s*, position of bluish silver high light, which could not be reproduced; I, unchanged golden film; II, iridescent magenta film; III, black underlying chitin.

Fig. 9.—Portion of collodion film with impression of wing of *Papilio agamemnon*, LINN. (See p. 10.) The surface structure of the scales may be clearly seen, and on the right are the small striated hairs, which are found on the green areas instead of scales.