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The origin of the colours in the plumage of birds

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1. Introduction

Great interest naturally attaches to the investigation of the colours that form a striking feature of the plumage of numerous species of birds. Even a cursory examination, as for instance the observation of the feathers under a microscope, shows that the distribution of colour in the material and its optical characters are very different in different cases, indicating that no single explanation will suffice to cover the variety of phenomena met with in practice. It is usual to distinguish between those cases in which the colour is chemical in origin and those in which it is physical or structural. It must not be overlooked, however, that in any particular instance both physical and chemical colouration may be jointly operative. Then again, it is usual to divide the structural colours of feathers into two classes: those of the *iridescent* type in which the colour changes very obviously with the angles of incidence and observation, and the *non-iridescent* class in which such change, if any, is not very patent. In the feathers of the tail of the peacock and in the gorgeous plumage which covers the head and neck of the Himalayan pheasant we have striking examples of iridescent colours. The non-iridescent type of colouration is also common and is shown by the feathers of certain birds, such as the jay, the kingfisher, the parrot and so on. It is proposed to describe in the present paper the results of a detailed study of the coloured plumage of the bird *Coracias Indica*. This is a species of jay, very common in Southern India, which furnishes readily accessible material for the investigation of this type of colouration of birds.

2. Some preliminary observations

Seen sitting with its wings folded up, *Coracias Indica* is not a particularly striking bird, though even in this posture its head, sides and tail show vivid colouration. It is when in flight that the gorgeous plumage of this bird is most strikingly seen, and museum specimens of the bird are therefore best mounted with the wings outstretched. The wings then exhibit a succession of bands of colours alternately a deep indigo-blue and a light greenish-blue; the tips of the wings show a delicate mixture of both colours. A remarkable feature is the striking variation in the appearance of the wings with their position relatively to the source of light and the observer. Held between the observer and the source of light, such as an open door or window, the wings appear dark and dull, while when observed with the light behind the observer, they have a brilliant sheen, and at some angles an enamel-like lustre. There is also a distinct difference in the colours exhibited in the two positions. With the light behind the observer, the predominant colours are deep blue and a light greenish-blue, while with the light facing the observer, the same regions exhibit respectively a dark indigo colour and a light blue tint.

Very noticeable changes in colour take place when the feathers are immersed in water and after some soaking the superfluous water is shaken off. The indigo-blue portions of the feather then appear green in colour, while the greenish-blue portions appear pinkish red. At the same time, the variation of colour with the position of the feathers relatively to the source of light and the observer becomes very conspicuous. The portions originally indigo-blue appear green in the damp feather only when the light is behind the observer. They change over to a dark blue and even a deep violet (depending on the angle of observation) when the feathers are held between the observer and the source of light. In the same way, the lighter regions appear pinkish red with the light behind the observer, but a light blue when viewed with the light facing the observer.

The foregoing observations indicate very clearly that the cause of the colouration is mainly physical. It should be remarked, however, that when the feathers are held against a bright source of light and viewed by transmitted light, the dark blue portions appear a deep brown, while the light blue portions are translucent and almost perfectly white. The presence of a dark pigment (melanin) is thus suggested in the darker portions of the feather and to a much less extent, if at all, in the lighter portions. It would not, however, be justifiable to infer from this that a difference in the amount of the melanin is *directly* responsible for the difference in colour between the dark blue and the light blue portions of the feather when viewed by reflected light.

3. Observations with the "Ultra-opak" microscope

Further insight into the nature of the colours is obtained when the feathers are examined microscopically. It is noticed at once that the characteristic colouration is confined entirely to the barbs of the feather. The usual method of microscopic lighting from below the stage is obviously unsuitable in the present case, and it is necessary to illuminate the barbs from above the stage. For a critical examination, a strong beam of light, as for instance from a pointolite lamp, may be projected on to the feather at a suitable angle. Some useful observations may be made in this way with an ordinary microscope or better still, with a binocular microscope. It has, however, been found that a much more interesting way of examining the feathers is to use the "Ultra-opak" microscope recently introduced by the firm of Leitz. In this microscope, the illumination of the object is secured by an incandescent lamp placed in a side tube attached to the microscope, the light from which is reflected down towards the object under study by suitable optical arrangements. The special feature of the instrument is that light does not pass down directly through the objective as in an ordinary metallographic microscope. Instead, it is reflected down through a ring-shaped aperture surrounding the objective and then through a cone of glass, polished flat at the lower end, which intervenes between the objective and the stage. In this way, an illumination of the objective itself is avoided, while the illuminated field can be made as bright as desired by controlling the lamp with a rheostat. The microscope itself is mounted on a cross slide fitted with ball bearings, so that it can be readily moved about and fixed in any position. The stage of the instrument is of considerable size, so that large objects such as the entire wing of a bird can be placed on it and any desired part may be conveniently examined under the very powerful illumination provided by the instrument.

The observations made with the "Ultra-opak" microscope are very significant. It is found that the colour of the barbs is by no means uniform even in the portions which appear ordinarily as dark blue or light blue respectively. The layer of colour in the barb appears divided up into a series of cells, polygonal in shape, and the colour varies individually from cell to cell. The appearances are particularly striking when the microscope is directed to a portion of the feather on the boundary between the dark blue and the light blue regions or, to a portion near the tips of the wings where the two colours intermix. The individual cells may then be seen showing a surprising range of colours. Some cells are violet in colour, some a deep blue or indigo, some lighter blue, some a bright green, some yellowish green, and here and there cells may be observed which are yellow or even orange in colour. Under the highest powers with which the "Ultra-opak" microscope is provided, it can be seen that the individual cell has a granular structure and that the different granules in a cell are usually of the same colour, though, occasionally, distinct differences in colour between the different granules in a cell may also be noticed.

The study of the wetted barbs under the "Ultra-opak" microscope is exceedingly interesting. When the barb is fully damp, the portions originally dark blue now show up as a bright green, while the portions originally light blue now become a light red. The variations in the colour of the individual cells are then much more striking, particularly so as the drying of the barb proceeds. In an individual barb, it is then possible to observe cells with colours ranging over practically the whole spectrum from a deep violet to a bright red, and the cellular structure of the barb is much more conspicuous than ordinarily. As each cell dries up, its colour changes and ultimately goes back to the original. During the process of drying, the cell boundaries may momentarily possess a different colour from the interior; for instance they may be picked out in red while the interior of the cell is a greenish yellow. The whole appearance is then very picturesque.

4. Is the blue of feathers a Tyndall effect?

Bancroft and others, including especially C W Mason[1], have put forward the theory that the non-iridescent blue colour exhibited by the feathers of numerous birds is a Tyndall effect due to the scattering of light by very fine air-bubbles or cavities contained in the substance of the barbs. Mason includes *Coracias Indica* in the list of birds examined by him in the investigations which are claimed to support the theory. The observations described in the preceding paragraphs, however, throw doubt on the correctness of this theory, at least so far as this particular bird is concerned. The surprising variety of colours exhibited by the individual cells which under suitable conditions cover the whole range of the spectrum cannot be reconciled with the idea of a simple scattering in accordance with the Rayleigh law (λ^{-4}) for small particles. We may of course attempt to evade the difficulty by postulating that we have to deal with scattering particles which are not sufficiently small for the Rayleigh law to be valid, or by assuming that the Tyndall blue is modified by the absorbing action of melanin or other pigment. The latter suggestion is negatived in the present case by the evident absence of pigment in the lighter parts of the feather which nevertheless show green, yellow or orange tints by reflected light and also red when wetted. As regards the former possibility, it may be mentioned that numerous experimental and theoretical investigations have been made on the subject of light-scattering by particles which are not small enough for the Rayleigh inverse fourth-power law of wavelength to be operative. We may for instance cite the experimental observations and the calculations based on the electromagnetic theory of light made by B B Ray for the case of small droplets of water suspended in air,[2] and small spheres of sulphur suspended in water.[3] These observations and calculations cannot be regarded as applicable without modification to the present case in which we are dealing with cavities having a *lower* refractive index than the surrounding medium. In the cases of particles having a higher refractive index than the surrounding medium, the most striking results of an increase of size which accompany a break-down of the inverse fourth-power law are: (a) a large increase in the forward scattering relatively to that in a backward direction, (b) disappearance of colour in the forward scattering, (c) the appearance of colour

[1] C W Mason, *J. Phys. Chem.*, **27**, 201, 1923.
[2] *Proc. Indian Assoc. Sci.*, **8**, 23, 1923.
[3] *Proc. Indian Assoc. Sci.*, **7**, 1, 1921.

varying with the angle of observation in other directions, these being most pronounced in the backward scattering, and (d) a large dependence of the intensity of the scattered light on the plane of polarisation except in the forward and adjacent directions. In the case of the colours exhibited by *Coracias Indica*, none of these features is observed. Actually, the layer of colour in the feathers appears much less luminous when viewed with the light facing the observer than in the opposite direction; immersing the feathers in a cell of benzene abolishes the surface reflexion at the exterior of the barbs without altering this particular feature of the internal colour.

Then again the colour in the forward direction though of low intensity is saturated in hue. Polarisation effects are hardly noticeable with *Coracias Indica*. Thus the observations seem unfavourable to the general idea that the colours are due to diffraction by spherical cavities, though in view of the strict inapplicability of the theoretical investigations to the present case, some reservation of opinion would be justifiable. It is not improbable, for example, that theoretical investigations for the case of a hollow cavity in a medium of much higher refractive index may actually indicate the backward scattering to be more intense than the forward one, as actually observed with *Coracias Indica*.

5. A possible alternative theory

The highly saturated nature of the colours, the fact that they change, though only slowly, with the angle of observation and the change of colour produced by the penetration of water into the barbs, all conspire to indicate that the phenomena, while undoubtedly due to the presence of cavities in the material of the barb, should be classed as interference rather than as diffraction effects. The succession of colours observed correspond to the colours of Newton's Rings in the second or third order and not to those of the first order. This may perhaps be regarded as a difficulty, since if very thin films are present, one would expect that colours of the first order should also be capable of being observed in individual cases. It is clear that further investigation of the problem of light-scattering by a spherical hollow cavity in a medium of higher refractive index is necessary, before we can definitely decide between the scattering and the interference theories of the colours of *Coracias Indica*. That these colours are not a simple Tyndall blue is evident enough. The difference between the diffraction and interference theories resolves itself into a question of knowing the exact form of the cavities responsible for the return of the light from within the barb. Only in the case of simple spherical cavities would we be justified in regarding the colours as a diffraction effect. With elongated or flattened cavities, the phenomena should be assimilated with those of interference.

It is obvious that elongated or highly flattened cavities would scatter light very differently indeed from simple spherical cavities. A cylindrical cavity, for example, would concentrate most of the light scattered by it along with the surface of a cone co-axial with itself and having its generating lines inclined to the axis at the same angle as the incident ray, but on the opposite of the normal. Then again, a flattened cavity would concentrate most of the scattered light in a single direction, namely, that of regular reflection. A simple spherical cavity, on the other hand, would distribute the scattered light impartially in all directions if it were sufficiently small.

Some insight into the form of the cavities responsible for the colours in *Coracias Indica* may be obtained by placing a feather on the rotating stage of an ordinary microscope and illuminating the same by a strong beam of light at a suitable angle. As the feather is rotated, positions are obtained in which the exterior surface of the barbs reflects light strongly and shows a brilliant white line superposed on the interior coloured background. The brightness of the colours is found to vary very strikingly at the same time, as the stage is rotated. This effect cannot be explained as due to a screening of the surface of the barbs by the barbules, inasmuch as the light is incident at a suitable angle to the surface of the barb and the latter is fully illuminated. Nor can it be ascribed to surface reflection depleting the intensity of the light entering the barb. The latter effect can completely be avoided by immersing the feather in a cell containing a suitable liquid placed on the stage of the microscope. It seems unlikely that such immersion would make any difference to the observed effects. We are thus forced to the conclusion that the cavities responsible for the colour reflection are extended structures capable of giving rise to interference effects rather than simple spherical cavities scattering equally in all directions.

6. Effect of penetration by liquids

In the preceding paragraphs we have already described the changes of colour produced by damping the feathers with water. Apart from the change of colour, such damping undoubtedly reduces the intensity of the colours. This is readily explained by the weakened reflections at the surface of the cavities when filled with water. If, instead of water, we use a liquid such as benzene of higher refractive index, the penetration is much slower but is ultimately more or less complete. On a rough inspection, it then appears as if the colours have disappeared. Placing the feathers under the "Ultra-opak" microscope, however, it is seen that the layer responsible for the colours, though only feebly luminous, can still be seen, the dark blue portions now appearing green and the light blue, dark red. In the absence of knowledge as to the exact extent to which the absorption of fluid might result in an enlargement of the cavities, it is not possible to definitely correlate the change of colour with the refractive index of the penetrating liquid. In a general way, however, it can be seen that the displacement of the colours towards the red end of the spectrum is what we should expect theoretically.

7. Summary

Observations are described with the feathers of *Coracias Indica* which throw doubt on the correctness of the theory that the blue of these feathers is a simple Tyndall effect due to the scattering of light by minute air cavities within the substance of the barb. Observations with the "Ultra-opak" microscope show that the coloured layers may exhibit tints ranging over the whole spectrum. A simple Tyndall effect is thus definitely insufficient to explain the observed phenomena. Further studies indicate that the cavities responsible for the colours are extended structures. The two alternative possibilities, namely, diffraction by cavities not small compared with the wavelength and interferences from the surfaces of minute films are considered and discussed, without a final decision being reached.