

1902, in Ware. The Dovekie has been taken at Greenfield and Belchertown where in 1872, large numbers were secured. The Leach's Petrel was taken September 2, 1900, at Agawan; October 11, 1905, at Hampden Ponds; and in October, 1908, at Smith's Ferry. A Black Skimmer was found exhausted in the latter part of August, 1893, in West Springfield. In 1877 or 1878, a number of Double-crested Cormorants were taken from small flocks near Springfield. Red-breasted Mergansers have occurred—one April 28, 1908, in Longmeadow and one prior to that in Northampton; also Gadwalls—one October 14, 1904, at Glastonbury, Conn., and one November 5, 1883, at East Hartford. Old-squaws, American, Surf and White-winged Scoters, and Brants have been either identified or taken near Springfield. Two species of Phalaropes have been known to use the Valley in the fall as well as the Purple Sandpiper, Red-backed Sandpiper and Willet.

By the keeping of migration dates up and down the Valley, museums, scientists and interested bird students have collected much valuable data relative to arrivals and migrations. It is hoped to establish a series of banding stations throughout the length of the Valley. Bird banding more than any other agency should reveal all and more than all that can be written emphasizing the importance of the Connecticut Valley as a highway for migration; and of its constant use, year in and year out, by thousands of migrants in both directions.

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BLUE FEATHERS¹

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PHYSICISTS distinguish between pigment and structural colors. Pigment colors depend on the chemical nature of the material and are due to the absorption of certain wave-lengths by the mole-

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cules. Structural colors depend upon, or are modified by, the physical arrangement of the material. The colors produced by a prism are structural colors and so are the diffraction colors of gratings and the interference colors of thin films. With turbid media in which the particles are small relatively to the wave-lengths of light, the shorter or blue wave-lengths are scattered much more than the longer or red wave-lengths. In consequence such a medium is reddish by transmitted light and bluish when seen from the side. These blues are called Tyndall blues, typical cases being the blue of the sky, of cigarette smoke, of skimmed milk, and of blue eyes. In all these cases of structural colors, the colors can be produced starting with materials which are in themselves colorless. The rain drops which give rise to the rainbow are colorless; a diffraction grating may be a sheet of colorless glass with parallel lines ruled on it; a thin film of a colorless oil will give us interference colors, and we can get the Tyndall blues by suspending a colorless powder in water. The arrangement of the material is what gives rise to the colors. In feathers the reds, yellows and blacks are pigment colors; the whites, blues, and the metallic colors are structural colors; and practically all the non-metallic greens are a structural blue and a pigment yellow.

A study of the question of structural colors in feathers indicated that this is apparently a problem calling for a co-operative research on the part of men representing different fields. This point of view was put before the Heckscher Research Council, and on July 1, 1921 a grant (No. 37) was made, for the study of structural colors in feathers, to a committee consisting of Messrs. Bancroft, Chamot, and Merritt, representing physical chemistry, chemical microscopy and physics respectively. As an unofficial member representing ornithology, the committee has had the enthusiastic co-operation of Mr. Louis Agassiz Fuertes, who was really responsible, initially, for the starting of the whole investigation. In addition, the work of the committee has been facilitated by the courtesy of Prof. A. A. Allen of Cornell University and of Dr. Frank M. Chapman of the Natural History Museum in New York, who have furnished many interesting feathers. For the experimental side the committee has been fortunate in securing the assistance of Mr. Clyde W. Mason, assistant in chemical microscopy at Cornell University.

It is to his skill and perseverance that the successful outcome of the investigation is due.

White is the most common and the simplest of the structural colors. We do not get the sensation of white when white light is reflected from a mirror but we do get it when white light is reflected diffusely or scattered from a surface. Thus powdered glass, chopped ice, snow, sugar, foam, clouds, paper, etc. appear white because of the light scattered from the surface. A block of ice or a pane of glass is transparent and not white. If a transparent, colored crystal, blue copper sulphate for instance, is powdered fine, the light scattered at the surface predominates so over the light which has passed through the crystals that these latter appear nearly white. If the powdered crystals are immersed in a liquid having practically the same index of refraction as the crystals, the amount of light reflected diffusely from the surfaces is reduced to a minimum and the powder appears blue if the large crystals were blue, or transparent if the large crystals were practically colorless. Oiled paper becomes translucent. The transparent "windows" in many business envelopes are made of paper which has been impregnated with material having very closely the same index of refraction as the paper, thereby doing away with the diffuse reflections which ordinarily make the paper appear white and opaque. Water colors get paler as they dry because the water is replaced by air. The difference in the indices of refraction between the medium and the pigment being greater, there is more light scattered from the surface of the pigment and this therefore looks paler. It has been stated¹ that the reason some flamingoes in zoological gardens are redder than others is because the red ones have more oil in their feathers, this making the feathers more translucent and intensifying the red.

All the so-called white pigments owe their whiteness to the diffuse reflection of light. Ground sand is not so effective a white paint as white lead because its index of refraction is too near that of linseed oil. If we had a drying oil with an index of refraction about equal to that of white lead, this substance would be worthless as a pigment, whereas sand would make a good one.

¹ Krukenberg: Vergleichend-physiologische Studien, 1 (5), 90 (1887).

The white color of flowers is due to the cellular, optically inhomogeneous, structure. The tiny cells, filled with juices, scatter the light very completely. In some flowers these cells may be seen with the naked eye, as in the narcissus, the petals of which have a frothy, white appearance. Crushing the flower destroys the minute structure and removes the juice, leaving a transparent mass. Birch bark can be made colorless and transparent by impregnation with cresol, etc. In this case the bark is porous and the pores are filled with air which can be seen to escape in bubbles when the cresol displaces it from the pores. The white bark of the sycamore behaves similarly, though here the outer surface of the cellular layer is distinctly rough, thus increasing the diffuse reflection and giving a chalky appearance, which disappears on impregnation with cresol. Certain butterflies (*Pieridae*) owe their whiteness¹ to the presence of uric acid in a very finely divided form. Large crystals of uric acid are colorless and transparent. The intensely white bellies of such fish as the mackerel and the flounder owe their color to crystals of guanin² which in themselves are colorless and transparent.

It is generally recognized that white in feathers is a question of structure;³ but there seems to be no definite statement as to the exact mechanism and consequently a more detailed study has been made. The whites fall into two classes: a white which disappears if the feather is treated with a liquid of the proper refractive index; and a white which is not changed by a liquid of any refractive index whatsoever. In both cases the sensation of white is produced by the diffuse reflection at a multitude of minute surfaces of optical inhomogeneity; but the two types differ in the nature of the inhomogeneity in structure.

The barbules of white feathers play the chief part in the sensation of whiteness when looking at a feather. The barbules of such typical white feathers as those of the white Leghorn, Turkey, Pigeon, Duck, Peacock, etc., are seen under the microscope to be

¹ Hopkins: Phil. Trans. 186 B, 661 (1896).

² Cunningham and McMunn: Phil. Trans. 184 B, 765 (1893).

³ Cf. Newbigin: Colors in Nature; Beddard: Animal Coloration; Poulton: Colours of Animals; von Bezold: Theory of Color in Relation to Arts and Industry; Gadov: Proc. Zool. Soc. London, 1882, 409.

colorless, transparent, more or less spatulate processes on the barbs of the feathers. They possess no significant internal structure, and when mounted in balsam, cresol, etc., are transparent and almost invisible to the eye. Their surfaces are often somewhat roughened. These innumerable, transparent, colorless barbules cause a large amount of diffuse reflection and consequently the feather appears white, exactly as snow, cotton, paper, etc., appear white.

When, however, the feather is wetted thoroughly with balsam, or cresol with an index of refraction of 1.54, which is practically that of the barbules, the feather becomes transparent and one may read through it with ease. The barbs themselves are not rendered transparent by this surface wetting and appear as white lines in the transparent plane of the feather; but they do not occupy a large proportion of the space and consequently the effect as a whole is one of transparency.

A similar type of whiteness is observed in the barbs and shafts of white feathers. In these the scattering takes place at the surface of pores in the walls of the cells of the barbs or at the surfaces of the bubble-like, cellular, pithy material in the core of the quill, these surfaces being in contact with air. The structures of these pores, bubbles, etc., are readily observable under the microscope. They are actually transparent and colorless if a thin section of the part of the feather in question is examined with moderate magnification. If the air in these pores and interstices is replaced by a liquid of the proper index of refraction, about 1.54, the sensation of whiteness disappears and the feather appears transparent. Since most feathers have the porous structures encased in a transparent, almost impermeable membrane of keratin, there is some difficulty in replacing the air by liquid. Prolonged soaking will do it; but the desired result may be obtained more rapidly by sectioning, and thus laying open, the porous part. Longitudinal, oblique, or transverse sections permit the liquid to penetrate the feather rapidly, the pores filling in a few minutes, the air in them bubbling out, as can be seen under the microscope. Cresol, with an index of refraction of 1.54, gave the best results. If the index of refraction of the liquid differs widely from 1.54, the whiteness

is not destroyed completely and only partial transparency is obtained.¹

The second type of white found in feathers is characterized by the fact that liquids of any refractive index whatsoever have no effect upon it. This type is found in most white quills (white turkey, goose, hen, etc.) and occurs usually in the outer sheath of keratin, which appears a translucent white to the naked eye. Microscopic examination shows that this keratinous sheath is fibrous and consists of numerous, elongated cells, packed closely together to form the horny layer. There are enough differences in the refractive indices of different portions of the material to cause diffuse reflection and a sensation of whiteness, which is not very marked because the differences in the indices of refraction are not large. Since the differences are due to the presence of two or more solids, addition of an organic liquid will not eliminate these differences and will not affect the whiteness.

The white or albino varieties of birds, which normally are colored, are white simply because of no pigment. The structure is, or may be, the same in the colored and the white varieties; but the absence of pigment permits the structural white being seen. Whitman¹ states that albinism is a deficiency of pigment (which may develop in later life) rather than any special development of white.

The non-metallic blues, such as the feathers of the Blue Jay, the Bluebird, the Indigo Bunting, and the Kingfisher are structural colors. There is no blue to be seen by transmitted light and nobody has ever succeeded in extracting any blue coloring matter² from any blue feather. Haecker and Meyer³ showed that the structural blue is what is known as Tyndall blue and is due to the scattering of light by minute air-bubbles in the horny mass of the

¹ The "clearing" of tissue, as a step in its preparation for study, is a process familiar to the biologist and is essentially similar to the treatment of the feather. If the cells of a tissue are filled with air or with a liquid having an index of refraction differing considerably from that of the cell walls, the finer details of the latter can only be brought out by making the mass more transparent through introduction of a liquid having practically the same index of refraction as the tissue. The mounting liquid, usually used is balsam with a refractive index of 1.54, which is close enough to that of most organic tissue to be satisfactory.

² Carnegie Inst. Pub. No. 257, 2 (1919).

³ Krukenberg: *Verleichend-physiol. Studien*, 1 (5) 98 (1881); 2(5) 154 (1882).

³ *Zool. Jahrbuch. Abt. Syst. Geog. Biol. Thiere*, 15, 267 (1902).

feather; but this view has not been accepted generally by the biologists. It is believed that the data now submitted will be conclusive as to the correctness of Haecker's theory.

A turbid medium, containing particles something less than 0.6 microns (0.0006 mm.) in diameter and having an index of refraction differing from that of the medium, is reddish by transmitted light and bluish by reflected light. The blue goes over to the violet as the particles become smaller. If the particles, which scatter the light, are sufficiently large to scatter the longer wave-length appreciably, the scattered light is no longer a clear, deep blue, but changes towards the white. Tyndall showed that increasing the size of smoke particles gave a whiter smoke. The blue of a turbid medium shows up best against a dark background because this serves to keep any transmitted light from reaching the eye. In fact, a blue which is quite marked against a dark background may appear whitish or almost colorless against a light background.

If the suspended particles and the medium have the same index of refraction, there can be no scattering of light at the surfaces of the particles and the Tyndall blue will disappear. As a matter of fact, even approximate agreement between the refractive indices of the particles and the medium is sufficient to cause a very marked decrease in the intensity of the scattered light. The behavior of a collodion jelly was found to show this fairly well. If a limpid, colloidal solution of collodion in an ether-alcohol mixture is allowed to evaporate slowly, a soft, turbid, bluish jelly is formed, the color being the Tyndall blue. If the jelly is immersed in a liquid with which the alcohol-ether mixture is miscible, the mixture will diffuse out fairly readily and can be replaced by the other liquid. This has been done with water, kerosene, cresol, cedar oil, monochlorobenzene, and other organic liquids. When the substituted liquid is cresol, the jelly ceases to be whitish blue and becomes colorless and transparent; its outlines being almost invisible in the cresol. When the excess cresol is poured off, the jelly looks like a clear, colorless piece of glass, though it has not lost its gelatinous character. The scattering of the light by the jelly has been eliminated by making the medium cresol, which has practically the same index of refraction as the collodion. The data in Table I show that the effect depends on the index of refraction of the liquid in the pores of the jelly.

TABLE I.

Liquid	Refractive Index (N)	Turbidity (Color)	Outline
Monobromo Naphthalene	1.66	marked	distinct
Carbon Bisulphide	1.625	marked	distinct
Iodobenzene	1.61	moderate	distinct
Bromoform	1.58	very slight	faint
Cresol	1.54	none	invisible
Chlorobenzene	1.525	none	invisible
Cedar Oil	1.51	none	almost invisible
Xylene	1.494	very slight	very faint
Turpentine	1.474	slight	distinct
Kerosene	1.443	moderate	distinct
Alcohol	1.37	moderate	distinct
Water	1.33	very marked	distinct

From the table we see that the bluish color is more marked, the greater the difference between the indices of refraction of the liquid and of the collodion; but that the effect is similar with monobromo naphthalene which has a higher index of refraction than the collodion, and with water which has a lower index of refraction.

The light scattered by a turbid medium is polarized provided the particles are small enough to scatter blue light. This polarization can be observed easily by viewing a beam of light in a turbid medium through a nicol prism, at right angles to the path of the beam. The vibrations of the scattered light are in the plane normal to the direction of the beam in the turbid medium, and a nicol prism, adjusted to intercept vibrations in this plane, renders the beam invisible. If the nicol prism is rotated, the beam is visible through it only when the nicol is in position to transmit vibrations normal to the direction of the beam. The light scattered by the turbid medium is cut out almost completely when the nicol is set to transmit only the vibrations in the plane parallel to the direction of the beam. This rather striking effect can be seen easily with blue smoke, collodion jelly, skimmed milk, partially devitrified glass—in fact with any medium which gives the Tyndall blue. If the blue is whitish, the polarization of the scattered light is not so complete and not all of the light can be cut out by the nicol prism.

A more sensitive means of detecting the polarization is by viewing the scattered light through a nicol prism with a "first

order red" gypsum plate between the nicol and the turbid medium. This arrangement is used by petrographers to detect slight polarization in the study of crystals with the petrographic microscope.¹ It substitutes a color change from greenish blue to reddish purple, when the nicol prism is rotated in a beam of polarized light, for the usual change from light to dark. The change in color can be detected more readily than the change in intensity, especially when the polarization is only partial.

Professor T. R. Briggs, of Cornell University, showed that a good Tyndall blue can be obtained by heating a Jena glass rod carefully until it devitrified partially. Still better results were obtained by Mr. Mason who heated a piece of Jena glass tubing in a combustion furnace at a temperature just below the softening point of the glass. Two hours heating is generally sufficient; but the time required is shorter at higher temperatures. It is best to allow the glass to cool at intervals and to examine it against a dark background. A strong clear blue results, which changes to an opal white if the heating is too prolonged. The blue color is due to the formation of tiny crystal nuclei which scatter the light. These particles can be seen under the microscope with 4 mm. or higher power objectives, if a horizontal beam of light is projected through a piece of the glass on which the microscope is focused. With careful focusing and some adjustment of the illuminating beam, the blue color seen in the field may be resolved into a dense mass of tiny points of blue light. With a little adjustment this crude ultra-microscope arrangement serves fairly well to detect the minute particles present in other Tyndall blues. The opal glass, which is obtained by longer heating, undoubtedly contains coarser crystals. Since the color by transmitted light is orange-red, the reflected light must theoretically be a bluish-white but the blue is lost to the eye.

By suitable length of heating the partially devitrified Jena glass tubes can be made to give blues ranging from deep indigo to pale sky blue or even to white. The color may be brought out most strikingly by painting the inside of the tube with black paint, so as to cut off the transmitted light. The blues of such specimens

¹ Johanssen: *Manual of Petrographic Methods*, pp. 386, 393.

rival the richest of those found in feathers and of course are stable at ordinary temperatures.

In the non-metallic feathers, so far as known, the color always appears in the barbs. We find that a typical blue feather, that of the Blue Jay, shows the following structure in the barbs:—

1. A transparent, colorless, horny, outer layer or sheath, 10–15 microns in thickness, which serves apparently as a protective coating for the barbs.
2. Beneath this is a layer of cells, polygonal as seen from the surface, about 15 microns in diameter and the same in depth. The boundaries of these cells are ordinarily invisible, and, by reflected light, the cells give the appearance of a thick layer of blue enamel. (Described by Fatio, who called it “*émail*.”)
3. Beneath the layer of cells, and occupying the central portion of the barb, lie closely packed, hollow, medullary cells which, contain a dark, granular pigment (melanin) mainly on the walls of the cells.

Gadow¹ summarizes his description of the barbs of a typical blue feather as follows:—

1. A transparent, apparently homogeneous, sheath of ceratinine.
2. One layer of prismatic (polygonal) cells.
3. A brownish pigment.

Gadow recognizes the prismatic or polygonal cells as the seat of the blue color; but his reasoning as to the cause of the color production is incorrect, as will be pointed out.

Longitudinal, transverse, and oblique sections show these relationships more clearly than does the barb as a whole. The blue color is localized plainly in the layer of cells immediately underlying the outer sheath of the barbs. Removal, by sectioning, of the outer sheath layer, or of the pigmented medullary cells does not affect the appearance of the blue cells, when they are examined by reflected light. It is evident that the blue of the feather originates in this layer of polygonal cells and a detailed study of them is therefore necessary for an explanation of its cause.

The cells are seen to be distinct and separate, like tiles in a floor. Their color is a turbid blue by reflected light and a turbid reddish-

¹ Proc. Zool. Soc. London, 1882, 409.

brown by transmitted light. A most striking phenomenon is that the cells, when laid bare by removal of the outer sheath or of the medullary portion of the barb, are rendered nearly colorless and transparent by immersion in xylene. The change takes place cell by cell; and, as it does so, the details of the structure become visible. The cell walls are seen to be 3-4 microns thick, apparently rough and granular on their inner surfaces, and with a central cavity, roughly spherical in shape and 4-5 microns in diameter. The blue color is apparently only in the cell walls. When the xylene evaporates, the blue color and the turbidity of the cells are restored. Other liquids behave similarly; but the amount of change varies with the refractive index of the liquid, the change being less striking when the refractive index is less than that of xylene (1.49). The blue color of the cell walls does not disappear completely and the cell walls are not rendered completely transparent unless the refractive index of the liquid is about 1.54 ± 0.04 , though the line cannot be drawn sharply. The index of refraction of the cell walls is very close to 1.54. Liquids with an index of refraction greater than 1.58 fail to destroy the blue color or to render the cell walls transparent.

Ortho-cresol is the most satisfactory of the liquids used, both as to refractive index, which agrees almost exactly with that of the cell walls, and as to the rapidity with which it penetrates the feather. Even the entire feather of the Blue Jay, with the blue barbs protected by a thick sheath of keratin, is permeated in about four days. The black pigment in the medullary cells becomes plainly visible and the entire feather appears black. When the ortho-cresol evaporates or is washed out with alcohol, the original color of the feather is restored perfectly. The results thus obtained agree with those of Haecker and Meyer¹ on blue *Cotinga* and *Malurus* feathers except that they make the index of refraction of the cell walls about 1.52 instead of 1.54. Their data are given in Table II, the first color being that for reflected light and the second for transmitted light.

Study of the actual process of permeation of the cell walls is rather difficult on account of the rapidity with which it proceeds

¹ Zool. Jahrb. Abt. Syst. Geog. Biol. Thiere, **15**, 267 (1902).

TABLE II.

	Refractive index for Na light	
Pure CS,	1.627	Distinct color, pale blue and pale yellow
CS, : C ₆ H ₆ = > 7 : 1 by volume	1.558	Distinct color, pale blue and pale yellow
CS, : C ₆ H ₆ = > 3 : 1 by volume	1.558	Traces of color
CS, : C ₆ H ₆ = 1 : 1 by volume	1.558	No color
Canada balsam		
Av. =	1.54	No color
Cedar oil	1.515	No color
Xylene	1.502	No color
Benzene	1.501	No color
Alcohol	1.362	Distinct color, light blue and golden yellow, changing to pale blue
Water	1.333	Strong color, sea-green and reddish yellow. Great transparency but pores visible.
Air	1.000	Strong color, cloudy blue and cloudy reddish yellow. Not transparent.

when the cells are exposed, as in a section, to the action of the liquid. Tiny air bubbles are often noted at the outer edges of the cells as the liquid penetrates, and a small bubble is often entrapped in the central cavity. As the liquid evaporates, air seems to be sucked suddenly into the cells through the walls, the central cavity fills with air, and the cell walls become blue again.

Careful observation shows innumerable, tiny pores, filling the cell walls and giving them a turbid, spongy appearance. A 4 mm. or higher power objective is necessary to reveal this porous character. Haecker and Meyer estimate the diameter of the pores at about 0.3 micron in a *Malurus* feather and at less than that in a *Cotinga* feather. A section of the cells in ortho-cresol appears practically invisible with the dark field illuminator. A few scattered points of blue light appear, which are probably pores from which the air has not been displaced by cresol. If the cresol is absorbed at one side of the cover glass by blotting paper, while

alcohol is applied at the opposite side, the cresol in the pores of the cell walls is replaced by alcohol, and the pores then show up plainly, the cell walls appearing filled with innumerable tiny points of blue light, distinguishable with difficulty as separate points. Water may be substituted for alcohol in the same way, and the intensity of the blue light increases. If the liquid in the pores is allowed to evaporate, the blue scattered by the air-filled pores is so bright as to give the effect of an almost solid color.

By transmitted light the dry preparation is yellowish-orange, this color disappearing when alcohol, or better cresol, replaces the air in the pores. This yellow or orange color, seen by transmitted light in the blue cells of blue feathers, has been confused with pigment color. Gadow¹ says that "the color of the cones [polygonal cells] is pale yellowish, or, if this is only the reflection of the underlying pigment, they are colorless." This is decidedly not the case, for the color exists unchanged even when the dark pigment backing has been removed by longitudinal or oblique sectioning and disappears completely when these polygonal cells are penetrated by a liquid of suitable refractive index. When thus permeated, these cells show no tinge of color but are transparent and colorless, thus proving conclusively the absence of any appreciable amount of pigment. When examined on a dark field, the cells are seen by virtue of the blue light which they scatter. The dark pigment layer which lies beneath the blue cells serves as a dark background to prevent transmitted light interfering with the production of the blue. If this dark pigment layer is removed by longitudinal sectioning, the blue color is seen only when the transmitted light is cut off by some sort of dark backing.

The Blue Jay feather is blue with black cross-bars and a white tip. If the white tip differs from the blue portion of the feather by not having any dark pigment, it should be possible to bring out the blue by suitable treatment. If surface reflections are eliminated by immersing the feather in a liquid with a refractive index of 1.54 for a time too short for the liquid to penetrate, and if the feather is then examined on a dark field by reflected light, a bluish color is plainly visible. Painting the back of the Blue Jay

¹ Proc. Zool. Soc. London, 1882, 409.

feather black with India ink makes the tip appear distinctly bluish. The blue is not so good as in the rest of the feather because the black background is not in as good a place as in the natural feather. The barbs of the white tip are reddish yellow by transmitted light. They are colorless when permeated by an appropriate liquid. Unless the background of India ink is supplied, the turbid structure of the white portion of the feather will not appear blue because the empty, unpigmented, medullary cells scatter white light like bubbles of air, and serve as a light background, thus obscuring the blue. If the medullary portion of the barb is removed by sectioning, there is no apparent structural difference between the porous cells in the blue and the white parts of the feather.

Removal of the pigment by prolonged bleaching with three per cent hydrogen peroxide destroys the blue color, though the blue is found to be unchanged if the pigment is not bleached completely. Examined on a dark field, the barbs of a feather which has been bleached almost perfectly, appear a pale, whitish blue, because of the medullary cells, which were black, now act to some extent as a light background, and therefore make the blue paler. The swelling of the feather is also a factor. When blue feathers are painted black on the back with India ink, bleaching does not destroy the blue color because the India ink is not acted upon.

Surface reflections from the outer layer of keratin of the blue barbs can be eliminated by immersing the feather in a liquid which has a refractive index of 1.54 and which does not penetrate too rapidly. A mixture of oil of cloves (1.538) and oil of anise (1.557) works well. Such a preparation consists essentially of the polygonal, cellular layer, surrounded by an optically homogeneous medium, because the keratin and the immersion liquid are practically identical optically. There is no change, therefore, in the light illuminating the preparation until it strikes the polygonal, cellular layer.

When a portion of a blue barb, mounted in this way and illuminated by a horizontal beam of light, is examined through the microscope as it lies on the stage, it appears fully as bright a blue as when seen under ordinary conditions. Examination by a nicol prism, mounted as an analyzer on the microscope, shows that

the scattered blue light is polarized, though not perfectly, and that the plane of vibration of the scattered light is normal to the direction of the incident beam. Rotating the analyzing nicol gives partial extinction when the plane of vibration of the nicol is parallel to the direction of the illuminating beam. Better results can be obtained by placing a "first order red" gypsum plate below the nicol. On rotation the color changes from greenish-blue to reddish-purple. Polarization of the scattered light is unmistakable, though far from complete. As an alternative method, the barbs may be illuminated by a horizontal beam of polarized light and the plane of polarization of the illuminating beam can be rotated. The intensity of the blue light is distinctly less when the vibrations of the polarized beam are in the vertical plane. A "first order red" plate may of course be inserted between the nicol prism and the preparation.

The incompleteness of the polarization of the scattered light must be due to the presence of some relatively large pores which scatter the light without polarizing it. Their presence would, of course, dilute all the effects which might otherwise be obtained if only very small pores were present. The presence of a greater number of larger pores is undoubtedly one reason why the white parts of the Blue Jay feathers do not give nearly as marked effects with polarized light as do the blue parts, even though the structures are essentially the same.

Haecker and Meyer¹ have shown that the variation in the intensity of the blue light reflected from a blue *Malurus* feather with varying wave-length of the incident light can be represented quite well by Rayleigh's formula for Tyndall blues.

Nearly all blue feathers show a change in color by reflected light to a greater or less degree, depending on the relative positions of observer, feather, and illumination. This is especially noticeable in the feathers of *Procnias viridis*, *Calliste lavinia*, *Pionus chalcopterus*, *Sialia arctica*, and other birds of similar bright blue color. When the observer faces the source of light and observes such a feather by reflected light, holding the feather below the line from the observer to the light, the feather appears a deep, almost

¹ Zool. Jahrb. Abt. Syst. Geog. Biol. Thiere, **15**, 267 (1902); Bancroft: Jour. Phys. Chem. **23**, 409 (1919).

indigo, blue. If the observer stands with his back to the light and examines the feather by reflected light, the feather appears a lighter more greenish blue. It is only the relative positions of illumination and observer to the feather that affect this color change and not the angle at which the light strikes the feather or the angle at which the feather is observed.

This phenomenon can easily be understood after examining an 'artificial blue feather' consisting of a partially devitrified Jena glass tube as previously described. Such a piece of glass is deep blue when seen against a dark background, while the transmitted light is yellowish orange. When the glass is held in such a position that both the blue scattered light and the yellowish transmitted light can reach the eye, the resultant color is a light, greenish blue, very similar to that observed with the feathers. In the feathers the color cells have walls of Tyndall blue, while the central cavities of these same cells are empty and may be compared to bubbles of air distributed more or less regularly in the turbid medium which forms the walls of the color cells. Bubbles appear relatively dark by transmitted light because a large proportion of the incident beam is reflected back at their surfaces. When the feather is between the observer and the source of illumination, though below the line connecting the two, the empty, bubble-like cavities of the color cells serve to some extent as a dark background for the Tyndall blue of the cell walls. When the observer has his back to the source of illumination, these cavities reflect some of the incident light back through the turbid medium to the eye, thus combining the reddish-yellow color of this light with the predominating blue color due to the scattering by the cell walls and thus giving a greenish-blue color to the barbs.

With dull blue feathers the blue is much less intense, appearing almost grayish, when the observer faces the source of light and examines the feather by reflected light with a large angle of incidence. When the observer is between the source of illumination and the feather, the blue color shows plainly by reflected light. This is very striking with *Andigena nigrirostris*, *Cyanocorax*, and, to a less degree, with other dull blue feathers. This may be explained as due to reflection from the surface of the feathers. Light, which falls perpendicularly on a transparent surface, is

mostly transmitted; but the intensity of the transmitted light decreases markedly and that of the reflected light increases correspondingly when the angle of incidence is large. With a medium having a refractive index of 1.55 less than five per cent of the light striking normal to the surface is reflected, the remainder being transmitted. At an angle of incidence of 75° twenty-six percent of the light is reflected, and sixty-two per cent is reflected when the angle of incidence is 85° . Consequently, when the angle of incidence is large, much of the light is reflected from the surface of the feather and does not enter the turbid medium at all. The blue is made paler by the white light reflected from the outer surface of the feather. When the barbules are dark, the resultant effect is grayish and dull whereas the blue color appears at its maximum intensity if there is very little reflection from the surface (illumination perpendicular) or if this reflection does not reach the eye (illumination and eye on same side of feather). This effect is mentioned because it influences the appearance of all feathers more or less and because it plays an important part with the structural blues in regulating the intensity both of the reflected and of the scattered light.

Another interesting property of blue feathers is that, in general, the color is rather easily modified by pressure, the lighter blues changing to deep blue or indigo when the barbs are compressed beneath a cover glass under the microscope. The dark blue appears first where the pressure is greatest as, for instance, where two barbs cross each other. Unless the pressure has been very severe, the original color is restored when the pressure is removed. Crushing or hammering usually destroys the blue completely. Since the indigo blue produced by pressure is a color which occurs frequently in feathers not under pressure, it must be caused by a change in the structure of the cell walls which give rise to the color. Pressure would be expected to decrease the size of the pores in these cell walls and should therefore give a deeper blue, which is exactly what happens. When the pressure has not been too great, the elasticity of the cell walls would restore the pores to their original size when the pressure was removed and consequently the original blue would return. Even the white tips of the Blue Jay feather show a distinct blue under the microscope when pres-

sure is applied, thus indicating that they possess essentially the same structure as the blue portion of the feather except that some of the pores in the cell wall are abnormally large. The change of color with pressure is shown best by barbs which are not armored by a thick sheath of keratin. Under pressure dark blue barbs appear black because the pores of the walls in the color cells become too small to affect light. The cell walls therefore become transparent, permitting the underlying layer of dark pigment to be seen.

As might be expected the color change is in the reverse direction—from dark blue to light blue—if the cell walls are made to swell. Dilute sodium or ammonium hydroxide solutions, cresol, phenol vapor, gaseous ammonia, sodium hypochlorite, hydrogen peroxide, and even water have marked swelling action on feathers, the effect on the cell walls being more striking with those barbs which have a relatively thin keratinous sheath layer, because the color cells are then more readily exposed to the action of the reagent. Water and the solutions of the alkalies have the most effect on blue feathers. The original blue color of the feather always becomes paler, the dark indigo blues changing to sky blue, and the light blues becoming almost white. When the reagent which causes the swelling is removed either by washing or by evaporation, the original color is restored. Pressure on the swollen barbs also restores the original color or may even make the barbs a darker blue.

This change of color on swelling explains the frequently observed, perfectly reversible change from blue towards white when certain blue feathers are wetted. The feathers, which show this change in a striking manner, are generally waxy in appearance and have prominent barbs with poorly developed barbules, and with only a thin outer layer of keratin. Typical feathers are those of *Calliste lavinia* and *Procnias viridis*. On a collecting trip Mr. L. A. Fuertes shot a specimen of *Procnias viridis*, which fell into the river and he was horrified to find that the bright blue bird was quite white when fished out of the water. Fortunately the color returned when the feathers became dry.

The effects caused by swelling are distinct from those due to penetration by liquids, for permeation by liquid always results in a greater transparency of the barb, while swelling tends rather

to decrease the transparency, as well as to change the color. However, a single reagent may cause changes both by reason of its swelling action and also because it penetrates the pores in the walls of the color cells. For instance, cresol, as it acts progressively on the color cells of a barb, first swells them, giving a white rounded appearance to the individual cells, and finally permeates the cell walls, rendering them transparent and colorless. The cell cavities may yet contain bubbles of air, which finally appear to dissolve in the cresol as it fills the cavities. Water or dilute ammonium hydroxide swells the color cell walls, causing white, and finally permeates these porous walls; but, on account of the low refractive index of these liquids, the cell walls are rendered only partially transparent. By reflected light the empty bubble-like cavities of the color-cells may be seen, appearing almost pinkish orange through the porous cell walls, the incident light passing through them twice before it reaches the eye, thus increasing the pinkish orange color which white of this nature transmits. It is possible that the dark brown color of the medullary cells aids in giving a brownish gray, tinged with pink, to the feather which has been subjected to long swelling and penetration by a liquid of refractive index markedly different from that of keratin. These peculiar appearances, observable only with special treatment, are of little significance, but an explanation of them in the light of the findings here presented seems necessary. It is not an essential part of the proof of the nature of the blue of feathers, however.

It is worth noting that when light and dark blue adjoin each other in the same barb, one shade of blue grades into the other cell by cell. The individual color cells are of one shade throughout, usually either light or dark blue, with few cells showing intermediate shades of color. The appearance is that of tiles in a floor, part of which is light blue, part composed of light and dark blue tiles, and part of dark blue tiles. Apparently the cells, developing as individuals, though side by side, have slightly different color-producing structure. This same character appears when several adjacent, apparently identical, cells are subjected to swelling. Some are affected much more rapidly than others, and appear markedly lighter in color, though uniform in themselves. This simply emphasizes the individual character of the cells, as units of the color-producing layer.

The general appearance of some blue feathers is influenced markedly by orientation alone. For example, the blue feathers of *Coracias indica* when viewed from a position inclined to the plane of the feather, appear brilliant blue when the barbs are seen crosswise of the line of vision and dull, darker blue, when they lie in the same direction as the line of vision. The same effect is noticed, to varying degrees, in other blue feathers viewed in similar positions, and is striking enough to be worthy of mention, though the explanation is simple enough. When the barbs lie crosswise of the line of vision, practically nothing but the blue color is visible; the barbules, of darker color, are almost hidden by the blue barbs, which are thicker and form a series of parallel ridges. Maximum color is observed under these conditions. When the position of the feather is such that the observer sees between the ridges the general effect is much dulled by the appearance of dark barbules which are visible in this position. This is exactly the same effect one sees in "changeable" or "two-tone" silks, which are woven so that from one position the threads of one color are visible, while from another position the other color is more prominent.

The character of the barbules influences the blue color to a considerable extent. If these are white the blue appears pale and transparent, while if they are dark the blue gains strength, opacity, and brilliancy in some positions. If the barbules are only slightly developed, the blue feathers have a waxy, enameled appearance, while if the barbules are yellow or red the color of the feather as a whole will be modified by this admixture.

Dark bars across blue feathers, such as those of Jays, *Procnias viridis*, and others, are seen to differ from the blue portions only in the layer of the color-cells, which are constricted, ill-developed, pigmented, and apparently do not possess the thick porous walls necessary for the production of blue.

Only one case was found in which the blue is not accompanied by underlying pigmentation. The blue tips of the feathers of *Procnias viridis* may be permeated by cresol so that they are perfectly transparent and colorless. No pigment is observed in the barbs of these feathers, though the barbules are dark. These barbs consist essentially of rods of turbid blue material (densely

packed color-cells) with rows of bubbles (the cavities of the color-cells) down the central part of the barb. These bubbles play an important part in causing the blue-green to blue color change with angle, discussed above. Since the blue of the barbs of the *Procnias viridis* feather is not inferior to other blues, it appears that the dark pigment is really not absolutely essential to production of a good blue, provided the color-cells have the proper structure, though it undoubtedly does intensify whitish or pale blues, while lending opacity to the feather.

It has not been the aim in this investigation to examine all known blue feathers, but rather to develop methods by which any given blue may be studied and its character determined. The feathers examined were chosen without reference to their order or family, and include widely differing types. Since the identical nature of the blues of birds of the different orders has never been questioned, and since no reason to doubt this has arisen in the course of this work, further study of this point was felt to be superfluous in the present investigation.

Blue feathers of the following birds have been examined and found to owe their color to the Tyndall blue: Blue Jay (*Cyanocitta cristata*), Yucatan Jay (*Cissolopha yucatanica*), Tanager (*Tersina* [*Procnias*] *viridis*), Arctic Bluebird (*Sialia arctica*), Parrot (*Pionus chalcopterus*), Ant Thrush (*Pitta cyanoptera*), Tangara [*Calliste*] *thoracica*, Painted Bunting (*Passerina ciris*), Bronze-wing Parrot (*Trichoglossus novae-hollandae*), Roller (*Coracias indica*), Jay (*Cyanocorax*), Fairy Bluebird (*Irena puella*), Blue and yellow Macaw (*Ara ararauna*), Purple Gallinule (*Ionornis martinica*), Indigo Bunting (*Passerina cyanea*).

Krukenberg¹ was unable to obtain any green coloring matter from green feathers and he therefore considered the non-metallic greens to be due to a combination of structural blue with pigment yellow. Since then, a green pigment, Turacoverdin, has been isolated; but it is found only in the *Musophagidae*, and can therefore be ignored when discussing other birds. Haecker² admitted Krukenberg's view as to most green feathers; but pointed out that olive green may be due to a yellow pigment combined with the

¹ Vergleichendphysiol. Studien, 1 (5), 98 (1881).

² Archiv. mikr. Anatomie, 35, 68 (1890).

dark brown or black pigment, melanin. Gadow¹ agrees with Krukenberg that only dark brown and yellow pigments are found in green feathers; but he does not accept Krukenberg's explanation of the cause of the color.

The color of green feathers is located in the barbs, just as is the case with the blue feathers. When a green feather is held against the light, only a dark brown, almost opaque, color is to be seen. The properties and structure of green feathers are the same as those of blue feathers, as regards polygonal color cells with porous walls, dark underlying pigment, yellowish color by transmitted light, change towards blue under pressure and away from blue on swelling, partial polarization of the scattered light, disappearance of color on penetration with liquid of proper refractive index, etc. In short, green feathers are identical with blue ones except for the one fact that the transparent outer sheath of keratin is yellow and not colorless.

In some green feathers the color of the barbs may vary from bluish green at one end to yellow at the other owing to changes in the intensity of the blue. In such feathers the barbules and medullary portion of the barbs are usually free from dark-brown pigment in the yellow parts of the feather thus destroying the blue; but the structure is the same throughout. Such yellow feathers can be made distinctly green by painting them on the back with India ink, just as the white tips of the Blue Jay feathers are made blue. Of course, only the yellow feathers having the proper structure will become green when thus treated. Haecker points out that the same effect can be produced by underlying black feathers on the bird acting as a dark background, though the resulting green is more imperfect.

Penetration by cresol, or other liquid of the proper refractive index, renders the color cells transparent and colorless. The dark brown medullary pigment and the yellow of the outer layer are seen plainly. The original color is restored on washing and drying. Prolonged extraction of green feathers with hot alcohol results in the removal of some or all of the yellow pigment, with the blue remaining as a structural color, unaffected by solvents.

¹ Proc. Zool. Soc. London, 1882, 409.

The most simple way of showing that green feathers are only blue feathers with a yellow outer layer is by scraping, with a knife or scalpel, the colored barbs of the feather. Green feathers become blue under this treatment and examination with the microscope shows that a transparent yellow layer has been scraped off the outside of the barbs, leaving the blue color cells exposed. Sections, of course, show the same features.

Another striking demonstration of the entirely different nature of the yellow and the blue in green feathers is afforded by their behavior when faded. When blue feathers are exposed in a "Fadometer" no loss of color results, but green feathers become blue in 20-40 hours exposure (equivalent to about 35-65 hours of direct sunlight). The pigment yellow of feathers is easily faded but the structural blue is unaffected.

It is possible to produce greens like those of feathers by covering a Tyndall blue medium (Jena glass, etc.) with a yellow varnish, while a blue feather dyed with a yellow dye, which does not penetrate to the color cells, becomes a pronounced green.

Parrots furnish excellent examples of green feathers; the Mexican Green Parrot (*Amazona*), *Trichoglossus novae-hollandae*, Blue and Yellow Macaw (*Ara*), all show greens which generally shade into yellow and blue. Other specimens studied include such Tanagers as *Tangara* [*Calliste*] *lavinia*, and *thoracica*, the Purple Gallinule, etc.

Some very pronounced and vivid greens, such as those of the Fruit Pigeons (*Ptilopus puella*, and *Ptilopus pulchellus*), Green Heron (*Butorides virescens*), etc., though lacking much of the brilliant lustre are nevertheless metallic colors, and not related to blue feathers. Their different nature is apparent under the microscope; the green color is entirely in the barbules, and is highly lustrous under the microscope while any further study only shows that we have here an entirely different type of color, which will be discussed later. Newbigin¹ discusses green in its relations to blue in Kingfishers and other birds.

As far as other pigments are concerned, apparently they are not found in combination with Tyndall blue in feathers to any con-

¹ 'Colour in Nature,' 288 (1898).

siderable extent, though the Blossom-headed Parakeet (*Palæornis cyanocephala*) is said to have blue barbs combined with red barbules, and the neck feathers of the Brazilian Hawk Parrot (*Deropterus accipitrinus*) have blue tips, while the middle of the feather is red, and the base is green. The blue tips are the typical Tyndall blue, with black barbules. Where the red coloration begins, the outer sheath layer surrounding the blue cells appears red, as does the base of the barbules. At this point there is actually a red transparent layer surrounding the blue cells, and the blue appears a pinkish purple. In the red part of the feather, however, the blue cells degenerate, the barbs are thinner, and the structure becomes that of a typical red feather. Near the base of the barbs the blue cells are developed somewhat, and the sheath layer is yellow, giving a green of the typical non-metallic sort. The modification of structure in the parts of the barbs where the red pigment exists is worthy of attention from the standpoint of the biologist. In some parrot feathers, which shade from red, yellow, and green, to blue, the structure of the blue and green parts does not appear to have degenerated completely in the red portion of the barbs, though no hint of the blue appears to be produced by it, but only white. Chandler¹ makes a point of various devices which Nature uses to produce similar color effects in feathers.

From the observations made on typical blue feathers it has been shown that the feathers satisfy the criteria chosen as a means of detecting Tyndall blue or the blue of a turbid medium. The scattered light is blue, the transmitted light yellowish; the blue requires a dark background to show up plainly; the blue may be rendered colorless and transparent by rendering the color-cells optically homogeneous; pores of dimensions of the order of the wave-length of blue light actually exist; the scattered light is polarized in the proper plane, and its intensity is inversely proportional to the fourth power of the wave-length; variations in shade of blue occur, and are apparently due to the presence of relatively larger pores. In short, the parallelism between non-metallic blues of feathers and the blue of a turbid medium is so complete that no reasonable doubt can exist as to their identity, particularly

¹ Univ. of Cal. Pub. Zool. 13, No. 11 (1914-16).

since no structures capable of acting as prisms, thin films, or diffraction gratings are present to be considered as possible causes of the color.

In the light of the evidence presented, Gadow's theory of the blue of feathers must be discarded completely. It is to be regretted that his explanation is still accepted and quoted, though it has been doubted and even disproved by several later investigators. A statement of his views seems necessary here, in order that their unsatisfactory features may be pointed out.

Gadow¹ ascribes the blue to ridges in the outer surfaces of the color-cells, which produce the color by diffraction, in the manner of a diffraction grating. His drawings show no ordered arrangement of these ridges, which would be necessary for a grating effect, nor does he explain how a grating could produce only the one color, blue. This error is a common one: gratings possess ridges and cause color; ridges are found in a colored substance, and the color is straightway ascribed to them. Gadow admits that the understanding of the production of the color would be "an almost super-human task. We know only the result, namely—blue color"; yet the laws of color production by gratings have long been established and grating colors possess definite properties which serve to identify them. The presence of ridges in the feathers is incidental. Most blue feathers show no signs of them.

Gadow has not definitely located the blue in the walls of the color-cells, nor has he recognized any connection between the color by reflected light (blue) and that by transmitted light (yellowish). He has not observed any change in color under the influence of a penetrating liquid, though if he studied sections mounted in balsam he could hardly have failed to notice some penetration. Apparently the blue of a turbid medium is not considered as a possible cause of color. Haecker² has pointed out the inadequacy of Gadow's explanation, but only in a later paper³ does he reach the conclusion that the blue of non-metallic feathers is the same as that of a turbid medium (Tyndall blue) and not a "diffraction color." He says that "the blue color is due to:

¹ Proc. Zool. Soc. London, 1882, 409.

² Archiv. mikr. Anat. 35, 68 (1890).

³ Haecker and Meyer: Zool. Jahrb. Abts. Syst. Geog. Biol. Thiere. 15, 267 (1902).

(1) The difference between the refractive indices of the cell substance and air without involving the hypothesis that this difference is distinctly greater for blue than for red.

(2) The small size of the pores whose diameter is small in comparison with a wave-length of light." ¹

The findings in the present paper confirm Haecker's theory completely, and emphasize the untenable nature of Gadow's views.

CONCLUSIONS.

1. Non-metallic blues of feathers are due to the scattering of blue light by very fine pores in the walls of the outer layer of cells of the barbs of the feather. This is the blue described by Tyndall, which is commonly observed in turbid media.

2. No blue pigments, and no other structural causes of blue color have been observed in non-metallic blue feathers.

3. Green feathers are essentially the same as blue feathers, except that the blue cells are overlaid by a transparent yellow layer.

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TWO NEW BIRDS FROM NICARAGUA.

BY WHARTON HUBER.

IN working over the ornithological material obtained by the 1922 Nicaraguan Expedition of the Academy of Natural Sciences of Philadelphia, I find two apparently undescribed forms which I have diagnosed and named as follows. My thanks are due now as always to Dr. Witmer Stone, Executive Curator of the Academy of Natural Sciences, for valuable help rendered and to Dr. Chas. W. Richmond of the U. S. National Museum for the loan of specimens for comparison. The color names used are from Ridgway's 'Color Standards' (1912).

***Lurocalis stonei* spec. nov.**

Type.—A. N. S. P. No. 75160 ♂, ten miles above mouth of Banbana River, Nicaragua, June 6, 1922. Collected by Wharton Huber.

¹ Cf. Rayleigh: *Phil. Mag.*, (4) **41**, 274 (1871); (5) **47**, 375 (1899); Bock: *Wied. Ann.*, **68**, 674 (1899).