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COMMUNICATIONS

THE INTRA-OCULAR COLOUR-FILTERS  
OF VERTEBRATES\*

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DETROIT

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Special Points

*Oil-droplets*<sup>36</sup>.—We have fully confirmed the reputed reduction of oil-droplet colours in secretive vertebrates and their absence in strictly nocturnal forms. In *Acipenser fulvescens*, *Xantusia vigilis*, *X. henshawi*, and *Heloderma suspectum* only perfectly colourless droplets were found. The presence of droplets in the sturgeons is set down in textbooks as doubtful; our observations

<sup>36</sup> The optics employed in our studies of oil-droplets were Zeiss apochromatic objectives, compensating oculars, and a B. & L. N.A. 1.40 aplanatic condenser. The illuminant was 6v. substage lamp with Corning "Daylight" filter.

appear to be the first confirmation of those of Leydig, made in 1853 (see Schultze).

*Lacerta ocellata*, *Gerrhonotus scincicauda* and *Crotaphytus collaris*, each representative of a family of bright-light lizards, showed colourless and deep lemon droplets in ca. 1:4 ratio. A fossorial lizard (*Aniella pulchra*) on the other hand revealed only unpigmented droplets which, unlike those of *Xantusia*, had an extremely pale yellow-green fluorescence.

A number of diurnal wild birds<sup>37</sup> were studied and found to have richly pigmented droplets. *Strix v. varia*, however, had only a few yellow droplets, the rest being unpigmented but faint bluish-green—the same situation as reported for *S. aluco* by Erhard (1924). The same reduction of red droplets noted by Erhard in a woodpecker was seen in the three American woodpeckers examined: *Dryobates pubescens medianus*, *Melanerpes erythrocephalus* and *Colaptes auratus luteus* averaged only 10.4 per cent. red droplets, as compared with 11 per cent. for the European woodpecker and 20 per cent. for passerines in general.

It was found almost impossible to locate the foveae in the fresh retinae of shot birds, as the post-mortem drainage of the aqueous produced extensive retinal detachment. The foveae were observed, however, in three species secured alive and tightly garrotted to maintain the intra-ocular tension during enucleation. In all of these—*Falco s. sparverius*, *Passer domesticus* and *Dryobates pubescens medianus*—the foveae contained only yellow droplets. The foveae of *Dryobates* was found to be relatively shallow, which is in keeping with the visual habits of this type of bird.

Only in *Colaptes auratus luteus* were any pigmented droplets found which were strongly greenish-yellow. In no bird was anything comparable to the "pure grass-green" droplet (reported for *Milvus regalis* by Kühne) found.

All oil-droplet pigments appear to be certainly carotinoids; they are easily soluble in alcohol, etc., and are present in normal amounts in albinotic birds (see Krause, 1894).

The greenish-yellow, yellow-orange, and red-purple pigments extracted from whole retinae by Kühne were named by him Chlorophan, Xantophan, and Rhodophan respectively. Kühne realized that two or all of these pigments might be present in a given droplet in particular proportions. Waelchli (1883), repeating the pioneer microspectroscopic work of Talma (1873), found the transmission spectra of the droplets themselves to differ from those of Kühne's extracts. Assuming each droplet to contain but a single pigment, Waelchli renamed the pigments Sphaero-

<sup>37</sup> *Falco s. sparverius*, *Dryobates pubescens medianus*, *Melanerpes erythrocephalus*, *Colaptes auratus luteus*, *Corvus b. brachyrhynchos*, *Cyanocitta alpestris praticola*, *Fermivora c. celata*, *Sturnella m. magna*, and *Passer domesticus*.

chlorin, Sphaeroxanthin, and Sphaerorhodin. We consider that if any specific names are to be used, those of Kühne have most justification; but still other extracts might be made from certain retinae (*e.g.*, *Milvus regalis*?) which would have different spectroscopic properties and deserve equally to be named. All attempts at a definite nomenclature of these pigments are perhaps idle at the present time. It may well be found that a profound alteration of colour accompanies a minor change in the molecule of a basic pigment substance from which all droplet pigments are derived. That, at least in the turtles, is suggested by the development of the colours (*v.i.*).

While individual variations in droplet pigmentations and sizes have been reported, the colours are remarkably constant within a species; some active control seems to be operative to prevent the influence of dietary variation in pigment intake which easily affects the colour of, say, the legs of fowls (see Palmer, 1922). It would be interesting, however, to attempt to influence the colour of the oil-droplets in some bird which is known to be capable of storing huge amounts of carotinoid (*e.g.*, *Serinus c. canarius*)<sup>38</sup>.

As Rochón-Duvigneaud (1929) has pointed out, there is no relation between droplet-colour assortments and plumage colours, though one apparent exception is to be noted. This is a green parrot, *Chrysotis levaillanti*, in which exceptionally greenish droplets occur (Kühne, 1882). There are no green pigments in parrots' feathers, however, so that the relation cannot be direct or passive. It *may* have evolved as an adaptation to a need for clear perception of the green values of the plumage of the mate, but is probably to be explained on other grounds as no such relation of droplet colours to "Schmuckfarben" is seen elsewhere.

A coincident relation of droplet and plumage colours might be expected in certain yellow birds, *i.e.*, the canary, where intensive "colour-feeding" might deepen the oil-droplet colours as it does those of the feathers.

We were unable to make precise microspectroscopic observations on single oil-droplets. It was found impossible, even with the retina pinned to a torus of paraffin in a watch-glass, to keep the fresh droplet within the minimal field of the Zeiss microspectroscope while swinging the Amici prism into place. Waelchli solved the problem by partially fixing the retina with chromic acid, thus immobilizing the droplets. The transmission spectra he thus obtained are probably no more representative of the properties of the droplets *in vivo* than are the spectra Kühne observed with extracts of the pigments, for in both cases chemical changes may have been produced by the treatment. Moreover, the curves figured

<sup>38</sup> The feathers of many birds contain pigments derived from the food; see Erhard (1929).

by Waelchli (1881) are based on purely visual estimates of the per cent. transmission of different wave-lengths and should be disregarded. The projection technique as employed by Roaf (1929a) promises the most reliable data for an investigator making a detailed study of droplet spectra.

The embryonic development of oil-droplet colours might be expected to show which of the colours of the multiplex mosaic is the "primitive" one. Conclusions as to phylogenesis might also depend upon whether the colours arise simultaneously and independently, or arise from each other (*e.g.*, red from yellow). Conflicting evidence in these regards was found in the three forms studied by us—*Sternotherus odoratus*, the domestic fowl, and the domestic pigeon.

*Sternotherus odoratus*, a turtle of the family Kinosternidae, hatches at a carapace length of 22.5 mm. (personal communication from Dr. Risley). Examination of a series of embryos supplied by Dr. Risley showed that the droplets appear at 10.5 mm. and are then colourless. By the 14.2 mm. stage some of the largest droplets had become lemon yellow. It was obvious that these had been derived from colourless ones, as no smaller yellow droplets were seen and all the droplets in the zone of growth (the periphery) were colourless. At 16 mm. some of the larger yellow droplets had deepened to a true orange, and by 19 mm. some of the orange droplets were beginning to redden, though the final ruby colour was not attained until after hatching.

In *Sternotherus*, then, the first colour to form is *yellow*; the orange droplets are formed from some of the yellow ones and the red droplets are later formed from some of the orange ones. This mode of development is in perfect accord with the phylogenetic process which the multiplicity theory supposes to have occurred.

Quite a different situation obtains in the pigeon; in a series of White King squabs we found that the droplets first appeared on the third day after hatching, at which time colourless, orange, and red droplets were already distinguishable. Yellow droplets were not seen until the sixth day, but by the fourteenth day these outnumbered either of the other two colours. There is nothing here which would support any theory of droplet function and the disagreement of the pigeon and turtle naturally throws grave doubt upon the validity of a "recapitulation" interpretation of the process in *Sternotherus*.

Two previous studies have been made of the droplet colours in chick embryos. Schultze saw no droplets until the eighteenth day of incubation, when *red* droplets were distinguishable; yellow ones did not appear until later.

Hahn (1916) studied Italian (Leghorn? Ancona?) and Wyandotte embryos and found that in both the droplets were visible

on the tenth day; they were "pale greenish" (*i.e.*, unpigmented). On the sixteenth day a few coloured droplets were noted, some "light yellowish-brown" and others "dark reddish-brown." Red and orange droplets were well demarcated on the seventeenth day, and Hahn concluded that the ruby droplets had formed from the reddish-brown ones of the previous day, the orange and yellow droplets being formed from the yellowish-brown ones.

Our own studies were made upon White Leghorn embryos. Five embryos of each age were studied and the counts averaged. All counts were made in the central fundus of the right eye, just nasal from the pecten. A  $\frac{1}{2}$  mm. square-ruled disc was used in the ocular to avoid counting any droplet twice and droplets were counted in 56 squares with a 4 mm. objective and 6.4 $\times$  ocular. The number of droplets in this area increased from 182 at the time of their appearance to 258 at hatching.

The counts were reduced to a per cent. basis and the results are given in Table II. Discrepancies between our findings and Hahn's must be laid to breed differences:—

TABLE II  
DEVELOPMENT OF OIL-DROPLET COLOURS IN THE CHICK

NO. DAYS INCUBATION	COLOURLESS	RED	YELLOW-ORANGE
Up to 13	0	0	0
14	100'00	0	0
15	90'40	9'60	0
16	78'54	21'46	0
17	0*	21'67	78'33
18	0	22'74	77'26
19	0	21'67	78'33
20	0	19'33	80'67
21	0	19'73	80'27

\* Colourless droplets were numerous in the periphery, and persist even in the adult.

Table II shows: (1) that all droplets, regardless of their final condition, are at first colourless; and (2) that the coloured kinds are independently derived from colourless ones and not from each other; the *red* droplets arise first.

While this situation is more clear-cut than that in the pigeon, it is equally disparate from that in the turtle. The only conclusion to be drawn is that the development of droplet colours in general affords no sure clue to the phylogeny of the colours, and supports

no theory as to their function. The basis for an hypothetical phylogeny and for a teleological interpretation must be sought in the comparative situation in adult vertebrates.

*Yellow Lenses.*—Yellow lenses (apart from those tinged by melanin in senile<sup>39</sup> and early cataractous lenses) were first seen<sup>40</sup> by Merker (1928) in *Sciurus vulgaris*. Without knowledge of this, one of us had found yellow lenses in snakes; after learning of Merker's work, an investigation of the Sciuridae was made, and a number of other vertebrates were examined with negative results. These studies were reported by Walls (1931); since that report, we have found yellow lenses in the woodchuck, *Marmota monax rufescens*, in the prairie-dog, *Cynomys ludovicianus*, and in Petromyzontid lampreys.

The Sciuridae of the world are well typified by our local forms, there being no type of Sciurid not represented by Michigan species. Having surveyed the local fauna we feel safe in asserting that all diurnal Sciuridae have yellow lenses and that the nocturnal sub-family Pteromyinae (flying squirrels) all have colourless lenses.

The lenses of the diurnal snakes average paler than those of squirrels. The deepest colour was found in *Malpolon* (see Walls, 1931), where the lens matches that of the average Sciurid. *Malpolon* is credited with very keen vision (Boulenger, 1913), but *Dryophis*, which has a highly developed fovea (temporalis; see Walls, 1932a) must have even sharper sight. We have not been able to examine the fresh lens of *Dryophis*, but would suggest that it may exceed that of *Malpolon* in depth of colouration.

Lamprey lenses compare favourably in colouration with those of racers such as *Coluber* and *Masticophis*. We have examined only two species: *Entosphenus appendix* (a brook type) and the landlocked marine lamprey of the Finger Lakes, *Petromyzon marinus*. Professor S. H. Gage kindly examined the lenses of fresh-killed breeding specimens of the latter form and sent us some living individuals which died a few hours before reaching us. He agreed with us that the lenses were quite yellow. Allowing for the difference in size, the lenses of these two species have about equal concentrations of pigment.

We have not attempted an accurate linear arrangement of these vertebrates with respect to the depth of colouration of their lenses, nor have we attempted any precise observations on the ontogenesis of the colouration. We hope that such efforts will be made,

<sup>39</sup> Including of course the lenses of many relatively young persons in whom the inception of nuclear sclerosis is accompanied by a definite yellow colouration.

<sup>40</sup> Yellow lenses and corneae were stated by Pütter (1912, p. 13) to occur in numerous fishes. Dr. Franz informs us that Pütter had only preserved and sectioned material, so that these colourations were certainly artefacts. Similarly, Plate's statement (1924, p. 611) concerning an amber colouration of the lenses of fishes and Cephalopods was based upon preserved material (correspondence with Dr. Plate).

however, either by ourselves or others, if some optical manufacturer can be persuaded to make a wedge of appropriate yellow glass for use as a standard<sup>41</sup>.

We have not been able to secure a device and feel that without it no accurate estimate of lens colourations is possible. We did find, however (as did Merker), that half-grown Sciurids had lenses slightly paler than those of adults. The lens of a new born *Thamnophis s. sirtalis* was colourless; on the other hand, a young (15 inch) *Malpolon monspessulani* proved to have a lens as dark as that of a full-grown (four to five foot) specimen.

Noviol "O" glass (the American Optical Co. product, *not* that of the Corning Glass Works, which is much paler although it has nearly identical transmission) in the usual 2 mm. layer, makes a convenient standard. This glass matches<sup>42</sup> the lenses of *Malpolon monspessulani* and of *Sciurus hudsonicus loquax*, *S. niger rufiventer*, and *Tamias striatus lysteri*. *Citellus t. tridecemlineatus* and *Cynomys ludovicianus* have lenses which are decidedly darker and match each other, while the lens of *S. carolinensis leucotis* is somewhat paler than Noviol "O".

This grade of Noviol glass is too pale to have an appreciable effect upon human vision (see Coblenz, 1932), but as we have already pointed out, the human eye is supplied with an intrinsic, much more effective short-wave absorbent to which such an external filter as Noviol "O" is but a small increment. One could form some notion of the effectiveness of unsupported Noviol "O" only if human subjects who lacked macular pigment were available for experiment<sup>43</sup>.

Our spectroscopic observations on yellow lenses have been scanty. Attempts were made to secure spectrograms, but we were not able to obtain the differentiation necessary to plot graphs of the transmission spectra; lacking a Goldberg wedge sufficiently small and dark, we were confined to superficial visual observations.

We employed a Zeiss microspectroscope with a 32 mm. objective, mounting the yellow lens in a small chamber 2 mm. deep, the transparent faces of which were formed by thin coverglasses. The lens was thus usually flattened slightly and this central portion was observed. The light source was a 100 watt blue Mazda lamp

<sup>41</sup> Such a wedge should be of A. O. Co. Noviol "O" glass, about three inches by one-half inch, tapering from 3 mm. thick to 0 and backed with a reversed wedge of colourless glass. The wedge should be mounted in a glass tray, under which is an adjustable white mirror, and made movable under a black mask in which variously sized apertures would allow the comparison of a lens with a circular, equal area of the wedge. The thickness of the yellow wedge at the point of matching would then be an accurate index of the colouration of the lens.

<sup>42</sup> All comparisons were made in a Syracuse glass of normal saline, over a white background, in daylight.

<sup>43</sup> Determinations of the visual acuity of sharp-sighted, filterless, diurnal vertebrates (e.g., pikas, trouts) with and without Noviol filters, might be possible and would be of interest.

at the level of the aperture of the comparison prism and one foot from the latter. The two spectra were made equally bright, and direct comparisons of a given lens with Noviol "O", or of either with the unmodified light were possible.

With the slit minimal, Noviol "O" was found to cut off the spectrum at about  $\lambda 4100$ , the lens of an adult *Tamias* at  $\lambda 4200$ , and the lenses of adult *Citellus* and *Marmota* at  $\lambda 4300$ . In all cases the transmitted blue was sensibly diminished, but no appreciable absorption was noted in the regions of longer waves.

We have gone as far as we could in determining the chemical nature of the pigment of yellow lenses and are satisfied that it is essentially the same substance in the three groups which possess it. The colouration is homogeneous even in crushed specimens under immersion lenses. For the pigment itself, we propose the name *lentiflavin* (NL.=lens-yellow). We will be glad to see this pigment identified with some colourant already known and named, but so far as we can judge from its chemical behaviour and non-granular condition, it is probably unique and deserving of a special name.

Merker (1928) states that he was able to extract the pigment from the lens of *Sciurus vulgaris* with dilute (50 per cent.) glycerine; he allows the reader to suppose that this took place in a few minutes. We have found no such solubility; the lens of *Tamias* after 28 hours in 50 per cent. glycerine<sup>44</sup> had shrunk somewhat, but had not changed in colour; a control in normal saline had lost all the yellow except for a tinge in the nucleus, which was gone 12 hours later. The lens of a *Citellus* had lost no colour after 23 hours in 50 per cent. glycerine; that of a *S. n. rufiventer* lost no colour in two hours in 10 per cent. and 50 per cent. glycerines, although parts of a teased lens became milky in the former concentration. The lens of a Blue Racer (*Coluber constrictor flaviventris*) was passed back and forth in these solutions and in pure glycerine for several hours; it became superficially milky in a few minutes in either solution and cleared upon being returned to pure glycerine, revealing the original colouration undiminished. An *Entosphenus* lens shrank a little when immersed in 50 per cent. glycerine for an hour, but showed no loss of pigment when compared with the control in saline.

There was certainly no solubility in the chemically pure glycerine employed. Concluding that Merker's glycerine must have contained an impurity (presumably acid, as chemists advised us that no other impurity would be prominent even in low grade glycerine) we placed a *S. h. loquax* lens in 50 per cent. glycerine acidulated with one drop of HCl per 10 c.c. The loss of colour was far too

<sup>44</sup> The National Aniline and Chemical Company's "Special—Absolute—Pure" grade.



slow to be observable, but after 24 hours the tremendously swollen lens had colour only in the centre of the nucleus. A control in neutral 50 per cent. glycerine shrank but lost no colour; it is to be noted that the loss of colour in acidulated glycerine was no more rapid than in normal saline.

Merker speaks of the colour coming out and tinging the solvent, when he proceeded to employ the now colourless lens in his experiments on fluorescence. He makes no mention of the swelling and softening which must have occurred had his glycerine been acid, and we can only suggest that his results may have been due to an over-correction of acid impurity of his glycerine by the manufacturer with alkali (*v.i.*).

The slow loss of colour in the normal saline suggested a possible solubility of the pigment in aqueous humour, which in turn might demand a continuous formation of the pigment in the living tissue. To test this, a *Citellus* eye was excised and placed unopened in normal saline in darkness at room temperature for 23 hours. The lens was then removed and compared with one taken from a fresh-killed individual; no difference could be seen. The first lens was now left in saline, in darkness, for 24 hours, when it was found to have lost a little yellow—just enough, in fact, so that it now matched Noviol "O" perfectly. After still another 24 hours it was slightly paler than the yellow glass standard. There is thus no bleaching effect of light and only a slow solubility in normal saline. The pigment in the intact animal is probably entirely stable with respect to light and contiguous fluids.

Dr. H. B. Lewis kindly undertook to find a substance which would remove the colour quickly, thus truly deserving to be considered an effective solvent. The usual solvents of physiological chemistry were tried, all of which were negative excepting alkali; a 1 per cent. or 2 per cent. solution of KOH or NaOH was very effective.

A 2 per cent. solution of KOH was found to dissolve out all the lentiflavin of *Tamias*, *Sciurus*, *Coluber* and *Entosphenus* lenses in from 30 to 60 minutes<sup>45</sup>. The solvent was tinged, showing that a true pigment was involved, not an optical phenomenon or a chromatic protein.

This alkali solubility is unusual for a true melanin (see Hammarsten, 1926). It is characteristic of the pigments of "melanoid"

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<sup>45</sup> The behaviour of lenses in weak alkali is worth description. The lens (*Tamias*, *Sciurus*) appears to shrink very slowly, maintaining a perfectly smooth surface. On close examination, however, it is seen that a hyaline, mucinous envelope has formed which increases in thickness as the coloured central part shrinks. This envelope is readily freed and then disintegrates in the alkali. After 45 minutes the firm central portion is no more than one-third the diameter of a control lens in saline, and at the end of an hour it is very small. The sharpness of the demarcation between centre and envelope, both as to colour and consistency, is striking. Similar changes were observed in the lenses of *Coluber*, *Entosphenus*, and *Rattus*.

tumours, however. Lentiflavin is thus probably related to the latter colourants; it is certainly not a carotinoid, being insoluble in alcohol, etc., and is not identical with the pigment of cataractous lenses, which is believed to be true melanin formed from tyrosine liberated by protein hydrolysis (Duke-Elder, 1929, p. 276)<sup>46</sup>

Further than this we cannot go at present. It is not known how close, chemically, the "melanoids" are to the true melanins; whether they can occur in albinos, or respond to the DOPA test, is likewise unknown. It will be of great interest to learn the condition of the lens in albino and melano squirrels. There are commercial breeders of albino squirrels, but their prices are prohibitive; wild albinos are rare, and we have not yet been able to secure one.

The lentiflavins of the three groups differ in minor respects. That of the Sciuridae exhibits an "indicator" reaction in the presence of alkali, the colour deepening markedly. This was not apparent in the case of *Coluber* or of *Entosphenus*. A *Malpolon* lens was seen to darken appreciably after a half-hour exposure to air; no such change was observed in *Sciurus* or *Entosphenus* lenses, but a thoroughly desiccated *Citellus* lens became almost orange (due perhaps solely to concentration rather than to any oxidation process). As previously mentioned the microscopically visible granules seen in sectioned lamprey lenses by Franz (1932) and Plate (1924; see p. 377) may be lentiflavin; whether it has here been artificially coagulated or actually exists in granules when fresh, we cannot say.

Differences are seen when the lenses are observed under the light of a clear tungsten-filament lamp or over black backgrounds in daylight. The lens of *S. h. loquax* appears to match Noviol "O" even under these conditions, while the lens of *S. c. leucotis* appears colourless under the artificial light and very pale over a black ground (on which Noviol "O" appears brownish). Other Sciurid lenses are a little greenish over a black ground, but this was not the case with *Petromyzon*.

<sup>46</sup> Through the kindness of Dr. Fralick of the University Hospital, we secured a number of freshly-delivered cataracts with yellow and brown nuclei. Immersion in cold 2 per cent. or 3 per cent. KOH or NaOH for two hours had no effect upon the pigmentation of such lenses. A yellow cataract immersed in cold 3 per cent. NaOH for two hours, then heated slowly to boiling during a half hour, and allowed to cool, slowly lost pigment and turned white and opaque; it was completely white after a total of five and a half hours in alkali. A brown cataract similarly treated was completely white only after 25 hours in 3 per cent. NaOH. Inasmuch as no loss of colour occurred until heat had been applied, and the lenses in alkali slowly swelled and fragmented radially, we feel that the loss of colour is to be ascribed to destruction or to dispersion of the pigment accompanying soluble proteins, *not* to a true solubility of the pigment.

Elschnig and v. Zeynek (1913) state that the pigment of black cataracts can be extracted by heating in 3 per cent. NaOH, but do not give the length of time involved. Gifford and Puntenny (1933) confirm this, and Dr. Gifford informs us that he has recently found heating to be unnecessary; but as stated above, we do not consider this a demonstration of solubility at all comparable with that of lentiflavin.

While there is little chance that the formation of lentiflavin would be influenced by diet, it may be that there is some direct influence of light as is the case with dermal pigment. The differences in lens pigmentation, in Sciurid species, which fit so well with their respective exposure to strong light, may even be automatically brought about by the amount of light to which the various species expose themselves. A crucial experiment would consist of dividing a litter of, say, *Citellus* sp. and raising half of the weanlings in darkness on a vitamin-adequate diet; the remainder would be raised in a strongly lighted cage and individuals of both groups sacrificed periodically for direct comparison of the lenses.

Yellow lenses may very well occur in still other vertebrate groups in addition to the Sciuridae, snakes, and lampreys. We would particularly suspect the diurnal geckoes such as *Phelsuma* and *Lygodactylus*, and such diurnal mammals as the so squirrel-like treeshrews (Tupaiaidae; see Lyons, 1913 and *cf.* Woollard, 1926, 1927).

The granular pigment reported by Plate (1924) in sections of median vertebrate eyes and in the "vitreous" of the spider-like Solpugidae probably has no significance for vision and may even be artefacts, but there is a possibility that yellow lenses or other yellow filters may occur in some invertebrates<sup>47</sup>. Those whose lenses and general ocular anatomy are most like the vertebrate, however (the Cephalopod molluscs) are apparently all nocturnal and should have no such filters (see Verrill, 1882, p. 97; Willey, 1902).

It is appropriate to call attention at this point to the fact that physiologically pigmented vitreous humours are unknown. There is no optical reason why a pigmented vitreous should not constitute an effective filter, but perhaps a continuous loss and replacement of the fluid portions of this body would drain the pigment away and make the vitreous an uneconomical location for it. The yellow pigmentation of the senile or cataractous human lens is permanent; that of the vitreous, in icterus, is only temporary.

*Yellow Corneae.*—Of the effective types of natural yellow filters the yellow cornea is the least regular in make-up and in distribution. It is expressed very differently in different species, and is lacking in a large number of fishes which, if our ideas are correct, should benefit from it or its equivalent.

With only a small number of freshwater fish species available to us in the living condition, we have been unable to make more

<sup>47</sup> Tillyard (1917) describes a reddish colouration of the corneal lenses of the ocelli in a diurnal dragonfly, *Austrolestes leda*. The ocelli are supposedly used only for very near vision and no connection of this phenomenon with the present problem is apparent to us.

than a preliminary survey; it is our hope that other investigators will be stimulated to add greatly to the scanty data of this subject.

Schiefferdecker's (1887) report is the only one we have found. He noted that the cornea of *Esox lucius* and *Cyprinus carpio* were yellow, the colour being present well down over the pupil, and thus necessarily "influencing the perception of colours." He does not mention the exact position of the chromatophores with reference to the laminations of the cornea, and we have made no histological investigation of this point, as it has seemed immaterial to our present purpose.

Among the species we have examined, *Esox vermiculatus* and *Amia calva* are conspicuous; these forms have an orange colouration of the extreme superior periphery of the cornea which shades rapidly into yellow, becoming paler opposite the pupil and lost below, so that the inferior periphery is practically colourless. In these cases the colour is produced by numbers of small xanthophores which are quite closely congregated; they are presumably non-migratory and identical with those of the head skin. The yellow pigment involved is probably ordinary ichthyocarin (Lönnerberg, 1931).

The excised fresh cornea of a large *Esox vermiculatus* was examined with the Zeiss microspectroscope; with the slit minimal, it was found that the portion opposite the pupil absorbed ca. 40 per cent. through the blue and violet regions and cut the spectrum off at about  $\lambda 4150$ . The more heavily pigmented dorsal area absorbed all of the blue and violet.

*Cottus bairdii* showed a very different situation. Although the pigmentation was quite heavy (cutting off the spectrum at  $\lambda 4200$ ) it was confined to the super-pupillary area and was formed by massive cytoplasmic processes descending waterfall fashion from the bodies of xanthophores situated at the superior corneal margin. The eyes of this form have a decidedly dorsad situs, and the pigmentation here seems to constitute rather an "eyeshade," protective against dazzle, than a filter in the strict sense<sup>48</sup>.

The eye-shade sort of arrangement, less well developed than in *Cottus*, was also found in *Cyprinus carpio*, *Perca flavescens*, *Poecilichthys coeruleus*, *Carassius auratus*, and *Notemigonus crysoleucus*. In these there was a conspicuous ventrad extension, dorsally, of the zone of xanthophores which in most fishes invade the entire circumference of the cornea for a short distance beyond the last of the melanophores.

Species in which there was no extra development, dorsally, of

<sup>48</sup> A very different type of eyeshade has been reported by Breder (1932), who interprets the umbraculum, or pupillary operculum, of certain fishes as having such a function; in some of these fishes, black pigment occurred in the dorsal part of the cornea.

this narrow yellow ring, sufficient to constitute even an "eye-shade," included the following:—

*Eucalia inconstans*, *Aplites salmoides*, *Ambloplites rupestris*, *Xenotis megalotis peltastes*, *Micropterus dolomieu*, *Umbra limi*, *Rhinichthys atronasmus*, *Semotilus atromaculatus*, *Catostomus commersonnii*, *Apomotis cyanellus*, *Eupomotis gibbosus*, *Percina caprodes*, *Helioperca incisor*, *Salmo salar sebago*, *Salmo gairdnerii*, *Lepisosteus platostomus*, and *Acipenser fulvescens*.

It would seem that only a small minority of fishes have a yellow filter through which they must look constantly. A few others look through a yellow screen only when their gaze<sup>49</sup> is directed rather sharply upward. The majority of species, however, have no filter for use under any conditions, and in such cases as the trouts, etc., this is frankly puzzling. The forms which do have the yellow cornea more or less developed are all shallow-water species, but apparently not even *Amia* and *Esox* are restricted by their filters to solely diurnal activity; both of these are included in Boulenger's (1929) list of forms which are, he believes, at least as active by night as by day.

The reason for the counter-shading of the coloured cornea from dark superiorly to pale or colourless inferiorly is perhaps simply the fact that the greater part of the incident light comes from above; the shading would thus be explained in the same terms as the differences in lens colouration in bright-light and dim-light Sciuiridae.

There are, however, two other possibilities, the first of which is the stronger: the fish can see upward into the air only within a definitely circumscribed overhead area, outside of which total reflection occurs, so that the fish sees the air-water interface only as a bright opaque surface. It is possible that the fish has most need for acute vision in a generally upward direction, as when it is searching for insects trapped in the surface film, or watching out for terrestrial and aerial enemies. This may be an important factor in the shading problem; a less likely possibility follows:

Schnurmann (1920) believes he has identified a type of yellow filter in the fish retina which, because we are doubtful of it, we have not included in our discussion of natural filters in general. Basing his hypothesis upon some work of Hess (1911*b*), Schnurmann postulates that the retinal pigment, fully expanded in light-adaptation, is so attenuated as to form translucent films about the visual cells. This pigment, he claims, becomes a yellow filter when greatly dispersed, although it forms a dark brown opaque

<sup>49</sup> Eye movement is not implied; we have in mind the portion of the visual field to which the animal's *attention* is directed. Probably but few fishes aim their eyes at all precisely, as only a few have been found to have a fovea (see Rochon-Duvigneaud and Roule, 1927; Verrier, 1928).

mass when retracted in dark-adaptation. Although it would seem that there would be no filtering action whatever upon those light-rays which are directed axially to the cones, Schnurmann considers the supposed action an adequate basis for the response of the dermal chromatophores to the yellow portions of the animal's background.

Assuming this filtering action to occur, and to affect vision, it would be most prominent in the dorsal portion of the retina, requiring a correspondingly less heavy deposit of pigment in the corresponding (inferior) portion of the cornea. We include this only because it is a possibility—not because we are at all in agreement with Schnurmann's hypothesis.

*Maculae luteae and Retinal Capillaries.*—We have seen that several investigators have explained the macular pigment as having the same function as the oil-droplets, according to their respective theories. One or two have been more specific and have compared the macula lutea with the general assemblage of *yellow* oil-droplets alone, but without knowledge of the still more perfect analogy afforded by conditions in the well-developed avian fovea itself<sup>50</sup>.

There have been denials, even recently<sup>51</sup> of the existence of a macular pigment in the living eye, but its presence is now certain. It has also been claimed that the yellowness of the macula is due merely to the extra thickness of the retina in that region, and that an equally yellow appearance can be produced anywhere in the periphery by doubling the fresh retina upon itself. This is also untrue, but suggests that perhaps the pigment may not be confined to the immediately circumfoveal region in those primates which have much higher percentages of cones than man, and are more strictly diurnal.

Woollard (1927), Kolmer (1930), and Menner (1931) have recently described sectioned material of such primates, some of which have practically as many cones as rods—the same high proportion of cones as in many lampreys and squirrels. The fresh retinae of such primates demand examination for the possible

<sup>50</sup> It is strange that Schultze, who was in possession of all the necessary information, never realized this situation. His statement regarding the presence of only yellow droplets in the foveae of the falcon, which we have quoted, occurs on p. 287 (1873). On p. 265 he had written: "In birds the number of cones is in general far greater than that of the rods, whilst in mammals the reverse obtains. In the retina of man and the monkeys, as is well known, it is only at the yellow spot that the cones exceed the rods in number; at the centre of this acutely perceptive area the rods entirely fail. The retina of birds resembles consequently the macula lutea of man throughout its whole extent, in the relative proportions of the cones to the rods, and this similarity is still further increased by the circumstance that the yellow oil globules in the outer segments of the cones of birds correspond to the presence of yellow pigment in the most sensitive area of the human retina."

<sup>51</sup> See Holm (1922), Nordenson and Nordmark (1928); the latter authors found no ophthalmoscopic appearance of macular pigment in eyes immediately *post mortem*, but neglected to employ red-free light.

presence of heavier and perhaps more extensive deposits of pigment than that of the human; these cone-rich primates have an approach to the (anomalous) human condition known as "universal maculosity," and since the visual-cell pattern of their general fundus is similar to that of the border of the human macula, a correspondingly broad pigmented area would not be surprising. Nocturnal primates, as is to be expected, have few or no cones, and have no fovea or, at most, a slight fovea externa (Kolmer, 1930). In at least one genus (*Galago*) a tapetum lucidum (Kolmer) and a vertical pupil (Mann, 1931) are both present.

Spectroscopic investigations of the fresh macula have shown that absorption is greatest in the violet and decreases regularly up to the green-yellow (see Schultze, 1873; Greeff, 1900; Parsons, 1924). Individual variation in the amount of macular pigment is considerable and within its limits are occasional cases of actual blue-blindness (*pseudo-tritanopia*; see Parsons, 1924, p. 192).

There seems to have been no published speculation hitherto as to the chemical nature<sup>52</sup> of the macular pigment, except by those who deny its presence *in vivo*. Two distinct possibilities are, however, indicated in the literature. The statement often seen, to the effect that brown eyes contain more macular pigment than blue ones, appears to derive solely from the observations of Huschke (1844)<sup>53</sup> If fully substantiated by enough additional observations to eliminate chance, this would indicate that the macular pigment is a form of melanin or a related pigment, subject, like dermal and hair pigments, to genic control.

Arguing strongly against this, however, is the easy solubility of the pigment in alcohol; this suggests rather that the substance is a carotinoid. Fully reliable microchemical tests for carotinoids have not yet been devised for animal tissues (Palmer, 1922, and recent personal correspondence), but indirect evidence on this point might be derived from a study of the individual variation by means of red-free ophthalmoscopy, and of the diet of the subjects. Cases of icterus *ex carotinaemia* should also be examined. The variation may then prove to have as its basis not the melanization of the body, but the intake of carotinoid-rich foods.

<sup>52</sup> The macular pigment has been called a "lac-dye" (see the American Encyclopedia of Ophthalmology, p. 2407), but this term is not chemically specific.

<sup>53</sup> On p. 727: "Seine Färbung ist im Auge von Kindern, blauäugigen, auch wohl von sehr alten und noch mehr von Erblindeten, vorzüglich bei Amaurotischen hellere, als bei Erwachsenen, braunen und gesunden Augen." Huschke's 1833-35 paper is sometimes cited in this connection, but we find no such statement therein; careless reading of the fourth paragraph on p. 19 (1833) is probably responsible.

Huschke unfortunately does not state whether the retinae were observed *in situ* or isolated; if in place against the background of the choroid, differences in appearance in blue and brown eyes might well occur, but would not necessarily indicate actual differences in the amount of the yellow pigment itself.

Man, unlike some vertebrates (Palmer, 1922), absorbs carotinoids unchanged; these pigments are circulated in the blood and deposited in various tissues. The retina is known to be extremely rich in Vitamin A (Holm and Bojesen, 1929; Yudkin, 1931; Smith *et al.* 1931), and our present knowledge that carotin is convertible into Vitamin A makes it seem probable that the mammalian retina takes in carotinoid continuously. With this in mind, we may tentatively interpret the macular pigment as a local deposit of carotinoid allowed to accumulate<sup>54</sup> to serve a special purpose. It is perhaps significant that the pigment is rarely present at birth (see Schwalbe, 1874, p. 430).

We have made no observations upon retinal capillary networks. Their probable effect as filters could be adequately gathered from published data on the spectroscopy of thin layers of whole blood and from the study of injected retinae, which we have not attempted to prepare. As an intra-ocular filter the retinal circulation admittedly plays a minor rôle, but as Schultze insists, its influence cannot be entirely disregarded.

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<sup>54</sup> Some chemical alteration of the carotin may occur; Valentin (see Huschke, 1844) claimed that the colour of the macular pigment deepened in the presence of mineral acid and partially bleached in the presence of strong alkali. Such performance is not characteristic of any known carotinoid. Valentin's experiments need repetition on isolated retinae, however, as his findings would be vitiated if the retinae were *in situ* against a background of melanized tissue.



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