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G. H. PARKER

THE MOVEMENTS OF THE RETINAL PIGMENT

WITH 13 ILLUSTRATIONS

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The Movements of the Retinal Pigment.

By **G. H. PARKER**, Cambridge (Mass.) U. S. A.

With 13 illustrations.

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I. Introduction.

The pigment cells in the eyes of many animals exhibit movements quite like those seen in the more usual types of dermal chromatophores. These movements, however, were not discovered until about half a century ago. Although as early as 1852 H. MÜLLER noted that the posi-

tion of the retinal pigment varied more or less in different animals, it was not till 1877 that BOLL and KÜHNE independently discovered that under the influence of light and darkness, the retinal pigment of the frog moved outward between the rods and cones and inward toward the bodies of the pigment cells. The movement of the pigment in the eyes of invertebrates was first recorded by EXNER for arthropods in 1889 and was subsequently described in these animals by STEFANOWSKA (1890), EXNER (1891), and SZCZAWINSKA (1891). In 1891 RAWITZ observed pigment movements in the eyes of cephalopods. Thus these pioneer workers identified retinal pigment migrations in the vertebrates, the arthropods, and the mollusks.

For a long time it was the opinion of most workers that the migration of pigment in the eyes of animals was due to the direct action of light upon the containing cells. However in 1885 ENGELMANN showed that a frog whose retinal pigment was in the position characteristic for darkness, and whose one eye was covered with a light-proof cap, would show a migration of pigment to the position for light in the covered eye if the uncovered one were exposed to light. ENGELMANN concluded from this observation that in the frog the two eyes are sympathetically related and that this relation is nervous. From the time of ENGELMANN's declaration to the present, investigators have attempted to show in one way or another that the retinal pigment of animals was to some extent at least under nervous control.

The importance of internal secretions for the movement of dermal chromatophores was pointed out as early as 1898 by CORONA and MORONI. It is therefore not surprising that in 1908 KLETT declared that adrenalin would influence the movement of retinal pigment also. According to him this internal secretion, if applied directly to the retina of the frog, would bring about a contraction of its pigment. In 1912 FUJITA without knowledge of KLETT's work, stated that the injection of adrenalin into a frog was followed by an expansion of its retinal pigment, a situation the reverse of that maintained by KLETT. To clear up this confusion the subject was reinvestigated by BIGNEY (1919) who gave unqualified support to FUJITA's claim. Thus the general view of investigators to-day, namely, that adrenalin even when present in very small amounts, induces a contraction of the retinal pigment was established. In this way the direct action of external environmental agents, of nervous influences, and of humoral factors have all been invoked as means of inducing migration in the retinal pigment of animals. In the following pages it is intended to present in the form of a summary the more important facts of retinal pigment migration and to point out the differences of opinion on some of the unsolved problems in this field.

II. Vertebrates.

1. Introductory.

The mobility of the retinal pigment in vertebrates was suggested by the observations of several investigators some years before its actual discovery. Thus in 1856 H. MÜLLER pointed out that this pigment varied in position in the eyes of different frogs, an observation subsequently confirmed by MORANO (1872). In 1867 CZERNY found that on excessive illumination of the frog's eye the retina could no longer be easily separated from the retinal pigment layer, a condition that led him to suggest that the processes of the pigment cells might have the contractility of a pseudopod and that the pigment particles might migrate back and forth in the cell process. The actual movement of this pigment was first demonstrated in 1877 by BOLL and by KÜHNE who independently discovered this phenomenon in the frog. Since that time a voluminous bibliography has grown up on this subject. Good surveys of the general field, some longer and others shorter, have been published by KÜHNE (1879), GARTEN (1907a), HESS (1913), AREY (1915a, 1928), ADLER (1928), and DITTLER (1929).

2. Occurrence of Pigment Migration.

Early in these investigations KÜHNE expressed the belief that a retinal pigment migration would be found in the eyes of all vertebrates, but this opinion has not been entirely confirmed. With the exception of the mammals, however, the majority of vertebrates show more or less movement of the retinal pigment. The eyes of fishes almost invariably exhibit a well pronounced pigment migration. This has been identified in many forms including *Perca* (VAN GENDEREN STORT, 1886, 1887a, 1887b; WUNDER, 1925a, 1925b, 1926a, 1926b); *Leuciscus* (PERGENS, 1896a; CHIARINI, 1904a, 1904b; GARTEN, 1907a; WUNDER, 1925a, 1925b, 1926b), the sea-eel and *Scorpaena* (HESS, 1902), *Abramis* (EXNER and JANUSCHKE, 1905; GARTEN, 1907a; AREY, 1916a; WUNDER, 1925b), *Ameiurus* (AREY, 1916a, 1916b, 1919a; WUNDER, 1925b), *Fundulus* (AREY, 1916a; WYMAN, 1922; GILSON, 1922), *Carassius* (AREY, 1916a; HIROSE, 1927; WUNDER, 1925b), *Gasterosteus*, *Gobio* (WUNDER, 1924, 1925b, 1926b), *Trutta*, *Rhodeus*, *Squalius*, *Lucioperca*, *Acerina*, *Blicca*, *Anguilla*, *Barbus*, *Lota*, *Cyprinus*, *Tinca* (WUNDER, 1925b), *Leucaspius*, *Phoxinus*, *Esox*, *Misgurnus*, *Cobitis* (WUNDER, 1925b, 1926b), *Coregonus* and *Salmo* (WUNDER, 1926a).

It is interesting to observe that in the brook lamprey *Entosphenus*, according to WALLS (1928), the retinal pigment though present shows no evidence of migration under changed illumination and that in certain elasmobranchs, such as *Scyllium* (MÜLLER, 1856, GARTEN, 1907a) and

Torpedo (GARTEN, 1907a), the pigment cells are completely devoid of pigment, a condition commonly characteristic of albino animals.

In amphibians the retinal pigment migration may be as pronounced as it is in fishes, and of the amphibians the frog of course has been most universally studied (BOLL, 1877a, 1877b; KÜHNE, 1877a, 1877b, 1879; ANGELUCCI, 1878; KÜHNE, 1879; ENGELMANN, 1885; GRADENIGO, 1885; VAN GENDEREN STORT, 1887b; HAMBURGER, 1888; FICK, 1889, 1891; VON KORANYI, 1892; NAHMMACHER, 1893; GAGLIO, 1894; CHIARINI, 1904a; 1904b; HERZOG, 1905; DITTLER, 1907; KLETT, 1908; LEDERER, 1908; FUJITA, 1912; AREY, 1919b; BIGNEY, 1919; DETWILER and LEWIS, 1926; SMITH, 1927). Excepting the toad, in which a pigment migration was identified by ARCOLEO (1890), the other amphibians in which this process has been sought and identified were the urodeles *Triton* (ANGELUCCI, 1898; VAN GENDEREN STORT, 1886; CHIARINI, 1904a, 1904b; GARTEN, 1907a), *Necturus* (AREY, 1916a) and *Amblystoma* (LAURENS and WILLIAMS, 1917). In these forms and especially in *Necturus*, the migration is said to be much less pronounced than in the frog.

The movement of the retinal pigment in reptiles was a question of much uncertainty to the older workers. ANGELUCCI (1878) was unable to decide whether or not there was a migration in the eye of the lizard or the turtle. BOLL (1881), who worked on the lizard, was left in equal uncertainty. ANGELUCCI (1890) subsequently identified a migration in the eye of *Testudo marina*, but he stated that it was much less pronounced than in the frog. CHIARINI (1906) also described a slight migration in the lizard. GARTEN (1907a), who worked on *Lacerta*, *Chameleon*, and *Ernys*, was unable to find any conclusive evidence for a migration in these three reptiles.

Contrasted with this uncertainty the more recent work has favored the view that reptiles show a slight but unquestionable pigment migration. DETWILER (1916) demonstrated such a movement of the retinal pigment in three turtles, *Chelopus guttatus*, *Chelopus insculptus*, and *Chrysemys picta*, and one lizard, *Sceloporus undulatus*. Notwithstanding the failure of ABELSDORFF (1898) and of GARTEN (1907a) to identify a migration in the crocodile, LAURENS and DETWILER (1921) demonstrated this process with certainty in *Alligator mississippiensis*. These positive results on reptiles were supported by DETWILER's further discoveries (1923, 1924a) of a pigment migration in the eye of the lizards *Eremias* and *Gecko*. It is therefore probable that reptiles in general will be found to show migrations in the retinal pigment indubitable but slight in character. The limited amount of these migrations as compared with what had been seen in the frog was what probably led to the confusion of the early workers.

In birds a retinal pigment migration is readily demonstrable. ANGELUCCI (1878) noted in the owl and VAN GENDEREN STORT (1887a, 1887b)

in the pigeon, an observation that was later confirmed by GARTEN (1907a). KRAUSE (1894) showed it in the common fowl, *Gallus domestica*. In all these instances the migration is much more pronounced than in reptiles and recalls in its conspicuousness the conditions found among the lower vertebrates.

In mammals a retinal pigment migration has never been satisfactorily demonstrated. ANGELUCCI's statement (1878) that such a migration can be shown in the rabbit was not confirmed by DEUTSCHMANN (1882). Nor is it probable that the difference claimed by CHIARINI (1906) for the retina of dogs exposed to direct sunlight or kept in the dark is reliable. GARTEN's careful tests (1907a) on the ape, ox, rabbit, and rat failed to demonstrate any significant differences and DETWILER's observations (1924b) on the field mouse and the bat showed a pigment, scanty in amount and motionless under changes of illumination. All in all these results lead to the conclusion that in mammals the retinal pigment migration is at best reduced to its lowest terms if in fact it occurs in these animals at all. That the mammalian retina adheres to the pigment epithelium slightly more tenaciously after the eye has been exposed to light than after darkness, has been urged in favor of migration, but this argument has proved far from convincing (EWALD and KÜHNE, 1878). It is to be inferred from the evidence thus far advanced that in man as in other mammals a retinal pigment migration is probably absent (AREY, 1915b) notwithstanding the assumption repeatedly implied in some of the less critical contributions (KLEIN, 1911; BARD, 1919; COBB, 1919).

In summarizing the foregoing account of the groups of vertebrates in which a migration of the retinal pigment has been investigated, it may be stated that the most extensive migrations are found in fishes and in anuran amphibians. Such changes are less evident in urodeles and still less so in reptiles. They are met with in unquestionable clearness in both day- and night-birds. Although in mammals there may be some slight evidence for pigment migration this evidence is very meagre, and it is more than probable that this process is scarcely recognizable as such in mammals including man.

That the pigment migration takes place to different extents in different parts of the retina in the same animal has been shown by HESS (1910) for the stickelback, frog, lizard, turtle, and swallow.

3. Retinal Pigment Epithelium.

The retinal pigment epithelium in vertebrates is a single layer of polygonal cells with one face resting on the choroid and the other on the free ends of the rods and cones of the retina. The individual epithelial cells of the retinal pigment layer are block-like in form and fit snugly one to the other as in a mosaic. Each cell has been described as com-

posed of three parts: a *base* comprising about half the cell next the choroid and composed of unpigmented cytoplasm containing usually one spheroidal nucleus or rarely two; a *body* next the retina and carrying a dense mass of pigment granules; and *cell processes* which emerge from the body and reach between the rods and cones as far at times as to the external limiting membrane. In the frog (ANGELUCCI, 1878), the number of processes for a pigment call varies from 10 to 40 according to the size of the cell. This provision appears to hold for most vertebrates but in *Lucioperca*, as described by WUNDER (1930), each cell carries as a rule only a single large blade-like process.

Oil, the lipochrin of KÜHNE (1879), occurs as droplets in the cell base of such vertebrates as the frog, owl, and rabbit. It is said to be absent from the hog, ox, and man. Myeloid or alemonoid granules, bodies with a wax-like appearance, have also been identified by KÜHNE (1882) in the bases of the pigment cells. They occur in amphibians, birds, and mammals including monkeys but not in man (AREY, 1928).

The most striking content of the retinal pigment cell is the melanin or fuscin granules, small bodies, usually dark-brown in color, that fill a large part of the body of the cell. Except in certain elasmobranchs already mentioned and in albino individuals, this pigment is characteristic of the retinal epithelium of vertebrates. It is ordinarily in two forms, granules and short rods. Both types occur in the body of the cell but the processes are occupied almost exclusively by the rods which are often arranged in series with their long axes parallel to that of the process. In the migration of the pigment the pigment rods are said to be much more active than the granules (VAN GENDEREN STORT, 1887a, 1887b). RAELMANN (1907) described the granules as enveloped in a special protoplasmic layer which MAJIMA (1925) regarded as a sheath. MIESCHER (1923) attributed to the granule a double nature, an albuminous base to which the pigment proper was held by adsorption.

Much uncertainty exists as to the origin of the retinal melanin pigment. LUNA (1911, 1912, 1913) believed that it arose from the mitochondria in the base of the pigment cell, an opinion that he finally abandoned (1917) and that was opposed by SMITH (1920). The view that it arose from the nucleus, as maintained by VON SZILY (1911), was opposed by CHAMPY (1911), HOOKER (1915) and SMITH (1920). Apparently the most that can be said about it is that it first appears in the cytoplasm of the pigment cell.

Guanin, a reflecting pigment, is also contained in the retinal pigment cells of certain vertebrates. In a member of animals such, for instance, as the cat, the eyes shine in the dark. This is due to the reflection of light that has entered the eye through the pupil and is turned outward again by a glistening layer in the choroid, — the choroidal tapetum. Beside this type of tapetum a number of vertebrates possess

a retinal tapetum composed of particles of guanin contained in the retinal pigment cells. This material was early recognized as a constituent of the retina in the fish *Abramis* by H. Müller (1856), and later by Kühne and Sewall (1880). It was subsequently identified in the alligator (Chievitz, 1889; Laurens and Detwiler, 1921) and in the crocodile (Abelsdorff, 1898). Its properties were fully described in *Abramis* by Exner and Januschke (1905) and by Garten (1907a) and it was identified in a number of bony fishes by Wunder (1925b, 1930). Of the 24 species of teleosts studied by Wunder (1925b) the following four gave clear evidence of a tapetum of guanin in the retinal pigment: *Lucioperca, Abramis, Acerina,* and *Blicca.* Wunder (1930) also found a retinal tapetum of guanin in *Pelecus.* All these fishes were normal inhabitants of dimly lighted waters. The guanin did not occur throughout the whole of the pigment epithelium of these retinas but was limited to special regions. Thus in *Lucioperca* (Wunder, 1930) a horizontal oval area rich in guanin and poor in melanin occupies the center of the retinal field. This is surrounded by a zone narrow anteriorly and posteriorly and broad above and especially below in which guanin is mingled with melanin. Finally the periphery of the retina is represented by a zone in which there is no guanin at all, and there is present a rich deposit of melanin. Thus the guanin is limited to the more nearly central portion of the eye of this fish and absent from its periphery. Similar and characteristic types of guanin distribution occur in the other fishes possessing this kind of pigment.

4. Retinal Pigment Migration.

The retinal pigment cells in those vertebrates that exhibit pigment migration undergo profound changes with differences of illumination (Figs. 1 and 2). Garten (1907a) has recorded six such changes. Under bright illumination the melanin moves from the base of the cell into its processes often crowding and distending their retinal ends; the cell body in consequence of the migration of melanin shortens on its vitroscleral axis (Angelucci, 1884), the nucleus migrates slightly toward the retina, the cytoplasm is said to change color, the oil drops lose color and disintegrate, and the pigment granules according to some authors are reduced in number and in depth of color. All these operations are reversed in the dark.

The migration of the melanin which is the most significant step in all these changes, is the one that has been followed by most investigators. It appears to occur for the most part within the limits of a fixed process by a kind of protoplasmic streaming. Some processes, however, show at least a certain amount of terminal extension and retraction as shown in *Lucioperca* by Wunder (1930), who claims that the activities of the pigment cells are due in part to amoeboid movement and in part to

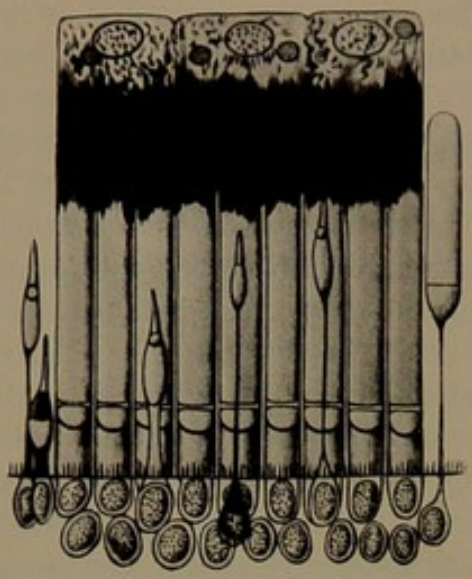

Fig. 1. Retina of a frog, *Rana esculenta*, that had remained in the dark 48 hours. Retinal pigment contracted. From VAN GENDEREN STORT, 1887b, Taf. 7, Fig. A.

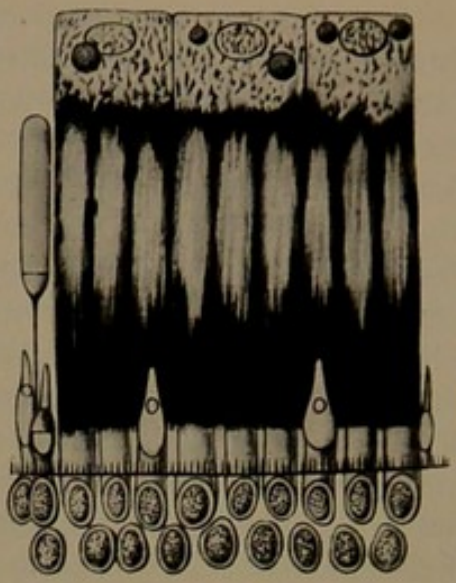

Fig. 2. Retina of a frog, *Rana esculenta*, that had remained in daylight 5 hours. Retinal pigment expanded. From VAN GENDEREN STORT, 1887b, Taf. 7, Fig. B.

internal streaming (Fig. 3). The movement of the melanin into the cell process in some way consolidates the union between pigment epithelium and retina, for, after the retinal migration has taken place, the two layers are almost inseparable as compared with their former loose connection. The melanin pigment was at one time supposed to be essential to the formation of visual purple in the rods, for when the pigment epithelium is loosened from the retina this substance fails to regenerate in the adjacent part of the retina even when it is fully cut off from the light. This failure, however, also occurs when the non-pigment-bearing cells of the albino are loosened from the retina, a condition which shows that the regeneration of the visual purple is dependent upon some other element in the retinal epithelium than its pigment.

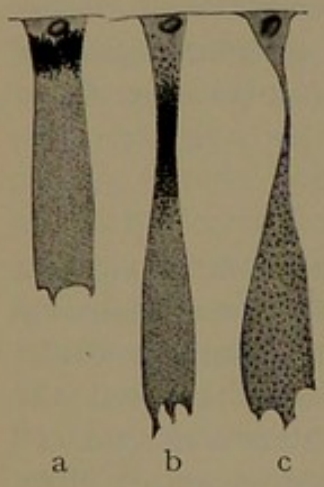

Fig. 3. Pigment cells from the middle region of the retina in the fish *Lucioperca sandra*; *a*, condition in darkness; *b*, in weak light; *c*, in strong sunlight. The melanin is shown as dark dots; the guanin as lighter dots. In the dark the melanin is next the choroid and the guanin occupies the retinal part of the cell. In dim light the melanin has moved toward the retina. In bright light the melanin and guanin are uniformly distributed through the retinal region of the cell. From WUNDER, 1930, p. 759.

The migration of the guanin in those eyes in which it occurs a matter of much uncertainty. The movement at best must be small and is doubtless more or less disguised by the change in position of the much more abundant melanin. KÜHNE and SEWALL (1880) were unable to discern a guanin migration in *Abramis* and ABELSDORFF (1898) failed to identify such a movement in the crocodile. EXNER and JANUSCHKE (1905), who reinvestigated

Abramis, succeeded in demonstrating a guanin migration and their observations were confirmed on the same fish by GARTEN (1907a). According to this author the guanin which in the light stretches from the retinal pigment almost to the external limiting membrane concentrates in the dark so as to draw away from both the retinal pigment cells and the external limiting membrane. In the half of the retina next to the external limiting membrane the direction of this concentrating movement in the dark agrees with that of the melanin migration; in the half next the retinal pigment it is the reverse. It is certainly remarkable, as several authors have noted, that in a given part of a cell two classes of pigment granules should be present and migrate in opposite direction. The guanin in the retinal pigment cells of *Lucioperca* has been well described by WUNDER (1930), but this author is doubtful whether or not a real movement of this pigment occurs. One feature, however, seems to be certain; the melanin migrates distally and proximally through the region in which the guanin particles remain relatively fixed (Fig. 3).

5. Time of Migration.

No systematic observations have been carried out on the rate of retinal pigment migration. A small amount of scattered data on this subject has been collected by GARTEN (1907a), but this is sufficient to give only a most general conception of what this field may yield. CHIARINI (1904a, 1904b) observed that the exposure of the eye of *Leuciscus* for 1 minute to sunlight was enough to start the distal migration of the pigment whereas it required from 4 to 5 minutes in the dark to start the reverse operation. These results were confirmed in all essentials by PERGENS (1896a, 1896b). VAN GENDEREN STORT noted that in a frog in daylight the distal pigment migration was completed in an hour but that in the dark the reverse movement required some four hours. AREY (1916a), who worked on three fishes exposed to either diffused daylight or darkness, found that in *Ameiurus* and in *Fundulus* full expansion or contraction was reached each in about one hour, and that in *Abramis* full expansion came in 45 minutes and full contraction in 30 minutes. It is clear from these few records that the movement of the retinal pigment is relatively slow, and that this migration is only of significance in the adaption of the given animal to its light environment in general. It is further evident from this standpoint that there is no reason to suppose that the inability of investigators to demonstrate a retinal pigment migration in mammals is due to the quickness of the migration as compared with the steps in preserving the tissue.

6. Temperature and Other Exciting Agents.

The first tests on the effects of temperature differences on the migration of the retinal pigment were carried out by EWALD and KÜHNE (1878)

on frogs, but since the animals on which they worked had been poisoned with curare with certain definite objects in view it is impossible to draw any unquestionable conclusions from their results. In 1885 GRADENIGO subjected frogs to a temperature of 30° C. in the dark and observed that the retinal pigment assumed full expansion. This was confirmed by ANGELUCCI (1890) and by FUJITA (1912). Meanwhile HERZOG (1905) without knowledge of GRADENIGO's work made similar observations and thus not only confirmed GRADENIGO but he showed further what at low temperatures (0°—14° C.) in the dark the pigment was also fully expanded. Between these high and low points, that is, over a range from 14° to 18° C., in the dark the pigment was fully contracted. AREY (1916a) confirmed in all essential respects the observations of HERZOG and showed further that in the particulars mentioned tadpoles behave as adult frogs do. In *Necturus* AREY could discover no very definite pigmentary effect from temperature changes. Subsequent investigations enabled DETWILER and LEWIS (1926) to reaffirm the main conclusions of HERZOG and of AREY.

In fishes the relation of temperature changes to the migration of the retinal pigment appears to have been investigated only by AREY (1916a) who studied for this purpose four fishes *Ameiurus*, *Fundulus*, *Abramis*, and *Carassius*. In all these both in light and in darkness the retinal pigment was expanded more at low than at high temperatures. At low temperatures the conditions were like those in the frog; at high temperatures the retinal pigment was by no means so fully expanded as in the frog.

Various drugs and anaesthetics have been applied to the retinal pigment. According to OVIO (1895) and to LODATO (1895) cocaine can arrest pigment migration. This effect can also be produced by ether (AREY, 1916a; WYMAN, 1922) and by carbon dioxide but not by chloretone or urethane (AREY, 1916a). Santonin (FILEHNE, 1900; SIVÉN and VON WENDT) apparently excites a slight expansion acting in this respect as light does. No effects were observed by FUJITA (1912) from strychnine and quinine. Increase or decrease of oxygen so long as the fishes subjected to the test remained alive does not influence the pigment migration (AREY, 1916a). Hormones have been little investigated in this respect. As stated in the introduction KLETT in 1908 was the first to report on the effects of adrenalin on retinal pigment. According to this investigator adrenalin in the frog induces in the light a contraction of the retinal pigment. FUJITA, without knowledge of KLETT's results, published in 1912 a brief statement on the same subject and declared that adrenalin caused the retinal pigment of the frog to expand. In consequence of this contradiction BIGNEY (1919) reinvestigated the subject and completely confirmed FUJITA. An injection of adrenalin into a frog according to BIGNEY induces at once an expansion of the retinal

pigment and a contraction of the dermal melanophores, a remarkable reversal of reponse. BIGNEY's results were subsequently confirmed by GILSON (1922) and, so far as they refer to the retinal pigment, by AREY (1919b) and by NAKAMURA and MIYAKE (1922). NONAKA (1931) has pointed out the importance of the neutrality of the adrenalin solution in this reaction. With progress in this field of research it is natural to expect that hormones or other humoral agents will be found to play an increasingly important part in these activities.

7. Migration and Adaptation.

It is now generally believed that the Duplicity-Theory of vertebrate vision is the best working hypothesis with which to approach the intricacies of retinal functions in these animals. According to this conception cones are concerned with distinct, colorful, bright-light vision and rods have to do with indistinct, colorless, dim-light vision. Vertebrates whose activities are carried out mainly in the day-time should be expected to have retinas in which cones are the predominant if not the exclusive element. Those whose activities are primarily nocturnal should have rods in excess. Vertebrates that may be active either at day or at night might be expected to have retinas with a mixture of rods and cones. In general these conditions are realized throughout the vertebrates (SCHARRER, 1929). The retinal pigment migration might, therefore, be expected to conform to this general conception and to serve as a means of adapting any given retina to its immediate surroundings. This interpretation has been accepted by AREY (1919a) who has sought to show that the vertebrate retina whose rods and cones as well as the pigment may under changes of illumination shift their positions is in consequence of these changes a mechanism of especially efficient vision.

This opinion can be well exemplified by the conditions of the retina for light and for dark adaptation as described by AREY (1919a) in *Ameiurus* (Fig. 4). In darkness the retinal pigment and the rod myoids are fully retracted and the cone myoid fully elongated. If this is the state in dim light the retina is well arranged for vision under such circumstances for the rods, elements for dim-light vision, are most fully exposed and the cones and pigment removed as completely as can be from the functional field. In bright diffuse daylight the retinal pigment is expanded, the rod myoid elongated, and the one myoid retracted. Here also the retina exhibits an appropriate adaptation, for the rods are covered by the pigment and the cones, the elements for distinct bright-light vision, are brought far enough forward to be accessible to the light and yet isolated one from the other by the surrounding pigment. Thus the retina is adjusted for sharp, bright-light vision. AREY (1919a) showed that the responses of the *Ameiurus* retina to dim light were essentially the same as to darkness and he therefore concluded that the

retinal changes already described were of adaptational value. Thus the retina of such a fish as *Ameiurus* may be regarded as a mechanism of really efficient vision.

WUNDER (1926b, 1930) has pointed out in detail a wide range of retinal adaptations among fishes. In confirmation of AREY (1916a) WUNDER showed on a much more extensive series of fishes that in dim-light species though the contraction of the melanin is complete its expansion is only partial, and that in bright-light forms expansion is complete and retraction partial, conditions to be expected on the assumptions already made. Hence as AREY pointed out (1916a, 1928) extreme expansion and extreme contraction do not occur in the same retina. WUNDER (1925b, 1926a) further pointed out that retinal guanin occurs only in such fishes as live in dim light or at great depths, and is often

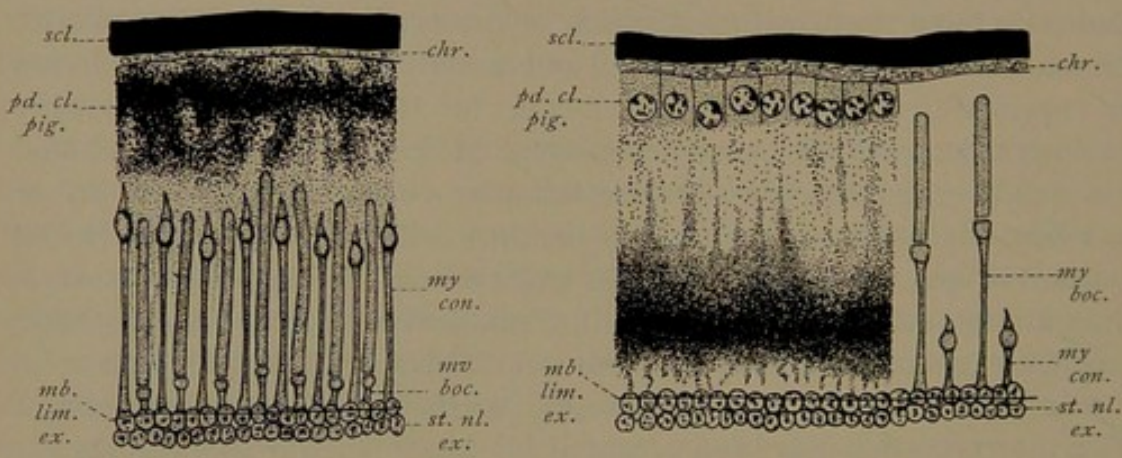

Fig. 4. Retina of a catfish, *Ameiurus nebulosus*, that had been subjected to total darkness (a) and to bright, diffuse daylight (b). In the dark the pigment is withdrawn toward the choroid; in the light it has moved toward the external limiting membrane. From AREY, 1919a, p. 344. *chr.* choroid; *mb. lim. ex.* external limiting membrane; *my. bac.* rod myoid; *my. con.* cone myoid; *pd. cl. pig.* base of pigment cell; *scl.* sclera; *st. nl. ex.* external nuclean layer; *st. pig.* pigment layer.

distributed over the retina in such a way as to meet special demands of illumination, as in the upper area of the retina as contrasted with the lower one in fishes whose vision included both upper (bright) and lower (dark) visual fields.

Interesting and accurate as many of these generalizations are they seem to apply only to the lower vertebrates. Here both the melanin and the guanin with their migrations appear to be harmoniously related to the type of vision in which both rods and cones play a part. In higher forms, however, a more specialized retina is present. Thus in some reptiles the retinas are provided exclusively with rods, in others with cones. Pigment migration, which according to the views already set forth mediate in the change from rod to cone vision and the reverse, ought to find no place in such a homogeneous retina. Nevertheless, to quote from only the more recent work, DETWILER (1916, 1923, 1924a)

found that in the pure cone retinas of the turtles, *Chelopus* and *Chrysemys*, and of the lizards, *Sceloporus* and *Eremias*, and in the pure rod retina of the *Gecko* small but unmistakable migrations take place. The fact that the pure rod retinas of the field mouse and the bat, nocturnal mammals, were found by DETWILER (1924b) to show no pigment migration is consistent with the general scheme of pigment relations already developed, but the additional fact that in man where both rods and cones occur, and yet presumably without pigment migration indicates that the scheme that applies with such completeness to the lower vertebrates has little relation to the higher forms. That many of these higher types adapt the retina admirably to dim and to bright light is most certain and yet it appears to be accomplished by means quite different from that exhibited by the vertebrates lower in the series. To some extent this condition raises the question whether what has already been done on the lower forms is really on as sound a theoretical basis as it appears to be.

III. Mollusks.

Although the mollusks, and particularly the cephalopods, have highly developed eyes, relatively little attention has been paid to their retinal pigment migration. In 1865 HENSEN intimated that the retinal pigment in cephalopods might be capable of migrating, but it was not till 1891 that RAWITZ actually demonstrated this movement. RAWITZ worked on three cephalopods: *Eledone*, *Sepia*, and *Sepiola*. In all these forms the retinas are composed of much elongated retinal cells arranged with great regularity and usually in groups of four or more. The center of each group is occupied by a receptive element, the rhabdome, probably the united product of the surrounding cells which not only contribute thus to an essential part of the retina but also carry in their core the retinal pigment. After one of these cephalopods had been kept in the dark for 24 or better 48 hours the pigment was found densely concentrated in the base of each retinal cell with a small number of straggling

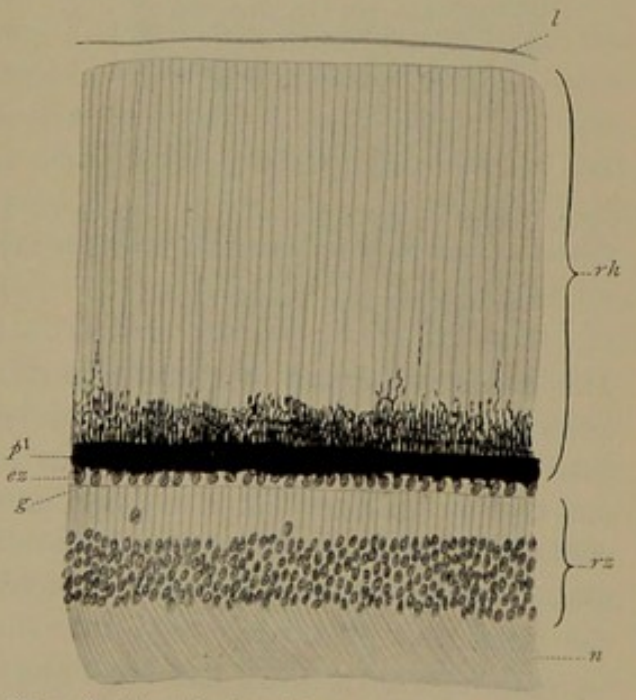

Fig. 5. Section of retina of *Sepia officinalis* showing pigment in position after 48 hours of darkness; all pigment inward (p^1). From RAWITZ, 1891, Taf. X, Fig. 2b.

granules distal to this position (Fig. 5). On exposing the animal to light more or less of the pigment still remained in the basal position but the rest is found scattered through the length of the retinal cell with a special accumulation at its distal end (Fig. 6). Thus in the light the retinal pigment must have moved distally and in the dark proximally. RAWITZ illuminated a part of the retina of *Eledone* leaving the rest of it in darkness, whereupon he found the pigment in the illuminated area distal in position and in the darkened area proximal. Thus a degree of regional independence was demonstrated. RAWITZ regarded the pigment and its movement as a means of protecting the retina from over-illumination.

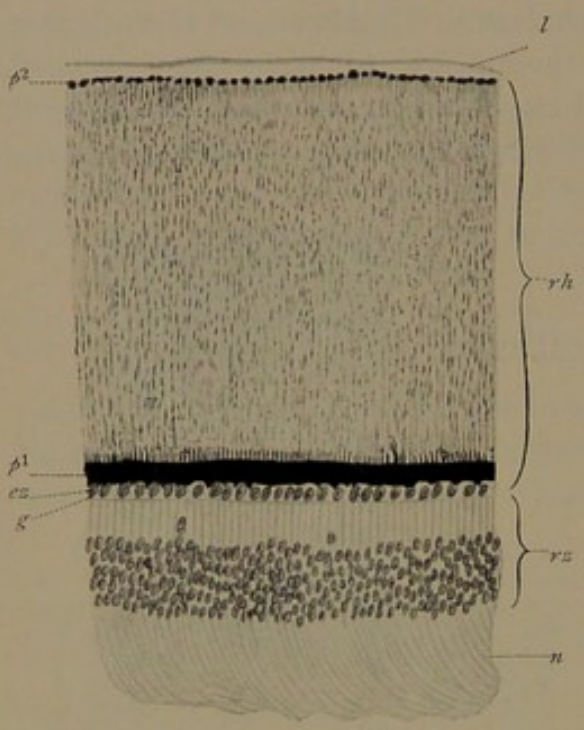

Fig. 6. Section of the retina of *Sepia officinalis* showing the pigment in the normal (light) position outward (p^2) and inward (p^1).
From RAWITZ, 1891, Taf. X, Fig. 1a.

HESS (1905) studied the condition of the eyes and retinal pigment in about a dozen species of cephalopods. From a structural standpoint he was led to distinguish three types of eyes: those with a relatively uniform retina (*Loligo*, *Todaropsis*), those in which the retina shows a differentiated band of longer and finer rods presumably for sharper vision (*Rossia*, *Scaeurgus*, *Eledone*, etc.) and finally those with a fovea (deep-sea cephalopods). In all the cephalopods investigated by HESS the pigment moved distally in the light and proximally in the dark as first demonstrated by RAWITZ. The times consumed in these migrations were found by HESS to be extremely diverse for the different species studied and were shorter than those implied in the tests carried out by RAWITZ. HESS pointed out that in an illuminated retina the color was brown or brownish red while in one from an animal kept in the dark the color was light gray. These color differences depend upon the relative positions of the migrating pigment.

Although little work has been done on the cephalopod eye still less has been carried out on that of gastropods. In 1906 SMITH stated that he was able to get only inconclusive experimental evidence of a retinal pigment migration in the fresh-water snail *Planorbis* and that he could find no evidence at all in favor of such a change in *Helix* or in *Limax*. Ten years later AREY (1916), also experimenting with *Planorbis*, recorded the following observations. Light induced in this snail a distal

migration of the retinal pigment which ended in about four hours. In darkness a proximal migration took place which required about five hours for its completion. High temperatures (30° C.) brought about a proximal migration and low ones (3° C.) a distal one. Both these reactions occurred in excised eyes, a condition suggestive of a direct response independent of nervous influence. AREY declared that the adaptional significance of these changes were to him quite obscure.

These few records on the movement of the retinal pigment in mollusks are sufficient to indicate this field as one open to future cultivation.

IV. Arthropods.

1. Introductory.

Arthropods are commonly described as possessing two kinds of eyes: — simple and compound. This division is perhaps more convenient than it is thorough-going, for it is more than probable that the so-called simple eyes are really subject to further classification (PLATE, 1924). Nevertheless this grouping will be adhered to in the present account for the reason that at least so far as pigment migration is concerned, the different types of simple eyes or ocelli have never been separately investigated.

2. Ocelli.

Very little attention has been given to pigment migration in the ocelli of arthropods. STEFANOWSKA as early as 1890 reported that after the arachnid *Phalangium opilio* had been in the light for some hours the pigment in its eye was in the main concentrated in the front of that organ and arranged in three layers; after it had been in the dark the pigment was generally diffused throughout the eye and arranged in two layers. In the same year SZCZAWINSKA stated that in the eyes of the spider *Epeira diadema* the pigment moves outward in the light and inward or toward the optic nerve in the dark. In another spider *Lycosa hortensis* she reported the reverse conditions and in the arachnid *Linyphia triangularis* she observed no migration at all. Much later in 1920 and 1921 HESS described pigment migration in the ocelli of the dragonflies *Calopteryx* and *Aeschna*. When these insects were brought from the light into the dark their ocelli became white in from a quarter of a minute to a minute. When they were carried from the dark into the light their ocelli became brown in from half a minute to a minute. Similar observations were made by SCHMITT-AURACHER (1923) on the larval ocelli of the moth *Euproctis chrysorrhoea*. HOMANN (1924), however, found that in the dragonflies *Calopteryx* and *Agrion*, the changes described by VON HESS though present were very much slighter than that author had indicated and took place at a rate much slower than what he recorded. HOMANN observed no pigment changes in the ocelli of certain

flies. KÖHLER (1925), who reported work on simple eyes done by LAMMERT, stated that in *Calopteryx* and *Agrion* the pigment migration though present was at best only partial. He was therefore led to believe that VON HESS was somewhat in error in his observations on dragonflies. No migration was observed by LAMMERT in the larval ocelli of moths and butterflies. From statements as conflicting as these it is impossible to draw with certainty any safe general conclusions. That some ocelli exhibit a pigment migration that may in a measure protect these organs against excessive illumination seems possible, but the subject is at best so poorly understood that it may be described as an essentially open field for investigation in which even the occurrence of the phenomenon itself is still more or less in question.

3. Compound Eyes.

a) Introductory. The movement of the pigment in the compound eyes of arthropods is a much more complex process than it is in the eyes of other animals. As a result much still remains to be investigated in this aspect of crustacean and insect vision and it is not surprising that the really important contributions to this subject are almost all of comparatively recent date. The condition of the pigment in the eyes of arthropods occupied to no small extent the attention of the older workers, but it was not until 1889 that the migration of this pigment was first seriously investigated. In that year EXNER published two papers on the physiology of insect vision in both of which the part played by the retinal pigment was considered. In the second of these papers (1889b) the relation of pigment migration to the vision of certain water-beetles was set forth with an analytic fullness that had never been approached before. These studies were the forerunners of EXNER's monograph on this subject, „Die Physiologie der facettirten Augen von Krebsen und Insecten", published in 1891.

Meanwhile in 1890 two independent investigations on the movement of the pigment in arthropod eyes had made their appearance, one by STEFANOWSKA and the other by SZCZAWINSKA. Notwithstanding the importance of these papers the theoretic conceptions advanced by EXNER in the publication already referred to were so sweeping and so fundamental that they literally dominated the whole of this field of research. In fact in all of the two score or more of papers on this subject that have appeared since the publication of EXNER's monograph, the authors have been chiefly concerned with a discussion of the problems raised by that publication, and have given very little attention to other possible matters. These comments are not to be taken as a reflection on the workers in this field. The problems brought out by EXNER's studies were so far-reaching that their solution called for years of work. Nor have these problems been fully solved yet (HESSE, 1929).

The migration of pigment in the compound eyes of arthropods is a subject that calls for a definite understanding of the structure of the organs concerned. From an anatomical standpoint compound eyes may be divided conveniently into two groups: relatively simple eyes such as occur in the lower crustaceans and more complex eyes which characterize the higher crustaceans and the insects (PARKER, 1891).

b) Simple Type of Compound Eye. The simpler eyes are well exemplified by those in *Gammarus*. In this amphipod each eye is a sessile more or less kidney-shaped body situated on the side of the head and is composed of relatively few ommatidia. Each ommatidium consists of a distal cone whose shape is such that it acts as a catoptric organ and causes to be absorbed or discharged all rays of light falling upon it except those that are parallel or very nearly parallel with its longitudinal axis. Proximal to the cone is the receptive element or rhabdome formed ordinarily from five retinular cells in each of which three portions may be distinguished, — a distal thin blade-like part applied to the sides of the cone, a middle attenuated portion carrying a segment of the rhabdome, and a proximal enlarged part below the basement membrane and including the nucleus. The attenuated inner end of the proximal portion passes over into the retinal nerve fiber. Such retinular cells carry the mass of melanin particles making up the black pigment of this type of eye. The interommatidial spaces in *Gammarus* are filled with reflecting pigment contained in cells whose nuclei may occur anywhere between the ommatidia and whose mass collectively constitutes the tapetum. Essentially this interpretation of the eye of *Gammarus* has been accepted by most of the workers on this subject including GRENACHER (1879), CARRIÈRE (1885), PARKER (1891, 1899), and BENNITT (1924).

SZCZAWINSKA's claim that the three parts of the retinular cell as just described are really three distinct cells is certainly quite erroneous. It is also probable that the opinion of STRAUSS (1926, p. 12) that what has been described in this account as the distal blade-like part of the retinular cell represents an independent cell secondarily fused with the true retinular cell is a mistaken view. STRAUSS in his monograph on the eyes of gammarids called attention to the difficulties in this interpretation and admitted that a separation between what he assumed to be the distal pigment cell and the retinular cell could not ordinarily be shown to exist.

A simple type of ommatidium such as that described for *Gammarus* appears to be found in the great majority of the crustaceans below the Schizopods. The images formed by such eyes are always apposition images and the cones of these eyes are catoptric cones in most cases probably unassociated with the migration of pigment.

In *Gammarus* and some allied forms, however, a pigment migration occurs. This was first described by SZCZAWINSKA (1890) and was studied

subsequently by PARKER (1899), by SMITH (1905), and by BENNITT (1924). All workers on this subject agree that in the dark the melanin pigment is absent from the middle portion of the retinular cell where it had previously cut off the tapetal pigment from the rhabdome and that it has moved into the adjacent proximal segment. In the light the middle portion becomes filled again with this pigment (Fig. 7). SZCZAWINSKA (1890) believed that the discharge of the pigment from the middle portion of the retinular cell was accomplished by a migration partly in an inward direction and partly in an outward one, but PARKER (1899) showed that this migration was chiefly, if not entirely, inward and that on the return of the pigment from the proximal part of the cell to the middle part, the proximal part was left with relatively little melanin in it.

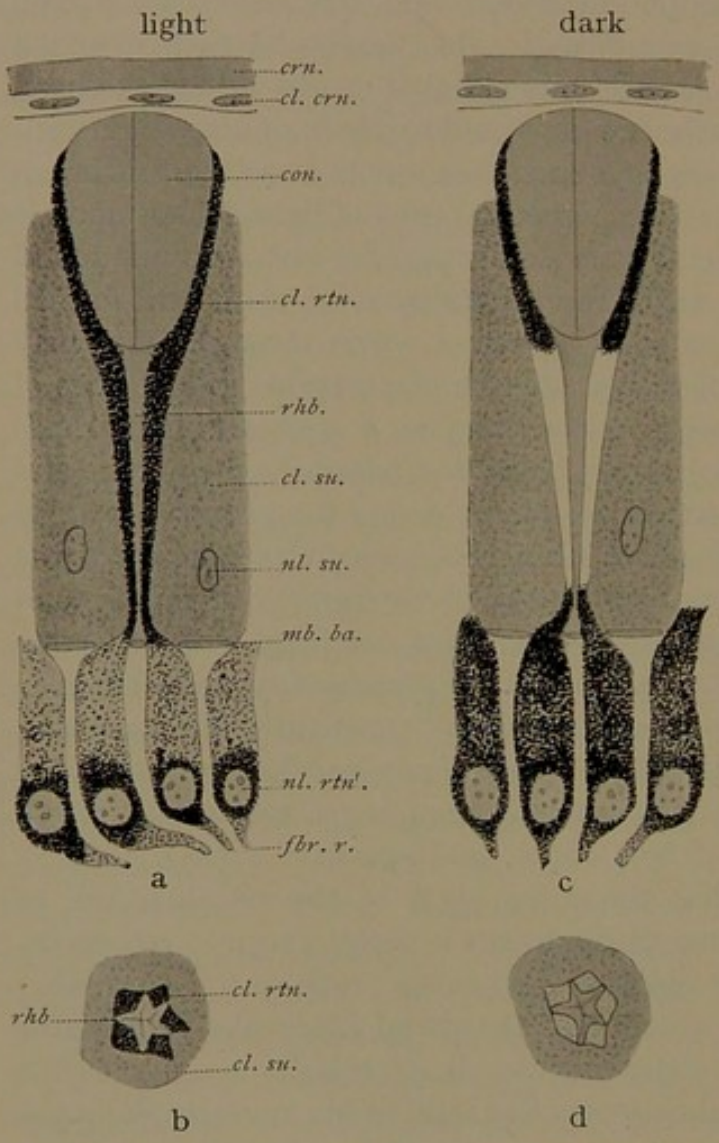

Fig. 7. Ommatidia from the eyes of *Gammarus ornatus* after exposure to bright light and to darkness. a and c longitudinal sections; b and d transverse sections in the region of the rhabdome. In the dark the pigment has moved from the region of the rhabdome to a position below the basement membrane; in the light it has returned to surround the rhabdome. From PARKER, 1899.

The intervals of time consumed in these migrations have been recorded by SMITH (1905) and by BENNITT (1924). In *Gammarus annulatus* the outward migration (in the light), according to SMITH, is for the most part accomplished in a quarter of an hour but may not be completed before a full hour. BENNITT showed that in *Gammarus locusta* the time intervals were influenced as might have been expected by the intensity of the light and by the surrounding temperature. The times of migration at different temperatures necessary to complete the movements are shown in Table 1.

As Table 1 shows the outward migration in the light is completed in much less time than the inward one (in the dark): at room temperature

Table 1. Time intervals in minutes for outward and for inward migrations of retinal pigment in the eyes of *Gammarus locusta* at different temperatures (BENNITT, 1924).

Outward Migration					
Degrees Centigrade	3.4	8	13.25	18.8	23
Time in Minutes	8	5	4	2.5	2
Inward Migration					
Degrees Centigrade	2.9	7	14	18.1	23.4
Time in Minutes	50	37	24	18	13

in the light in about two and a half minutes and in the dark in about 18 minutes. The process has a temperature coefficient of approximately 2 and hence may be assumed to involve chemical activity as might be expected. The migration in the light takes place in shorter time as the light increases in intensity. At 0.0031 candle-meter the migration requires 14 minutes; at 0.011 candle-meter 6 minutes and at 0.072 candle-meter 4 minutes.

The means by which this migration is effected has been worked out by BENNITT (1924) in *Talorchestia longicornis*. If measurements of the volumes of the middle segment and of the proximal segment in this amphipod are compared for the two conditions of illumination important relations will be disclosed (Table 2).

Table 2. Volumes in cubic μ of the middle and of the proximal parts of the retinular cells from *Talorchestia longicornis* under different degrees of illumination (BENNITT, 1924).

	Light	Dark
Middle Part	4495.64	1770.64
Proximal Part	2208.65	4341.42
Total	6704.29	6112.06

As Table 2 shows, the outward migration of the pigment in bright light is accompanied by a considerable enlargement of the middle segment into which the pigment passes, and a corresponding reduction of the proximal segment from which it migrates. The inward migration involves a reversal of these conditions. In each instance the recipient segment is about twice the size of the donating one. BENNITT concluded from these measurements that the pigment migrations are accomplished by what may be described as a voluminous streaming back and forth of the cell protoplasm of so vigorous a nature as to be fairly described as a surging. In this way the pigment granules are carried bodily back and forth. The migration of the pigment results in the exposure or the covering up of the reflecting pigment, steps which intensify the illumina-

tion of the rhabdome in dim light and reduce it in bright light. Such eyes probably maintain under all conditions an apposition image and show no tendency to pass over into a superposition state even in extreme darkness.

The significance of these changes for the phototropism of *Gammarus* has been worked out by SMITH (1905), who showed that when an animal with the pigment in the dark position is exposed to horizontal illumination it remains essentially indifferent for some 10 minutes, after which it becomes distinctly positive, a state which increases markedly till it reaches a maximum in about an hour when the pigment has assumed the full light position.

Very little attention has been given to the pigment migration in the eyes of other lower crustaceans. According to SZCZAWINSKA (1890) a slight distal concentration of pigment occurs when the eyes of *Branchipus* or of *Phronima* are exposed to the light, but this is so slight that EXNER (1891), who studied the eyes of *Phronima* independently of SZCZAWINSKA, was unable to discover any sign of migration at all. Although the eyes of *Phronima* and of *Branchipus* exhibit at best very little pigment migration, the eyes of certain other lower crustaceans, as for instance those of *Gammarus* and of *Talorchestia*, show such marked activity in this respect as to invite an extended study of this phenomenon in other related forms.

c) Complex Type of Compound Eye. The more complex type of compound eye, judged from the standpoint of its pigment migration, is found in the higher crustaceans and in the insects. In an ommatidium of such an eye from among the crusaceans there may be as many as three kinds of pigment cells disposed around a transparent central axis. The distal portion of this axis is occupied by the cone which is dioptric in function and which extends inward to the receptive element or rhabdome in the proximal portion of the axis. The most distal band of pigment in this type of eye is the iris or distal pigment contained in cells which are usually two in number for each ommatidium and which together surround the cone in sleeve-like fashion. The proximal or retinular pigment is contained in the retinular cells which to the number of eight, one often rudimentary, envelop the centrally located rhabdome. The rhabdome as a matter of fact is made by the fusion of the inner differentiated faces of the functional retinular cells whose outer cytoplasmic portions are filled with pigment granules. The pigment of the distal and of the proximal cells consists of melanin particles; hence the pigmented parts of these cells are black in appearance. The third kind of pigment, the reflecting pigment, is white, at least when viewed by reflected light, and is contained in cells that fill the somewhat irregular spaces between the proximal ends of neighboring ommatidia. This kind of pigment may reach out to the front face of the distal pigment cells

and inward to a point below the basement membrane. It is believed to be made up of guanin particles and is collectively designated as the tapetum. The retinal nerve fibers are inward prolongations from the proximal pigment cells, one for each functional cell and hence seven or eight for an ommatidium. They pass proximally from the bodies of the cells through perforations in the basement membrane to terminate in the subjacent optic ganglion. They are relatively coarse and their substance may be invaded to a considerable extent by the proximal melanin pigment which may thus make its way from the bodies of the retinular cells to situations well below the basement membrane.

The ommatidia in the eyes of insects have the same general structure as have those in the higher crustaceans. In insects as in crustaceans the transparent axis of the ommatidium is occupied by a distal cone or cone-like body and a proximal rhabdome. This axis is surrounded by two tiers of pigment cells, the distal or iris cells and the proximal or retinular cells both of which ordinarily contain an abundance of melanin. In addition to these two sets of pigment cells accessory black cells may also be present. A reflecting pigment or tapetum is not known to occur in the eyes of insects, but its place is taken by a mat of very fine tracheal tubes which occupy the space between the bases of the ommatidia and which in consequence of their contained air reflect light efficiently. The innervation of the insect retina agrees with that in crustaceans.

The *distal* or *iris pigment*, as already stated, surrounds the transparent axis of the ommatidium at the level of the cone. In an ommatidium from one of the higher crustaceans this pigment is contained in two opposing cells. The distal pigment often exhibits an extremely active migration. In bright light it is proximal in position abutting against the proximal pigment; in darkness it occupies a distal location between the cones (Fig. 8). When the distal pigment is at its innermost position the eye is assumed to act as an apposition eye; when it has reached its outermost position the eye may function as a superposition organ. Thus the migration of the pigment is assumed to regulate the light leading to a given rhabdome, numerous avenues when the light is dim, few when it is bright (Fig. 9).

At least two types of movement are known to occur in the distal pigment. In the first type the distal cells that together form a sheath around the transparent axis of the ommatidium slip as a whole up and down on this axis (Fig. 8), a movement the extent of which can be measured by the distance over which the nucleus of the cell moves (Parker, 1897). Judging from the figures given by various authors this type of movement is well exemplified in the following macrurans: *Palaemon* (Szczawinska, 1890; Exner, 1891; von Frisch, 1908; Trojan, 1913; Mossler, 1915), *Palaemonetes* (Herrick, 1891; Parker, 1896, 1897; Congdon, 1907; Welsh, 1930a), *Nika*, *Sicyonia* (Exner, 1891),

Macrobrachium (WELSH, 1930b), in the brachyurans, *Pisa*, *Portunus* (EXNER, 1891), and in a large number of insects chiefly nocturnal; among the beetles *Lampyris*, *Cantharis*, *Dyticus*, *Colymbetes*, *Hydrophilus* (EXNER, 1891; KIRCHHOFFER, 1908), *Melolontha*, *Geotrupes*, *Cicindela* (KIRCHHOFFER, 1908), among the moths *Lasiocampa*, *Spilosoma*, *Porthesia*, *Catocala* (EXNER, 1891), *Plusia* (KIESEL, 1894), *Agrotis* (DEMOLL, 1911) and a host of others (MERKER, 1929b, 1929c).

The time consumed in the first type of migration appears to have been measured directly only in the crustaceans *Palaemonetes* and *Palaemon*. In *Palaemonetes* according to PARKER (1897) the inward migra-

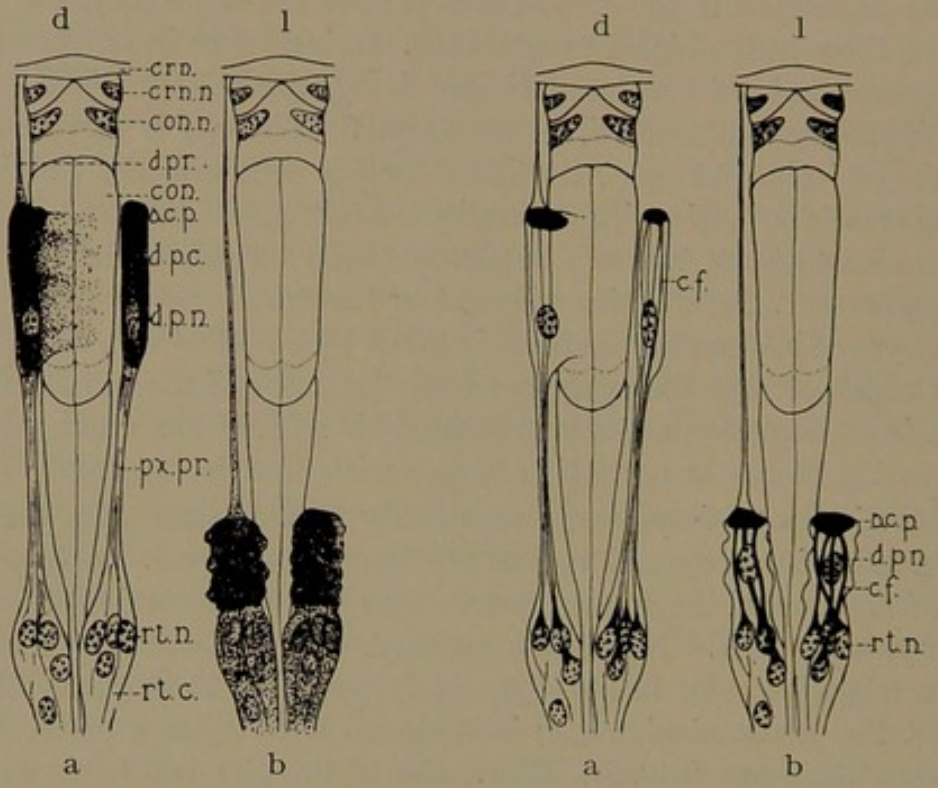

Fig. 8. Ommatidia from the eyes of *Palaemonetes vulgaris*, showing the conditions due to extreme darkness (d) and extreme light (l) in preparations with the natural pigment intact (a) and after depigmentation (b). In the dark the iris or distal pigment is outward and the retinal pigment inward in position; in the light the reverse is true. The contractile fibrils (*c.f.*) of the distal pigment cells are shown thickened in the light and attenuated in the dark. From WELSH, 1930a, p. 464.

tion, which occurs when the animal is placed in the light, requires for its completion from 90 to 105 minutes, the outward migration, in the dark, from 105 to 120 minutes. In *Palaemon* VON FRISCH (1908) recorded shorter intervals, for the inward migration 45 minutes and for the outward one within 60 minutes. These records were confirmed on the same crustacean by MOSSLER (1915) who showed that the inward migration required from 45 to 50 minutes and the outward one 60 to 70 minutes. WELSH (1930a) repeated PARKER's tests on *Palaemonetes* and obtained essentially similar results for the outward migration, 90 to 120 minutes, but shorter records for the inward migration, 50 to 60 minutes. By a direct method of observation on the living crustacean WELSH showed

an average for the inward migration of 40 minutes and for the outward one of 90 minutes. He likewise demonstrated considerably individual variation in the determinations from different shrimps. Notwithstanding these variations it is probable that PARKER's determinations for the inward migration are somewhat too long. However this may be, a general survey of the whole body of records points clearly to two conclusions: first, the migrations whether they be outward or inward in direction are always relatively slow, and, second, the inward migration (in the light) in any set is always accomplished in less time than the outward one (in the dark) in the same set.

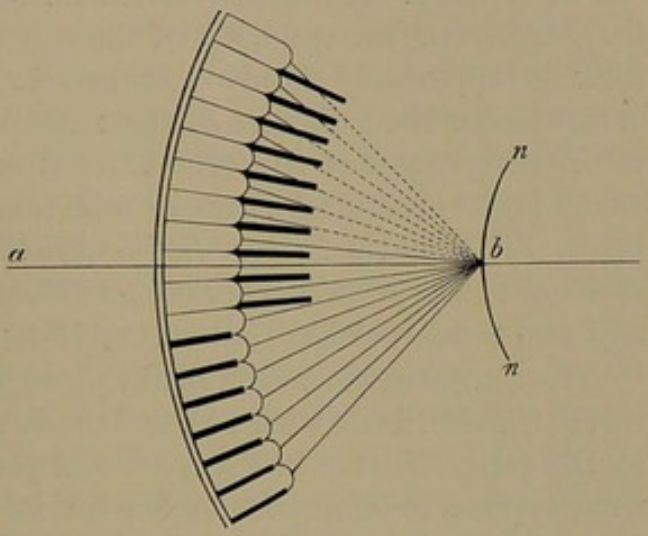

Fig. 9. Diagram showing the effect of the migration of the iris or distal pigment in the compound eye. The axial ray of light is indicated by the line *a b*. In the lower part of the figure the pigment is in the position for dim light and the eye admits lateral rays; in the upper part it is in the position for bright light and the eye excludes lateral rays. From EXNER, 1891, p. 64.

By repeated determinations on one individual WELSH showed with his improved technique that in the dark the migration starts slowly, then speeds up, and finally slows down again before it stops entirely. When, in such a set of observations, distance travelled is plotted against time a sigmoid curve results. The same general changes in rate were seen when the migration in the light was recorded except that as the movement approached completion a second but much slighter acceleration occurred. WELSH also observed that a migration started in the light would continue in the dark in the same direction for as much as 20 minutes.

It is commonly assumed that in the moths and other night insects the time necessary for the disappearance of glow which occurs when the animal is transferred from darkness to light is a measure of the period necessary for the inward migration of the distal pigment. This period ranges from 3 to 25 minutes (EXNER, 1891; KIESEL, 1894; DEMOLL, 1917; MERKER, 1929a) a period that is probably approximately accurate for this type of migration. It must, however, be remembered that the disappearance of glow may be determined by migrations in the proximal pigment as well as in the distal pigment and that determinations based upon glow are at best only indirect determinations.

The mechanism of the first type of movement in the distal pigment cells has been assumed by TROJAN (1913) and by MOSSLER (1915), who have studied this process in *Palaemon*, to be akin to protoplasmic

streaming. PARKER (1897) had previously suggested that in *Palaemonetes* the change in position might be the result of combined amoeboid and muscular movements. The operation was studied in detail by WELSH (1930a) in *Palaemonetes*. In the dark condition of the eye in this shrimp the body of the distal pigment cell has roughly the form of a flat double plate covering approximately two of the four sides of the cone. Distally it is continued as a fine fiber that reaches from the cell-body proper to the cuticula and has a length of about that of the cell-body itself. Proximally another fiber, somewhat coarser than the first, extends from the body of the cell to the retinula. This proximal fiber is apparently firmly attached to the proximal retinular cells. When under the influence of light the distal pigment cell moves from the neighborhood of the cone to that of the retinula, the distal fiber elongates to over three times its original length, the proximal fiber contracts till it is no longer distinguishable as such, and the cell-body shortens to about half its former length, becoming much expanded laterally and roughly folded (HERRICK, 1891; PARKER, 1897).

WELSH noted that each distal pigment cell contained in its interior three or four fibrils which extend from the distal end of the cell-body to the proximal end of the proximal process where they terminate in what appears to be very intimate relations with the nuclei of the proximal pigment cells (Fig. 8). When the distal pigment-cell migrates proximally these fibers shorten to one-fourth or one-fifth of their former length and correspondingly thicken. They are, therefore, believed by WELSH to be myofibrils, responsible in the main for the inward movement of the distal pigment cell. Their contraction is fairly represented by the movement of the cell as a whole which when plotted is sigmoid in form, a further intimation of their muscular nature. Myofibrillar agents were claimed as components of the compound eyes in insects by LEYDIG (1855, 1864) and, though they were denied as such by CLAPERÈDE, (1860), their presence was again asserted by EXNER (1891, p. 69). If these fibrils in *Palaemonetes* are really myofibrils, as WELSH's evidence appears to indicate, this record is the first for the occurrence of such elements in crustaceans.

Although the inward migration of the distal pigment cells appears to depend chiefly on the contraction of myofibrils, its outward migration cannot be so explained, for the distal processes, so far as is known, contain no such fibrils. In the outward migration these processes shorten while the cell-bodies and the proximal processes elongate. That the outward migration is due in part to a primitive type of protoplasmic contraction in the distal process is entirely possible, and the fact that the distal process shortens consistently, and that the cell-body moves first slowly, then more rapidly, and finally again slowly, are indicative of some muscle-like action. It is still possible, however, that the motion

is amoeboid. It must, however, be kept in mind that the means for the outward migration of the distal cells is quite unknown.

The second type of pigment migration as shown by the distal cells is one in which the cell-bodies remain essentially motionless at the level of the cones and their contained pigment granules move inward into the long proximal processes of the cells (in the light) and back again to the bodies of the cells (in the dark). In this type of migration the cell body is without a distal fiber but possesses a very long proximal one which, like that in the first type reaches from the cell-body to the retinula (Figs. 10 and 11). The second type of pigment migration is exemplified in the following macrurans: *Astacus* (Szczawinska, 1890; Exner, 1891; Parker, 1895; Bernhards, 1916), *Scyllurus*, *Pagurus* (Exner, 1891), *Cambarus* (Bennitt, 1924), probably *Palinurus* (Exner, 1891), in the brachyurans *Dromia* and *Maja* (Exner, 1891), and in the insects *Notonecta* and *Corixa* (Bedau, 1911).

The means by which the pigment granules from the cell-body make their way into the proximal process and back again has never been determined by experimental test, but is generally assumed to be the result of protoplasmic streaming. When the process is densely loaded with pigment granules, as happens after the eye has been exposed for some time to strong light, the retina must approximate that of one arranged for apposition images though not so completely so as in the first type of migration. The outward movement of the pigment of course renders the situation favorable for a superposition image as was true in the first type of migration.

It is not to be supposed that the two types of pigment migration discussed in the proceeding paragraphs are to be regarded as strictly distinct and separate. Undoubtedly in many cases where the cell-body migrates as a whole more or less internal movement of pigment also takes place. Thus both methods of pigment change may occur in the same eye. This seems to be true of the eye of *Galatea* judging from the descriptions by Szczawinska (1890) and by Exner (1891). Here a limited amount of actual cell movement is associated with a migration of pigment from the cell-body into the proximal process and back again. However most crustaceans and insects exhibit one type of migration to the exclusion of the other.

A migration of the distal pigment could not be identified by Exner (1891) in *Squilla*, nor was it observed or expected in insects that live in strong sunlight, such as the beetles, *Cetonia*, *Tropinota* (Exner, 1891) and many butterflies (Demoll, 1909).

The *proximal* or *retinular pigment* is the second type of pigment in the more complex form of compound eye. This pigment, as already stated, surrounds the rhabdome and is contained in the group of proximal or retinular cells, usually eight in number, that envelop that structure.

It is composed of melanin granules and hence it is black in appearance. It moves under the influence of light in such different ways in the crustaceans and in the insects that its activities in these two groups will be considered separately.

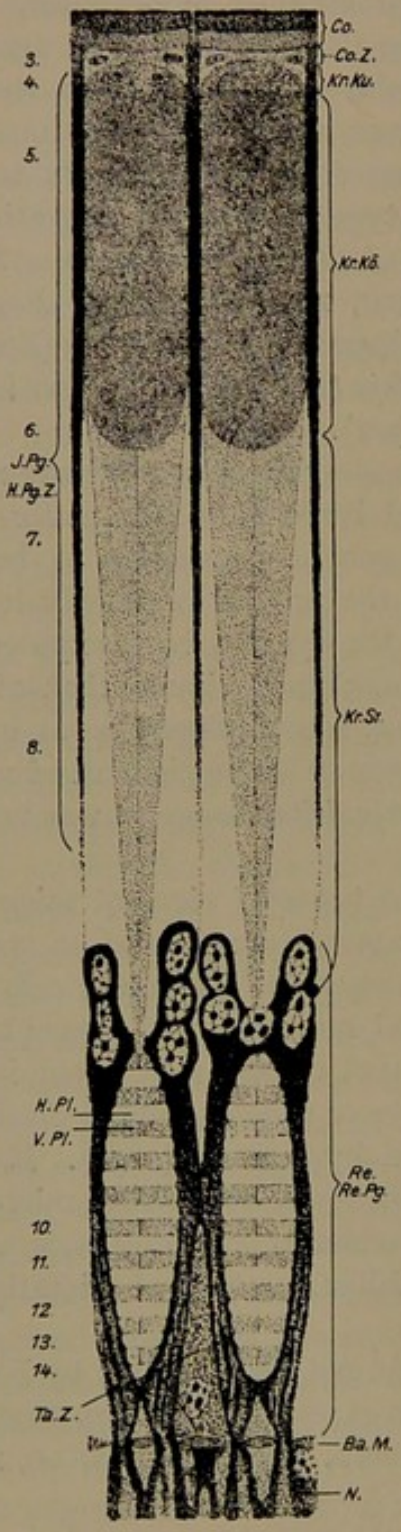

Fig. 10. Longitudinal section of two ommatidia of the crayfish, *Astacus fluviatilis*, showing the pigment in the light position. The iris or distal pigment is in the extreme inward position, the retinal pigment in the extreme outward one.
From BERNHARDS, 1916, p. 684.

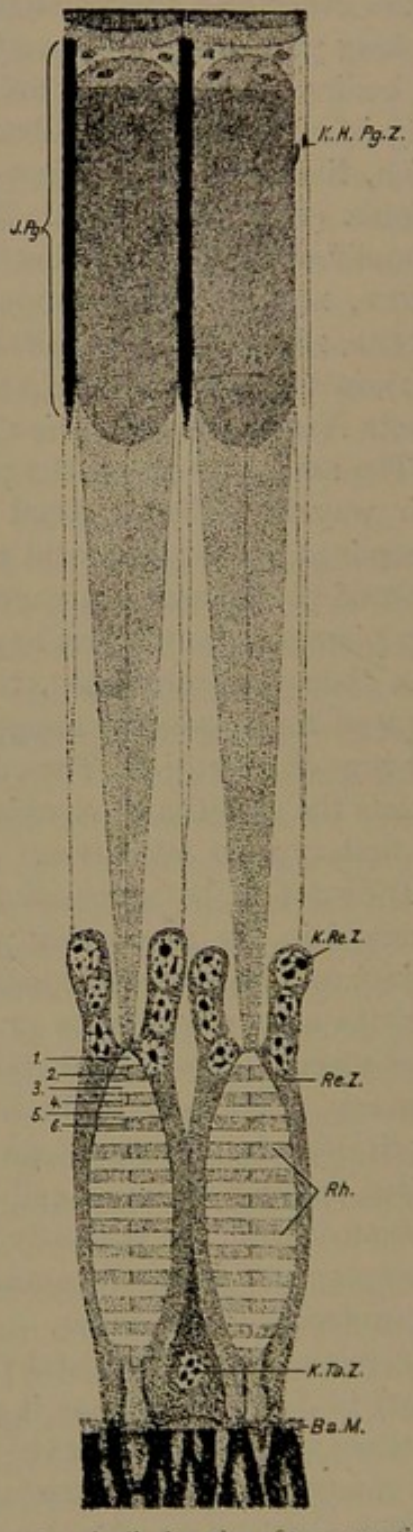

Fig. 11. Longitudinal section of two ommatidia of the crayfish, *Astacus fluviatilis*, showing the pigment in the dark position. The distal pigment is in the extreme outward position; the retinal pigment in the extreme inward one.
From BERNHARDS, 1916, p. 685.

The *proximal pigment* in *crustaceans* in its light phase commonly fills the proximal retinular cells from their fibrous extensions below the basement membrane to their nucleated distal ends. In its dark phase it is usually limited to the fibrous portion of these cells below the basement membrane (Figs. 8, 10, 11). In terms of migration the proximal pigment may be said to move outward in the light and inward in the dark — the reverse of the distal pigment. As a consequence the distal and proximal pigment masses approach one another in the light and separate in the dark. In bright light the proximal pigment is so placed as to admit rays to the body of the rhabdome only at its distal end and to cut off all possibility of the adjacent reflecting or tapetal pigment from playing the part of a reflector. In the dark position the whole rhabdome is exposed laterally as well as distally to light and the tapetal pigment may turn rays that have passed through a part of the rhabdome back into that structure. The proximal pigment is believed therefore to have the function of controlling the amount of light that acts on the rhabdome, and this function is carried out chiefly in connection with the reflecting pigment. In this sense these two pigments act as a unit.

Proximal pigment showing the type of migration described in the last paragraph has been recorded in the following macrurans: *Astacus* (Szczawinska, 1890; Exner, 1891; Parker, 1895; Bernhards, 1916), *Cambarus* (Congdon, 1907; Day, 1911; Bennitt, 1924, 1932a, 1932b; Bennitt and Merrick, 1932), *Homarus* (Bennitt, 1932a), *Palaemon* (Szczawinska, 1890; Exner, 1891; von Frisch, 1908; Trojan, 1913; Mossler, 1915), *Palaemonetes* (Parker, 1896, 1897; Congdon, 1907; Castle, 1927; Bennitt, 1929, 1932a), *Galatea* (Szczawinska, 1890; Exner, 1891), *Palimurus*, *Sicyonia*, *Nica*, *Scyllarus* (Exner, 1891), and in the following brachyurans: *Dromia*, *Pagurus*, *Pisa*, *Portunus* (Exner, 1891), *Cancer*, *Carcinides*, and *Libinia* (Bennitt, 1932a). Exner (1891) was unable to identify this type of pigment migration in *Maja* and in *Squilla*.

The time consumed in the movement of the proximal pigment in crustaceans is not far from that required in the migration of their distal pigment. In *Palaemonetes*, according to Parker (1897), the outward migration of the proximal pigment (in the light) takes from 30 to 45 minutes and the inward migration (in the dark) from 45 to 60 minutes. In the proximal pigment of *Palaemon* von Frisch (1908) found that the outward movement requires 25 minutes and the inward one 75 minutes. In the sets of records from these two crustaceans it will be seen that the migrations in the light require less time than do those in the dark (Mossler, 1915), a condition already noted for *Gammarus* (Bennitt, 1924). Further the migrations of the proximal pigment both in the light and in the dark are accomplished for the two crustaceans under consideration in shorter times than are those of their respective distal

pigment masses. In *Palaemon*, however, the migration of the proximal pigment in the dark is completed in 75 minutes, although the distal pigment requires only 60 to 70 minutes. These features of pigment migration are recorded in Table 3.

Table 3. Comparison of times in minutes for the migration in the light and in the dark of the distal and the proximal pigment in *Palaemonetes* and *Palaemon*. F, VON FRISCH; M, MOSSLER; P, PARKER; W, WELSH.

	Palaemonetes	*Palaemon*
Light migration, distal pigment (inward) . . .	90—105 P.	45 F.
„ „ „ „ „ . . .	50—60 W.	45—50 M.
„ „ proximal pigment (outward)	30—45 P.	25 F.
Dark „ distal pigment (outward) . . .	105—120 P.	60 F.
„ „ „ „ „ . . .	90—120 W.	60—70 F.
„ „ proximal pigment (inward) .	45—60 P.	75 F.

No special attempt has been made to investigate the means by which the migration of the proximal pigment is accomplished. It is generally assumed that it is the result of some form of protoplasmic movement (PARKER, 1897; MOSSLER, 1915) such as that shown by BENNITT (1924) for *Talorchestia*. The opinion advanced by ROSENSTADT (1896) that proximal pigment may percolate forward into the distal mass and the reverse, and thus establish a kind of pigment infiltration from one part of the retina to another has never received any substantiation and is probably erroneous (DEMOLL, 1910).

A *reflecting pigment*, the so-called *tapetum*, has been identified in the interretinular spaces of most crustaceans. The full inward migration of the retinular pigment, as occurs ordinarily when these animals are kept in the dark, exposes this reflecting pigment in such a way that, as already described, light which has entered the eye from the outside and which has passed through the rhabdome once may be reflected back again into that structure or even out of the eye. In this way the repeated application of weak light to the rhabdome may make possible stimulation, a step which might not have been accomplished by a single passage of the light through this organ. Light which after one or more such reflections escapes from the eye is believed to be responsible for the glow often seen in the eyes of many crustaceans which have been kept for some time in the dark. This light plays an important part in the phenomenon of pseudopupil to be considered later. In bright light the reflecting tapetum is covered by proximal black pigment and no such reflection is possible nor is there any need of this reflection if the hypothesis just referred to be correct. Assuming the function of the crustacean tapetum to be simply that of a reflector it is not necessary that this pigment exhibit movements of its own; all that is needed for

its part in the action of the eye is that it should be covered or uncovered by other pigment such as the melanin pigment in the proximal cells. General quiescence, appropriate to this method of action, seems to characterize the tapetum in most crustaceans (EXNER, 1891; PARKER, 1895). Nevertheless in *Palaemonetes* PARKER (1897) believed that there was evidence of slight migration. This opinion has been supported by the observations of TROJAN (1913) and of MOSSLER (1915) on *Palaemon*, and fully confirmed and much extended by those of WELSH (1932) on *Palaemonetes* and especially on *Macrobrachium*. In these two crustaceans according to WELSH the tapetal pigment migrates inward in the light and outward in the dark, and thus comes into more intimate relations with the rhabdome where its reflecting action would be of most importance. PARKER (1897) expressed the opinion that the reflecting pigment changed position in that its cells were capable of amoeboid motion. WELSH suggested (1932) that in addition to amoeboid activity the protoplasm of the reflecting cells was probably capable of a surging motion, such as had been indicated for the retinular cells in *Talorchestia* by BENNITT (1924). Nothing, however, is really known, experimentally or otherwise, about the means of migrations for this pigment.

If the relation of the reflecting pigment to the retinular pigment in crustaceans as summarized in the preceding paragraph, be correct one would expect to find that all eyes which possess a tapetum would exhibit an appropriate type of movement in their proximal pigment, and such seems to be true. It is, however, conceivable from what has already been stated that a proximal pigment migration might be present but without a tapetum as appears to be the case in *Pagurus* and in *Portunus* (EXNER, 1891). Where no migration of proximal pigment occurs as in *Maja* and in *Squilla* (EXNER, 1891), no tapetum should be expected, and EXNER reported both these forms as devoid of this structure. Such conditions support the general contention originating with EXNER (1891) that the crustacean tapetum is a reflecting layer whose physiological activity is dependent upon the movements of the proximal retinular pigment.

The *proximal pigment in the compound eyes of insects* is ordinarily massed around the rhabdome and is probably contained always in retinular cells, but the outlines of these cells in the usual histological preparation are often so vague and indistinct that some writers have been inclined to believe that this pigment is not within cells proper but in the open spaces adjacent to the rhabdome. This opinion, however, is probably erroneous. EXNER (1891) stated that he was never able to detect any evidence of migration in the proximal pigment of insects. He and others therefore assumed that in these animals the changes in the pseudopupil and other like phenomena following changed illumination were to be ascribed entirely to the movement of the distal cells. Never-

theless in 1909 DEMOLL showed that in certain butterflies (*Pieris napi*, *Melitaea athalia*, *Pararge megera*, *Bupalus pinnarius*, *Thecla rubi*, *Gonopteryx rhami*, *Vanessa urticae*, *V. polychloros*, *V. io*, and *V. levana*) that live in alternating shadow and sunlight as on the edges of woods and other like places, a pupillary glow could be obliterated by appropriate illumination in from 4 to 6 seconds and revived in the dark in from 4 to 5 seconds. This phenomenon was not observable in closely related species, such as *Pieris brassicae*, *Papilio machaon* and others, which inhabit the open fields. DEMOLL further showed that, as might be expected, a pigment migration was associated with the production and obliteration of the glow (Fig. 12). When the glow was to be seen the retinular pigment was found well below the basement membrane, and when it had been obliterated this occupied the region over the distal face of the optic ganglion. Whether in this position the glow was lost by the spreading of the pigment over a tapetum of tracheal tubes or by covering the reflecting bases of the rhabdomes was not definitely determined. That some reflecting material close to the basement membrane was quickly covered and uncovered is clear and the very short distance over which the necessary pigment migration took place explains the relative rapidity of the change.

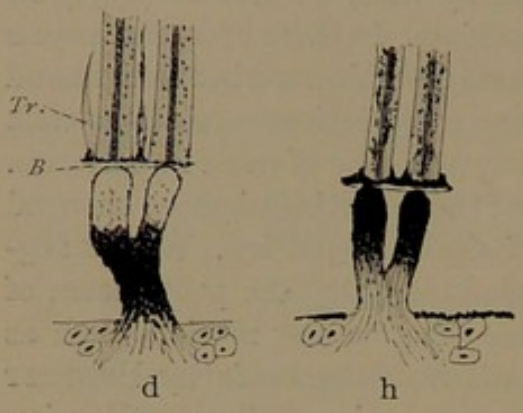

Fig. 12. Proximal zone of the retina of *Vanessa urticae*. The pigment is shown in the position for the dark (d) and for the light (h). From DEMOLL, 1909, p. 466.

DEMOLL's observations on the rapid change in glow in these butterflies were abundantly confirmed on a large number of such insects by MERKER (1929 a, 1929 b) who, however, left the structural side of the question untouched and consequently was not in a position to state with certainty the part played by the distal and the proximal pigments in these operations. Following the work of DEMOLL, KIRCHHOFFER (1908) published an account of the pigment migration in the eyes of the tiger beetle *Cicindela*. In this insect the proximal pigment moves inward in the dark and outward in the light but not enough, according to KIRCHHOFFER, to allow anything but an apposition image. The migration, however, is by no means inconsiderable. In 1911 BEDAU reported on the pigment migration in the eyes of the water boatmen *Notonecta* and *Corixa*. In these insects a much more considerable migration of the proximal pigment takes place than that described for butterflies by DEMOLL. In fact the photomechanical activity in the proximal cells of *Notonecta* even exceeds that in crustaceans. In a brightly illuminated *Notonecta* the pigment in the cells next the rhabdome, which in this

summary have been called proximal pigment cells, is more or less uniformly distributed throughout the length of the cells. In the dark, however, a part of this pigment migrates outward toward the distal end of the containing cell and a part inward to a position even below the basement membrane. In this way the middle region of the retina becomes devoid of pigment. This type of migration is remarkable as compared with that in other compound eyes in that the proximal pigment becomes divided into two parts: one inner and the other outer. The inner part migrating inward, as does *all* the proximal pigment in the higher crustaceans, and the outer part migrates outward, a novel direction as compared with the movement of the proximal pigment in the eyes of other arthropods. The migrations of the proximal pigment are supplemented by the movements in the pigment of what may be called the proximal accessory cells which occur in *Notonecta* at the level of the rhabdome. This pigment migrates inward in the dark and outward in the light thus following the movement of the pigment in the proximal part of the proximal cells proper. As already noted in this account the ommatidium of *Notonecta*, according to BEDAU contains not only proximal accessory cells but also distal ones and in these, as already stated, the pigment moves outward in the dark and inward in the light. The retina in *Notonecta*, like that in the higher crustaceans seems arranged, therefore, to produce a superposition image in the dark and an apposition one in the light. This opinion, however, calls for experimental test. When it is remembered that EXNER (1891) was unable to detect any pigment migration at all in the proximal region of the insect's retina, it is plain from the results recorded in the last few paragraphs that this field is far from exhausted; in fact it has scarcely been touched and will doubtless well repay extended investigation.

d) Types of Compound Eyes and Times for Pigment Migration. It may be well here to survey briefly the types of compound eyes as established by the several kinds of pigment migration exhibited and to compare the times necessary for these migrations. At least seven such types may be distinguished. They are indicated in outline in Table 4.

Table 4. Types of compound eyes based on pigment migration; m, migratory pigment; n, non-migratory pigment; p, present.

Type	Retinal Pigment		Tapetum	Glow
1. *Gammarus*	m		n	?
	Dist. Pig.	Prox. Pig.		
2. *Gonopteryx*	n	n	n	p
3. *Vanessa*	n	m	n	p
4. *Porthesia*	m	n	n	p
5. *Notonecta*	m	m	?	?
6. *Astacus*	m	m	n	p
7. *Palaemon*	m	m	m	p

The simplest type of compound eye is well represented by that in *Gammarus* (PARKER, 1897) in which the retinular pigment next the rhabdome moves inward in the dark and outward in the light (Fig. 8). At ordinary temperature, as already stated, inward migration requires 18 minutes, the outward one 2.5 minutes (BENNITT, 1924). Such a relatively slow change probably meets the adaptive needs of an animal which, like *Gammarus*, spends part of its time in open sunlight and part under stones. The image formed in such an eye would be under all conditions an apposition image.

The second type of eye is represented by *Gonopterix*, a butterfly of the open fields. In this type the distal and proximal pigment show little or no migratory activity (MERKER, 1929a, p. 347), and thus conforms to what has long been supposed to be characteristic of insects active in continuously strong sunlight. The bright spot in the center of the pseudopupil in this eye is evidence of some form of tapetum though the exact nature and location of this structure are not known. Such insects are active in sunlight but retire and come to rest in dim light or darkness. Their retinal images are presumably apposition images.

The third type, represented by *Vanessa* and a number of other butterflies (DEMOLL, 1909), shows no migratory activity in the distal pigment and very little in the proximal pigment. Such migration as the proximal pigment shows is in the neighborhood of the basement membrane (Fig. 12). Here in the light the pigment moves outward to the bases of the rhabdomes; and in the dark, it moves inward to the proximal side of the membrane. By this means a tapetum, presumably tracheal in nature, is alternately covered and uncovered. The image in this eye must be an apposition image rendered more effective in dim light by the action of the tapetal layer. The inward migration requires only some 4 to 5 seconds, the outward one 5 to 6 seconds. These relatively rapid changes probably adapt the eye in this butterfly to the sudden changes in illumination that it must suffer in flying from shadow to sunlight and the reverse. Butterflies with this type of eye frequent the edges of woods, copses, and similar places and are not usual inhabitants of the open fields.

The fourth type of eye is represented in the moth *Porthesia*. In this insect the distal pigment migrates inward in the light and outward in the dark. The proximal pigment is non-migratory. A tracheal tapetum is present. When the distal pigment is at its innermost position (apposition image in bright light) only a dark pseudopupil is observable. When it is outermost in position (superposition image in dim light) a large luminous pseudopupil is visible. A moth in this condition in the dark by reflected light seems to have an eye with a glowing coal of fire as its center. The luminous pseudopupil thus outlined gradually diminishes in size in full light till it finally disappears as a glowing dot (Fig. 13).

This change in the light, a change that may be described as the conversion of a superposition eye into an apposition one, takes place in from a few minutes to about half an hour (3 to 25 minutes, EXNER, 1891; 15 minutes, DEMOLL, 1917; 17 minutes, MERKER, 1929a) depending upon the species of moth under examination. The change is relatively slow and probably has to do with the adaptation of the eye of these moths to the slow diurnal change in light intensity. This type of eye is limited to insects (DEMOLL, 1917, p. 183) and occurs commonly in moths and other night forms.

In the fifth type of eye as represented by that in *Notonecta* both distal and proximal pigments migrate (BEDAU, 1911). In the light the distal pigment moves inward and the proximal outward and their approach one to the other favors an apposition image. In the dark the

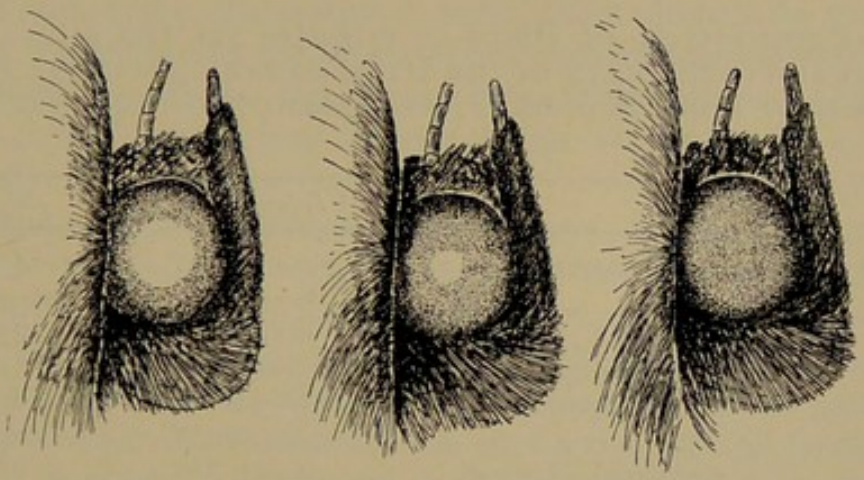

Fig. 13. Surface view of the right eye of the moth, *Plusia gamma*. In the dark there is a large pseudopupil (a); this diminishes in the light (b) and finally disappears (c). From MERKER, 1929a, p. 315.

two masses of pigment separate and a superposition image may result as is also probably true in the ephemerids (ZIMMER, 1898). In this respect the eyes of *Notonecta* are more like those in crustaceans than those in the majority of insects. It may not be irrelevant to note that the water boatmen resemble the crustaceans not only in the structure of their eyes but also in that they are water-inhabiting animals. It would be extremely interesting if it could be shown that this similarity in the structure of the eye depended in any real way on the similiarity of the environment of the two sets of animals. Presumably, a tapetum is present in *Notonecta*, but thus far no record of it appears to have been made nor of the times required for the pigment migrations.

The sixth type of eye is well illustrated by that in *Astacus* (Figs. 10 and 11). In the light the distal pigment of this eye moves inward and within the cell and the proximal pigment moves outward thus favoring an apposition image (PARKER, 1895). In the dark these pigments reverse their movements and the condition for a superposition image is ap-

proximated. A granular, quiescent tapetum is present and is effective as a reflector in dim light. The intervals of time necessary for the migrations just recorded appear never to have been measured. Without doubt they are relatively long and in magnitude very close to those given for the next and seventh type.

In the seventh type, as represented by *Palaemon* and by *Palaemonetes*, for the two crustaceans are very closely related, the plan of pigment migration is the same as in the sixth type except that in the seventh the distal pigment cells migrate as whole cells and intracellular migration is mostly absent (Fig. 8). Further, in the seventh type the tapetal pigment is migratory instead of stationary as in the sixth. The times necessary for various migrations in the eyes of type seven are given in Table 5 where it will be seen that they are all relatively long, that con-

Table 5. Comparison of times in minutes for the migration in the light and in the dark of the distal and the proximal pigment in *Palaemonetes* and *Palaemon*. F, VON FRISCH; M, MOSSLER; P, PARKER; W, WELSH.

	Palaemonetes	*Palaemon*
Light migration, distal pigment	90—105 P.	45 F.
„ „ „ „	50—60 W.	45—50 M.
„ „ proximal pigment . .	30—45 P.	25 F.
„ „ tapetal pigment . . .	45—60 P.	
Dark „ distal pigment	105—120 P.	60 F.
„ „ „ „	90—120 W.	60—70 M.
„ „ proximal pigment . .	45—60 P.	75 F.
„ „ tapetal pigment . . .	105—120 P.	

sequently these migrations may be regarded as of adaptive significance only in so far as a general diurnal change in illumination is concerned. As might be expected these eyes, like those of the sixth type, acquire a luminous pseudopupil in the dark and lose it in the light.

What might be regarded as representing still an additional type of compound eye are the remarkable visual organs found in the deep-sea euphausids and described by CHUN (1893, 1896). Each of these eyes is peculiar in that it is divided into a frontal and a lateral organ both of which are entirely devoid of retinal pigment and possess only limited traces of iris pigment. The structure of these eyes is appropriate for the extreme of dim-light vision and as the euphausids that possess them live at such depths in the ocean that the only light available to them is that from the luminescent organs of themselves and other animals, their eyes may be said to be well adapted to their conditions of life. Apparently the eyes of these forms are permanently set for this type of vision under which circumstances pigment migration would be superfluous.

A general survey of the contents of this section leads to the conclusion that all migration times except in the third type of eye (butterflies of the edge of woodlands) are relatively long and so far as they are means of visual adaptation they must apply only to the most general changes in illumination. It is also clear that in most instances the movements that occur in the light require less time than those that take place in the dark. The only exception to this rule is in the very brief periods recorded for the third type of eye, 4 to 5 seconds in the dark and 5 to 6 seconds in the light. These records are, however, so close that they may be considered open to possible subsequent revision. Finally, if distal (iris) and proximal (retinular) pigment cells are compared, the proximal cells will be found as a rule to require less time to accomplish their pigment migrations than the distal ones do. In this instance there is also one exception, namely that recorded by VON FRISCH (1908) of 75 minutes for the proximal cell pigment migration in the dark, and only 60 minutes for the corresponding distal pigment migration in the light. Here apparently the distal cells act in less time than the proximal ones.

e) Pseudopupil and Glow. That the eyes of a moth may glow in the dark like coals of fire was known to the older naturalists. This glow and the peculiar central spot seen in many compound eyes were studied by LEYDIG (1864) who recognized that the spot moved over the creatures eye as the observer shifted his position. In consequence of this peculiarity LEYDIG called the spot a pseudopupil to distinguish it from a true pupil such as occurs in the vertebrate eye. Both glow and pseudopupil were very fully investigated by EXNER in 1891. An account of the markings and coloration of the insect eye has recently been published by FRIZA (1928).

A coarse pseudopupil can be easily seen with a hand lens in such a simple eye as that in *Talorchestia*. Such a pupil shifts in position with the movement of the observer. It is, however, not known whether this pseudopupil alters with the migration of the retinular pigment as this pigment changes from a light position to a dark one or the reverse, nor is it known whether this eye shows a glow at any phase if its pigment migration.

In the apposition eyes of insects such as are shown in the second, third, and fourth types of eyes in the classification used in this summary, a well pronounced pseudopupil is ordinarily present. This consists commonly of a single central or chief pseudopupil surrounded by a ring of six secondary ones which may in turn be encircled by twelve others (EXNER, 1891; DEMOLL, 1917). The exact arrangement and composition of these elements depend in part upon the grouping of the ommatidia and in part upon the magnification under which they are inspected. In the majority of insects the ommatidia have hexagonal facets and a cor-

responding arrangement. Hence their principal pseudopupil is surrounded by six secondary ones. Under the low magnification used by EXNER (1891) in the study of these phenomena, the chief and accessory pseudopupils must have consisted of groups of ommatidia. But in DEMOLL's investigations (1917) the magnification was such that the central dark spot was the blackness seen in looking down the length of the single black-walled ommatidial tube directly in line with the observers eye, and the surrounding six secondary pseudopupils were the corresponding dark ends of the six surrounding ommatidia. These dark spots stand out in contrast with the lighter pigment that fills the space between the ommatidia proper. Where this interommatidial space is as darkly pigmented as the walls of the ommatidial tubes are, pseudopupils both principle and secondary, though present, cannot be recognized, — a condition seen in many beetles (DEMOLL, 1917). Pseudopupils may be associated with no observable glow, with a single shining point as in *Papilio* (DEMOLL, 1917, p. 169), with a group of bright points (DEMOLL, 1917, p. 169) or with a more general glow as in most moths. When a moth showing such a glow is brought into moderate light much of the surface of the eye is seen to glow (Fig. 13), after which the glow is restricted to a central area that steadily decreases in size till it finally disappears as a minute point in the middle of that part of the eye that is opposite the observer (MERKER, 1929a, p. 315, Fig. 3). The steps by which this spot disappears and the period of time necessary for its disappearance suggest at once that the change is due to the inward migration of the distal or iris pigment, an explanation that was first proposed by EXNER (1891) and was subsequently accepted by most workers including DEMOLL (1917).

In superposition eyes such as are represented by types six (*Astacus*) and seven (*Palaemon*) there is a well marked pseudopupil which at night gives way to a general glow. This has been described by DAY (1911) in the crayfish *Cambarus*. In this animal in daylight the eye presents a dark central spot, the pseudopupil, framed by a lighter peripheral area. At night this pupil vanishes and the whole eye when examined by a flash light glows with a bright metallic-orange light. After exposure to light for several minutes thc metallic orange fades to a dull yellow and with this change the dark area in the center appears. The pseudopupil in these eyes is therefore a feature of the daytime. DAY 1911, p. 321) noted in his account of these phenomena that the retinular pigment was concerned with the exposing and the covering of the tapetal layer. The pseudopupil, however, was without doubt dependent upon the migration of the distal or iris pigment (EXNER, 1891; DEMOLL, 1917). In this respect the pseudopupil of the superposition eye is like that of the apposition eye.

The glow in the compound eye is always the result of reflection and

never due to inherent light. In this respect it is like the shining of the cats eye in the dark. The reflecting layer is the tapetum, a body of guanin-like granules in the crustaceans and a mass of fine tracheal tubes in the insects. These reflecting materials are either covered up from the light or exposed to it by the migration of the retinular pigment. The glow is due in part at least to the turning back of light which has traversed the rhabdome once. To any one who has witnessed in dim light the glow of such an eye as that in *Palaemonetes*, it seems hardly possible that the glow itself is a mere escape of unused light. The eyes under such circumstances are so conspicuously bright that this display would seem to have some real significance in the shrimp's biology. Possibly it is a means of bringing animals together in very dim light where the only visible evidence of their presence is the pair of glowing eyes in an otherwise dim and uncertain background. The same may be true of moths which in the faint evening light exhibit a retinal glow as conspicuous as that seen in many crustaceans.

f) Rhythmic Migration. The pigment-migrations in the compound eyes of arthropods, except in the third type described in the present summary, take place so slowly as to enable the animals to do little more than to become adapted to the changes from day to night or the reverse. Hence in most arthropods with compound eyes there may be said to be a rough daily rhythms in their retinal pigment migrations dependent upon the changes in general illumination.

In 1894 KIESEL made the interesting discovery that when a moth is kept continuously in the dark for several weeks it will show alternate periods of glow and of absence of glow corresponding in general to day and night. This general statement is based on KIESEL's observations on two noctuids, one of which lived in the dark for eleven days and the other for twenty-two days, and showed during these periods a rhythmic alternation of presence and absence of glow. As moths are ordinarily quiet and devoid of glow in the day time KIESEL interpreted the absence of glow in the dark as evidence of a kind of sleep. Although this interpretation may be questioned, it is perfectly evident from KIESEL's observations that pigment migration in the compound eye may be induced by other means than a change in illumination. KIESEL's observations were repeated and fully confirmed by DEMOLL (1911, p. 170; 1917, p. 186). The pigment that took part in this rhythmic response is believed on good ground by these authors to be the distal or iris pigment.

In 1930 WELSH also discovered a daily rhythm in the movements of the pigment in the eyes of the Cuban fresh-water shrimp *Macrobrachium*. When the distal pigment of this shrimp is observed, it is found to be inward during the day and outward at night. These are the appropriate positions for vision in superposition eyes in bright light and in dim light. If now a *Macrobrachium* is put under artificial, bright,

constant illumination it will be found that at about six o'clock in the evening the distal pigment, notwithstanding the illumination, will move outward as though the shrimp were in the dark. Here it will remain during the night, and at about five o'clock in the morning it will move inward again. Thus contrary to what would be expected from the light conditions, the distal pigment maintains a peripheral position overnight to regain a deep one as morning returns. It is a remarkable fact that in this shrimp the proximal pigment takes no part in this migration, a state of affairs that shows very conclusively the independence of the distal and the proximal cells. A solution of chloretone of 0.01 per cent strength had no influence on adaptation to the light in this animal, but did slow down its dark adaptation and entirely obliterated the daily rhythm just described. WELSH's observations afford the first evidence of this type of rhythm in the retinal pigment of crustaceans.

The observations made by WELSH were soon followed by other more or less similar ones by BENNITT (1932b), who found that the proximal pigment of the crayfish, *Cambarus*, after having taken up during the night the characteristic proximal position will assume in continued darkness alternate partly distal and complete proximal positions. The distal positions are never those produced by full light but they are so pronounced as to leave no doubt about them. Like the responses of *Macrobrachium* these in *Cambarus* represent a daily rhythm that could be observed for several days. This instance differs from that reported for *Macrobrachium* in two important particulars; first it is shown by the proximal and not by the distal cells, and second, it occurs in continuous darkness and not in light.

These rhythms recall other similar activities, as indicated by WELSH (1930b), such as the rhythmic change in the chromatophores of the skin of *Hypolyte* as observed by GAMBLE and KEEBLE, and the similar observations of MERKER on the chromatophores of *Idothea*. SLOME and HOGBEN observed that in the South African frog *Xenopus* the melanophores are more contracted at midnight than at midday even when the animal is kept in constant darkness. The occasion of the retinal pigment rhythms have been attributed by some to nervous influences and by others to hormones in the blood but without any confirmatory evidence one way or the other (DEMOLL, 1911; WELSH, 1930b; BENNITT, 1932b).

g) Internal Environment. The daily rhythms of the retinal pigment discussed in the last section call for some other form of stimulating agency than light. Such agencies may be expected in the internal environment especially in the blood. WELSH (1930b) showed that when the base of the eyestalk of *Macrobrachium* was ligated so as to interfere with the flow of the blood the diurnal migration of the distal pigment in this shrimp was checked. Although it might be maintained in this

instance the ligation interfered with nervous transmission rather than with the flow of blood, it is more than probable that the interference was with humoral agents and that some hormone was prevented from reaching the retina. BENNITT and MERRICK (1932) showed that in *Cambarus* kept in the dark, oxygen deficiency produced by overcrowding or by passing carbon dioxide or nitrogen through the respiratory water, induced an outward migration of the proximal pigment, a movement contrary to that induced by the absence of light. This position of the pigment is also called forth by anesthesia and by death. Lack of oxygen, anesthetization, and death are all associated with low metabolism and it may be that in this condition there is discharged into the blood some metabolite which, hormone-like in action, may bring about in the absence of light the outward migration of the proximal pigment.

This opinion is supported by the observation of CONGDON (1907) that in *Cambarus* and in *Palaemonetes* low temperatures are associated with an outward migration of proximal pigment. Here too low temperature may be associated with low metabolism. It is also to be remembered that, according to CONGDON, high temperature induces an inward migration of this pigment and that these temperature conditions have the opposite effect on the distal pigment, an inward movement of this pigment with low temperatures and an outward one with high temperatures. In this respect heat is like darkness and cold is like light.

Scattered though these observations are, they are sufficiently decisive to show that in the compound eye the pigment migrations are by no means exclusively controlled by light or its absence, and that the internal environment with its humoral agents in the form of hormones and other like secretions as well as temperature differences may play a significant part in these operations. Such agents must always be kept in mind in attacking the many problems of the compound eye. This is conspicuously true of the general question of the interrelation of eyes as indicated in the movements of the retinal pigment.

V. General Considerations.

1. Functions of the Retinal Pigment.

The function of the dark or melanin pigment of the retina has been variously stated. That it absorbs light is obvious. What is accomplished by the absorption is by no means clearly understood. Some of the earlier investigators attributed to this process the primary function of transforming light-energy into that form of energy appropriate for stimulating the visual apparatus (DAY, 1911). In this way KÜHNE (1878) believed that the mechanical agitation of the pigment by light might stimulate the rods and cones or that the end-products of chemical decomposition of the pigment by light might affect the same end. No

support has been found for such hypotheses. Moreover since albino animals, whose retinas are devoid of pigment, may have good vision, it is evident that the retinal pigment has no such primary function. Even the regeneration of visual purple in vertebrate eyes, which is known to depend upon an intact retinal epithelium, is due, as already stated, to some other constituent of the epithelium than the pigment (HOSOYA, 1929a, 1929b).

The majority of investigators, particularly the more recent ones, have generally agreed that the absorption of light by the retinal pigment is a means of eliminating light that would otherwise be disturbing to the sharpness of the visual image or overpowering in stimulation. This opinion has been espoused by STEFANOWSKA (1890), SZCZAWINSKA (1890), EXNER (1891), PARKER (1895), HESSE (1902), GARTEN (1907b), DONISELLI (1907) and a host of modern workers.

The reflecting pigments, guanin and the like, also serve as a means of dissipating light that would otherwise be disturbing to the retinal image. At least this seems to be the obvious function of the reflecting pigment which is located on the outer faces of the distal pigment in the compound eyes of *Palaemonetes*. No one, however, can observe the glow of the eyes of such crustaceans in dim light without being impressed with the idea that this glow is more than the mere escape of excess light from a over-supplied eye. It is not improbable, as suggested in an earlier part of this paper, that such a glow may play some part in enabling these shrimps to find one another in dim light. But the principal function of the reflecting pigment is admitted by almost all workers to be that of a reflecting mechanism whereby light which has passed through the somewhat transparent receptive element, rod, rhabdome, or other like part, is again sent through that part to reenforce the process of stimulation when the light is very faint. Judging from the opinions expressed by most investigators, this holds true of arthropods (EXNER, 1891) as well as of vertebrates (EXNER and JANUSCHKE, 1905; WUNDER, 1925b, 1926a, 1930).

2. Light as an Activator of Retinal Pigment Migration.

The natural stimulus for the retinal pigment migration is daylight from the full intensity of sunlight to the dim light of night. At the hands of the experimentalist animals whose retinal pigments were to be tested have been subjected to a range of artificial lights from those of the most powerful lamps to complete darkness. AREY (1919a) has shown that the effect of very dim light is the same as that of complete darkness and that the efforts of many investigators to attain for their tests unquestionable darkness is an undue refinement.

The so-called white light of the ordinary experiment is by no means a homogeneous stimulus. It is made up of a mixture of pure colored

lights, best described by their wave-lengths, which vary more or less in proportional amounts for each source. In this mixture one element may be much more effective than another and it is natural to inquire into these relations in considering the initiation of retinal pigment migration. Such an inquiry calls for a certain degree of analysis. Any given pure light may become effective as a stimulus either because of its innate qualities as represented by its wave length, recognized crudely by its color, or in consequence of its quantity. It is conceivable that a very small amount of a very effective ray may equal in stimulating power a very large amount of a very ineffective one. Hence in testing the stimulating quality of given pure lights for pigment migration it is necessary to know not only the approximate wave-length of the light but also the quantity of light impinging upon the receptor. Most investigators have failed to take into account these two separating factors.

Much of the early work on colored lights was done on the frog. In 1878 ANGELUCCI (1878, 1882a, 1882b) declared that the response of the retinal pigment in this animal was the same to red light as to darkness, but was greater to blue light than even to white light. ENGELMANN (1884) also declared for the great effectiveness of blue light. VAN GENDEREN STORT (1887), however, believed that the highest efficiency was shown by green light. In none of these investigations, however, was quantity of light taken into account. PERGENS (1899) attempted to remedy this defect by the use of a Ritchie photometer for equating the lights and declared in favor of the series red, yellow, green, blue with blue as the most effective element. When the intensity of the series was low the sequence became green, red, yellow, blue. HERZOG (1905), who reinvestigated the subject, confirmed in the main the work of PERGENS in that he concluded that of the extremes of the spectrum red was much less effective than blue as an exciting agent. MAKI (1931) has very recently shown that a pigment migration can be induced in the frog's retina by ultraviolet light.

In invertebrates KIESEL (1894) emphasized the importance of ultra red, but VON FRISCH (1908), who worked on butterflies and moths, concluded that violet was most effective, blue less so, and the remaining spectral colors least effective and indistinguishable among themselves. DAY's work (1911) on the crayfish, *Cambarus*, was made with lights equated by use of a radio-micrometer and led him to conclude that blue-violet ranked very close to green and yellow and much above red. Thus it appears that with the exception of VAN GENDEREN STORT, who placed green first, all other workers agree in regarding violet or blue as the most effective colored light in inducing retinal pigment migration. Of recent years MERKER (1929a, 1929b, 1929c) has shown that ultra-violet rays may penetrate the eyes of insects and there set up pigment migra-

tions such as are called forth by ordinary light. He has also discussed the problem of the fluorescence of the arthropod eye in relation to the external source of light, a subject investigated as early as 1911 by HESS.

3. The extra-retinal Control of Pigment Migration.

Does the retinal pigment migration in animals take place in consequence of the direct effect of the environmental illumination upon the responding cells or is the operation more in the nature of a reflex in that the stimulation of a receptor by the light induces changes which finally spread to the retinal pigment and excite it as an effector? This rather categorical statement of the problem by no means exhausts its possibilities, for, in consequence of the complexities of the situation, it is conceivable that direct stimulation and reflex activity may be so intertwined in the actual performance as to make it impossible to declare in favor of one type of explanation over the other.

If the responses of the retinal pigment are direct responses to the light that enters the eye and if this pigment is normally not open to influences in other ways, there should be no possibility of controlling the position of the pigment in one eye by inducing changes in the other. This problem has been worked on extensively in the vertebrates especially in the frog but with no generally conclusions results. ENGELMANN as early as 1885 declared that if one eye in a frog was covered so as to be inaccessible to light and the other eye was illuminated, the pigment of the closed eye would assume a position characteristic for the light. This observation led to the hypothesis of retino-motor fibers which has played an important role in the subsequent discussion. ENGELMANN's contention was supported by GRIJNS (1891), NAHMMACHER (1893), LODATO and PIRRONE (1901), and HERZOG (1905) on frogs, and by BIRCH-HIRSCHFELD (1906) on the pigeon. AREY (1916b) arrived at the same conclusion in experiments involving the cutting of the optic nerve in the fish *Ameiurus* though he was unable to obtain similar results from certain other fishes, *Abramis* and *Fundulus*. In his summary of the question DITTLER (1929) favors ENGELMANN's view. A considerable number of investigators, however, were unable to obtain confirmatory observation. Thus HAMBURGER (1888) who worked on the frog could not note a change in the covered eye and GERTZ (1911) and especially FICK (1889, 1890, 1891, 1895), in a series of contributions, also opposed ENGELMANN's view. Later FUJITA (1912) and HESS (1913) entered the field in opposition and most recently of all SCHARRER (1929b) has been unable to get anything but negative evidence from a study of the two fishes *Gasterosteus* and *Phoxinus*.

Evidence on this question from arthropods is equally inconclusive. KIESEL in 1894 observed, as already noted, that the appearance and disappearance of glow in the eyes of moths occurred at night in the

absence of light. Without experimental evidence he attributed this nocturnal alternation to central nervous changes comparable to sleep (absence of glow) and induced through a nervous control of the retina. DEMOLL (1910, 1911, 1917) favored this interpretation and pointed out (1910) that when a beam of light with parallel rays falls on a compound eye the effective light is that which penetrates an ommatidium to its base and stimulate its rhabdome and not that which falls upon the sides of the adjacent ommatidia and is taken up by their pigmented wall. From the stimulated rhabdome to the rest of the responding retina it would seem as though mediation must be by transmission amounting essentially to a nervous reflex. DEMOLL (1911) advanced the hypothesis that from the arthropod brain a steady flow of tonic impulses may be supposed to pass into the retina holding the pigment in the dark position. When light enters the retina this flow is inhibited, migration takes place, and the so-called light position is assumed. Without adding new evidence TROJAN (1913) concluded that what has been already discovered was in favor of a nervous control of pigment migration.

Among the latest workers BENNITT (1924), experimenting on *Cambarus* on the lines of ENGELMANN's experiment, found that when light was thrown into a newly exposed dark-adapted eye of this crustacean it was followed by an outward migration of the proximal pigment in the opposite covered eye. He also found that in a light-adapted animal the illumination of one eye prevented the opposite covered eye from completing the migration toward the dark state. Experiments of this type with like results were subsequently reported by BENNITT (1932a) for *Cambarus, Cancer, Carcinides, Libinia,* and *Homarus.* WELSH (1930b) included nervous control as one of the possible factors in explaining the diurnal rhythm of pigment migration in the shrimp *Macrobrachium.*

VON FRISCH (1908) as a result of many experiments on insects and especially on crustaceans was left in much uncertainty as to the nervous control of retinal pigment. He obtained no pigment migration on stimulating electrically the optic nerves of insects or crustaceans, and his experiments on *Palaemon* in which one eye was illuminated and the other covered yielded no conclusive records. PARKER's results (1897) on the other hand showed with *Palaemonetes* a light condition so generally in illuminated eyes and a dark one in covered eyes that he was led to conclude that the migration in the two eyes was quite independent of nervous control. Using a much improved technique CASTLE (1927) carried out tests on the same shrimp and was unable to get evidence in favor of nervous control. Thus in the arthropods as in the vertebrates the observations of various workers on the relations of retinas one to the other are conflicting and contradictory.

Tests on eyes or parts of eyes have also yielded results far from uniform. That the pigmentary system of the compound eye in such

a crustacean as *Palaemon* can be profoundly disorganized by overstimulations was abundantly shown by MOSSLER (1915). Parts of one retina may exhibit different conditions of pigment migration in consequence of different degrees of illuminations. This was observed by EXNER (1891) in *Sphinx* and by DEMOLL (1910) in other insects. Eyes severed from the individual have shown much diversity in their pigment responses. PARKER (1897) found that when four excised light-adapted eyes from the shrimp *Palaemonetes* were left two hours in darkness in three there was some appropriate migration and in the fourth complete migration. In *Palaemon* on the other hand VON FRISCH (1908) got no evidence whatever of migration from eyes that had been cut off or fragmented. Circulatory disturbance, as VON FRISCH suggested, may have been the occasion of these results. In isolated eyes of *Talorchestia* BENNITT (1924) found that a pigment migration took place in the light but not in the dark. When the whole head of this crustacean was cut off and tested before the tissues had died, the retinal migration in the dark occurred as well as that in the light. Thus the results on severed eyes are quite as diverse as are those on attached eyes.

The confusion that characterizes this whole body of work is probably due to the failure on the part of the earlier investigators to recognize a factor which has been clearly seen only in the last few years.

This factor is humoral or hormone control which, judging from recent work, may be of great importance in this connection. It was long ago pointed out that no nerves are known to go to the distal or iris cells of the compound eye and it is also known that the vertebrate retinal pigment is unprovided with nerves. Nothwithstanding this absence of nerves the iris pigment in some arthropods particularly insects appears to respond to nervous influences and the recorded observations of sympathetic migrations in the paired eye of vertebrates are too numerous and too well attested to be explained away as the result of purely faulty technique. May it not be possible that these obscure relations in reality are due to hormone intervention? If the receptors of eyes such as the retinulae and the rod and cone cells, on being activated by light or by darkness were to give out susbtances appropriate to these states, the adjacent pigment cells, iris cells or retinal pigment cells, might well respond to such substances in so appropriate a way as to stimulate nervous control. The secretory action of the retinal pigment has often been suggested (AYRES and KÜHNE, 1878; GAD, 1894; MIYAKE, 1931) and KOLMER (1909) believed he had identified such secretions in droplets found by him on the rods especially in vertebrates from fishes to mammals. These droplets were subsequently shown by DETWILER (1924a) to come in all probability from the outer segments of the rods and not from the retinal pigment, a source subsequently admitted by KOLMER

(1925) and quite in line with the suggestion of the humoral control of the retinal pigment as described in this paragraph. That such secretions might be taken up by the blood and carried from one eye to another is entirely possible in which case an easy explanation might be offered for the sympathetic relations between eyes that apparently have been met with from time to time.

That such a view is not far-fetched is shown by PERKINS' discovery (1928) that in the light the eye stalk of *Palaemonetes* elaborates a material that when carried through the blood brings about a contraction of the bodily chromatophores of this animal. KROPP (1929) has also found, what is still more to the point, that extracts of the eyes of dark-adapted tadpoles or *Fundulus* when injected into the corresponding light adapted animals will cause an expansion of the dermal melanophores. All these conditions illustrate the modern doctrine of neurohumoralism (PARKER, 1932), and till the problem of the nervous control of retinal pigment is approached with the proper check on this aspect of the subject no conclusive advances are likely to take place. These humoral possibilities have already been hinted at by BENNITT (1924, 1932a) and by WELSH (1930b). It is perhaps premature to suggest at this stage a solution of the problem with which this section opened. Evidence of direct stimulation of retinal pigment is sufficiently strong to make it a possible factor. But there is also equally strong evidence of an external control nervous or humoral. Under such circumstances it is probable that the final solution will show the process to be a complex one. Like the beat of the vertebrate heart the migration of the retinal pigment may be a process essentially inherent in the pigment cell itself and yet under such a degree of nervous or humoral control that at times it appears to be purely of this type of action.

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