ments of the vacuum evaporation rate of single-crystal surfaces as a function of temperature. Complementary studies of vaporization are carried out to determine the reaction steps leading to the desorption of the vaporizing species. The rates of vacuum sublimation of solids, which undergo marked chemical rearrangements (association or dissociation) upon vaporization, are lower $(\alpha \ll 1)$ than the maximum equilibrium sublimation rate. For these solids a particular chemical reaction is the ratecontrolling vaporization step. Solids which do not exhibit appreciable structural rearrangements during sublimation may have vacuum evaporation rates equal to the maximum rate. For clean materials of this type, the structure of the vaporizing surface (dislocations, atomic steps, ledge concentrations) plays a more dominant role in determining the rate of vaporization. Once the reaction steps which lead to sublimation are known, the sublimation rates can be changed by several orders of magnitude

by a suitable adjustment of the conditions of sublimation, such as the addition of impurities, illumination, and the introduction of dislocations or vacancies.

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The Optics of Insect Compound Eyes

Microcomponents with dimensions near a wavelength of light cause observable optical effects.

W. H. Miller, G. D. Bernard, and J. L. Allen

In the 1800's, when Müller (1) and Exner (2) made the first important advances toward understanding the optical function of compound eyes, their theories of function were based on only the most obvious anatomical details. Nevertheless, these theories are widely respected even now. Müller proposed that the radially arranged facets of compound eyes are stimulated principally by light coming from the directions they

face. If each ommatidium acts as a unit, the eye sees an erect mosaic image comparable to a newspaper halftone, but about 100 times coarser. Exner agreed with this theory for the eves of diurnal insects, but for certain nocturnal insects in the dark-adapted condition he found evidence that a large part of the dioptrics functions to project a coarse erect image on the photoreceptors. This finding differed from that predicted by Müller's mosaic theory in which the individual facets are held to transmit light only to their own photoreceptors.

In recent years it has become evident that the dioptrics of insect eyes are more complex than early investigators had

thought. In fact, as better microscopes and microscopic techniques have evolved, numerous additional dioptric components, characterized by dimensions of the order of a wavelength of light, have been discovered. Some of these components, such as the crystalline tracts and rhabdomeres, by their very existence have forced examination of Müller's and Exner's theories. The finding of other structures, such as the corneal nipples and various periodic layered structures, have called attention to the possibility of more subtle optical processes. All these microcomponents pose interesting problems about the nature of their interaction with light and the consequences of this interaction for the function of the eyes and for other biological processes of the animal. Before turning to these problems, we will review the basic construction of the compound eye (3).

Gross Anatomy of the Compound Eye

The compound eves of insects are composed of a large number of ommatidia (little eyes). The ommatidia are hexagonally or rectangularly packed over portions of the insect's head (Fig. 1). The outermost part of each ommatidium, the cornea, is an extension of the

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chitinous cuticle and is usually a planoconvex lenslet that is transparent, as are the deeper optical structures. The gross structure of the optical pathway of some insect ommatidia is depicted schematically in Fig. 2. Beneath the cornea lies the crystalline cone, most of which is enveloped by cells containing lightabsorbing pigment. The photoreceptor organelles are rod-shaped and are called rhabdomeres. They lie just beneath the crystalline cone in many day-flying insects such as the flies (Fig. 2, D and F). There are usually seven or eight rhabdomeres in each ommatidium. These rhabdomeres of the sensory retinular cells appear to be neurally independent since each retinular cell gives rise to its own nerve fiber (4). The fly's rhabdomeres are separate and also optically independent (5, 6). Even in arthropods with fused rhabdoms, the individual rhabdomeres, or at least local regions of the rhabdom, can function independently (7).

The ommatidia of many day-flying butterflies have a short, thin cylindrical extension of the crystalline cone-the crystalline tract; this prominent optical component separates the crystalline cone from the rhabdomeres (Fig. 2C). The rhabdomeres of butterflies are optically fused into a single rod, the rhabdom, but the individual retinular cells retain their separate nerve-fiber outputs. The eye of the skipper (superfamily Hesperioidea) (Fig. 2B) is transitional in form between the typical day- and night-flying insects. In this eye there is a clear separation of almost a millimeter between the rhabdom and the crystalline cone. The crystalline cone is connected to the rhabdom by eight filamentous extensions of the retinular cells that travel as a bundle between the two structures. This bundle, the crystalline tract, is surrounded by "iris" cells that are transparent and devoid of pigment granules. In the night-flying moths the filamentous extensions of the retinular cells are fused into a single cylindrical crystalline tract. Iris cells of the nightflying moth contain a migrating, lightabsorbing pigment that is shown in the light-adapted position in Fig. 2A. In the dark-adapted condition the pigment is entirely withdrawn distally between the crystalline cones. The rhabdomeres of moths and skippers are also optically fused (8).

The ommatidium is not only a basic anatomical unit; it is also a fundamental functional unit whose optical properties are important in determining the re-

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Fig. 1. Swammerdam's (30) rendering (1734) of the head and compound eyes of a bee. The right eye is partially dissected.

solving power of the compound eye (9). Components of the compound eye of insects are quite small. For instance, the corneal lenslets are only about 30 micrometers in diameter. Because of diffraction effects, the resolution of a lens becomes poorer as the lens gets smaller. For the best resolution without blind spots, a compound eye should have lenses large enough for the resolution angle to be comparable to the interommatidial angle. The typical diameter of a facet (about 30 micrometers) is optimum in this sense (10). Blurring of the image for various reasons is partially compensated for by neural sharpening (11).

Small as the corneal facets are, they are still large in comparison to the wavelengths of light visible to the insect, which range from about 0.3 to 0.7 micrometer. In fact, because of diffraction limitations, the very function of these lenslets depends on their being large with respect to a wavelength of light. It may seem surprising, then, that compound eves contain a variety of optical components with characteristic dimensions near a wavelength of visible light. We will discuss the following examples of such components: crystalline tracts, the corneal nipples, corneal layering, and periodic layered tracheolar structures.



Fig. 2. Schematic drawing of ommatidia in longitudinal section and in the light-adapted condition of (A) moth, (B) skipper, (C) butterfly, (D) fly, and in cross section of (E) butterfly and (F) fly; a, cornea; b, crystalline cone; c, crystalline tract; d, "iris" cell; e, tracheolar tapetal structures; f, nerve fibers. Stippling represents pigment granules; heavy solid areas represent rhabdoms; heavy solid lines beneath ommatidia represent basement membrane.

Crystalline Tracts

The crystalline tract is 2 micrometers in diameter (about five wavelengths) in the butterfly, 4 micrometers in the moth, and 10 micrometers in the firefly beetle. The tract varies in length from 20 micrometers in the butterfly to about 1000 micrometers in some moths. Two conditions must be fulfilled in order that the tract perform an optical function in the eye. First, the refractive index of the tract must be higher than that of the surrounding material. Second, light must be focused on the beginning of the tract. If these conditions are met, the tract will act as a fiberoptic light pipe and guide light to the rhabdom.

Although Exner was aware of the existence of tracts and at first postulated that they could conduct light by total internal reflection, he later dismissed this possibility. His final theory completely ignored their presence (2). He derived this theory principally from investigations of firefly corneas with their attached crystalline cones, but with the tracts and other mechanically soft parts of the eye removed and replaced by diluted glycerol. In this preparation, at a depth formerly occupied by rhabdoms, he discovered a superposition image formed by light converging from a score or more facets illuminated by a point source. He reasoned that the dark-adapted compound eye of the living insect should function in the same way and postulated that the refractive index of the crystalline cone is higher at the center than at the periphery, so that the combination of cornea and cone could act as a lens-cylinder. An incoming light wave emerges from the cones at angles that are negatives of the entrance angles, and an erect superposition image is formed at the half-radius of the approximately spherical eye. According to Exner's theory, light-adapted eyes with crystalline tracts function in the same way as eyes without tracts because the migrating iris pigment intercepts all but the on-axis rays (Fig. 3).

Exner Challenged

Exner's theory has been questioned in recent years by workers who suggest that the tracts have an optical function. The tracts in crustacean eyes have a higher index of refraction than their surroundings. These tracts could act



Fig. 3. Exner's (2) schematic diagram to illustrate the formation of a superposition image in dark-adapted eye. The distance n - - - n is a plane in the rhabdom area. When dark-adapted, pigment is withdrawn between cones (lower part of figure) and incoming rays from many facets are focused at b. When in light-adapted condition, pigment sheaths are located more proximally (upper part of figure) and only on-axis rays reach b.



Fig. 4. Fraction of power received by different parts of rhabdom plotted as a function of source location for broad-band source. The symbol Θ_{inc} is the angle the incident light makes with the ommatidial axis. The symbols ρ_8 and ϕ_8 are the polar coordinates of the focused spot at the beginning of the tract. Theoretical calculations for six-sector model of rhabdom. This model predicts substantial differences in power received by various sectors for a broad-band source centered about 0.360 micrometer, but a smaller difference for radiation centered about 0.550 micrometer. [From Allen (14)]

as light guides to conduct the light from the cone to the rhabdom (12). Furthermore, although tract propagation has not been observed, a superposition image as detected in Exner's experiment has not been found in the crustacean eyes with tracts (5).

Even though the evidence strongly suggests that tracts in crustacean eyes function as light guides, such a conclusion cannot be indiscriminately applied to the insects, or even to a particular family of insects, because the anatomies of various tract eyes are different. The firefly beetle used in Exner's most important experiments possesses crystalline cones that are structurally part of the cornea. Corneal layering may provide a mechanism for the graded refractive index that Exner postulates as the function of his lenscylinder; only quantitative measurement can settle this question. For the present, Exner's experiments with the firefly corneas have been confirmed in detail (5), but how the complete eye functions is still an open question (13).

For the tobacco hornworm moth and certain other moths and skippers we have direct experimental and theoretical evidence that the tract functions as a light guide and that no useful superposition image such as that postulated by Exner exists (14). The refractive index of the crystalline cone of the hornworm moth is not sufficiently graded to function as Exner's lens-cylinder; it is constant to less than 1 percent. The combination of cornea and crystalline cone focuses an image at the beginning of the tract for normally incident light. A theoretical model based on geometric optics shows that about 80 percent of normally incident light is focused on the tract. All other light passing through the crystalline cone and cornea is sprayed out the proximal end of the cone in such a way as to make it doubtful that it could be utilized in a superposition image. The refractive index of the tract is 1.523 and that of the iris cell is 1.371; thus the tract should function as a light guide. That it does so is confirmed by direct observation of eyes that were sliced near their bases and removed from the insects' heads (15).

Even though the cornea-crystalline cone focuses an image on the beginning of the tract, it cannot transmit the image because a small tract, such as this one is, transmits optical energy in discrete patterns or modes. The number of modes that a tract can transmit is deter-

mined by the diameter, wavelength, and refractive index of the tract relative to the surround (16). According to theoretical calculations, the tract of the hornworm moth supports about 50 modes; however, the diffraction limitation of the lens ensures that most of the energy is transmitted in only a very few modes of lower order. Each of these modal patterns propagates along the tract at a distinct phase velocity, with the result that the modes are scrambled in relative phase. Therefore, no image in the usual sense should be available at the rhabdom. However, information about the image could be carried to the rhabdom by modes. For instance, the theory predicts that the degree to which incident light from a point source lies off the axis of an ommatidium could be inferred from the relative excitation of the individual rhabdomeres in a dark-adapted eye (Fig. 4). Furthermore, according to our theory, polarization information contained in the image is carried by the modes to the rhabdom. Earlier physiological studies (17) have shown that the compound eye of the insect and its rhabdomeres are sensitive to polarization.

As the eye adapts to light, pigment envelops the tract and bleeds it of energy with the modes of higher order undergoing greater rates of attenuation and the mode of lowest order having only about half the attenuation of the next higher mode. Thus the pigment and tract together function as a longitudinal pupil (5). Our theory predicts that the lowest-order mode alone is the dominant mechanism of light transmission in the light-adapted eye.

Since the information contained in the higher-order modes does not reach the rhabdom in the light-adapted state, the resolution of the tract eye might be better when dark-adapted than when light-adapted, because more information would be available to the retinular cells in the dark-adapted condition. Whether the information is actually utilized is another question.

The amount of energy given up to the pigment by a minute segment of the tract is proportional to the energy contained in that segment. Therefore, the logarithm of energy delivered to the rhabdom should be linearly related to pigment position; maximum energy would be transmitted to the photoreceptor when the pigment is withdrawn between the cones, and minimum energy when the pigment is fully extended along the tracts. Physiological measure-

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ment of the sensitivity of moth eyes as a function of pigment position confirms the expected sensitivity changes (18). For the moths that have been studied we conclude that both the lightand dark-adapted eyes function by tract propagation (14). Therefore, the function of the tract is to guide light to the rhabdom and to act as a longitudinal pupil (5, 18).

The compound eyes of diurnal skippers are an exception. Because the "iris" cells do not contain pigment, the tract cannot perform as a longitudinal pupil. Nevertheless, evidence derived from observations on eyes sliced near their bases and removed from the insects' heads indicates that the light is largely confined to the tracts in these eyes. Because the skipper is a diurnal animal with a tract eye, it is to the skipper's advantage to have emptied the "iris" cells of pigment. Information carried along the tract by the modes of higher order, which would otherwise be lost in the iris pigment, should reach the rhabdom. The light-adaptation mechanism, so useful for a nocturnal animal, should be much less useful for a diurnal animal.

Only a few species of insects have been examined in our preliminary studies. Because of variations in anatomy from order to order among animals with compound eyes containing tracts, the results outlined above cannot safely be generalized. The conclusion that tract propagation occurs in dark-adapted eyes has been confirmed for the sphinx moths *Manduca* and *Elpinor*, the giant silkworm moths *Cecropia* and *Polyphemus*, and the skipper *Hobomok*. Whether this is true for the eyes of the firefly and for scores of other tract eyes awaits further experimental work.

Optical Microcomponents

The corneal lenslets of the compound eye are poor lenses, because their small size causes substantial diffraction. The smallness of the facets is a constraint on the system imposed by the size of the insect head. The crystalline tracts are even smaller in diameter than the facets. This causes further deterioration of the optical quality of the eye, a disadvantage that is balanced by the wide dynamic range of the light-adaptation mechanism.

Small as the crystalline tract is for an optical component, it still measures from five to ten wavelengths in diameter and hence is easily visible in the light microscope. There are a number of microcomponents that are smaller still; for the most part, these are not resolvable in the light microscope, but they can be observed with the electron microscope. Although they have dimensions smaller than a wavelength of light, these microcomponents cause observable optical effects and can have a beneficial effect on the performance of the eye.

Corneal Nipples

The compound eyes of many insects are coated with a hexagonal array of conical protuberances, the corneal nipples (19, 20). They are about 0.2 micrometer from tip to base and center to center, which corresponds to roughly half a wavelength of light near the middle of the spectrum. Figure 5 is an electron micrograph of the front surface of a corneal facet from a monarch butterfly. It shows the nipples in a section taken normal to the corneal surface. The nipples act as an antireflection



Fig. 5. Electron micrograph of section taken normal to front surface of cornea in monarch butterfly, showing corneal nipples at the interface between air and the cornea. Nipples are about 0.2 micrometer from center to center and tip to base. They function as a broad-band antireflection coating (19).



Fig. 6. Schematic diagram which indicates distribution of glow coloration over the left compound eye of the monarch butter-fly. [From (23)]

coating, reducing reflection from the aircornea interface about 1000-fold over the entire visible band. The transmission of light through the cornea is correspondingly increased by about 5 percent, which is the intensity reflection coefficient for a smooth interface be-



Fig. 7. An electron micrograph of section taken along the ommatidial axis of modified tracheoles lying proximal to butterfly rhabdom. Light spaces are air in living animal; thickness is about 0.123 micrometer; taenidial platelet thickness is about 0.088 micrometer. This structure is a reflection interference-filter and causes the blue glow indicated on the schematic of Fig. 6. [From (23)]

tween the cornea and air. The array of corneal nipples in insects that are inactive and vulnerable during daylight hours may principally be used for camouflage by reducing the mirror-like corneal reflections that might otherwise attract predators. For animals that are active at night the nipples may possibly play a role in increased sensitivity near the absolute threshold of vision (19). This has not been proved; although it seems doubtful because of the small increase in transmitted intensity afforded by the nipples, it is a possibility. A third use could be to prevent reflection of light back to the rhabdoms in darkadapted eyes with tracts (14). There is a strong tapetal reflection in such eyes; reflection of a portion of this tapetal light from the front corneal surface back into the rhabdoms as the remainder passes out of the eye could create ghost images or otherwise interfere with visual perception. The suppression of this reflection should be beneficial for night vision.

The corneal nipples can be regarded as an impedance transformer somewhat similar to the cones in an anechoic chamber. The nipples make a gradual transition between the refractive indices of air and the cornea. By using layeredmedia analysis, which approximates a continuous transition, one may predict that the system will possess low reflectivity (19). However, such an analysis fails to take into account the periodic structure of the nipples. One optical effect that may be explained by this periodic structure is the hexagonal outline of dim bluish light that is reflected from nippled corneas. This blue reflection is probably caused by diffraction from the array of corneal nipples. A small fraction of the incident light is diffracted from the nipples into the cornea and is then scattered from facet intersections out of the eye. Detailed understanding of the interaction of the nipple array with light is an interesting, unsolved problem in electromagnetic theory.

Tracheolar Microcomponents

The nipples are conspicuous mainly in the low visibility with which they endow the surfaces they coat. Other microcomponents, periodic layered structures, are conspicuous in a more conventional way; they cause brilliant and highly visible reflections. Examples of such reflections are well known for



Fig. 8. Glow spot in the eye of a *Hobo-mok* skipper. Spot is bluish and about ten facets in diameter. [From (25)]

crustaceans and for many orders of insects. One of the best known of these phenomena is eye shine of the moth. The compound eyes of dark-adapted moths glow as hot coals in reflected light. Scientific interest in this eye shine arises from the work of Leydig (21), who discovered that the glow originates in the reflection from the tracheole layer just underlying the rhabdoms. Moth glow disappears when the eye is lightadapted, because the incident light is absorbed by the distal pigment that has migrated to surround the tracts (22). Moth glow is easily observed with the naked eye.

Butterfly Glow and Its Origin

A large number of diurnal Lepidoptera also exhibit glow, but in these animals the glow can be seen only with the ophthalmoscope or a similar instrument that allows observation and illumination from the same direction. Exner (2) first described butterfly glow. He observed an evanescent red spot in the center of the main pseudopupil.

We have investigated glow in a number of butterflies and have usually found a pattern of different colored glows distributed over the eye (Fig. 6); colors of shorter wavelength are observed in the dorsal ommatidia and longer wavelengths in the ventral ommatidia.

The most proximal end of each rhabdom terminates in a fusiform multilayered device (Fig. 7) that functions optically as an interference filter to reflect incident light in the rejection band of the filter back through the rhabdom and out of the eye where it can be observed as glow (23). Light in the passband of the filter is absorbed by a layer of proximal pigment. To illustrate how the filter functions we will discuss the filter (Fig. 7) which comes from an ommatidium displaying blue glow. The dense layers are cytoplasmic platelets derived from the taenidial ridges of a tracheole. The less dense space between the platelets would contain air in the living animal. The cytoplasmic plates in this filter are about 0.088 micrometer thick, whereas the intervening air spaces are about 0.123 micrometer thick. If the normally incident light has a wavelength of 0.49 micrometer, the air spaces are one-quarter wavelength thick. On the reasonable assumption that the refractive index of the cytoplasmic plates is 1.4, the plates are also one-



Fig. 9. Electron micrograph of longitudinal section showing modified taenidial ridges surrounding sensory part of skipper ommatidium. Period of ridges is approximately 0.180 micrometer. Diffraction from this structure causes skipper glow shown in Fig. 8. [From (25)]

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quarter wavelength thick, this wavelength being measured in the cytoplasm.

Reflections from the boundaries between air and cytoplasm all add in phase at the distal end of the filter, creating a large net reflection that propagates back through the rhabdom and out of the eye. The reflections all constructively interfere for the following reasons. (i) The Fresnel reflection coefficient is positive for a light wave going from cytoplasm to air but is negative going from air to cytoplasm. A negative reflection coefficient may be regarded as a 180° shift in phase between incident and reflected waves. (ii) This phase shift added to the 180° shift in phase incurred in a round trip through a given layer one-quarter wavelength thick implies perfect constructive interference for all the reflected waves.

From theoretical calculations one can predict that if white light is incident on this filter, a band of wavelengths approximately 0.104 micrometer wide and centered around 0.49 micrometer will be reflected, whereas light outside this band will pass through the filter and be absorbed in the proximal pigment. Therefore, the fusiform multilayered structure at the proximal end of the butterfly rhabdom is a quarter-wavelength interference filter and is the cause of the colored glow.

A filter taken from a part of the eye that displays red glow has platelet and air space dimensions corresponding to one-quarter wavelength of red light. The reason for variation of color in glow over the eye of the butterfly (Fig. 6) is a corresponding variation in the thickness and spacing of the filter layers from region to region in the eye.

The reason for the rapid disappearance of butterfly glow during direct illumination is probably basically the same as for the moth. We have observed pigment migration enveloping the short tract of this eye, which could account for evanescence of the glow (24).

Skipper Glow and Its Origin

The compound eye of the diurnal skipper is of particular interest because the skippers have features in common with both the moths and butterflies. Although these animals are day fliers, their compound eyes resemble those of the moth in that they contain long crystalline tracts. But the "iris" cells surrounding the tracts are devoid of pigment; thus the tracts cannot be bled of energy by pigment. Furthermore, there is good optical isolation between the sensory parts of the ommatidia that are surrounded by pigment-bearing cells.

The skippers display a bluish or greenish glow, which resembles the butterfly glow in not being visible under conditions of natural lighting, because it is very directional and must be observed from the same angle as the illumination. An area about ten facets in diameter lights up (Fig. 8) and, as might be expected from the lack of pigment in the "iris" cell, the glow remains even after the eye has been exposed to strong light for many minutes.

The retinular cells in each ommatidium are surrounded by modified tracheols so that any incoming light wave meets a succession of cytoplasmic ridges alternating with air spaces (25). This is indicated schematically in Fig. 2B and in the electron micrograph of Fig. 9, which is a section taken parallel to the ommatidial axis.

Incoming light propagating into the retinular cell along the ommatidial axis meets a periodic structure, the taenidial ridges of the tracheole cell. Because the period is approximately 0.18 micrometer, theory predicts that a single diffracted wave should exist within the ommatidium for free-space wavelengths shorter than approximately 0.52 micrometer. This diffracted wave propagates back out of the eye, causing the glow. For the free-space wavelengths longer than approximately 0.52 micrometer, there are no propagating dif-



Fig. 10. Left compound eye of horsefly *Hybomitra lasiophthalma* photographed in normally incident light. Dark stripes are blue; light stripes are orange. Colors caused by corneal interference-filter such as shown in Fig. 11.



Fig. 11. Electron micrograph of section taken normal to corneal surface from a bright facet of *Hybomitra lasiophthalma*. Dense layers are about 0.089 micrometer thick, rare layers about 0.112 micrometer thick. The set of dense and rare layers functions as a transmission interference-filter. [From (26)]

fracted orders present within the ommatidium.

As shown in Fig. 9, the taenidial ridges are composed of cytoplasmic ridges about 0.070 micrometer wide separated by air spaces about 0.11 micrometer wide. For wavelengths corresponding to bluish hues these dimensions are about one-quarter wavelength in each region, which for layered media is a condition for maximum reflection at normal incidence. For the skipper we interpret this as a mechanism for maximizing the energy in the diffracted wave for blue light. Such considerations lead us to believe that the source of the bluish glow in skippers is diffraction from the taenidial ridges of the tracheole cells that surround the retinular cells.

The glows of both skipper and butterfly are moderately saturated colors produced by periodic structures. Moth glow is typically an unsaturated warm color, and, although we know that this glow originates by light reflected from the tracheoles, there is as yet no detailed understanding of this phenomenon. Another type of highly visible reflection that superficially resembles the glow is caused by specialized layering in the cornea.

Corneal Layering

Many compound eyes of dipterans, especially those of Tabanidae, show colored reflection patterns when illuminated with white light. For instance, the compound eye of the female horsefly *Hybomitra lasiophthalma*, when viewed from the same direction as the illumination, shows a pattern consisting of five dark stripes predominantly bluish and four bright stripes predominantly orange (Fig. 10). The pattern consists of



Fig. 12. (Left) Theoretical characteristics of transmission filter for typical 12-layer horsefly blue filters (_____) and orange filters (-----). (Right) Theoretical characteristics of transmission filter for typical 20-layer deerfly blue filters (_____) and orange filters (_____) and

reflections originating from a small part of each corneal facet that is locally flat. The colored reflections are a constant feature of the eyes of living animals, of fixed eyes, and of isolated corneas. Patterns of colored eyes of other dipterans, rather than exhibiting stripes, may be uniform in appearance or subdivided into irregular areas, or may even consist of alternating rows of two types of facets having different colors.

These colored reflections are caused by a specialized system of alternating dense and rare layers located just beneath the distal corneal surface (26, 27). By means of the Zernike phase contrast system of light microscopy, it has been established that these layers differ in optical refractive index. Using the Leitz interference microscope, we inferred that the refractive index of the individual layers was about 1.74 for the dense layers and 1.40 for the rare layers. An electron micrograph of a cornea of the H. lasiophthalma taken normal to the surface (Fig. 11) shows the set of six rare and six dense layers. From the thickness of these layers measured in electron micrographs and the refractive indices of the layers measured in the interference microscope, we constructed a theoretical model to predict the reflection and transmission properties of the corneas. The calculations show these layer systems to be transmission interference-filters composed of quarter-wavelength layers which function in the manner described above for the reflection interferencefilters of the butterfly eyes. The behavior of the reflection properties of dipteran corneas as a function of incident angle and wavelength is supported by the calculations. The number of layers in the filter sets we have encountered ranges from six in parts of certain tabanid and dolichopodid eyes to 20 in the corneas of deerflies. Typical theoretical characteristics of transmission filters are shown for filters having 12 and 20 layers (Fig. 12).

Biological Significance of the Filters

We have discussed two types of filtering structures found in the compound eyes of insects. The first type is represented by various tapetal structures that cause eyeshine in moths, butterflies, and skippers, and the second by transmission filters found in the corneas of dipteran flies. The eyes of many vertebrates contain structures analogous

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to these two types of filters. These are the tapetum lucidum and the colored oil droplets, respectively (28).

The tapetum lucidum in the vertebrate eye is a mirroring device located proximal to the receptors and is often present over only a portion of the fundus. It causes a reflection that is usually colored, although unsaturated. The hue may be located in practically any region of the spectrum. The tapetum is thought to (i) optically improve contrast by enhancing brightness differences in the retinal image and (ii) aid sensitivity by increasing the intensity of light in the photoreceptors (29). Maximizing brightness differences in the image on the photoreceptors requires that the tapetum should be a perfect reflector in the sense that all the energy is reflected specularly and not diffusely and that the photoreceptors should be relatively transparent.

Many properties of the tapeta of vertebrates are shared by the invertebrate tapeta. The arguments for contrast and sensitivity enhancement may be applied to filters of the moth, skipper, and butterfly and in certain cases may be broadened to include optical enhancement of color contrast. The tapetal filter in the butterfly creates a colored reflection that is relatively saturated. In this case, differences in image intensity are increased only for a restricted band of wavelengths, and only selected color contrasts are enhanced. Because photoreceptor absorption is probably at least 20 percent, intensity differences can at most be increased by about 80 percent by a tapetal filter, for the reasons mentioned above. However, if instead a transmission filter is inserted between the incident light and the photoreceptors, as with the oil droplets of the vertebrate or the corneal filters of the invertebrate, this limitation on contrast enhancement is removed.

Colored oil droplets in a vertebrate retina are located in cones between the inner and outer segments; light must first pass through the oil droplets before entering the outer segments of the cone, the sites of photodetection. Droplets of different colors may occur in the same retina and may be organized into fields characterized by the predominance of a particular color. These oil droplets are thought to enhance color contrasts in particular parts of the visual field. An example is the pigeon, in which the ventronasal droplets are yellow, giving maximum contrast of objects seen against the sky by eliminating the blue

The color filters in the corneas of dipterans do not fall into any easily recognizable pattern such as occurs in the pigeon. For this reason it is more difficult to state definitely that they serve a similar function without direct experimental proof. Still, the preponderance of evidence suggests that they serve as a color-contrast filter system for vision (26, 27). In fact, all the filters we have described are probably optical devices that enhance contrast. Although the corneal lenslets and the tracts of the compound eye tend to smear the retinal image, the eye's optical microcomponents tend to enhance contrast and sharpen the optical image.

Summary

Exner's classical theory of the function of compound eyes with crystalline tracts ignores the presence of the tracts for the dark-adapted eye. The tracts perform an optical function in the eyes of certain moths and skippers whether light- or dark-adapted. The lenslet of the corneal-crystalline cone focuses an image at the beginning of the tract. Although the image is not transmitted, theory predicts that some information about the image could be guided to the rhabdom. The tract and migrating pigment together also function as a longitudinal pupil.

In addition, compound eyes contain dioptric components with characteristic dimensions smaller than a wavelength of light. Corneal nipples act as an antireflection coating that aids camouflage and may reduce ghosts. The specialized layering in corneas of certain dipterans probably serves a contrast-filtering function for vision. Tracheolar interference filters of lepidopterans act as tapeta that may enhance both sensitivity and the optical contrast of the retinal image.

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