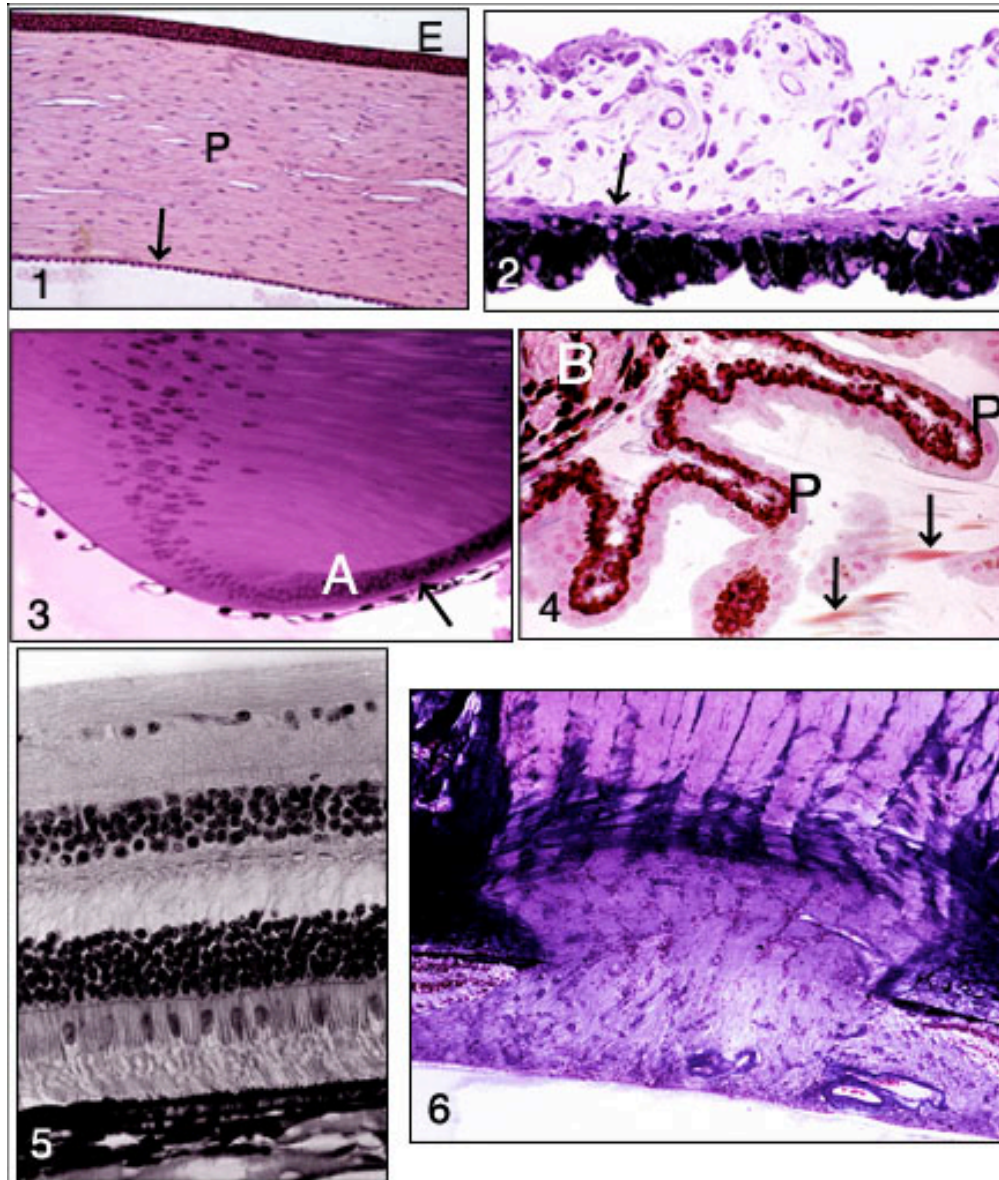


## Eye



1. Cornea. Note the corneal epithelium (E), substantia propria (P), and corneal endothelium (arrow).

2. Iris. The stroma of the iris separates the posterior surface covered by two rows of cuboidal pigmented cells from the anterior surface (top). Note the dilator of the iris (arrow).

3. Lens. Note the anterior lens cells (A), capsule (arrow), and the lens fibers making up the lens substance.

4. Ciliary processes (P) covered by ciliary epithelium. Note the zonule fibers (arrows) and the ciliary body (B).

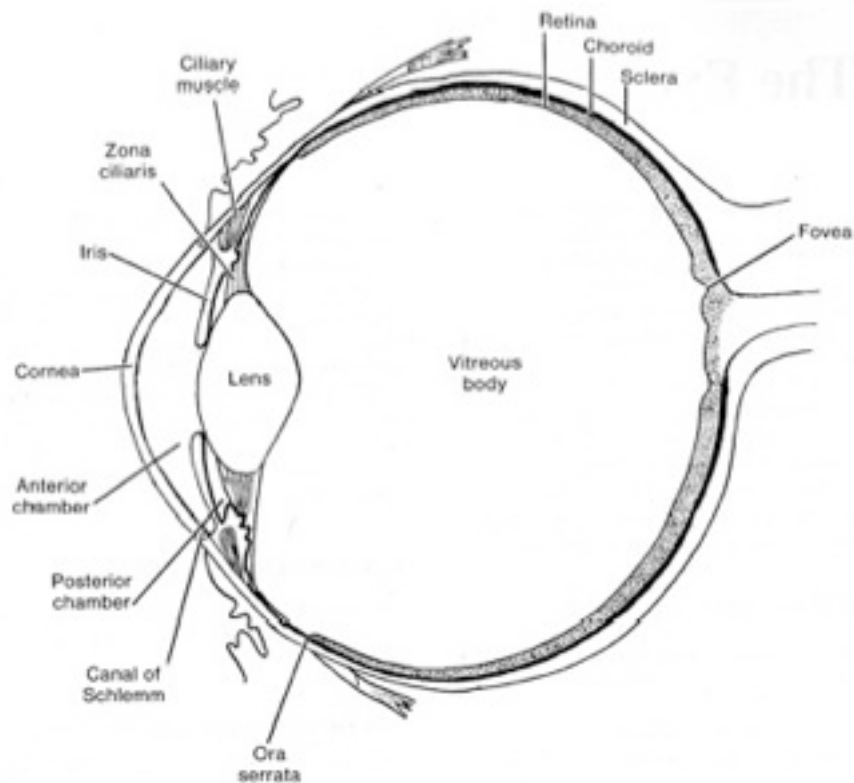
5. Neural retina. Identify: pigment epithelium, layer of rods and cones, external limiting membrane, outer nuclear layer, outer plexiform layer, inner nuclear layer, inner plexiform layer, ganglion cell layer, layer of nerve fibers, and internal limiting membrane.

6. Optic disc.

Eyes are photoreceptors containing systems of convex surfaces that transmit and focus light on a surface sensitive to the intensity and wavelength (color) of light. Images formed there are transmitted to the brain, where they are interpreted, correlated, and translated into the sensation of sight. Eyes can regulate the amount of light admitted and change their focal lengths. The eyes are almost spherical and are located in and protected by bony sockets provided with a padding of fat. Because the eyes are offset from each other, the images formed are correspondingly offset and provide for binocular vision. Integration of the binocular images results in a three-dimensional quality of sight through which depth and spatial orientation are recognized.

## **General Structure**

The wall of the eyeball consists of an outer corneoscleral coat, a central coat called the uvea, and an inner coat called the retina. The corneoscleral coat is subdivided into a smaller, transparent, anterior cornea that allows light to enter the eye and the sclera, a larger white segment. The sclera is a tough fibrous layer that protects the delicate internal structures of the eye and helps maintain the shape of the eyeball. The uveal coat consists of the choroid, ciliary body, and iris. The choroid is the vascular part of the uvea, immediately beneath the retina. It is continuous with the ciliary body, which forms a belt-like structure around the interior of the eyeball, just forward of the anterior margin of the retina. The ciliary body controls the diameter and shape of the lens, which focuses light on the retina. The iris, the last portion of the uvea, is continuous with the ciliary body and has a central opening, the pupil, whose diameter can be changed to regulate the amount of light passing into the eyeball. The retina consists of pigment-containing photoreceptors that, on exposure to light, produce chemical energy that is converted into the electric energy of nerve impulses. A chain of conducting neurons in the retina transmits the impulses to the optic nerve. The optic disc is the point where nerve fibers from the retina gather to form the optic nerve and leave the eyeball. The interior of the eyeball is subdivided into an anterior chamber, a posterior chamber, and a vitreal cavity. Each is filled with a transparent medium that helps maintain the shape and turgor of the eye. The anterior and posterior chambers are continuous through the pupil and contain a watery aqueous humor, which provides nutrients for the anterior structures of the eye. The large vitreal cavity is filled with a viscous, transparent gel called the vitreous humor or vitreous body.



A diagrammatic sketch of general eye structure.

### **Corneoscleral Coat**

The corneoscleral coat forms the outermost layer of the eyeball and consists of the cornea and sclera.

### **Sclera**

The sclera forms the tough, opaque, fibrous outer tunic of the posterior five-sixths of the eyeball. It varies in thickness in different regions but averages about 0.5 mm. It is composed of flat bundles of collagen that run in various directions parallel to the scleral surface. Delicate networks of elastic fibers and elongated, flattened fibroblasts extend between the collagen bundles. Melanocytes occur in the deeper layers. The sclera thins and forms a fenestrated membrane, the lamina cribrosa, at the point where fibers of the optic nerve penetrate the sclera to exit the eye. The sclera protects the interior of the eye, aids in maintaining its shape, and serves as the site of attachment for the extrinsic muscles of the eye.

### **Cornea**

The transparent cornea is the most anterior part of the eye. It is about 11 mm in diameter, approximately 0.8 mm thick near the center, and 1.00 mm at the periphery. Its curvature is considerably greater than that of the posterior sclera. The cornea is uniform in structure throughout and consists of corneal epithelium, Bowman's membrane, substantia propria,

Descemet's membrane, and corneal endothelium. The corneal epithelium is stratified squamous with a smooth outer surface and averages about 50  $\mu\text{m}$  in depth. It usually consists of five layers of large squamous cells that have few organelles but often contain glycogen. The superficial cells retain their nuclei, and their external surfaces form numerous fine ridges (microplicae) that help retain moisture on the corneal surface. The epithelium lies on a distinct basal lamina. The lateral membranes of adjacent cells are extensively interdigitated and joined by numerous desmosomes. The corneal epithelium contains many free nerve endings and is very sensitive to a number of stimuli, especially pain. The basal lamina of the corneal epithelium lies on the outer layer of the substantia propria and is called Bowman's membrane; it ends abruptly at the peripheral margin of the cornea. Bowman's membrane has a homogeneous appearance and consists of a feltwork of small collagen fibrils (type I) and lacks elastin. The substantia propria, or stroma, forms the bulk of the cornea. It consists of numerous bundles of collagen fibers (type I and type V) arranged into 50-70 broad sheets called corneal lamellae that run parallel to the corneal surface. The collagen bundles in each successive lamina run in different directions and cross at various angles. Adjacent lamellae are knit tightly together by interlacing collagenous fibers. The fibers, bundles, and lamellae of collagen are embedded in a matrix of sulfated proteoglycans rich in chondroitin sulfate and keratosulfate. These proteoglycans are not present in the sclera. Flattened fibroblast-like cells, the keratocytes, are present between the bundles of collagen fibers. Blood vessels and lymphatics normally are absent in the substantia propria, although occasional lymphoid wandering cells are seen. Descemet's membrane is a homogeneous membrane, 6 to 8  $\mu\text{m}$  thick, lying between the posterior surface of the substantia propria and the corneal endothelium. It corresponds to a thick basal lamina secreted by the corneal endothelium. It is resilient and elastic, although elastic fibers are not present, and appears to consist mainly of the type VIII form of collagen. The corneal endothelium lines the inner surface of the cornea and consists of a layer of large, hexagonal squamous cells. Tight junctions join the apices of the cells, and the cytoplasm contains numerous mitochondria and vesicles. The cells are involved in transporting materials from the anterior chamber. The transparency of the cornea is due to the uniform diameter and orderly arrangement of collagen fibers and to the properties of the ground substance. The cornea is avascular and depends on the aqueous humor and blood vessels of the surrounding limbus to supply its nutrients. Ion pumps of the corneal endothelial cells maintain a critical fluid level within the substantia propria. If excess fluid accumulates, the cornea becomes opaque. Corneal endothelial cells do not divide after birth and therefore are not replaced. Each person is born with a complete complement of corneal endothelial cells.

## **Limbus**

The limbus represents a zone of transition 1.5 to 2.0 mm wide between the transparent cornea and the opaque sclera. The outer surface bears a shallow groove, the external scleral sulcus, where the more convex cornea joins the sclera. A similar structure, the internal scleral sulcus, lies on the inner surface of the limbus. The scleral spur is a small ridge of tissue projecting from the posterior lip of the internal scleral sulcus and attached anteriorly to tissue that comprises the outflow system for fluid in the anterior chamber. The limbus is further characterized by the terminations of Bowman's and Descemet's membranes. The collagen fibers and bundles of the cornea become larger here and their arrangement more irregular as they blend with those of the sclera. Numerous small blood vessels form arcades in this region and nourish the peripheral portions of the avascular cornea. Descemet's membrane is replaced by the spongy trabecular meshwork attached to the anterior part of the scleral spur. It

contains numerous flattened, anastomosing trabeculae that consist of collagenous fibers and ground substance covered by an attenuated endothelium that is continuous with the corneal endothelium. The trabeculae form a labyrinth of spaces that communicate with the anterior chamber. Between the bulk of the limbal stroma and the trabecular meshwork, a flattened, endothelial-lined canal, Schlemm's canal, courses around the circumference of the cornea. Aqueous humor enters the trabecular spaces from the anterior chamber and crosses the endothelial lining of the trabeculae, the juxtacanalicular connective tissue, and finally, the endothelium of the canal to enter its lumen. Several channels arise from the peripheral wall of the canal to join veins in the limbus and eventually drain to episcleral veins. Obstruction to the drainage of aqueous humor causes a rise in intraocular pressure, a characteristic of the condition called glaucoma.

## **Uveal Layer**

The uvea, the middle vascular coat of the eye, is divided into choroid, ciliary body, and iris.

## **Choroid**

The choroid is a thin, brown, highly vascular membrane that lines the inner surface of the posterior sclera. Its outer surface is connected to the sclera by thin avascular lamellae that form a delicate, pigmented layer called the suprachoroid lamina. The lamellae mainly consist of fine elastic fibers between which are numerous large, flat melanocytes and scattered macrophages. The lamellae cross a potential cleft, the perichoroidal space, between the sclera and choroid to enter the choroid proper. The choroid proper consists of three regions. The outer vessel layer is made up of loose connective tissue with numerous melanocytes and contains the larger branches of ciliary arteries and veins. The central choriocapillary layer consists of a net of capillaries lined by a fenestrated endothelium; these vessels provide for the nutritional needs of the outer layers of the retina. The choriocapillary layer ends near the ora serrata. The innermost layer of the choroid is the glassy (Bruch's) membrane that lies between the remainder of the choroid and the pigment epithelium of the retina. With the light microscope it appears as a homogeneous layer, 1 to 4  $\mu\text{m}$  thick. Ultrastructurally it shows five separate strata made up of basal laminae of capillaries in the choriocapillary layer, the pigment epithelium of the retina, and between them, two thin layers of collagen separated by a delicate elastic network.

## **Ciliary Body**

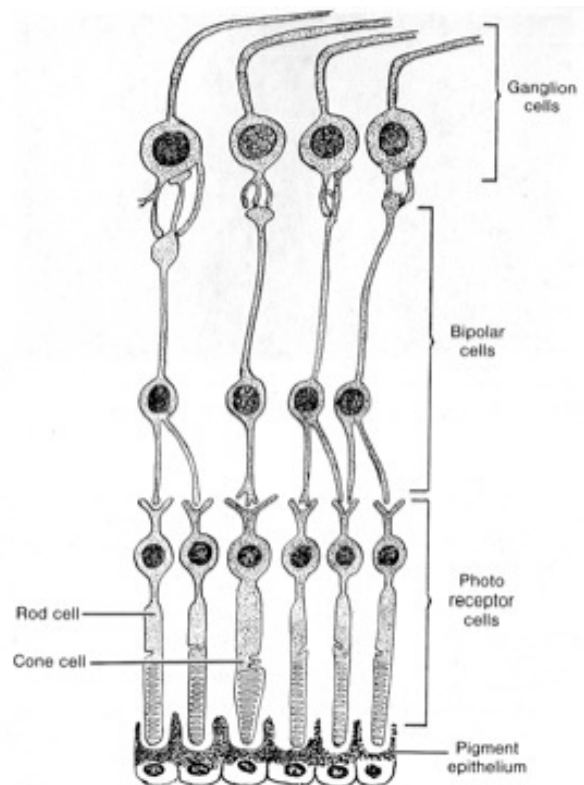
The ciliary body is located between the ora serrata of the neural retina and the outer edge of the iris, where it attaches to the posterior aspect of the scleral spur at the corneoscleral junction. It forms a thin triangle when seen in section with the light microscope and consists of an inner vascular tunic and a mass of smooth muscle immediately adjacent to the sclera. The internal surface is covered by ciliary epithelium, a continuation of the pigment epithelium of the retina that lacks photosensitive cells. Ciliary epithelium consists of an inner layer of nonpigmented cells and an outer layer of pigmented cells, each resting on a separate basal lamina; it is unusual in that the cell apices of both layers are closely apposed, apex-to-apex. The outer pigmented cell layer is separated from the stroma of the ciliary body by a thin basal lamina continuous with that underlying the pigment epithelium in the remainder of the retina. The basal lamina of the nonpigmented layer lies adjacent to the posterior chamber of the eye.

and is continuous with the inner limiting membrane of the retina. The basal plasmalemma of the nonpigmented cells shows numerous infoldings and is involved in ion/fluid transport. The cells contain numerous mitochondria and a well developed, supranuclear Golgi complex. The adjacent pigmented cells of the outer layer also show prominent basal infoldings, and the cytoplasm is filled with melanin granules. The apices of cells of the inner, nonpigmented epithelium are united by well-formed tight junctions that form the anatomic portion of the blood-aqueous barrier, which selectively limits passage of materials between the blood and the interior of the eye. The ciliary epithelium elaborates aqueous humor, which differs from blood plasma in its electrolyte composition and lower protein content. Aqueous humor fills the posterior chamber, provides nutrients for the lens, and posteriorly, enters the vitreous humor. Anteriorly, it flows from the posterior chamber through the pupil into the anterior chamber and aids in nourishing the cornea. It leaves the anterior chamber via the trabecular meshwork and Schlemm's canal to the episcleral veins. In its anterior part, the inner surface of the ciliary body is formed by 60 to 80 radially arranged, elongated ridges called ciliary processes, which are lined by ciliary epithelium and contain a highly vascularized stroma and scattered melanocytes. Zonule fibers, which hold the lens in place, are produced mainly by the nonpigmented cell layer of the ciliary epithelium and are attached to its basal lamina. They extend from the ciliary processes to the equator of the lens. Most of the ciliary body consists of smooth muscle, the ciliaris muscle, which controls the shape and therefore the focal power of the lens. The muscle cells are organized into regions with circular, radial, and meridional orientations. Numerous elastic fibers and melanocytes form a sparse connective tissue between the muscle bundles. The ciliaris muscle is important in eye accommodation, and when it contracts, it draws the ciliary processes forward, thus relaxing the suspensory ligament (zonule fibers) of the lens, allowing the lens to become more convex and to focus on objects near the retina.

## **Iris**

The iris is a thin disc suspended in the aqueous humor between the cornea and lens and has a central, circular aperture called the pupil. The iris is continuous with the ciliary body at the periphery and divides the space between the cornea and lens into anterior and posterior chambers. The anterior chamber is bounded anteriorly by the cornea and posteriorly by the iris and central part of the lens. The posterior chamber is a narrow space between the peripheral part of the iris in front and the peripheral portion of the lens, ciliary zonule, and ciliary processes. The two chambers communicate through the pupil. The anterior surface of the iris is irregular due to numerous fissures or crypts. The margin attached to the ciliary body forms the ciliary margin; that surrounding the pupil is the pupillary margin. The stroma of the iris consists primarily of loose, vascular connective tissue with scattered collagenous fibers, melanocytes, and fibroblasts embedded in a homogeneous ground substance. The anterior surface lacks a definite endothelial or mesothelial covering but is lined in part by a discontinuous layer of melanocytes and fibroblasts. Tissue spaces of the stroma often appear to communicate with the anterior chamber. The posterior surface is covered by two rows of cuboidal, pigmented cells that are continuous with the ciliary epithelium. Where it passes onto the posterior surface of the iris, the inner nonpigmented layer of the ciliary epithelium becomes heavily pigmented. Cells of the outer layer have less pigment and are modified into myoepithelial cells to form the dilator of the iris. The dilator of the pupil consists only of a single layer of radially arranged myoepithelial cells whose contraction increases the diameter of the pupil. The sphincter muscle consists of a circularly arranged, compact bundle of smooth muscle cells near the pupillary margin. Contraction of the sphincter muscle reduces the

diameter of the pupil. The iris acts as a diaphragm, modifying the amount of light that enters the eye, thus permitting a range of vision under a variety of lighting conditions. The color of the iris is determined by the amount and distribution of pigment. In the various shades of blue eyes, melanin is restricted to the posterior surface of the iris, whereas in gray and brown eyes



A diagrammatic sketch illustrating the basic three-neuron chain system of the retina.

melanin is found in increasing concentration within melanocytes present throughout the stroma of the iris. In albinos, melanin pigment is absent and the iris takes on a pink color due to the vasculature of the iridial stroma.

## Retina

The retina, the innermost of the three tunics, is a delicate sheet of nervous tissue that forms the photoreceptor of the eye. The outer surface is in contact with the choroid; the inner surface is adjacent to the vitreous body. The posterior retina consists of an outer pigment epithelium and an inner neural retina (retina proper). The retina decreases in thickness anteriorly, and the nervous component ends at a ragged margin called the ora serrata. The thin prolongation of the retina extends anteriorly to cover the ciliary processes as the ciliary epithelium and covers the posterior aspect of the iris, where it forms the iridia retinae. The forward extension of the retina consists only of the pigmented layer and an inner layer of columnar epithelial cells; the

nervous component is lacking. The neural retina is anchored only at the optic disc, where nerve fibers congregate before passing through the sclera to form the optic nerve, and at the ora serrata. Although cells of the pigment epithelium interdigitate with photoreceptor cells of the neural retina, there is no anatomic connection between the two components of the retina, and after trauma or disease, the neural retina may detach from the pigment epithelium. The exact center of the posterior retina corresponds to the axis of the eye, and at this point, vision is most perfect. The region appears as a small, yellow, oval area called the macula lutea. In its center is a depression about 1.5 mm in diameter called the fovea centralis, where the sensory elements are most numerous and most precisely organized. Nearer the periphery of the retina, neural elements are larger, fewer, and less evenly distributed. About 4.0 mm to the nasal side of the macula lutea is the optic disc, the site of formation and exit of the optic nerve. Lacking photoreceptors, this area is insensitive to light and forms the "blind spot" of the retina.

## **Neural Retina**

Except for the extreme periphery and the fovea centralis, the neural retina is made up of the following layers, listed in order from the choroid, as seen with the light microscope: (1) layer of rods and cones, (2) external limiting membrane, (3) outer nuclear layer, (4) outer plexiform layer, (5) inner nuclear layer, (6) inner plexiform layer, (7) ganglion cell layer, (8) layer of nerve fibers, and (9) internal limiting membrane. The layer of rods and cones represents the inner and outer segments of rods and cones. The rod outer segments appear as darker-staining rods and are more numerous than the cone outer segments. The latter are larger and exhibit a conical shape. Lying between this layer and immediately adjacent the outer nuclear layer is the external (outer) limiting membrane. It appears as a fine discontinuous line and is formed by junctional complexes between the scleral tips of Müller's cells and adjacent photoreceptor cells. The outer nuclear layer consists of the cell bodies and nuclei of the rods and cones. The outer plexiform layer consists primarily of rod spherules, cone pedicles and dendrites of bipolar neurons. Nuclei and cell bodies of bipolar neurons, horizontal, amacrine and Müller's cells constitute the inner nuclear layer. The inner plexiform layer is made up of axons of bipolar neurons, dendrites of ganglion cells, and processes of amacrine cells. Ganglion cells and scattered neuroglial cells form the ganglion cell layer. The nerve fiber layer is made up primarily of unmyelinated axons from ganglion cells and processes of Müller's cells. The very thin internal limiting membrane is formed by the vitreal processes of Müller's cells and their basement membrane.

The structurally complex neural retina consists essentially of a three-neuron conducting chain that ultimately forms the nerve fibers in the optic nerve. The neural elements of the basic conducting chain are photoreceptors (rod and cone cells), bipolar neurons, and ganglion cells. When stimulated by light, photoreceptor cells transmit an action potential to the bipolar neurons, which in turn synapse with ganglion cells. Unmyelinated axons from the ganglion cells enter the layer of retinal nerve fibers and unite at the optic disc to form the optic nerve, which transmits the impulse to the brain. Other intraretinal cells are either association neurons (horizontal cells, amacrine cells) or glial cells. These elements are organized into the various layers of the retina.

## **Glial Cells**

The largest and most prominent glial elements in the neural retina are Müller's cells, which extend between the outer and inner limiting membranes of the retina. Their cytoplasmic



processes run between the cell bodies and processes of neurons in the retina and provide physical support for the neural elements. The basal lamina of Müller's cells lies adjacent to the vitreal body and forms the inner limiting membrane of the retina. The apices of Müller's cells are joined to adjacent photo receptor cells by junctional complexes and form the outer limiting membrane. The cytoplasm is rich in smooth endoplasmic reticulum and contains abundant glycogen. In addition to providing structural support, Müller's cells are thought to aid in the nutritional maintenance of other retinal elements and have been equated with astrocytes of the central nervous system. A small number of spindle-shaped glial cells also are present around ganglion cells and between axons that form the nerve fiber layer of the retina.

## Photoreceptor Cells

The two types of photoreceptors are rod cells and cone cells. Rod cells are long, slender cells that lie perpendicular to the layers of the retina. They are 40 to 60  $\mu\text{m}$  long and 1.5 to 3.0  $\mu\text{m}$  wide, depending on their location in the retina, and number between 75 million and 170 million in each retina. The scleral (outer) third of each rod, called the rod proper, lies between the pigment epithelium and the outer limiting membrane. The scleral end of the rods is surrounded by processes that extend from the underlying pigment epithelial cells; the inner or vitreal end extends into the outer plexiform layer. Each rod proper consists of outer and inner segments connected by a slender stalk containing nine peripheral doublets of microtubules. The doublets originate from a basal body in the vitreal end of the inner segment, but the connecting stalk differs from a typical cilium in that it lacks a central pair of microtubules. The outer segment contains hundreds of flattened membranous sacs or discs of uniform diameter. These sacs contain rhodopsin, the substance responsible for absorption of light. After exposure to light, rhodopsin changes its molecular configuration from cis to trans and breaks down, resulting in hyperpolarization of the plasmalemma of the rod cell, with formation of an electrical potential that is transferred to dendrites of associated bipolar cells. After stimulation, rhodopsin is rapidly reconstituted. The inner segment consists of an outer scleral region called the ellipsoid (which contains numerous mitochondria) and a vitreal portion that houses the Golgi complex, free ribosomes, and myoid. Microtubules are numerous in both regions. The myoid region contains elements of granular and smooth endoplasmic reticulum and synthesizes and packages proteins that are transported down the connecting stalk to the scleral end of the outer rod segment to be used in the assembly of new membranous discs. Older sacs are shed from the tips of the rods during the morning hours and are replaced by new discs. The discarded discs are phagocytized and destroyed by cells of the pigment epithelium. The remainder of the rod cell consists of an outer fiber, a cell body, and an inner fiber. The outer fiber is a thin process that extends from the inner segment of the rod proper to the cell body, which contains the nucleus. The inner fiber joins the cell body to the spherule; a pear-shaped synaptic ending that contains numerous synaptic vesicles and a synaptic ribbon. The latter consists of a dense proteinaceous plaque that lies perpendicular to the presynaptic surface, often bounded by numerous vesicles. The cell body and nucleus of the rods are located in the outer nuclear layer of the retina; the spherule lies within the outer plexiform layer. Cone cells are 75  $\mu\text{m}$  or more in length at the fovea, decreasing to 40  $\mu\text{m}$  at the edge of the retina. Each retina contains between 6 million and 7 million cones. In general, cone cells resemble the rods but are flask-shaped with short, conical outer segments and relatively broad inner segments united by a modified stalk similar to that of rod cells. The membranous sacs of the outer cone segments differ in that they may remain attached to the surrounding cell membrane and decrease in diameter as they approach the tip of the cone. The inner segment, also called the ellipsoid

portion, shows a region with numerous mitochondria and a myoid part that contains the Golgi complex and elements of smooth and granular endoplasmic reticulum. As in rods, the cones synthesize proteins that pass to the outer segments, where they are used in the formation of new membranous sacs. Older sacs appear to be shed in the evening and are phagocytized in the pigment epithelial cells. Unlike those in rod cells, the sacs decrease in size as they approach the tip of the cone. The visual pigment of cone cells, iodopsin, is associated with the outer segments. Absorption of light and generation of an electrical impulse are similar to that occurring in rods. Cones function in color perception and visual acuity, responding to light of relatively high intensity. Detection of color is believed to depend on the presence of several pigments in the cones, whereas rods are thought to contain only one form of pigment. Three different categories of cones have been described. Long wavelength cones that respond best to the red range, middle wavelength cones that respond to the green range, and short wavelength cones that respond best in the blue range. Except for those in the outer fovea, cones lack an outer fiber, and the inner cone segment blends with the cell body. The nuclei of cone cells are larger and paler than those of the rods and form a single row in the outer nuclear layer, adjacent to the outer limiting membrane. Each cone has a thick inner fiber that runs to the outer plexiform layer, where it forms a club-shaped synaptic ending, the cone pedicle, which synapses with processes from bipolar and horizontal neurons. Thus, photoreception results when light is absorbed by visual pigments in the rods and cones. The photoactivated pigment activates a G protein, transducin, which then stimulates a phosphodiesterase to hydrolyze intracellular cyclic GMP. This action closes sodium channels, hyperpolarizes the photoreceptor, and slows glutamate release at the synaptic terminal. In this way, the photoreceptor cells respond to light and pass on the generated action potential to neurons of the inner retina and ultimately to the brain.

### **Bipolar Cells**

Like photoreceptor cells, bipolar cells lie perpendicular to the retinal layers with their cell bodies and nuclei in the inner nuclear layer of the retina. They give rise to one or more dendrites that extend into the outer plexiform layer, where they synapse with terminals of photoreceptor cells. A single axon extends into the inner plexiform layer and synapses with processes from ganglion cells. Several types of bipolar neurons have been described: Rod bipolar cells make contact with several rod cells; flat cone bipolar cells form synapses with several cone pedicles; invaginating midget and flat midget bipolar cells synapse with a single cone pedicle. Bipolar cells relay impulses from the rod and cone cells to the ganglion cells of the next layer.

### **Ganglion Cells**

Dendrites of ganglion cells synapse with axons of bipolar neurons and represent the third and terminal link in the neuron chain. Axons of the various ganglion cells pass along the vitreal surface in the nerve fiber layer of the retina and join other axons at the optic disc to form the optic nerve. Although several morphologic varieties of ganglion cells have been described, two forms have been identified by their synaptic relations with bipolar neurons. Diffuse ganglion cells synapse with several types of bipolar cells, and midget ganglion cells, a monosynaptic type, synapse with a single midget bipolar cell.

## **Association Neurons**

The cell bodies and nuclei of horizontal cells lie in the inner nuclear layer. Their dendrites enter the outer plexiform layer and synapse with a single cone pedicle. The axons also enter the outer plexiform layer and run parallel to the adjacent retinal layers to end on terminal twigs that synapse with several rod spherules. Although the functional significance of horizontal cells is not clear, because they synapse with cones of one area, with rods of another area, and with bipolar cells, it has been suggested that they may raise or lower the functional threshold of these cells. Amacrine cells are pear-shaped neurons that lack axons but have several dendrites. The cell bodies lie in the inner nuclear layer, and their dendrites extend into the inner plexiform layer. Perikarya of interplexiform cells also lie in the inner nuclear layer and send processes to both plexiform layers. They receive input from amacrine cells, and their output is with both horizontal and bipolar neurons. All three types of association neurons are thought to act to modulate the passage of impulses from the photoreceptors to ganglion cells. These association neurons allow for the integration of signals between adjacent groups of photoreceptors.

## **Fovea Centralis**

The fovea centralis is a funnel-like depression on the posterior surface of the retina, in direct line with the visual axis. At this point, those vitreal layers of the retina which are beyond the outer nuclear layer are displaced laterally, giving light an almost free pathway to the photoreceptors. The central region of the fovea, about 1.5 mm in diameter, consists only of cones that are longer and thinner than cones elsewhere in the retina. They are closely packed and number about 25,000 to 35,000. Vision is most acute in this part of the retina.

## **Pigment Epithelium**

The pigment epithelium of the retina consists of a simple layer of hexagonal cells that tend to increase in diameter near the ora serrata. Their basal cell membranes show numerous infoldings with associated mitochondria and are thought to be active in transport. The basal lamina contributes to the glassy (Bruch's) membrane of the choroid as seen by the light microscope. The lateral cell membranes of adjacent cells show some interdigitations and, near the apex, are united by tight junctions. Two types of cytoplasmic processes arise from the apices of the cells: cylindrical sheaths invest the tips of the rod and cone outer segments, and elongated microvilli extend toward photoreceptor cells. The cytoplasm is characterized by abundant mitochondria near the base of the cell and by many lipofuscin and melanin granules. Pigment epithelial cells may show numerous residual bodies that contain remnants of phagocytized membrane material shed by rod outer segments. Pigment epithelium absorbs light after it has passed through the neural retina, thereby preventing reflection within the eye, and the apical tight junctions prevent undesirable substances from entering the intercellular spaces of the neural retina. The pigment epithelium also stores vitamin A, a precursor of rhodopsin, needed by the outer rod membranes.

## **Vascular Supply of the Retina**

The outer nuclear and plexiform layers and the layer of rod and cone inner segments lack blood vessels. Capillaries of the choriocapillary layer of the choroid nourish these parts of the

retina. Nutrients cross the pigmented epithelium to enter the intercellular spaces of the outer neural retina. Retinal vessels arising from the central retinal artery, which enters the eye in the optic nerve, supply the inner layers of the retina. Capillary networks from this source lie in the nerve fiber layer and in the inner plexiform layer.

## **Lens**

The lens is a transparent, biconvex epithelial body placed immediately behind the pupil between the iris and vitreous body. It is about 10 mm diameter and 3.7 to 4.5 mm thick. The posterior surface is more convex than the anterior surface. The lens consists of a capsule, anterior lens cells, and lens substance. On its anterior and posterior surfaces, the lens is covered by a homogeneous; proteoglycan-rich capsule 10 to 18  $\mu\text{m}$  thick. A single layer of cuboidal cells, the anterior lens cells, lies immediately beneath the capsule and forms the epithelium of the lens, which is restricted to the anterior surface. The posterior surface has no epithelium. The apices of the anterior lens cells face inward, toward the lens; the basal surfaces rest on a basal lamina. Anterior lens cells contain ion pumps that maintain the proper hydration of the lens. Near the equator of the lens, the cells increase in height and gradually differentiate into lens fibers that make up the bulk of the lens, referred to as the lens substance. The lens grows throughout life by addition of new fibers to the periphery of the lens substance. The outer layers of the lens substance form the cortex. Nearer the center, the lens substance consists of condensed, concentrically arranged fibers that give it a more homogeneous appearance; this area is called the nucleus of the lens. At the equator of the lens, the anterior lens cells elongate and push into the lens to lie beneath the epithelium anteriorly and the capsule posteriorly. As the cells increase in length, they lose their nuclei and their basal attachment to the capsule and become lens fibers that show a homogeneous, finely granular cytoplasm with few organelles. They appear hexagonal in cross section and measure 7 to 10  $\mu\text{m}$  in length. The lateral membranes of the lens fibers (cells) in the cortex show large protrusions that interdigitate with concavities in adjacent fibers, in a ball and socket manner. Nexus junctions are common at these points. The ball and socket joints maintain the relative positions of the fibers as the lens changes shape during focusing.

The lens is avascular and derives nourishment totally from diffusion of material from the aqueous humor and vitreous body. The lens is held in place by a system of fibers called zonule fibers that make up the suspensory ligament of the lens. Zonule fibers arise from the ciliary epithelium that covers the ciliary processes and attach to the lens capsule just anterior and posterior to the equator of the lens. Zonule fibers consist of small bundles of fine filaments, approximately 12 nm in diameter, which may correspond to the microfibril (glycoprotein) component of elastic fibers. The ciliary muscle controls the thickness and convexity of the lens. If the ciliary muscle contracts, the ciliary body and choroid are pulled forward and centrally, releasing tension on the zonule fibers, and the lens "sags" to become thicker and more convex. This permits focusing on near objects. When the ciliary muscle relaxes, the zonule fibers are placed under tension, and the lens becomes thinner and less convex to focus on far objects.

## **Vitreous Body**

The vitreous body is a colorless, transparent, gelatinous mass that fills the vitreal cavity. It is 99% water and contains hyaluronic acid and other hydrophilic glycosaminoglycans, as well as thin fibrils of collagen (type II and type XI) arranged randomly in a network. The fibrils are most

prominent near the periphery. A few cells, the hyalocytes, and occasional macrophages are present in the outermost parts of the vitreous body. Hyalocytes may be responsible for the formation and maintenance of the vitreous body. A thin, cylindrical network of fibrils, the hyaloid canal, extends from the optic disc to the posterior surface of the lens. It represents the site of the embryonic hyaloid artery. The vitreous body provides nutrients to the lens and adjacent structures and maintains the correct consistency and shape of the eye.

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