THE ZONULE OF ZINN: ITS ORIGIN, COURSE, AND INSERTION, AND ITS RELATION TO NEIGHBORING STRUCTURES

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THE ZONULE of Zinn is small, it is difficult to see, and its function is not wholly apparent. The fibers are hard to define, they do not stain well with ordinary stains, their origins and insertions are not easy to determine, and their courses involve an appreciation of three dimensions and of many neighboring structures. For all these reasons the zonule has enjoyed the continuous academic interest of anatomists during the last two centuries. With the appearance of the two major theories of accommodation, by Helmholtz (1) and by Tscherning (2-5), and with the introduction of the intracapsular cataract extraction, and, finally, as a result of the possible relation of the pull of the zonule to retinal detachment, knowledge of the anatomy of the zonule has found practical application.

In recent years there have been excellent papers on the zonule. The most comprehensive have been by Loddoni (6), Moreno (7), and Lauber (8, 9). Strangely enough, the zonule has not been discussed in the English literature, except in relation to certain clinical problems or as part of a larger anatomic study. Troncoso (10), in describing the anterior segment of the eyeball of man and of certain vertebrates, gives a careful description of the zonule. Minsky (11), Goldsmith (12), Kirby (13-15), and Vail (16, 17) describe the zonule as they think about the problems of cataract extraction. These are excellent studies, but, beyond these, there is need for a review, and for confirmation, of some of the major works on this structure.

REVIEW OF THE LITERATURE

Early anatomists thought of the zonule as part of the anterior face of the vitreous. Petit, in 1723 (18), by injecting air between the zonule and the vitreous, defined a space which still carries his name. He described the zonule as a folding of the anterior face of the vitreous, which passed to the anterior face of the lens. The posterior fold of the vitreous extended across the posterior face of the lens, the space between the two folds being the canal of Petit. This view of the zonule was also held by Winslow (19) and Cloquet (20). Zinn (21, 22), however, felt that it was composed of material entirely different from that of the vitreous; he appreciated its fibrillar character and its toughness. He described it as a separate membrane passing from the region of the ora serrata to the anterior surface of the lens. The face of the vitreous then formed a sheet lying posteriorly, which passed to the posterior surface of the lens. This view remained essentially unchanged into the middle of the nineteenth century, and is reflected in the writings of Cobbold (23), Kölliker (24), Hannover (25, 26), and Müller (27, 28). Although Müller did not change this general concept, he did point out that the epithelium of the pars ciliaris retinae was different from that of the retina proper, that it was much thinner, and that it might represent rods and cones, Müller cells of the retina, ganglion cells, or merely undifferentiated cells. He noted that the zonule was intimately adherent to this epithelium near the ora serrata, was fused to the internal limiting membrane, and might be classed among the glass lamellae of the eye. Hannover (26), by injecting air, found a space about the equator of the lens. He thought this lay between the vitreous and the zonule; but it is now known to lie between the two faces of the zonule, and is called Hannover's canal.

Our present knowledge of the zonule of Zinn may be said to have developed from the writings of Merkel (29) and Schwalbe (30), in 1870. During the next 50 years most of what we know of this structure was assembled. In recent years the introduction of the slit lamp and the possibility of physical and chemical studies have opened new avenues of research on the zonule.

The discussions which have been carried on since 1870 concern-

ing the zonule have been so extensive that chronological listing of the contributions would be confusing. However, by tracing a few problems which have appeared in the literature it will be possible to indicate most of the important communications on this subject.

THE STRUCTURE FROM WHICH THE ZONULE ARISES

The zonule has been described as arising from nearly every structure lying in its neighborhood. It is in close association with the vitreous and was considered by the early anatomists to be part of that structure (18-20, 22, 25, 31-32). More recent writers, such as Szent-Györgyi (33), DeWaele (34), Dejean (35, 36), and Kölliker (37) have thought of the zonule as a condensation at the anterior face of the vitreous. Duke-Elder (38) and Lauber (9) have pointed out many similarities between the substance of the zonule and that of the vitreous. Retzius (39) and Hocquard and Masson (40) agreed that the zonule may have the same origin as the vitreous, although it may be of slightly different composition. Kölliker (37, 41) thought that both the vitreous and the zonule were formed as extensions from the unpigmented cells of the ciliary body. Berger (42) and Rabl (43, 44) described the zonule as a condensation in the vascular part of the primary vitreous which lies about the lens. Druault (45, 46), Dejean (35, 47, 48), Baldwin (49), and Troufesco (50) believed that the zonule is mesodermal in origin and that it is related to the vascular portion of the primary vitreous.

The zonule has been considered to be formed from the retina. Haemers (51) thought that both the zonule and the vitreous are derived from the retina. Arnold (52) stated that the zonule is a membranous extension from the retina. Many other authors thought the zonule is not particularly related to the retina, but is formed, in one way or another, from the epithelium of the ciliary body. Claeys (53), Heiberg (54), Kölliker (37, 41), Addario (55, 56), and Schoen (57, 58) saw the zonule as protoplasmic extensions from the nonpigmented epithelial cells. According to Claeys (53), Terrien (59, 60), and Schwalbe (61), these extensions are equivalent to Müller's fibers of the retina. Carlini (62), Agababow (63), and Sbordone (64) suggested that they may be glial fibers. But Hannover (65) had previously pointed out that the

ciliary epithelium cannot be considered to be equivalent to any particular type of cell in the retina.

A great many authors have stated that the zonule may form as an extracellular substance from the ciliary epithelium (66). Damianoff (67) and Truc and Vialleton (68) suggested that it is a secretion. Magitot and Mawas (69), Mawas (70-73), and Pignède (74) described it as exoplasmic substance which also forms the internal limiting membrane of the ciliary body. Carrère (75) indicated that Mawas meant a glass membrane. Bach (76) suggested a cement substance binds the zonular fibers to the ciliary epithelium. Czermak (77), Hess (78), Salzmann (79), Müller (27), and Angelucci (80) looked upon it as a substance akin to the glass membranes of the eye or as an extension from the internal limiting membrane of the ciliary body.

Lenhossék (81, 82) suggested a mixed origin, the part near the ciliary body coming from the epithelial cells, the midpart being mesodermal from the vascular part of the primary vitreous, and the part near the lens being from the cells of the lens. Brailey (83) and Circincione (84) thought that there is a double origin, mesodermal and epithelial.

Opinion today is in favor of the zonule being ectodermal in origin (Mann, 85, 86; Vail and Mertz, 87). The lens capsule appears before the zonule can be seen; therefore, the zonule must arise from the ciliary epithelium (69).

IS THE ZONULE A MEMBRANE OR IS IT MADE UP OF FIBERS?

Schwalbe (61) and Merkel (88) described the zonule as made up of fibers, and this view has been agreed upon by many (42, 56, 62, 77, 79, 89-95). Schoen (96, 97), who conceived of each fiber as an extension from a cell of the unpigmented epithelium, saw the zonule as fibers with an occasional bit of cement substance between. Ulrich (98), Dessauer (99), and Henderson (100) thought of the zonule as a membrane. The method that an investigator used in examining this structure greatly affected his understanding of its architecture. Using the slit lamp, Egger (94), Kahmann (101), and Duverger and Velter (102) noted that the zonule appears as fibers. Troncoso (10), Beauvieux (103), Dejean (36, 47), Goldsmith (12), and Moreno (7) agreed upon this general appearance,

but after dissecting the zonule under the microscope they felt that it is really formed of fibers with an intermediary substance. Loddoni (6) and Duke-Elder (104) indicated that there is not sufficient interfibrillar substance to stop fluid. Schwalbe (105), Ulrich (98), Mawas (70), and Wolfrum (128) saw the zonule in microscopic sections as formed of fibers and intermediary substance. Most of the authors who studied sections, such as Berger (42), saw the zonule as fibers, although by this method of examination the interfibrillar cement substance may well have been precipitated (106).

If the zonule is membrane, it should block any passage between the posterior chamber and the face of the vitreous. When air is injected it stays in the canal of Petit (18, 12, 10) or in Hannover's canal (26). However, air will not pass through small openings, and leakage across this membrane must be tested with solutions of dyes. Schwalbe (30) and Merkel (29) were greatly influenced in their opinion that the zonule was composed of fibers by their observation that solutions of dyes could cross the zonule. Subsequently Angelucci (80, 107), Czermak (108), Berger (42), and Pagenstecher (109) have all found that dyes pass through. Aeby (110), with air and dyes, and Goldsmith (12), with air, dyes, and barium, could find no passage. Comberg (111) noted movement of blood through the zonule after intraocular hemorrhage, and MacMillan (112) observed that inflammatory cells during uveitis were not stopped at the zonule. Loddoni (6) has summed up the findings in the literature by saying that there is not enough interfibrillary substance to stop fluid from crossing the zonular membrane.

OF WHAT IS THE ZONULE COMPOSED?

Much has been learned of the composition of the zonule by analyzing its staining properties. While it does stain with Weigert's neuroglial stain (63) and aniline blue (103), most authors have been struck by its resistance to acids and to alkalis and its refusal to accept stains (8, 28, 62, 70, 71, 73, 74, 78-80, 113, 114). Because of these characteristics the nature of its substance has been in question. Schulze (115), Angelucci (80), and Haensell (116) suggested that it is hyalin, and Carlini (62) felt that it is elastic or glial; Schwalbe (117), Agababow (63), and Lauber (8) considered

that it might be elastic; Dejean (118, 48) and Wolfrum (113) saw it as collagen; and Müller (27), Salzmann (79), Carrère (75), and Hess (78) saw it as a glass membrane. Recently, Wislocki (119) has greatly clarified the situation. He has pointed out that the zonule stains like a basement membrane, and that in its staining characteristics it is comparable to Reissner's membrane in the third ventricle and the tectorial membrane of the inner ear (120). He noted that the zonule stains deeply with periodic acid-Schiff reagents (121-123) and with the chrome alum hematoxylin component of Gomori's stain (124). He considered that it is a mucopolysaccharide secreted by the ciliary epithelium.

The details of the structure of the zonule and some of its physical and chemical properties are of interest. It is generally agreed that the fibers are formed of fibrils (8, 79). The fibers tend to have flat sides and squared edges. They may be considered either squared or triangular in outline (12, 16, 79, 108). The fibers vary in size; the larger are about 35 microns in diameter (79). Berger (125) noted that they are refractile. Lauber (8) observed that they are birefringent, and therefore different from collagen. This optical property must reflect a regular orientation of the molecules in the fibers. Pflugk (126) and Lauber (9) noted that they are extremely elastic, much more elastic than is the lens capsule. This may account for the fact that the lens capsule rolls outwards when it is broken.

THE DETAILS OF THE ORIGIN OF THE ZONULE IN THE CILIARY EPITHELIUM

The early anatomists (18, 19, 20), who considered the zonule to be part of the vitreous, saw no need for the zonule to take origin from any other structures. As its distinct composition was realized other possible origins were considered.

The details of the origin of the zonule in the ciliary epithelium have been discussed extensively in the literature. The view that the fibers attach to the internal limiting membrane of the ciliary epithelium has been expressed repeatedly (29, 62, 63, 92, 98, 99, 127). Since the time of Müller (27) many have considered that the zonule and the internal limiting membrane of the ciliary epithelium are glass membranes, and part of a single system (77, 79,

93, 114, 117). Schwalbe (117) noted that on the ciliary processes, and Wolfrum (128) noted that near the ora serrata, where the zonular fibers do not attach, there is no internal limiting membrane.

The depth to which the zonule penetrates among the epithelial cells has not been settled. Many workers have traced fibers from the zonule, or from the internal limiting membrane, to between the unpigmented epithelial cells (49, 53, 63, 67, 77, 128, 82, 98, 83). Wolfrum (128), Pignède (74), and Mawas (70) could trace them to the membrane deep to the unpigmented cells. Terrien (59) saw the fibers between the pigmented epithelial cells. Berger (130) and Redslob (131) could trace the fibers from the internal limiting membrane to the connective tissue beneath the pigmented epithelium; and Troufesco (50) and Metzner (132) found attachments of the zonular fibers to the ciliary muscle. The different authors' views on the nature of the zonule account for some of the variation in opinion concerning how deeply the fibers attach. The men who believed the zonular fibers are an extension of the protoplasm of the unpigmented epithelial cells could not see deep attachments (57, 133); those to whom the zonule was a glass membrane could see fibers between epithelial cells (27, 77, 93, 117); those who saw the zonule as fibers from Müller's cells could trace extensions into the pigmented epithelium (53, 59).

Lange (134) and Schultze (114) noted that the epithelial cells in the pars plana ciliaris slope toward the lens along the direction of the zonular fibrils, whereas the cells in the region of the valleys were cuboidal and not sloping.

THE ORIGIN OF THE ZONULE AT THE ORA SERRATA

The early anatomists (18, 19) thought that the vitreous attaches to the pigmented part of the eye at the ora serrata, and that the zonule comes off as a separate fold. That the vitreous, the retina, and the zonule are fused in the region of the ora serrata was noted by Iwanoff and Arnold (31), Schwalbe (105), and Merkel (129). Agababow (63), Kahmann (101), Druault (135), Mawas (70), and Merkel and Orr (136) wrote that the zonule is attached right up to the ora serrata. Schultze (114), Hocquard and Masson (40), Iwanoff and Arnold (31), and Merkel (129) stated that the zonule

pulls upon the retina. Lauber (9) noted that at certain places the zonule attaches to the retina at the ora serrata, whereas at other places it is distant from the retina. Retzius (39) described supratraction of the retina resulting from the pull of the zonule. Schoen (97), Berger (42, 125, 137), Dessauer (99), and Alexander (138) observed that the zonule attaches to the retina at the spikes of the retinal tissue and believed that these points of attachment result in the formation of the spikes. Schoen (97), Retzius (39), Berger (42), and Dessauer (99) found that in children the ora serrata is ill defined but that with age the zonule draws on the retina and causes the spikes. But Schultze (139) and Keibel (140) pointed out that the spikes of the ora serrata are closely related to the development of the ciliary processes and are present in the fetus.

Many authors have stated that the final fibers of the zonule fall 1 mm. to 1½ mm. short of the ora serrata (31, 53, 55, 56, 59, 79, 92, 94, 99, 141). Kölliker (37), Dessauer (99), and Addario (55, 56) thought that the last 1½ mm. is the area of attachment of the vitreous, and Wolfrum (128) saw no internal limiting membrane in this region. The attachment of the zonule to the vitreous as well as to the ciliary epithelium in the region of the ora serrata has been noted by many writers (28, 31, 34, 40, 42, 79, 98, 108, 127, 101, 142). Dessauer (99), Claeys (53), and Topolanski (92) could see no attachment to the vitreous, but merely to ciliary epithelium.

THE COURSE OF THE ZONULE AND ITS RELATION TO THE CILIARY PROCESSES

One of the long-debated problems concerning the zonule is its relation to the ciliary processes. This is intimately connected with the problem of whether the zonular fibers are actually attached to the ciliary processes. If the zonular fibers are attached to the processes, then the processes themselves are merely one part of the large area of attachment. If the zonular fibers bypass the ciliary processes, then the processes must lie in clefts in the total zonule. Presumably the processes can move in these clefts and can secrete fluid into these clefts.

Müller (27), Pignède (74), Redslob (131), Merkel (129), Retzius (39), and Angelucci (107) all considered the zonule to be attached to the ciliary processes. Schultze (114) realized that if the zonular

fibers did attach to the processes the processes themselves would need to be supported, and such supporting fibers he found running from the region of the ora serrata to the posterior surfaces of the processes. Magitot and Mawas (69) and Mawas (70-73), Egger (94), Loddoni (6), Wolfrum (128), and Lauber (9) all noted zonular fibers attaching to the processes, but felt that these are relatively unimportant. Wolfrum (128) and Vail (16) saw the zonular fibers attaching to the sides only. Schwalbe (117) could find no fibers attaching to the ciliary processes and noted that there is no internal limiting membrane in this region. Many other authors have felt that the ciliary processes are essentially free and that the zonular fibers merely pass by (9, 42, 44, 49, 53, 62, 63, 143). Pütter (144) described two types of ciliary processes: one which has a suspensory function, and another which regulates intraocular pressure. MacDonald (145) noted, in the rabbit, two types of processes: one with a clear, gelatinous stroma, the other with a dense, fibrous stroma. Kahmann (101) and Walls (146) pointed out that in certain animals, such as the cat, there are two types of ciliary processes, small and large. The zonular fibers attach to the small ones but pass by the large ones. In man he felt that the ciliary processes are essentially free.

If the ciliary processes lie free it should be possible to find clefts in the zonule between the ciliary processes and the lens. Such clefts have been described by many authors (9, 44, 60, 61, 92, 114, 128, 143, 147, 148). They were described as triangular, with the base toward the ciliary processes and the apex toward the lens. The fibers bounding the clefts meet to form columns of insertion passing sagittally around the equator of the lens. Ulrich (98) observed clefts which opened when eserine was used. No clefts were seen by Troncoso (10).

It is widely agreed that the zonular fibers attach to the ciliary epithelium in the valleys between the ciliary processes, to at least the *sims* (149) of the ciliary body. Garnier (93), Gallenga (150), and Druault (135) have described zonular fibers attaching at the back of the iris. Loddoni (6), Schoen (97), Merkel and Orr (136), and Lauber (9) confirmed this attachment and indicated that it is rare in adults, but common in children.

One of the longest and most widely debated controversies in the

literature has been over the question of whether the zonule forms a cross. The classical description is that of Retzius (39). The fibers from the anterior lens capsule pass backward through the valleys between the ciliary processes toward the ora serrata. The fibers from the posterior lens capsule fan out from this insertion toward an origin all across the ciliary valleys. The result is a cross. This crossing of fibers has been repeatedly observed (10, 40, 42, 62, 77, 91, 103, 114, 131, 101, 142, 151, 68). Kahmann (101) and Schultze (114), who saw the crossing, felt that it took place in different planes, so that the fibers passing from the posterior capsule into the ciliary valleys were not in direct apposition with the fibers passing backward towards the ora serrata. Brailey (83), Egger (94), and Schwalbe (117) could see an occasional crossing, but considered it unimportant. Interestingly enough, Topolanski (92), Angelucci (107), Wolfrum (128), and Claeys (53) could not see a crossing.

The anterior face of the zonule has been considered to be concave forward, and the posterior face to be concave backward (6, 57, 101, 152). Stilling (153), Schoen (154), and Henderson (100) made this an important basis for their theories of accommodation.

The literature leaves no doubt that the zonular fibers break into fibrils approximately ½ mm. before they touch the lens capsule (6, 9, 60, 79, 114, 117, 131).

THE INSERTION OF THE ZONULE ON THE LENS

Brücke (155), Brailey (83), Schulze (115), Merkel (29), and Schwalbe (30) described fibers from the zonule fixing to both the anterior and the posterior faces of the lens. Since their time this observation has been amply confirmed (39, 77, 92, 94, 98, 127, 156). Wolfrum (128), Terrien (157), Aguilar (158), and Troncoso (10) have carefully described an anterior and a posterior line of insertion about the lens. The anterior line of insertion is farther from the equator than is the posterior line. Hasner (159) saw the zonule inserting at the equator of the lens, along sagittal lines. Hess (78) noted that only in an occasional section can fibers be seen in the equatorial region. Schultze (114) and Schwalbe (117) described those fibers which insert at the equator as passing in sagittal lines

to join the anterior and posterior lines of insertion. Terrien (160) noted that the fibers forming the sagittal lines of insertion on the lens come out of the valleys between the processes. Lauber (9), Rabl (44), Wolfrum (128), and Walls (146) described fibers passing from either side of the ciliary processes to form lines of insertion which run sagittally about the equator of the lens. These lines of insertion, which therefore correspond to the processes, also correspond to the bumps, or the crenations, about the lens (6, 44, 92).

In addition to the crenations at the border of the lens, tent-like figures were noticed in the lens capsule by Rabl (44), Wolfrum (128), and Topolanski (161). These obviously result from the tug of the zonular fibers and are probably artefacts.

The zonular lamella, with the zonular fibers inserting into it, was first described by Berger (130). This observation has been amply confirmed (9, 39, 60, 82, 127). Garnier (93) and Cattaneo (162) felt that the zonular lamella was part of the zonular system. Busacca (163, 164), with silver impregnation methods, beautifully demonstrated the zonular lamella. He observed that it is a thin layer lying on the surface of the cuticular portion of the lens capsule. In the equatorial region fine fibrils from the zonular lamella enter the cuticular portion of the capsule. Wislocki (119) noted that the zonular lamella stains deeply with Gomori's stain (124) and with periodic acid-Schiff reagents (121, 123) and, in fact, has the same staining qualities as does the zonule proper. He observed that it stains metachromatically with toluidine blue and that it is probably composed of acid mucopolysaccharide. It is interesting that, in 1890, Anderson Stuart (165) suggested that a cement substance binds the zonule to the lens. The cement substance must be between the zonular lamella and the cuticular portion of the lens capsule. Rupture between these layers has been repeatedly observed (14, 17, 166-174). In each case the border of the lens at the site of rupture was found to be clean, indicating that the break must have occurred between the zonular lamella and the cuticular portion of the lens capsule. Elschnig (175) and Vogt (176) introduced the subject of exfoliation of the lens capsule, which is undoubtedly exfoliation of the zonular lamella.

DOES A CANAL OF PETIT EXIST?

When the fallacy in Petit's early views was realized the presence of the canal of Petit had to be reassessed. There were several reasons for thinking that a canal of Petit does not exist. First, those who thought the zonule is formed from the vitreous considered the zonule as merely part of the anterior face of the vitreous and, therefore, no canal of Petit is present (88, 107, 177). Secondly, those who felt that the zonule is made up of fibers saw no need for a canal of Petit (55, 56, 62, 77, 79, 88, 91, 92, 94). Virchow (106) summed up this view by stating that, if the zonule is indeed fibers, there is a volume between the posterior surface of the iris and the face of the vitreous which can be divided into a prezonular, a zonular, and a postzonular space. The posterior chamber and the canal of Petit do not need to be described as separate. Other authors felt that the canal of Petit is not present because in the living eye the face of the vitreous does lie against the zonule; only following shrinkage after death, or with injection of air or solutions, can a canal of Petit be formed (31, 45, 46, 93, 103, 108, 110, 178, 107, 118, 179). Topolanski (92), Kolmer (180) (in the chimpanzee), Salzmann (79), and Troncoso (10) have agreed that the space is potential and have also noted that the vitreous extends to clothe the valleys between the ciliary processes. Berger (42) stated that not only can a canal be produced by the injection of air, but it is present in old age and after death as a result of anterior retraction of the vitreous and of exudate or hemorrhage in the area. Other authors could see a real space between the zonule and the face of the vitreous—a space which they did not believe to be an artefact (6, 34, 96, 98, 99, 109, 83, 181). Schwalbe (117) and De-Waele (34) felt that no canal of Petit is present in children, although it is present in adults. A. Trantas (182) and N. Trantas (183, 184), Berliner (185), Werner (186), and Mawas (187) could see a space between the zonule and the face of the vitreous in the living eye.

If the zonule is made up of fibers, Hannover's canal between the anterior and posterior zonule fibers can hardly be considered to exist. However, free space at such a location in the zonular system has been described (6, 12, 98, 103, 110, 130, 101, 151, 102).

METHODS

All the eyes that were examined were human. The material came from several sources. Sixty-three eyes were obtained at autopsy, being taken from two to eight hours after death. These eyes were all normal, that is, death was from a cause not related to the eyes and the eyes were known from the hospital records to be essentially normal. Eighteen eyes obtained at operation were used. These eyes were removed because of pathologic changes which had left the zonular apparatus intact. Finally, material was taken from thirty old blocks of eyes which had been stored following previous sectioning. These eyes also had intact zonules and lenses.

The greater part of the study was devoted to the *examination of whole specimens.* Exploratory search was made for the best method of preparing the material and examining the zonule. Specimens were examined after they had been dried, after suspension in saline, in 70 percent alcohol, in 5 and in 10 percent formalin, in glacial acetic acid, and after various stains had been applied. Finally, five methods of preparing specimens were found useful. Practically all the observations on gross material were made on specimens prepared in these ways.

1. Fresh eyes were immersed in normal saline, a window was cut in the globe, and the zonule was examined. Most of the eyes were examined in the fresh state and were then placed in fixative.

2. After the original examination in saline, the eyes were immersed in 70 percent alcohol, which was changed three times in the first three days. The eyes so prepared did not decompose and the zonular fibers were slightly easier to see than when the eyes were suspended in saline. The alcohol changed the appearance; the ciliary processes became smaller, the lens became opaque and white, and small, tent-like points of traction appeared where the zonule inserted on the lens. The zonular fibers looked the same; the interfibrillar substance could not be seen in the fresh or in the fixed preparations.

3. Gross specimens were stained with periodic acid (Appendix A).

4. Gross specimens were cleared in benzyl benzoate and oil of

wintergreen (Smith, 188). Some of these specimens were depigmented with hydrogen peroxide, some were left with the pigment intact (Appendix A). Some of the specimens which were stained with periodic acid were cleared in oil of wintergreen and benzyl benzoate (Appendix A).

5. Celloidin blocks, of eyes that had formerly been sectioned, were trimmed and cleared in oil of wintergreen (Appendix A).

Cutting a window to view the zonule was done in several ways. Finally, two principal methods were used in preparing specimens.

1. A coronal cut was made in the fresh eye, right through the eyeball, about 10 mm. behind the limbus. The anterior half of the globe was mounted in a bottle with a flat wall, the cut surface pressed against the side of the bottle. The posterior aspect of the zonule could then be viewed through the side of the bottle. If a view of the anterior aspect of the zonule was desired a small incision was made at the limbus, with a Graefe knife, and the cornea was cut away with scissors. The iris was torn away, using fine forceps. The full anterior face of the lens, the anterior surface of the ciliary processes, and the torn base of the iris were then visible. If the eyeball was not to be viewed when fresh, a small opening was made in the sclera, the globe was placed in 70 percent alcohol, and was later prepared for viewing.

2. The specimens that were cleared in benzyl benzoate were examined both intact (the clearing allowing a view into the interior of the eye), and after windows had been cut into the globe. When benzyl benzoate was used on celloidin blocks, the celloidin did not dissolve. The blocks were trimmed to present the zonule to good advantage.

Several other methods of viewing the specimens were tried. If the eye is viewed from above, through the surface of a fluid, using a dissecting microscope, the study is not satisfactory. The surface moves with each tremor of the laboratory and the details are difficult to explore. By far the best method of viewing is through the flat wall of a bottle, using the slit lamp. The flat wall is stable, the specimen can be firmly pressed against it, the position for viewing is comfortable, and the slit of the slit lamp is as useful as the magnification of the microscope in making apparent the structures (Troncoso, 10).

For the *sectioning of the specimens* three methods of fixation were used; with 5 percent formalin, with 70 percent alcohol, and with Carnoy's solution (Appendix B). The formalin was a valuable general fixative, and the alcohol was used if the specimen had already been viewed as a whole preparation. The Carnoy's fixative was valuable when studying the intercellular tissue. It was used particularly with the toluidine blue and the periodic acid stains.

Sections of the specimens were cut in coronal, sagittal, and oblique planes. They were stained with hematoxylin and eosin, iron hematoxylin (Van Gieson's), Masson's trichrome, toluidine blue, periodic acid, and Gomori's chromic hematoxylin (ponceau method). The periodic acid stain of Hotchkiss (121) was the most valuable (Appendix B). It stains the zonular fibers and the lens capsule blue and leaves the surrounding structures unstained. A counterstain then sharply differentiates the fibers. Metanil yellow gives the most striking contrast. Gomori's chromic hematoxylin, ponceau method, was useful (Appendix B). It stains the zonule and zonular lamella blue. Unfortunately it stains the surrounding connective tissue deeply and is therefore mainly valuable where the zonule lies free.

In selected areas attempts were made to cut serial sections. This was not found particularly helpful. Zonular fibers are seen, often, as minute points in space. They are not always near structures which can be used as landmarks. Attempts to trace individual fibers by serial sections were therefore confusing. In certain selected areas, such as at the spikes of the ora serrata, a succession of sections was cut and was found helpful.

Some of the specimens were studied while teasing the zonular fibers with a small pick. Injection of air, and ink, into the zonule and the region of the zonule was also tried. These examinations were interesting and they revealed points which could not be seen in the intact specimens. However, this type of examination was not easy to control, the possibility of producing artefacts was great, and the results could only be interpreted with caution. Goldsmith (12) has thoroughly described such dissections, and I cannot add anything. Therefore they are left out of this work.

The final source of material was clinical cases. Twenty-one eyes were seen on which an iridectomy had been done, two in which an

iridodialysis had occurred, three in which there was a partial dislocation of the lens, and four which had aniridia. Also many normal eyes were examined, searching for the zonule. This material was considered subsidiary to the main study and was principally used as a control, or as a check for artefacts in the prepared specimens.

RESULTS

Many of the controversies on the anatomy of the zonule have been reviewed. The observations in this study are presented in the form of a description of each region in which the zonule lies. Although the stand that is taken on each point in controversy is obvious, the reasons for each opinion are not always easy to present. They can be seen in the descriptions, in the figures, and to some extent in the discussion. Finally, it must be remembered that the arrangement of the structures is not regular, or geometric, and that the descriptions aim at the general design of the tissues.

THE ORIGIN OF THE ZONULE IN THE REGION OF THE ORA SERRATA

Before describing the terminations of the zonule at the ora serrata it is necessary to outline the architecture of the ora itself, particularly as it relates to the pars ciliaris retinae. The anterior boundary of the retina is raised above the neighboring pars plana ciliaris (Fig. 1). When the beam of a slit lamp is brought in from the posterior aspect, like a cliff this boundary casts a shadow on the pars plana ciliaris. The retina is gray, containing a number of dark cystic areas, and is in sharp contrast with the dark-brown color of the pars plana ciliaris. The anterior border of the retina is a series of bays, separated by spikes which point toward the lens. The boundary is sharpest, or the cliff is most precipitous, in the region of the spikes, and it is least marked in the region of the bays. Each spike of retina points along a fine, dark, pigmented band which, in turn, can be followed to a valley between two ciliary processes. This pigmented band has a rough inner surface in comparison with the smooth surface of the rest of the pars plana ciliaris. As the band is traced forward, the roughness increases to become the plicae ciliares between the ciliary processes. Most specimens display this arrangement; each bay of the ora serrata corresponds to a

ciliary process, each spike corresponds to a valley between processes. A few specimens do not show such regularity (Fig. 2). A bay may span two ciliary processes and an intervening valley, or the plicae ciliares may be almost as large as the ciliary processes themselves, so that the pattern is broken.

In the gross specimens the zonular fibers lying across the pars

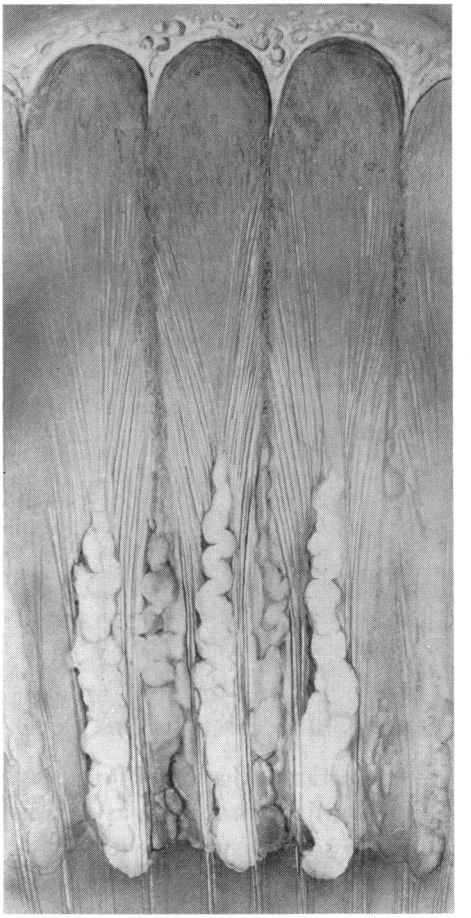

FIGURE 1. GROSS SPECIMEN VIEWED FROM BEHIND TO SHOW THE ZONULE IN RELATION TO THE CILIARY PROCESSES AND THE ORA SERRATA

This shows an extremely regular arrangement. Each spike of the ora serrata lies opposite a plica ciliaris. The zonule lies along each side of each ciliary process, and diverges as a fan towards the spikes and their anterior extensions. (Periodic acid stain.)

plana ciliaris look like a mat. Although fibers pass backwards from the whole width of each bay between two ciliary processes, they are particularly concentrated at the sides of the posterior ends of the processes. From this location the fibers diverge in the shape of a fan, arching across the pars plana ciliaris in broad sweeps toward

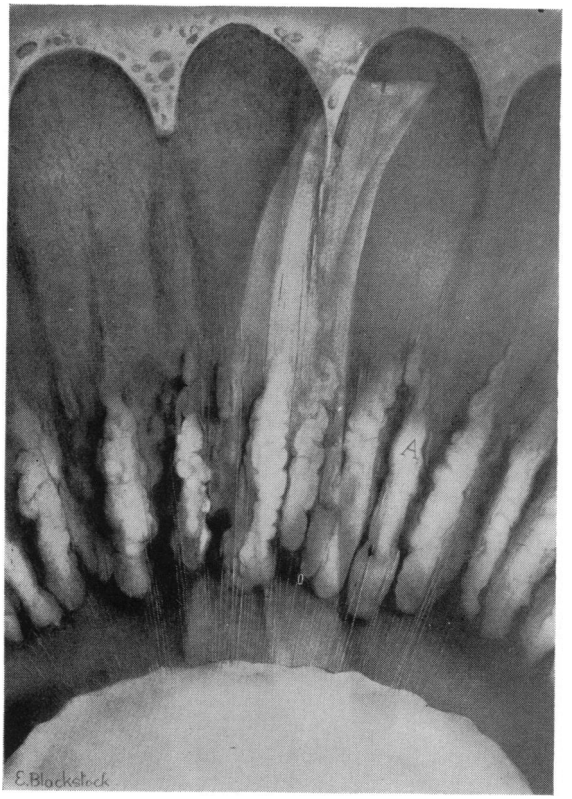

FIGURE 2. GROSS, FRESH SPECIMEN TO SHOW THE WHOLE REGION OF THE ZONULE FROM BEHIND
The light outlines the face of the vitreous, passing from the posterior surface of the lens to the ora serrata. The ora serrata appears raised. The spikes of the ora have a very irregular relation to the ciliary processes. The processes protrude posterior to the zonule, through clefts among the fibers, A. The crenations on the lens, lying approximately opposite the process, are apparent.

the spikes of the ora serrata (Fig. 1). The fibers from all across the valleys between the ciliary processes, as well as the fibers lying at the sides of the processes, all sweep, with gentle curves, toward the spikes of the ora serrata. As each spike corresponds to a plica ciliaris, the fibers from the region of the plica ciliaris, the fibers from the floor of the valley, and the fibers from the adjacent sides of the neighboring ciliary processes all arch towards one spike. The striated sheen of zonular fibers on the pars plana ciliaris can be traced right to the spikes.

The bays of the ora serrata correspond to the ciliary processes. At the posterior end of each ciliary process the thick mass of fibers lying at either side sweeps away from the process, and away from the corresponding bay of the ora serrata, towards a spike. As a result, fibers can only be traced to within about 1½ mm. of the ora serrata at the bays; the ciliary epithelium in the depth of each bay is bare of zonular fibers.

Sections through this region confirm and add to the observations which were made on the gross specimens. The increased thickness of the retina, as compared with the ciliary epithelium, and the sudden termination of the retina, forming a sharp edge at the ora serrata, are immediately apparent. In most sections the zonular fibers can only be traced to within 1½ mm. of the retina. However, in an occasional section the terminal fibers pass right to the retina. In a group of sections cut serially, and in the anterior–posterior plane, it is possible to trace the terminations of the zonular fibers from a point where they are 1½ mm. from the retina to a point where they draw directly on the retina. The majority of sections, in which the zonular fibers do not reach the retina,

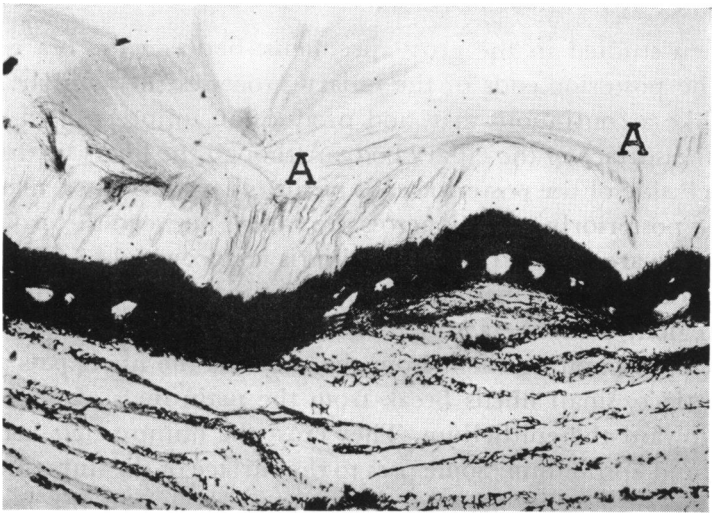

FIGURE 3. A CORONAL SECTION ACROSS THE PARS PLANA CILIARIS JUST ANTERIOR TO THE SPIKES OF THE ORA SERRATA

The zonular fibers are in groups, A A, with clear spaces between. The vitreous is intimately associated with each group of fibers. (Gomori's stain, x 40.)

corresponds to the bays of the ora serrata. The occasional section, in which the zonular fibers extend to the retina, corresponds to a spike of the ora serrata.

In the region of a bay of the ora serrata the zonular fibers terminate in two structures. As these fibers come to their posterior ends they break into minute fibrils. Many of the fibrils turn towards the ciliary epithelium and insert between the epithelial cells. Other fibrils show no tendency to turn towards the epithelium, but extend into the adjacent vitreous. The point where an individual zonular fibril ends in the vitreous cannot be defined. If staining with periodic acid is taken as the criterion of a zonular fibril, then the fibrils end far short of the ora serrata. If lines of traction through the vitreous are considered part of the zonular system, then the zonular fibrils extend to the retina.

Coronal sections just anterior to the spikes of the ora serrata show clusters of zonular fibers separated by clear areas (A A, Fig. 3). This arrangement occurs because the fibers are forming into groups as they converge on the spikes of the ora serrata.

THE ORIGIN OF THE ZONULE IN THE REGION OF THE PARS PLANA CILIARIS

When studied in the gross specimens, between the ora serrata and the posterior ends of the ciliary processes the zonular fibers look like a continuous mat, and produce an uninterrupted sheen over the surface of the ciliary body. Although the fibers lie thickest on each side of the posterior ends of the ciliary processes, they also extend posteriorly from all across the valleys between the processes, so that no area of the pars plana ciliaris is uncovered by fibers.

Sections show the manner in which the zonule takes origin across this region. The fibers run parallel to the ciliary epithelium, a thin cleft separating them from the cells. As the fibers pass across the surface, small fibrils break from the main mass of fibers and turn toward the epithelium. They cross the minute cleft between fibers and epithelium. Some pass to the surface of the unpigmented cells, others extend between the cells to be lost in the layer of pigmented cells (Fig. 4). The inner surface of the unpigmented cells is clothed by a limiting membrane which stains with the Hotchkiss stain, and with Gomori's stain, exactly as does zonule. It

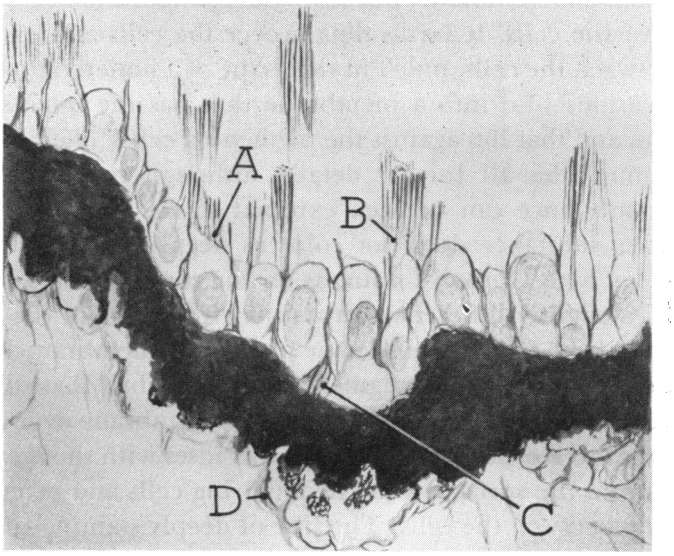

FIGURE 4. A SECTION THROUGH THE PARS PLANA CILIARIS SLIGHTLY POSTERIOR TO THE CILIARY PROCESSES

The zonular fibers, B, are sending fibrils to the ciliary epithelium. Fibrils touch at the surface of the unpigmented cells, A, and also pass between the cells. Traces of a blue staining cement substance are visible deep to the unpigmented epithelium, C. Deep to the pigmented epithelium a blue staining membrane has retracted from the pigmented cells, D. (Periodic acid stain, counterstained with hematoxylin, x 230.)

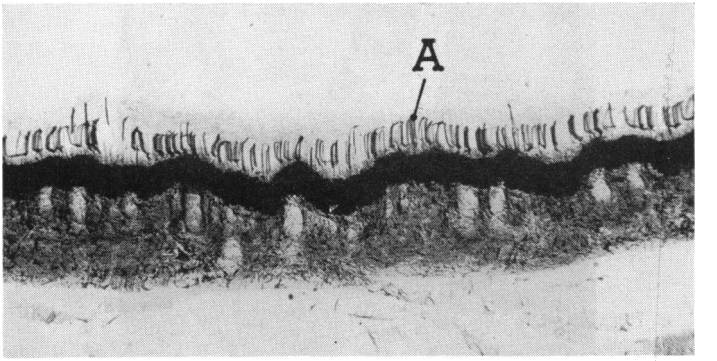

FIGURE 5. A CORONAL SECTION ACROSS THE PARS PLANA CILIARIS ABOUT HALF WAY BETWEEN THE ORA SERRATA AND THE CILIARY PROCESSES

The zonular fibers, A, are evenly distributed over the surface and are sending minute fibrils into the epithelium. (Periodic acid stain, counterstained with metanil yellow; x 34.)

is not a smooth membrane, but takes the configuration of the inner surface of the cells. It forms domes over the cells and extends as walls between the cells, much in the shape of a honeycomb. Deeply the extensions fuse into a membrane that has the same staining reactions, and that lies against the pigmented cells. The pigmented epithelium hides all further details, although traces of a blue-staining substance can be seen external to the pigmented layer. The latter substance does not color as deeply by the Hotchkiss method, or with Gomori's stain, as do the zonular fibers. It probably has a slightly different composition from that of the zonule. The fibrils from the zonule become part of the membrane limiting the inner surface of the unpigmented cells. A fibril that strikes on the surface of a cell fuses into the limiting membrane over the cell. A fiber that strikes at a cleft between cells fuses with the membrane coming from the surface of the neighboring cells and extends as a sharp line between the cells. The line of deeply staining substance between the cells is lost into a similarly staining membrane between

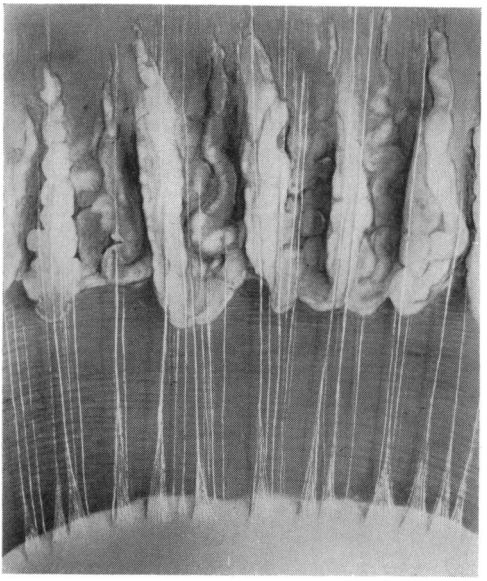

FIGURE 6. GROSS SPECIMEN VIEWED FROM BEHIND

This is from a man of sixty-eight years; a child would show many more fibers. The light is coming from the right and the fibers are illuminated against the right side of each process. The grouping of the fibers on the lens opposite the processes and the terminal fibrils at the lens can be seen. (Periodic acid stain.)

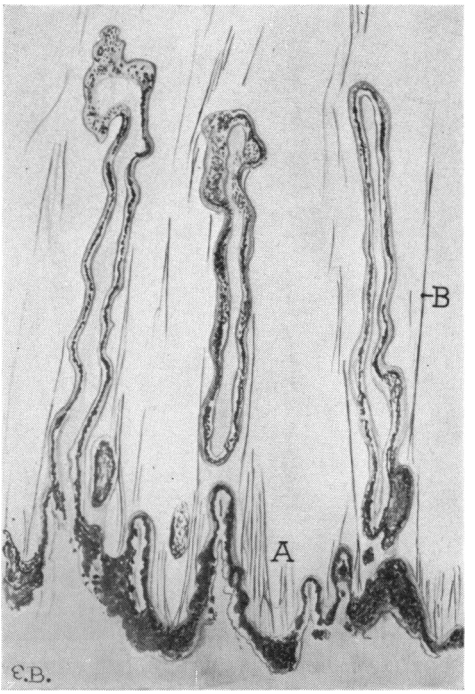

FIGURE 7. A SECTION NEAR THE POSTERIOR END OF THE CILIARY PROCESSES The zonule passes by the processes, B, and seems to support them. It attaches to the floor of the valleys and to the plicae ciliares. An interfibrillar matrix is present among the fibers in the valleys. (Periodic acid stain, counterstained with metanil yellow; approximately x 35.)

the unpigmented and pigmented epithelium. This architecture gives the impression that the pull from the zonule is transferred over the top and down the sides of the unpigmented cells, and into the deep intercellular substance.

This manner of origin of the zonule is evident across all the pars plana ciliaris (Fig. 5). The unpigmented epithelium varies in appearance. Posteriorly it is columnar, the cells sloping slightly towards the lens, or in the direction from which the zonular fibrils come. More anteriorly the cells are shorter and fatter, until near the posterior ends of the ciliary processes they are approximately cuboidal in shape. Despite this variation in the shape of the unpigmented cells, the attachments of the zonular fibrils are essentially the same across the whole region. Furthermore the origin is continuous. While the attachment at the spikes of the ora serrata is

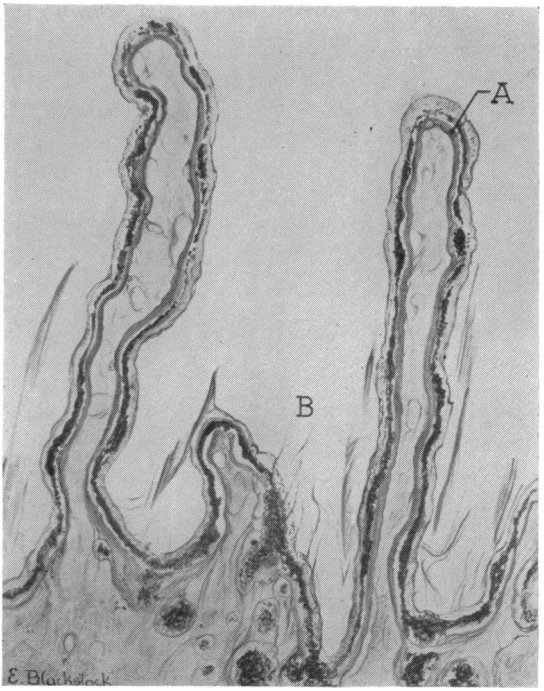

FIGURE 8. A CORONAL SECTION THROUGH THE CILIARY PROCESSES

A membrane lies deep to the epithelium of the ciliary processes, A. The zonular fibers pass by the processes and insert into the epithelium of the valleys and of the plicae ciliares. (Periodic acid stain, counterstained with metanil yellow; approximately x 65.)

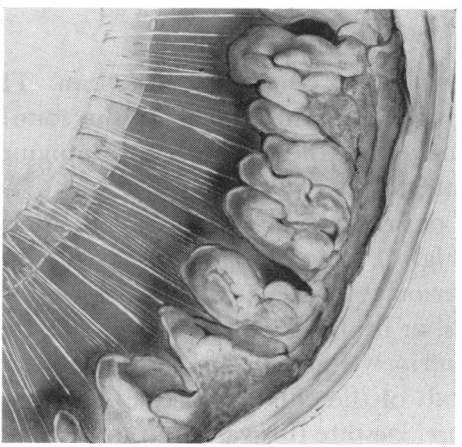

FIGURE 9. GROSS SPECIMEN OF ZONULE FROM IN FRONT

The processes are protruding well anterior to the zonule. Where the angle of view is direct the clefts among the fibers which contain the processes are visible. The small mounds on the lens are due to fixation, but they show the groups of insertions lying opposite the processes (see Figure 13). (Periodic acid stain.)

firm, the attachment across the pars plana ciliaris is extensive. The attachments of fibrils to the epithelium end at the spikes of the ora serrata, 1½ mm. from the retina in the bays of the ora serrata, and extend anteriorly into the valleys between the ciliary processes. In the anterior part of the pars plana ciliaris there are a few small processes, or plicae ciliares. The zonular fibers send fibrils to these processes. So far as the attachment of zonule is concerned, they do not appear to be differentiated from the surrounding epithelium.

THE ORIGIN OF THE ZONULE IN THE VALLEYS BETWEEN THE CILIARY PROCESSES

Gross specimens viewed from the posterior aspect are of little help in studying the origin of the zonule in the valleys between the ciliary processes. The zonular fibers that pass from the lens into the valleys between the ciliary processes lie like columns along the sides of the processes and give the appearance of supporting the processes (Fig. 6). At first glance some fibers seem to insert into the processes, but more careful study always reveals that such fibers pass onward, extending deeply into the valleys or backward toward the ora serrata. The floors of the valleys cannot be seen.

Coronal sections show the zonular fibers passing between the ciliary processes (Fig. 7). Some of the fibers extend into the depth of the valleys to attach to the epithelium of the valley floor. Those fibers that pass to insert at the floor break into many fibrils. The break may occur far up the sides of the processes, so that a wide fan of fibrils spreads across the valley, or the break may occur close to the epithelium of the floor, when only a small fan spreads to a few cells. The fibrils fuse into the internal limiting membrane and pass between the unpigmented cells to the underlying pigmented cells (B, Fig. 8). The substance that forms the membrane on the surface of the unpigmented cells, also the fibrils between and the membrane deep to them, stains the same as do the zonular fibers. This is essentially the arrangement seen across the pars plana ciliaris.

The attachment is present across the valleys and is dense at the edges of the floors of the valleys, but then it stops (Fig. 7). A short distance up the sides of the processes all attachments have ended; there only remain those fibers that are passing by the processes in their course to some distant point.

There are some small processes, or plicae ciliares, in the depth of the valleys. The zonular fibrils attach on and between the epithelial cells of these processes, in the same manner as to the rest of the epithelium of the valleys.

The anterior end of the attachment of the zonular fibers in the valleys is of interest. The ciliary processes extend anterior to the

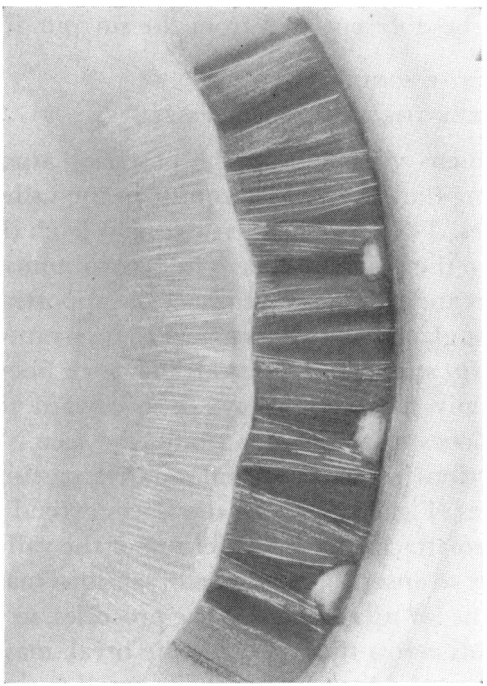

FIGURE 10. VIEW OF THE ZONULE AND CILIARY PROCESSES THROUGH A SURGICAL COLOBOMA OF THE IRIS, SEEN WITH THE SLIT LAMP AND CORNEAL MICROSCOPE

The ciliary processes protrude through gaps in the zonule. The crenations at the equator of the lens are opposite the ciliary processes. Through the lens the zonular fibers are seen passing to a posterior coronal line of insertion.

fibers of the zonule. Whole specimens viewed from in front (Fig. 9), and living eyes in which the zonule is exposed (Fig. 10), show the ciliary processes lying in clefts between the zonular fibers and protruding anterior to the most anterior fibers. Occasionally fibers will be seen lying in front of a process. Careful study always shows, however, that the cleft carrying the ciliary process is present, but is

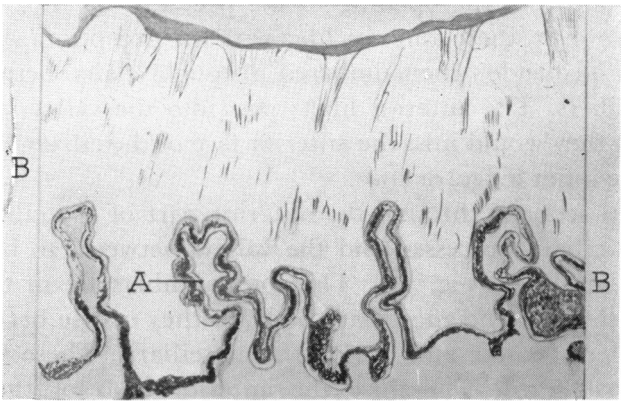

FIGURE 11. CORONAL SECTION PASSING NEAR THE POSTERIOR END OF THE POSTERIOR CHAMBER

Lines of insertion of zonule on the lens are at the top of the picture. Traces of an interfibrillary matrix can be seen near the lens. The anterior face of the zonule lies between B and B. The ciliary processes lie, unencumbered by zonule, in the posterior chamber. A basement membrane under the epithelium of the processes is apparent, A. (Periodic acid stain, counterstained with metanil yellow; approximately x 35.)

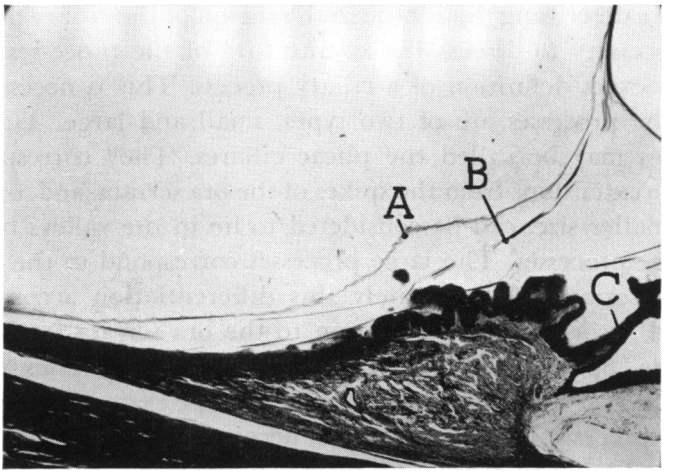

FIGURE 12. A SAGITTAL SECTION

The face of the vitreous, A, lies free, behind the zonular fibers, B. The canal of Petit ends where the vitreous and zonule touch the lens capsule, and where the vitreous and zonule come together over the pars plana ciliaris. A ciliary process, C, lies in front of the zonule, in the posterior chamber. (Periodic acid stain, counterstained with hematoxylin; x 25.)

oblique, and that the opening to the posterior chamber is at an angle. However, these anterior fibers are the exception, since most processes protrude unencumbered through clefts between the zonular fibers. The anterior fibers pass into the valleys at such a level that they would miss the anterior face of the ciliary body, and end at the inner ledge, or *sims*.

Coronal sections through the anterior part of the ciliary body show the ciliary processes, and the valleys between, to be free of the zonular fibers (Fig. 11). The zonular fibers lie in the space between the lens and the ciliary body, as they course between the anterior lens capsule and the pars plana ciliaris. These fibers are passing backward. Therefore the anterior ends of the ciliary processes and the anterior surface of the ciliary body lie free of fibers, in immediate contact with the posterior chamber. In sagittal sections the ciliary processes protrude anterior to the zonular fibers that pass from the anterior lens capsule to the ciliary body (Fig. 12). These fibers pass in such a direction that they would leave the anterior face of the ciliary body free.

THE RELATION OF THE ZONULE TO THE CILIARY PROCESSES

Before describing the zonule in the region of the ciliary processes it is necessary to discuss the architecture of the processes and to give an exact definition of a ciliary process. This is necessary because the processes are of two types, small and large. The small processes may be called the plicae ciliares. They correspond to anterior extensions from the spikes of the ora serrata, and, owing to their smaller size, can be considered to lie in the valleys between the large processes. The large processes correspond to the bays of the ora serrata. Unfortunately this differentiation according to size and according to the relation to the ora serrata is not quite adequate. Specimens vary. Some of the small processes may be nearly as large as the large ones. Some bays are extra wide, bridging several processes. Therefore it is necessary to search for other criteria which may distinguish plicae ciliares from ciliary processes proper.

There are five such criteria. First, true ciliary processes can be distinguished as those processes to which zonular fibers do not attach. By comparison, the zonular fibers do insert into the epithe-

lium of the plicae ciliares. There are four other peculiarities of true ciliary processes that depend upon, or occur with, the lack of attachment of zonular fibers. First, the internal limiting membrane that covers the inner surface of the unpigmented epithelial cells of the pars plana ciliaris, of the valleys between the ciliary processes, and of the plicae ciliares, and that has the same staining reactions as the zonular fibers, is not present over the ciliary processes. The cells of the ciliary processes show the inner cell wall and nothing more. Second, the pigmented epithelium of the ciliary body becomes unpigmented as it is traced over the ciliary processes. In the region of the unpigmented epithelium there are no attachments of zonular fibers, whereas in the areas of pigmented epithelium there are many attachments. The lack of pigmented epithelial cells in the ciliary processes seems to contraindicate the insertion of the zonular fibers. Third, in the region of the ciliary processes, deep to the two layers of the epithelial cells, is a thick membrane (A, Fig. 8). This stains by the Hotchkiss method and is clear with hematoxylin and eosin (189). This membrane lines the deep surface of the epithelium throughout the ciliary processes, thinning as it passes into the valleys between the processes. Moreover, it does not extend forward into the iris, nor does it continue backward into the pars plana ciliaris. Although one might imagine that such a thick membrane is designed to take the tug from the zonular fibers, it is in this area that the zonular fibers do not attach. The membrane must have some other purpose. Finally, the ciliary processes contain many capillaries and a loose, clear, gelatinous stroma. The stroma of the plicae ciliares carries few capillaries, and is dense and fibrous. This density would be necessary to withstand the pull of the zonular fibers. The loose stroma of the ciliary processes would withstand no pull and would be no support to the ciliary processes. The nature of the stroma in the processes is strong confirmation of the fact that no zonular fibers insert into them. The clear, gelatinous appearance suggests that the ciliary processes have a different function.

In summary, true ciliary processes, the relation of which to zonular fibers will be described, are defined as those (a) which have no attachments of zonular fibers, (b) which have no internal limiting membrane covering the first layer of epithelial cells, (c) in

which the deep layer of epithelium is unpigmented, (d) which show a distinct membrane deep to both layers of epithelium, and (e) which have a loose, gelatinous stroma. These true ciliary processes tend to be larger than the plicae ciliares and tend to correspond to the bays of the ora serrata.

In gross specimens, studied from the posterior aspect, the zonular fibers passing from the lens into the valleys between the ciliary processes form columns which lie along the sides of the processes (Fig. 6). The posterior fibers, or those near the peaks of the processes, pass toward the ora serrata; the anterior fibers disappear into the depths of the valleys. From the continuous sheet of fibers on either side of each process no fibers can be traced to an insertion in a process. Some of the fibers passing into the valleys break into fibrils before they descend out of sight, but no fibers near the processes break into fibrils or turn toward the epithelium. The tops of the processes are free, either lying in the cleft between the columns of fibers or protruding posterior to the zonule towards the vitreous. There is no suggestion that the zonular fibers form a cross as they lie against the ciliary processes. The succession of fibers down the sides of each ciliary process is dense and forms a continuous mat, but the individual fibers tend to be parallel.

When gross specimens are studied from the anterior aspect, both in the prepared specimen and in the human eye, columns of fibers, which are coming from the lens, are seen to pass along the sides of the ciliary processes behind their anterior extremities (Figs. 9, 10, 13). The processes lie in clefts among the zonular fibers, undoubtedly the same clefts that were seen from the posterior aspect. There must be a free passage through these clefts, about the ciliary processes, between the posterior chamber and the canal of Petit. From the anterior aspect there is no indication of a crossing of the zonular fibers.

When the gross specimens are cleared in oil of wintergreen and benzyl benzoate the details of the course of the zonular fibers in the valleys can be seen. The individual fibers in the columns at the sides of the ciliary processes lie parallel. They are going from the pars plana ciliaris toward the lens. Between these columns, and opposite the valleys, are fibers that take origin in the floors of the valleys and that insert on the posterior surface of the lens. The

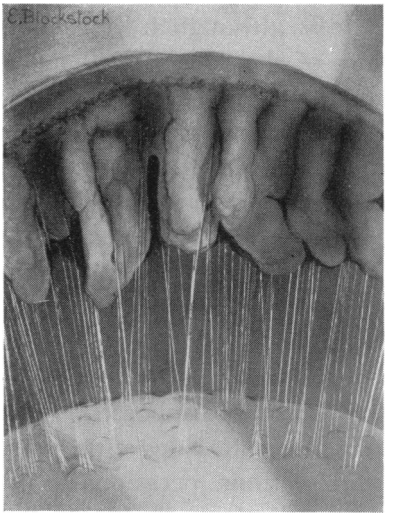

FIGURE 13. GROSS SPECIMEN OF ZONULE FROM IN FRONT
The light is coming from the right and the zonular fibers are illuminated against the right side of the processes. The processes protrude in front of the zonular fibers. Where the angle of view is correct the processes can be seen lying in clefts among the fibers. The small mounds on the lens are due to the fixation, but they show the groups of insertions lying opposite the processes. (Periodic acid stain.)

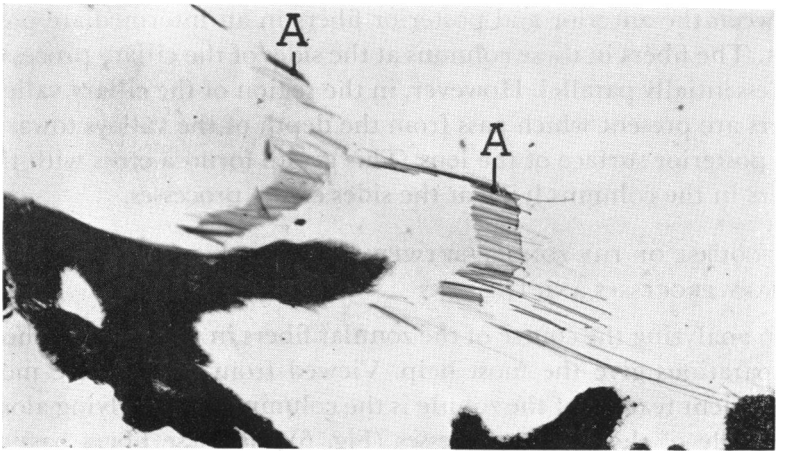

FIGURE 14. A SAGITTAL SECTION THROUGH A CILIARY PROCESS
Two columns of zonular fibers, A A, lie adjacent to a ciliary process. The cut is oblique to the direction of the zonular fibers. The ciliary process undoubtedly extended up between the columns of fibers during life. (Gomori's stain, x 60.)

groups of fibers from the valleys therefore cross the columns at the sides of the ciliary process, although at different planes. The larger group lies at the sides of the processes, the smaller group passes from the valleys.

Sections supplement the knowledge gained from the gross specimens. In coronal cut the zonular fibers pass in straight lines along the sides of the processes and seem to support them (Fig. 7). Fibrils do not turn off to insert into the processes. The clefts between the zonular fibers are open posteriorly, there is no hood of fibers, and the ciliary processes have free access to the posterior chamber. More anteriorly, coronal sections, with the zonular fibers cut as they leave the lens, show the anterior ends of the ciliary processes lying in the posterior chamber, unencumbered by the zonule (Fig. 11). The zonular fibers pass along the sides of the ciliary processes more posteriorly. In sagittal sections, occasionally, a sheet of zonular fibers that represents a wall of zonule beside a ciliary process can be found (Fig. 14). The anterior fibers in these columns can be traced from the anterior face of the lens through the depth of the valleys between the processes towards the ora serrata. The posterior fibers in the columns extend from the posterior surface of the lens, past the processes near their apices, toward the ora serrata. Intermediate fibers, which insert about the equator of the lens, lie between the anterior and posterior fibers in an intermediate position. The fibers in these columns at the sides of the ciliary processes are essentially parallel. However, in the region of the ciliary valleys fibers are present which pass from the depth of the valleys towards the posterior surface of the lens. This group forms a cross with the fibers in the columns lying at the sides of the processes.

THE COURSE OF THE ZONULE BETWEEN THE CILIARY PROCESSES AND THE LENS

In analyzing the course of the zonular fibers in this region, whole preparations give the most help. Viewed from behind, the most prominent feature of the zonule is the columns of fibers lying along each side of the ciliary processes (Fig. 6). As these fibers passing toward the lens leave the ends of the ciliary processes they form the sides of empty clefts (Fig. 1). The fibers on either side of each cleft come together to a single point of insertion on the lens, or the

two walls of each cleft fuse to form a line of insertion that passes sagittally about the equator of the lens. Therefore, the clefts that enclose ciliary processes when traced towards the lens take the form of triangular spaces, with the bases towards the ciliary processes and the apices towards the lens. Between these strong, prominent masses of fibers is a lesser number of fibers that pass from the valleys between the processes (Fig. 2). They end at the posterior line of insertion on the lens, adjacent to the fibers which support the ciliary processes but opposite the valleys between the processes. When these are traced into the depth of the valleys they quickly extend out of sight.

When the whole preparations, either prepared specimens or the living eye, are viewed from in front, the appearance is similar to that from behind (Fig. 13). The columns of fibers that enclose the ciliary processes go towards the lens. As they do so they come together to form a single sagittal line of insertion on the lens. The clefts so produced have their bases towards the ciliary processes and their apices towards the lens. Between the columns of fibers which lie beside the ciliary processes are a smaller number of fibers which pass into the valleys between the processes.

Microscopic sections do not add greatly to the findings from the whole specimens. The zonular fibers are seen as straight lines. They have a squared or a cuboidal outline when stained with hematoxylin and eosin, a finer but rectilinear outline when stained by the Hotchkiss method, and almost a rounded outline when stained with Gomori's chromic hematoxylin. Near the lens, as the fibers break into fibrils, a faint, clear substance enmeshes the fibrils and fibers. Near the ciliary processes the fibers are concentrated together and adhere to form a continuum. In coronal sections successive columns of fibers are cut across (Figs. 11, 18). The fibers in each column extend along the side of a process in one direction and to a point of insertion on the lens in the other direction. A few fibers lie between these regularly placed columns, and pass toward the ciliary valleys. Sagittal sections show a prominent posterior line of fibers that passes from the posterior surface of the lens, toward the apices of the ciliary processes, and on toward the pars plana ciliaris. This line has a gentle curve, with the concavity facing backwards (Fig. 12). A prominent anterior line of fibers

passes from the anterior surface of the lens toward the depth of the ciliary valleys. This line often has a gentle curve with the concavity facing forward. Between these two lines of fibers, in about one section in ten, a column of fibers comes from the ciliary body and passes to an insertion about the equator of the lens

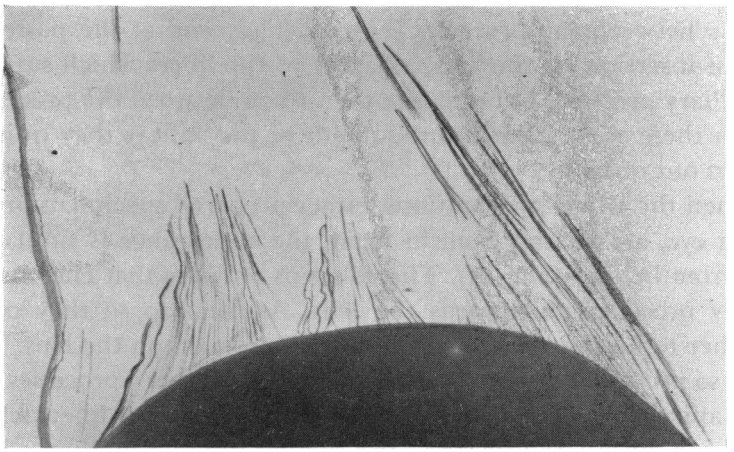

FIGURE 15. A SAGITTAL SECTION AT THE EQUATOR OF THE LENS
The face of the vitreous lies at the left. The zonular fibers break into fibrils close to the lens. The fibrils form an almost continuous line of insertion across the equator of the lens. (Masson's trichrome stain, x 91.)

between the anterior and posterior insertions (Fig. 15). A few fibers can be seen passing from the region of the *sims* of the ciliary body toward the posterior line of insertion on the lens.

THE INSERTION OF THE ZONULE ON THE LENS

The whole specimens, from both the anterior and the posterior aspect, show the zonular fibers ending in successive lines of insertion which lie sagittally about the equator of the lens. Although there is some variation from specimen to specimen, the columns of fibers on either side of a ciliary process come together at the equator of the lens to form a single sagittal line of insertion. Few fibers insert on the capsule between these lines. Therefore, the insertion of the zonule, as a whole, appears as successive lines, separated by spaces that show few points of attachment of the zonule to the lens (Fig. 9).

In addition to these anterior-to-posterior lines of insertion, there

is a line at which the zonular fibers attach running about the circumference of the lens approximately 1½ mm. anterior to the equator. A second line runs similarly about the circumference of the lens approximately 1 mm. posterior to the equator of the lens. Extending out across the lens capsule for approximately 1 mm. from each of these lines of insertion are faint striae. These are seen when the light of the slit lamp is focused to bring out the sheen of the lens in this region. They give the impression that they are an extension of the zonular fibrils along the capsule of the lens, or that they represent lines of traction radiating from the insertion of the zonule towards the poles of the lens.

The junctions of the successive sagittal lines of insertion and the two coronal lines of insertions are interesting (Fig. 6). As they approach the lens the zonular fibers break into diverging pencils of fibrils which fuse into the lens capsule. As a result the final insertions of the sagittal columns of fibers are as sagittal bands of fibrils. At the posterior and anterior ends of these columns the zonular fibrils diverge and pass extensively into the neighboring coronal lines of insertion. The spreading of the fibrils from each fiber into the sagittal band of insertion is in all planes, whereas the spreading of fibrils into the coronal line of insertion is essentially in the coronal plane. The two lines of insertion meet and the sagittal lines lose many fibrils to the coronal insertions.

The equatorial border of the lens is crenated. These crenations take the form of gentle waves or undulations which can be seen from both the posterior and the anterior aspect (Figs. 2, 10). They end at approximately the anterior and the posterior coronal lines of insertion of the zonular fibers. The protruding parts of the crenations correspond to the place where fused sagittal columns of fibers insert and lie opposite ciliary processes. The valleys of the crenations are relatively untouched by inserting fibers and lie opposite the valleys between ciliary processes. There are often fewer crenations than there are ciliary processes, because occasionally one crenation will span two processes.

Study of microscopic sections adds many details concerning the terminations of the zonular fibers. In sagittal sections the fibers, which are passing both to the anterior and to the posterior coronal lines of insertion, lie tangential along the globe and imperceptibly

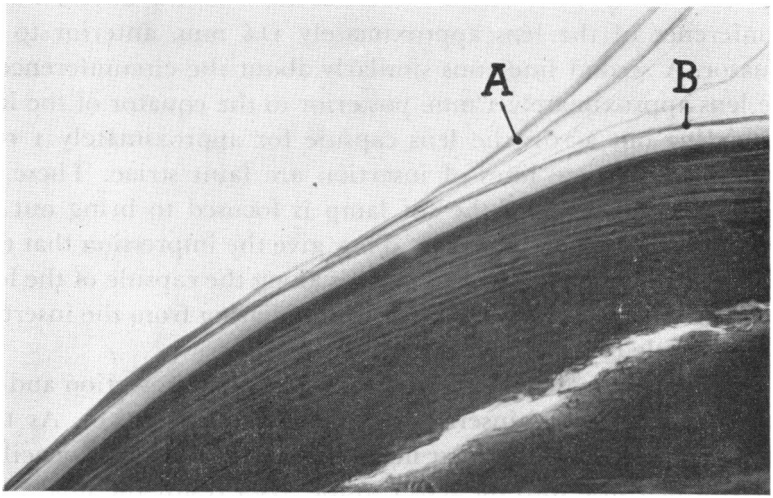

FIGURE 16. A SAGITTAL SECTION THROUGH THE LENS
The zonular fibers, A, are passing to the anterior line of insertion on the lens. The zonular lamella, B, stains more darkly than does the cuticular part of the capsule. The zonule fuses into the zonular lamella. (Gomori's stain, x 91.)

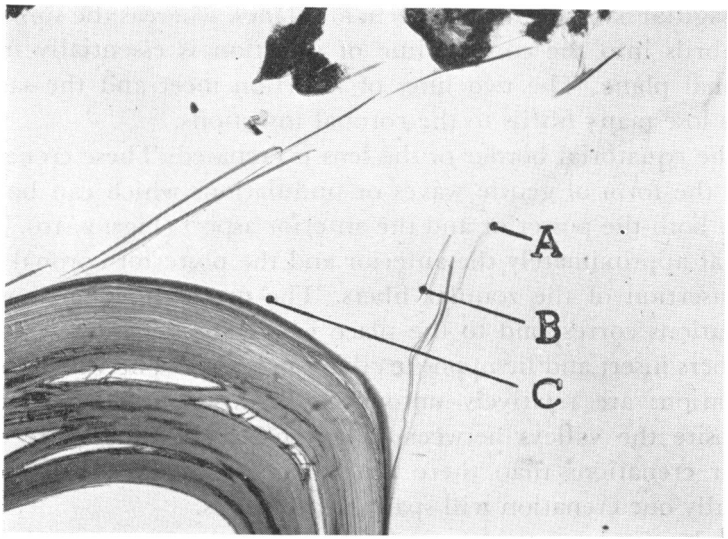

FIGURE 17. SAGITTAL SECTION AT THE EQUATOR OF THE LENS
The face of the vitreous lies at A. It comes in contact with the lens at the posterior line of insertion of the zonular fibers, B. Hannover's space, C, lies between the prominent anterior and posterior zonular fibers. No zonular fibers insert on the lens at its equator. (Periodic acid stain, counterstained with hematoxylin; x 40.)

fuse to become part of the zonular lamella of the lens capsule (Fig. 16). Some fibrils separate from the fibers, but most pass into the lens capsule as part of the main mass of fibers. Only in occasional sections is the insertion of the zonular fibers into the equatorial region of the lens shown (Fig. 15). This occurs when the section happens to pass through a sagittal line of insertion of the zonule. In most sections no fibers pass to the equator of the lens (Fig. 17). Before inserting, the equatorial fibers break into fibrils which diverge as a fan and fuse into the zonular lamella over a considerable area. In coronal section, the zonular fibers approach the equator of the lens in successive groups, corresponding to the fusing

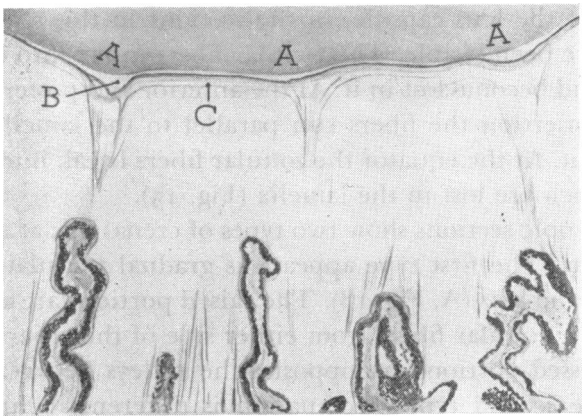

FIGURE 18. CORONAL SECTION THROUGH LENS AND CILIARY PROCESSES
The crenations of the lens lie at A, A, A. At B are tent-like elevations of the zonular lamella (C), of the cuticular portion of the capsule and of the subcapsular epithelium. Both the crenations and the folds of capsule lie opposite groups of zonular fibers, which in turn lie opposite ciliary processes. (Periodic stain, counterstained with metanil yellow; approximately x 40.)

columns of fibers from the sides of the ciliary processes (Fig. 18). Near the lens the fibers break into many fibrils which insert into the zonular lamella over considerable distance. If the cut is anterior to the equator, near the anterior line of insertion, the zonular fibers approach the lens as a continuous line of fibers. Close to the lens they break in the coronal plane into many fibrils, and insert continuously along the anterior coronal line of insertion. At the posterior coronal line of insertion the arrangement is the same. Near the lens a clear matrix encloses each group of fibrils.

The zonular lamella of the lens capsule is of particular interest. By the Hotchkiss method and with Gomori's chromic hematoxylin it stains as do the zonular fibers. With both stains it appears dark blue—almost black with Gomori's stain—and is sharply separated from the paler cuticular part of the lens capsule (Fig. 16). The zonular lamella can be traced all around the lens. It is thickest at the anterior and at the posterior coronal lines of insertion of the zonule, and is slightly thinner at the equator of the lens. It can be traced across the anterior pole of the lens, where it is quite thin. It also can be traced across the posterior pole of the lens, although here it shrinks to a faint, dark blue line. Although it may be possible to show fibrils passing from the zonular lamella into the cuticular part of the lens capsule, in the sections in this study no such fibrils have been visible. The zonular fibers insert into the zonular lamella and become lost in it. At the anterior and posterior coronal lines of insertion the fibers run parallel to the lamella, and just fuse with it. At the equator the zonular fibers break into a brush of fibrils which are lost in the lamella (Fig. 15).

Microscopic sections show two types of crenations at the equator of the lens. The first type appears as gradual undulations of the border of the lens (A, Fig. 18). The raised portions are at the insertions of the zonular fibers from either side of the ciliary processes, the depressed portions are opposite the valleys between the processes. The second type of crenation is different; it appears as a sharp tenting. The zonular lamella is drawn outward, being separated from the cuticular part of the capsule. The underlying cuticular part of the lens capsule is sharply tented (B, Fig. 18). At the peak of the tent there may be a separation between the inner surface of the lens capsule and the underlying lens fibers, so that a small space is formed. This type of tenting always corresponds to the exact location of a lens fiber and its terminating fibrils. It is obviously due to the pull of the lens fiber and is probably an artefact, the result of fixation and shrinking.

THE RELATION OF THE ZONULE TO THE POSTERIOR CHAMBER

The posterior chamber is that volume bounded behind by the zonule, by the iris in front, the ciliary body to the side, and the lens towards the axis of the eye. The lens is in contact with the posterior

chamber over an area between the anterior line of insertion of the zonule and the line where the iris touches the lens. The ciliary processes form part of the posterior wall of the posterior chamber because they protrude through clefts in the zonule and jut into the space. The small bay between the ciliary processes, the zonule, and the neighboring lens has been called the *recessus camerae posticus* of Kuhnt.

The controversial question concerning the extent of the posterior chamber has been how far this chamber insinuates between the zonule and the ciliary body. As there is a wide attachment of zonular fibers in the valleys between the ciliary processes, the posterior chamber as a continuous cleft is shut off. In the region near the ciliary epithelium the zonular fibers break into many fibrils and are enmeshed in a continuous gelatinous material. It is therefore doubtful if any significant flow of fluid could take place in this region. The ciliary processes protrude into the posterior chamber through clefts between the zonular fibers. Similarly the ciliary processes in these clefts protrude posteriorly into the space between the ciliary body and the vitreous. Therefore the posterior chamber can hardly be considered to be cut off on its posterior aspect by the zonule. The clefts in which the ciliary processes lie indicate that a free passage is available between the canal of Petit and the posterior chamber. If fluid is formed at the ciliary processes it can flow unimpeded either towards the canal of Petit or towards the posterior chamber.

THE RELATION OF THE ZONULE TO THE ANTERIOR FACE OF THE VITREOUS

The canal of Petit is the space between the zonule and the face of the vitreous. It ends axially where the vitreous attaches to the lens and at the sides where the vitreous attaches to the ciliary body. Embryologically, the canal of Petit is said to contain the remnants of primary vitreous, and the "face of the vitreous" is merely the separation between the primary and the secondary vitreous (Mann, 85). In the adult the face of the vitreous is a definite surface and the canal of Petit contains an aqueous fluid.

In whole preparations the face of the vitreous can be seen behind the zonule (Fig. 2). The vitreous touches the lens just posterior to

the posterior line of attachment of the zonule to the lens, the *ligamentum hyaloidea-capsulare* of Wieger (190). This contact is a line passing completely about the lens, 1½ mm. posterior to its equator. As the vitreous is traced from this point toward the ora serrata it lies free and posterior to the zonule, but gradually approaches it until over the pars plana ciliaris it is in contact with the zonular fibers. In the region of the bays of the ora serrata there is a broad direct application of vitreous to the surface of the ciliary body. At the spikes of the ora serrata the free anterior face of the vitreous passes directly onto the retina. The cleft between zonule and vitreous, therefore, ends posteriorly at the bays of the ora serrata, where the vitreous applies directly to the ciliary epithelium. At the spikes of the ora serrata the cleft between vitreous and zonule merely ends with the application of the anterior face of the vitreous to the inner surface of the retina.

Sections show a similar picture (Fig. 12). The anterior face of the vitreous ends at Wieger's capsulo-hyaloid adhesion. As the face of the vitreous is traced towards the ora serrata it approaches the zonule and comes to lie in contact with the zonular fibers over the pars plana ciliaris. In the bays of the ora serrata the zonular fibers are not present. The vitreous applies directly to the ciliary epithelium and the fibrils of the vitreous seem to fuse to the surface of the epithelial cells. The internal limiting membrane, which was described as part of the zonular system, is not present and therefore the application of the fibrils of vitreous to the ciliary epithelium is direct. Where the zonular fibers pass to the retina, in the region of the spikes, the vitreous lies free until it touches the inner surface of the retina.

THE ZONULE AS A MEMBRANE OR AS A COLLECTION OF DISTINCT FIBERS

Whether the zonule is a membrane or a collection of fibers is a difficult question to answer. In whole, fresh specimens no ground substance can be seen between the fibers. Dissection, drying, or the injection of air or fluids may form artificial surfaces. When fixative or preservative is used the matrix between the fibers may be precipitated or destroyed. The appearance in the sections suggests that the zonule is made up of individual fibers. However, fixing and staining may have destroyed or precipitated the matrix between

the fibers. Whether or not a matrix is present between the zonular fibers, there are distinct, larger clefts which give free passage between the space in front of and the space behind the zonule. These clefts lie about the ciliary processes and extend nearly to the lens. They are not clefts of single fiber width but are sizable, too big to be bridged by a diaphanous cement substance. Because they contain the ciliary processes they cannot be bridged. Whether or not there is cement substance between the zonular fibers, because of these larger spaces the zonule cannot be considered a continuous or an effective membrane between the posterior chamber and the vitreous cavity.

In the whole preparations used in this study, intact, separate fibers passed from the lens to the ciliary body. In the microscopic sections the fibers were square or rectangular in outline, and lay free, without surrounding substance. However, at certain places, namely near the origin and near the insertion of the fibers, a diffuse interfibrillar matrix was present. The zonule would appear to have some interfibrillar matrix, but this is not present between the large fibers or in the large clefts about the ciliary processes.

CLINICAL OBSERVATIONS

Owing to the difficulty in preparing good specimens and particularly to the possibility of artefacts resulting from fixation and shrinkage, there are several clinical observations which are valuable contributions to the knowledge of the zonule. Because of the zonule's location little of it is within view, and that bit is not easy to examine (74, 187).

If a coloboma of the iris is present, or if there has been a subluxation of the lens, a direct view of the zonule is available. Even if the eye is normal, by the use of strong mydriatics and with the aid of a goniolens it is possible to obtain a direct view of the zonule with the slit lamp. However, in the normal eye the view is so restricted that it is of little value. When the pupil has been dilated to its maximum it is still necessary to look obliquely across the anterior chamber. The direction of vision is such that the rounded anterior face of the lens near the anterior line of insertion of the zonule cuts off observation. Only a short length of zonule is visible.

But in the normal eye it is not hard to see the zonule through

the lens (Werner, 186). The lens must be clear and the pupil must be capable of dilation to about 8 mm. This dilation is necessary if the iris opposite the zonular fibers being viewed is to be retracted sufficiently to allow an extremely oblique view across the lens. The zonule can then be seen with the ophthalmoscope or with the corneal microscope. The observation with the microscope is considerably easier if the rays from the slit lamp are brought into the line of observation through the microscope. The slit must be adjusted up or down, so that the reflex from the equator of the lens is not blinding. The view is slightly improved by firmly indenting the sclera over the ciliary body adjacent to the fibers which are to be viewed (Trantas, 184; Berliner, 185). Also it may be of benefit to dilate the pupil with 10 percent neo-synephrine only, and then have the patient exert marked accommodation during the examination. This makes the lens slightly rounder and the course of the rays to and from the area to be observed more direct. These last two aids may be helpful, but they are not necessary. To view the zonule with the ophthalmoscope a small, bright beam is best. The focus on the zonular fibers must be accurate.

Figure 10 is drawn to show the zonule in a young man who had a surgical coloboma of the iris. Three years before the figure was drawn a nail had perforated the cornea without touching the underlying structures. The iris had prolapsed and had been removed surgically. Recovery had been uneventful and there had been no further complication. His refractive error had not changed.

The points which have anatomical interest are, first, that the ciliary processes protrude into the posterior chamber through clefts in the zonule. Second, the zonular fibers are in groups or bands about the ciliary processes. Third, the crenations that are present in the anatomic specimen can be made out in the living eye. Fourth, the zonule can be seen through the lens. Its passage to the posterior coronal line of attachment is apparent. Two other observations of interest can usually be made on the living eye. One did not show in this particular eye and is not drawn. A faint grey line can be seen circling the lens just axial to the posterior coronal line of insertion of the zonular fibers. This is the location of the capsulo-hyaloid attachment of Wieger (190, 94). The other object of interest was out of focus posteriorly. In young, healthy eyes the

anterior face of the vitreous lies free, behind the zonule (187, 191, 102).

When the iris is intact the view is confined to the zonular fibers seen through the lens. With the ophthalmoscope or the slit lamp it is possible to see the zonular fibers passing to the posterior coronal line of insertion, and to appreciate a variation in the reflex coming from the equator of the lens, which is due to the crenations of the lens.

DISCUSSION

The interpretation of the anatomy of the zonule that is given in this paper leads naturally to a discussion of certain points of anatomic and physiologic interest.

THE CROSSING OF THE ZONULAR FIBERS

The question of a crossing of the zonular fibers has been controversial. Crossing can be seen in sections but is not apparent in the gross specimens. There are two explanations that may account for the discrepancy. First, in the gross specimens viewed from the posterior aspect, most of the fibers from the lens form into columns about the ciliary processes. There is a smaller number of fibers which are not part of these columns; these lie opposite the valleys. After passing deeply into the valleys they are lost from view. Fibers from this group would cross fibers from the anterior surface of the lens deep in the valleys, and the crossing would not be visible. In the specimens cleared with oil of wintergreen and benzyl benzoate these two sets of fibers can be seen.

Secondly, the view that one can trace a given fiber from a given location on the lens to a given spot on the ciliary body is not fully correct. In the region of the ciliary body the fibers form into sheets and masses which, in the matter of transmitting pull, may be considered a continuum. A fiber which enters this continuum loses its identity and can hardly be traced out the other side. But this is unimportant, since force transmitted along this fiber will be carried into the mass of fibers and spread to many. Although it is possible to trace a fiber from the depth of a valley, and another fiber passing backward toward the posterior surface of the lens, and to imagine a straight line joining these two, that does not mean that this is all

one fiber, but rather that this is one direction of force. The fiber passing to the epithelium of the valley floor may have come from some other location than the posterior lens capsule, or may be composed of fibrils which are parts of fibers from several locations on the lens. The zonule may better be considered a continuum which receives certain forces from its origin, fuses these, and then distributes them to its insertion. Although there are fibers which cross other fibers, it is wise not to place too much emphasis on these individuals. It is better to consider that the zonule carries crossing lines of force between the ciliary body and the lens.

There is a second crossing of zonular fibers which does occur and which is distinct from the major crossing described in the literature

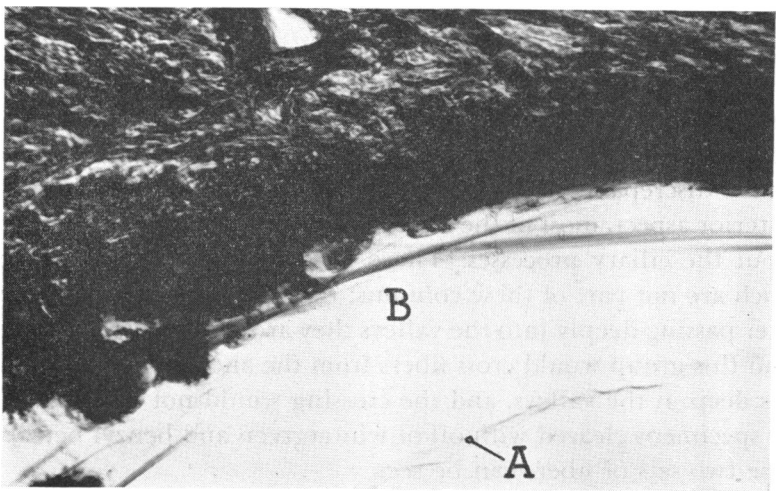

FIGURE 19. A SAGITTAL SECTION THROUGH THE CILIARY BODY JUST BEHIND THE SIMS

The face of the vitreous lies at A. At B the zonular fibers form a cross. Fibers from the lens on the left are crossing fibers from the pars plana on the right. (Gomori's stain, x 101.)

(Fig. 19). Some fibers from the pars plana ciliaris insert on the ciliary body near the *sims* or on the plicae ciliares. Zonular fibers going to the lens take their origin in this area. The result is a crossing which lies near the epithelial surface and is visible in sections, but passes unnoticed in the gross specimens.

THE FUNCTION OF ACCOMMODATION

In the literature adequate support can be obtained for the view that the zonule attaches to the ciliary processes, but there is equally good support for the view that it does not. Those who have described the zonule as attaching to the ciliary processes have realized that the zonule would pull over the soft processes. Therefore, struts, or zonular fibers tying the pars plana ciliaris to the processes, have been found (40). Such struts are an unnecessary complication. In this study zonular fibers inserting on the processes could not be found. That there are no attachments is confirmed by the lack of fibrils breaking from the fibers about the processes, by the lack of an internal limiting membrane on the processes, and by the loose gelatinous stroma of the processes.

It is known that the ciliary processes move towards the lens during accommodation, in fact, they may almost touch the lens (78, 102, 157, 192-197). If there were fibers connecting the processes to the lens one would expect the lens to retract as the processes move in, which does not occur. The processes must be carried passively along the clefts in the zonule during accommodation. They must transmit no lines of force and take no direct part in accommodation.

The fibers that pass from the pars plana ciliaris to the plicae ciliares, and to the ciliary body near the *sims*, must maintain the distances between points all across the pars plana ciliaris and into the valleys between the ciliary processes. Although the zonular fibers are elastic and there may be some elongation or contraction, still this surface probably moves as a whole during accommodation.

Whether the fibers draw more strongly on the lens or are relaxed during accommodation, the architecture of the zonule suggests that a comprehensive view must be taken of the action of this structure. Physiologically the zonular fibers lie in groups or sheets. Sheets of fibers attach coronally and sagittally to the lens, lie at the sides of the ciliary processes, and cover the pars plana ciliaris. The action of one fiber cannot be separated from the action of the rest. The pull of fibers from many points of origin fuses into a sheet of force over the pars plana ciliaris. When the pars plana ciliaris moves it must move as a whole. Fibers to many points of insertion on the lens receive a common drag from large groups of fibers.

When the zonule pulls on the lens it must exert force throughout wide areas of insertion. From an anatomic point of view the zonule is made up, to a large extent, of fibers; from a physiologic point of view the zonule is composed of wide areas of force.

THE INFLUENCE OF THE ZONULE ON THE DEVELOPMENT OF DETACHMENT OF THE RETINA

The importance of a tear or a hole in the etiology of retinal detachment is established. The possibility of a pull from the zonule deforming and tearing the retina has not been proved. Whether the zonule reaches right to the retina at the ora serrata or falls slightly short of it has never been decided. Topolanski (92) states that the origin of the zonule is 1½ mm. anterior to the ora serrata, and he reflects the views of many others. Schultze (114) indicated that the zonule attaches directly to the retina, and there are other authors who support this view. The statement in this paper—that the zonule reaches the retina at the spikes of the ora serrata but falls 1½ mm. short in the bays—is a compromise. It is not new, but it explains the disagreement which has continued on this point over the years. Both of the old views are correct, for the one gives the appearance at a bay, the other at a spike of the ora serrata.

Not only does the zonule attach at the spikes of the ora serrata but also the fibers arch away from the bays to concentrate there. The pull from the zonule must be focused at the spikes of the ora serrata and into the neighboring retina. Also the two layers of ciliary epithelium near the ora serrata are more firmly fused together than are the retina and the pigmented epithelium. Therefore, a pull at a spike would probably produce wrinkles in the retina radiating from the spike, and lines of force following the contours of the bays. These lines of force along the bays would cause strain between the retinal epithelium and the unpigmented ciliary epithelium. Whether he has considered such an analysis or not, Schepens (198) has drawn wrinkles in the retina radiating from the spikes of the ora serrata, holes in the retina posterior to those wrinkles, and cystic changes and holes which go on to disinsertion along the contours of the bays of the ora serrata. Such changes would be what one might expect from a consideration of the arrangement of the zonule in this region.

THE BASE OF THE VITREOUS

The region of the ora serrata, the base of the vitreous, and the posterior terminations of the zonular fibers are so interesting and so important that they are worthy of special description (9, 97, 199). Here is an area, a band about the eye, in which many important structures end. The zonule ends here, but that has little significance unless the other structures coming to the area are described. The vitreous has its base here, being attached by successive pads of adhesion in the bays of the ora serrata. The retina terminates here. There is some cleavage possible between the retina and the pigment epithelium, but little between the two layers of ciliary epithelium. The pigment epithelium passes right through the region, but is thick in the area of the pars plana ciliaris adjacent to the ora serrata (9). The choriocapillaris under the retina stops and only veins lie under the ciliary epithelium at the base of the vitreous (9, 117, 200). The ciliary muscle attaches deeply, and because of the thick fibrous tissue in the choroid, draws on the pigment epithelium.

This is a major location of fixation in the eye. The unpigmented ciliary epithelium is bound to the pigmented epithelium, which in turn is bound to the underlying fibrous tissue of the choroid and to the fibers of the ciliary muscle. The vitreous has its most firm attachment to the epithelium in the area. On the one side the zonule and on the other the retina find their final attachments in this firm base. The motions which are possible about the area, in the vitreous, between the vitreous and retina, between the retina and the pigment epithelium, between the pigment epithelium and the choriocapillaris, and of the zonule itself, are all stopped here.

Finally, this area of fixation itself probably moves. It is firmly attached to ciliary muscle, and with contraction of that muscle the whole area is drawn towards the scleral spur.

INTRACAPSULAR CATARACT EXTRACTION

There are a few anatomic observations which might be made concerning intracapsular cataract extraction. The zonule attaches to the zonular lamella of the lens capsule. This stains similarly to the zonular fibers and may be considered part of the zonule. The

separation at intracapsular extraction is undoubtedly between the cuticular and the zonular lamella of the lens capsule (13). After intracapsular extraction zonular tags are not found on the lens (16). During this study 50 lenses that were taken intracapsularly at operation were examined by the methods which have been described. In all the lenses no zonular lamella was visible at the equator; only some small tags of zonular substance remained in the region of the anterior and posterior coronal lines of insertion. Cadiat (203) and Carroll and Berke (204) have noted, in the eyes of animals, that after intracapsular extraction a membrane of zonule remains against the vitreous. Dislocation of the lens through the zonular lamella is well known (166-173, 176, 201, 202). The cement substance binding these two layers together must be strong in youth, weak in old age. Cutting the zonular fibers (D'Andrade, 205) would help little to break the zonular lamella in intracapsular extraction.

If the zonular fibers are pulled from the eye it is likely that pigment from the pigment epithelium of the ciliary body will come with them. It has been pointed out that the internal limiting membrane of the ciliary epithelium, the supporting substance between the unpigmented cells, and the membrane deep to the unpigmented cells are essentially part of the zonular system. If the zonular fibers are torn from the eye, because this system does reach to the pigmented layer it is likely that pigment will come with the fibers (99). This is occasionally seen at operation, for example when a secondary membrane is grasped by forceps and drawn forcibly from the eye.

THE FORMATION AND THE CIRCULATION OF THE AQUEOUS

The zonule and the structures to which it attaches are so intimately related to the site of formation of aqueous and to the passages through which that fluid must flow that some discussion is worth while. The anatomy of the zonule would suggest that the aqueous is formed at the ciliary processes, not at the pars plana ciliaris, or in the valleys between the processes, or at the plicae ciliares in the valleys. The findings indicating this are several. The zonule attaches not to the ciliary processes, but to the other struc-

tures. The zonular fibrils with their interfibrillar matrix would be a distinct bar to any sizable flow of fluid from the pars plana or from the floors of the valleys. The internal limiting membrane of the ciliary epithelium, which is part of the zonular system, would be a hindrance to the flow of aqueous and is not present over the ciliary processes. Secretion through a glass-like membrane at the surface of all layers of epithelial cells is not a usual arrangement in the body, nor is it a likely one. In the areas where the zonule attaches the ciliary body has a dense, fibrous stroma, no choriocapillaris (9, 187, 199), and a pigmented epithelium. At the ciliary processes, where the zonule does not attach and where the aqueous may be formed, there is a clear gelatinous stroma containing capillaries, a peculiar membrane which lies under the epithelial cells, and no pigmented epithelium. The unpigmented epithelial cells stain by the Hotchkiss method suggesting that they contain substances that support an active metabolism. A membrane that separates tissue with different metabolic activities and across which work may be done is here present (206). The ciliary processes lie in clefts that are designed to carry aqueous forward to the anterior chamber and backward to the vitreous. The anatomic relationships of the zonule all suggest that the pars plana ciliaris, plicae ciliares, and valleys between the ciliary processes are the origin of the zonule. The ciliary processes are physiologically unrelated, merely lying in clefts in the zonular system, and are advantageously devised and situated for the secretion of aqueous.

SUMMARY

Compromise can be reached on several of the controversies which have enlivened the literature on the anatomy of the zonule during the last two hundred years:

1. The zonule is not part of the vitreous but it is intimately associated with the vitreous in the region of the ora serrata.

2. It is not necessary for vitreous to penetrate through the zonule to reach its attachment to ciliary epithelium, because the area in the bays of the ora serrata allows direct application.

3. Both those who have said that the zonule reaches the retina and those who have said that it stops one or more millimeters from

the retina are correct, but another dimension must be considered. It reaches the retina at the spikes of the ora serrata and it falls short of the retina at the bays.

4. Similarly, the zonule pulls on the retina at the spikes of the ora serrata and does not pull on the retina at the bays.

5. The zonule is formed of fibers, but in certain areas it contains an interfibrillar meshwork. Despite the similarity to a membrane, there are clefts about the ciliary processes which are too big to be bridged by a matrix and which indicate that this diaphragm has no properties that limit the flow of aqueous.

6. There is a crossing of zonular fibers. However, this is an interpretation which is not broad enough in its concept. The zonule could better be thought of as broad areas of origin, large masses of connecting fibers, and large areas of insertion. A fiber might be traced from an area of origin into an area of connection, but by that time the fibrils are so fused that the fibers of insertion can be considered as different, or new, fibers. The fibers lying beside the ciliary processes are parallel, but the fibers passing from the lens into the valleys between the processes pass more deeply and give the appearance of crossing.

7. A canal of Petit does exist. It is seen in microscopic sections, in gross specimens, and in the living eye.

8. Hannover's canal can be distinguished between the anterior and posterior fibers of the zonule. However, it is not continuous around the lens, for it is broken by the many columns of fibers that form the walls of the clefts about the ciliary processes.

9. The zonule does not attach to the ciliary processes, and the processes appear physiologically unrelated to the zonule.

APPENDIX A

PREPARATION OF GROSS SPECIMENS

PERIODIC ACID STAINING OF GROSS SPECIMENS

The fresh eye, or the eye after examination in saline, is placed in 70 percent ethyl alcohol for one day. A window is then cut, either through the sclera or through the cornea, which will eventually be used to view the zonule. The specimen is then treated as follows:

1. Place in ethyl alcohol, 70 percent, for 3 days
2. Wash in distilled water for 10 minutes
3. Place in periodic acid, 0.5 percent, for 2 to 5 minutes

4. Wash in distilled water
5. Immerse in Schiff's reagent for 5 to 10 minutes
6. Place in sulfurous acid solution, 3 changes, 3 minutes each
7. Wash in distilled water for 5 to 10 minutes
8. Place in 70 percent ethyl alcohol, for mounting

CLEARING GROSS SPECIMENS WITH BENZYL BENZOATE AND OIL OF WINTERGREEN

The eye is fixed in 5 percent formalin and a window is cut. It is then placed in:

1. Two changes of distilled water, for 24 hours each
2. Three changes of hydrogen peroxide, 15 percent, for 24 hours each
3. Distilled water, for 24 hours
4. Ethyl alcohol, 50 percent, 70 percent, 80 percent, 95 percent, for 3 days each
5. Four changes of absolute ethyl alcohol, for 3 days each
6. Two changes of benzene, for 48 hours each
7. Oil of wintergreen, 4 parts, and benzyl benzoate, 3 parts, for mounting

CLEARING GROSS SPECIMENS WITH BENZYL BENZOATE AND OIL OF WINTERGREEN AFTER STAINING WITH PERIODIC ACID

After the specimens have been stained with periodic acid and returned to 70 percent alcohol, place them in the following solutions:

1. Ethyl alcohol, 70 percent, overnight
2. Ethyl alcohol, 95 percent, overnight
3. Two changes of absolute ethyl alcohol, for 1 hour each
4. Two changes of benzene, for 1 hour each
5. Benzyl benzoate and oil of wintergreen, for mounting

CLEARING CELLOIDIN BLOCKS WITH BENZYL BENZOATE AND OIL OF WINTERGREEN

The specimens are placed in baths as follows:

1. Alcohol, 70 percent, overnight
2. Alcohol, 95 percent, for 2 days
3. Two changes of absolute ethyl alcohol, for 1 day each
4. Two changes of benzene, for 1 day each
5. Oil of wintergreen and benzyl benzoate, for mounting

APPENDIX B

PREPARATION OF MICROSCOPIC SECTIONS

FIXATION

Immerse in formalin, 5 percent, or ethyl alcohol, 70 percent, or Carnoy's solution.

Carnoy's solution:

Glacial acetic acid	10 c.c.
Absolute ethyl alcohol	60 c.c.
Chloroform	30 c.c.

EMBEDDING

Use the celloidin method. Cut sections and transfer them to ethyl alcohol, 70 percent.

PERIODIC ACID STAIN

Staining Method

The sections in 70 percent alcohol are treated as follows:

1. Wash in water for 5 minutes
2. Place in periodic acid, 0.5 percent, for 5 minutes
3. Wash in distilled water
4. Place in Schiff's reagent for 15 minutes
5. Place in sulfurous acid, 3 changes of 2 minutes each
6. Wash in water for 5 to 10 minutes
7. Counterstain in metanil yellow, 1 percent, for 15 to 30 seconds
8. Rinse in water
9. Place in ethyl alcohol, 95 percent, for 15 seconds
10. Place in absolute ethyl alcohol for 30 seconds
11. Place in absolute ethyl alcohol and xylol for 30 seconds
12. Place in xylol. Mount section in Permount

Staining Solutions

1. Periodic acid: 0.5 percent in distilled water
2. Schiff's reagent: Boil 200 c.c. of distilled water and add 1 Gm. of basic fuchsin and stir. Cool to 50°C. and filter. Then add 20 c.c. of normal hydrochloric acid and 1 Gm. of anhydrous sodium bisulphite. Keep in a dark place. The fluid takes one to two days to become orange, or straw colored, and it is then ready for use.
3. Sulfurous acid rinse:

Sodium metabisulfite, 10 percent	6 c.c.
Normal hydrochloric acid	5 c.c.
Distilled water	100 c.c.

4. Metanil yellow:

Metanil yellow	1 Gm.
Distilled water	100 c.c.

GOMORI'S CHROMIC HEMATOXYLIN, PONCEAU METHOD

Staining Method

The sections in 70 percent alcohol are treated as follows:

1. Place in potassium permanganate for 1 to 2 minutes
2. Wash in running tap water for 1 to 5 minutes

3. Bleach in potassium bisulfite, 2.5 percent
4. Wash in running tap water for 10 minutes
5. Stain with chromic hematoxylin
   (a) at room temperature for 15 minutes to 1 hour, *or*
   (b) at 50°C. for 5 to 30 minutes
6. Rinse in distilled water
7. Differentiate in 0.5 to 1 percent hydrochloric acid
8. Wash until slide appears blue
9. Place in ponceau (of Masson trichrome) for 10 to 30 minutes
10. Rinse in 1 percent acetic acid
11. Place in phosphomolybdic acid, 1 percent, for 5 to 10 minutes
12. Place in acetic acid, 1 percent, for 1 to 5 minutes
13. Dehydrate in absolute ethyl alcohol (dropper method)
14. Clear and mount in salicylic balsam

Staining Solutions

1. Potassium permanganate: Aqueous potassium permanganate, 2.5 percent; sulfuric acid, 5 percent. Mix 1 part of each of these solutions with 6 to 8 parts of distilled water.
2. Sodium bisulfite solution: Aqueous solution, 2 to 5 percent.
3. Phosphomolybdic acid: Aqueous solution, 1 percent.
4. Chromic Hematoxylin: Mix equal volumes of 1 percent aqueous hematoxylin and 3 percent aqueous chrome alum. To each 100 c.c. of the above mixture add 2 c.c. of 5 percent potassium dichromate and 1 c.c. of 5 percent sulfuric acid. This mixture is ripe after 48 hours, and will keep in the ice box for many months. It should have a deep, opaque, somewhat purplish, blue shade. Filter before use.
5. Ponceau: Fuchsin S, 1 percent, 1 part; acid Fuchsin, 1 percent, 1 part; ponceau de xylidine, 1 percent, 4 parts. This is the stock solution. For use, dilute 10 c.c. of stock solution with 90 c.c. of 1 percent acetic acid.

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