ELECTRON MICROSCOPE OBSERVATIONS ON THE SUBMICROSCOPIC ORGANIZATION OF THE RETINAL RODS*

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PLATES 68 TO 71

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The submicroscopic organization of the rod cell of the retina has been studied by polarization optical analysis (1) and more recently by electron microscopy (2, 3). These investigations refer principally to the outer segment of the rod in which a transversally oriented, layered structure has been recognized. In electron microscope observations of thin sections of guinea pig rods, Sjöstrand (2) describes the outer segment as composed of a pile of double membranes or discs which are connected in series by means of short stalks. Each of the membranes of the disc is described as having a thickness of about 30 A; they enclose together a compartment of only 70 to 80 A in height.

In another paper Sjöstrand (3) analyzes the inner segment of the guinea pig rod concentrating particularly on the description of the long slender mitochondria, which in aggregation constitute the so called ellipsoid. Furthermore he describes a bundle of thin submicroscopic fibrils connecting the outer with the inner segment of the rod and suggests that the fibrils may be involved in the conduction of excitation between the two segments.

The observations that will be reported here on the fine structure of the rod cell of the albino rabbit are to a considerable extent confirmatory of those of Sjöstrand. However, our description of the rod cell will put in evidence some new details of structure, and a different interpretation of some of the structures will be advanced.

In sections cut normal to the surface of the retina we were struck by the structural similarity of the connecting fibrils with cilia (4). These observations led us to study transverse sections of the connecting fibers at different levels and the electron micrographs obtained showed an even more striking resemblance to cross-sections of cilia. This finding led us to search into the classical cytological literature and, as it will be mentioned later on, we found that several authors had pointed out the probable ciliary nature of the external segment of both rods and cones. This literature refers principally to the development of these photoreceptors and for this reason it will be analyzed in a second paper dealing with the submicroscopic morphogenesis of the rod (5).

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Furthermore in the present work several morphological components of the inner segment will be described. In addition to the mitochondria, they comprise the vacuolar elements of the so called endoplasmic reticulum of Porter (6) the dense particles described in other cells by Palade (7) the elements representing the Golgi complex and the neuroprotofibrils which concentrate in the rod fiber.

Technique

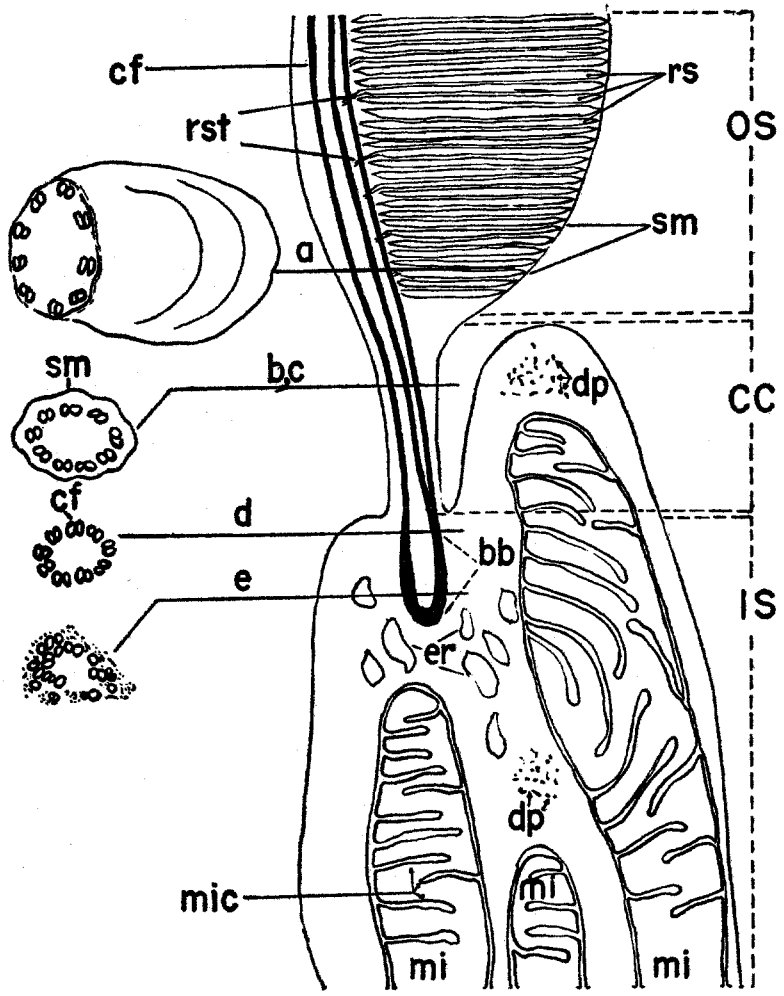
This study was carried out on the retina of albino rabbits and mice. Under ether anesthesia the eyeballs were exposed and opened. Following separation of the vitreous the fixative was directly flooded upon the retina. After a few minutes of fixation, fragments of retina were detached and sectioned into small pieces for further fixation for 1 to 4 hours. As fixative Palade's (8) buffered osmium tetroxide with minor modifications was used. The pH of the solution, which included Ringer with a double concentration of Ca^{++}, was 7.4. The material was dehydrated, embedded in methacrylate and sectioned with a Porter-Blum (9) microtome. Proper orientation of the blocks was provided to make sections normal to the surface, but tangential and oblique sections were also made. The sections were selected for thinness on the basis of interference colors. The micrographs were taken with an RCA-EMU electron microscope with a compensated objective lens at magnifications ranging between 5,000 and 10,000 diameters.

OBSERVATIONS

The region of the rod cell that will mainly be described here is shown in a longitudinal section in Fig. 1 and Text-fig. 1. In the upper part, the outer segment constituted by a stack of membranous elements and surrounded by a surface membrane is observed. This outer segment is connected to a depression or recess in the inner segment by means of a short bundle of filaments. In this particular case the bundle is 700 mμ long, 160 mμ wide near the inner segment and widens up to 240 mμ before reaching the outer segment. The penetration of the bundle into the inner segment is better seen in Fig. 3 in which the filaments can be followed for a short distance below the cell surface. Soon they become continuous with a round basal body consisting of a diffuse shell of dense material surrounding a less dense core. Figs. 1 and 3 also show that this bundle of connecting filaments is surrounded by a thin surface membrane which is continuous with that enveloping the outer and the inner segments. This membrane is better illustrated in the cross-section of this region of the rod (Fig. 11).

Outer Segment.—The membranous elements which constitute the outer segment are best described as flattened sacs or cisternae lying parallel to one another and extending transversally over almost the entire width of the rod segment (about 1 μ) (Text-fig. 1).

These flattened sacs are limited by a thin, homogeneous membrane of about 30 A and have a cavity which seems to be very sensitive to fixation



TEXT-FIG. 1. Composite diagram based on the electron micrographs of Figs. 1, 2, 3, 4, 6, 7, and 8 showing in longitudinal (right) and cross-sections (left) the region of the rod cell described in this paper. The part marked *OS* corresponds to the outer or receptor segment of the rod constituted by the flattened rod sacs (*rs*), which are in close connection with the surface membrane (*sm*) and sometimes can be seen to be connected by short tubules (*rst*) with the cilium. *CC* indicates the free portion of the connecting cilium and *IS* the most distal region of the inner segment containing large mitochondria (*mi*) with mitochondrial cristae, the basal body (*bb*) of the cilium, vacuoles of the endoplasmic reticulum (*er*) and dense particles (*dp*). In the diagram the continuity of the surface membrane of the outer and inner segments through the connecting cilium is emphasized. On the left side, cross-sections of the connecting cilium at different levels are shown, (see further description in the text and in the original electron micrographs).

and other technical handling. As indicated by Sjöstrand (3), in the best preserved material this cavity is essentially virtual with only a minute space between the paired membranes. On the other hand very frequently the two membranes become separated leaving a variable space in between. This kind of artifact is however helpful in revealing the real structure of the sacs. As shown in Fig. 2 the two membranes are continuous with one another and seem in some instances to be attached to the surface membrane, where they end in a V or Y structure. Furthermore the contact between the outer surface of the neighboring sacs is maintained even when the cavity of the sac widens.

In surface view these flattened sacs are not perfect circular discs. They are horseshoe-shaped owing to an incision or depression at one point in the margin. The superimposition of the sacs is such that the incisions of the different elements coincide. For this reason, in the longitudinal sections of the outer segments it is possible to observe a "cavity" which corresponds to the series of incisions and which is continuous with the insertion of the connecting fibers. Along this cavity the membranes of the sacs also end in a V configuration (Fig. 2) or they are continuous with small tubular projections which frequently have a criss-cross disposition. The connection and significance of these tubular projections, which have a diameter of about 100 to 150 A, is uncertain. Some light may be shed on the problem by the study of the development of the discs during the morphogenesis of the rod outer segment; a study to be presented in another paper (5).

The Connecting Cilium.—The bundle of filaments that connects the inner and the outer segment is best studied in cross-sections. The approximate level of the cross-section of Figs. 4 to 10 is indicated in the longitudinal section of Fig. 3 (see also Text-fig. 1). Furthermore, the height can be easily determined by the structure of the neighboring formations. There are three definite regions in this bundle of filaments, a middle part where it is free surrounded only by a surface membrane, an upper part which is connected with the outer segment, and a lower portion which penetrates into the recess of the inner segment and is continuous with the basal body.

The middle free portion is illustrated in Figs. 5, 8, 9, and 11. It has a striking resemblance with the structure of a cilium (4) and for this and other reasons, the entire structure will be described as the *connecting cilium.* Within the round or oval shaped area delimited by the surface membrane, there are nine peripheral filaments embedded in a rather dense matrix and surrounding a less dense core in which sometimes (but very seldom) it is possible to find the cross-sections of two single filaments (Fig. 5). Electron micrographs of higher resolution show that each one of the nine peripheral filaments is a pair, each unit having a diameter of about 160 A (Figs. 8 and 9). It is an interesting fact

that the distance from one pair to the next and to the limiting membrane are quite constant. This would indicate an organization of the matrix material surrounding each pair of filaments, a suggestion further supported by the fact that the surface membrane shows wavy projections opposite each pair of filaments (Figs. 8 and 9). In the thinnest cross-sections the filaments show a less dense core which gives them the appearance of sectioned tubules (Figs. 8 and 9).

The upper portion of the connecting cilium enters the outer segment of the rod. At the point of entry, the surface membrane of the cilium is continuous with the membrane surrounding this part of the rod. The filaments penetrate deeply into the outer segment in the region corresponding to the incisions into the rod sacs (Figs. 1, 3, 4, and 10). In the adult rod it is difficult to follow these filaments within the outer segment and to recognize their endings and connections with the rod sacs. However the study of the morphogenesis of this segment indicates that some of the filaments may extend almost up to the end of the rod and that very possibly they are related to the individual rod sacs (5).

The lower portion of the connecting cilium has no longer a membrane since it has penetrated into the inner segment (Fig. 6). The nine pairs of filaments are much closer and less distinct being embedded in a rather dense matrix. Also the core shows an electron density that is higher than that in the free portion of the connecting cilium.

The basal body is round or oval shaped (Fig. 3). It seems to be symmetrical in some sections but in others there are indications of an asymmetrical construction (Fig. 7). It is composed of a clear center and a rim of numerous circles, probably cross-sections of tubules or filaments embedded in a dense matrix. In our material it has not been possible to demonstrate whether these elements are continuous with the nine pairs of filaments of the connecting cilium. The longitudinal sections indicate only that there is continuity between the filaments of the cilium and the dense peripheral material of the basal body (Fig. 3).

Inner Segment.—The inner segment of the rod shows two distinct regions; a distal one connected by the cilium to the outer segment, and a proximal one which continues into the rod fiber.

The distal region corresponds essentially to the so called ellipsoid of classical histology and is mainly composed of large longitudinally arranged mitochondria with the typical internal structure (10). It is an interesting fact that in the most distal part of the inner segment and opposite to the insertion of the cilium there is a very large mitochondrion (Fig. 1). This disposition can be better appreciated in a cross-section passing at this level (Fig. 11). At a lower level in the ellipsoid proper, the cross-section shows the inner

segment packed with mitochondria. In Fig. 12 twelve cross-sections of mitochondria can be seen. They all show the characteristic mitochondrial structure with the two enveloping membranes and the folds of the inner membrane to constitute the so called mitochondrial cristae (10).

In addition to the mitochondria, the cytoplasm contains a number of vacuoles probably corresponding to sections through portions of the so called endoplasmic reticulum (6) and aggregates of the fine particles of high electron density described by Palade (7) in other cells. The intervening cytoplasmic matrix is generally amorphous, but in some high resolution electron micrographs it shows very fine (less than 50 A), irregularly arranged filaments (Fig. 11).

The proximal region of the inner segment is shown in Fig. 13. The mitochondria are completely absent in this region and are also lacking in all the rest of the rod cell down to the terminal spherule (11). Within the light amorphous matrix and surrounded by the surface membrane the following submicroscopic components can be observed:

(*a*) *Golgi complex:* Occupying the central part of this region there is a tight group of longitudinally arranged fine canaliculi, small dense vesicles, and some large clear vacuoles which have resemblance with the Golgi complex observed in other cell types (12). In Fig. 13 this substance is little developed and is only represented by two islands of grouped dense vesicles of about 400 to 500 A in diameter and probably by some of the large clear vacuoles in the vicinity. It is interesting to note the fact that the dense particles are absent from the Golgi complex.

(*b*) *Endoplasmic reticulum:* This component is probably represented by the vacoules and short canaliculi which are surrounded by the dense particles.

(*c*) *Dense particles* of about 80 A are seen dispersed in the matrix of the cytoplasm on both sides of the central region. They tend to be attached to the membrane limiting the endoplasmic reticulum but there are also clusters of them dispersed throughout the matrix.

(*d*) *Neuroprotofibrils:* A distant fibrillar component is present in this proximal region of the inner segment. This is constituted by long protofibrils of smooth edges varying in diameter between 160 and 200 A and mainly disposed along the length of the segment. These protofibrils, which are similar in size and shape to those found in nerve axoplasm (13) tend to collect and form a definite bundle at the exit of the rod fiber.

The Rod Fiber.—The proximal part of the inner segment is continuous with the rod fiber which has essentially the characteristics of a nerve axon surrounded by a double membrane and constituted by a tight bundle of parallel neuroprotofibrils (Fig. 13). All the other components found in the inner

segment are lacking here and only a sparse intervening matrix is observed between the neuroprotofibrils.

DISCUSSION

In his study of the ultrastructure of the inner segment of the rod Sjöstrand (3) states that: "The connection between the outer and inner segments is maintained by a specialized structure, composed of a bundle of fibrils running between the proximal part of the outer segment to the distal part of the inner segment. Except for this connection the two segments are completely separated, each one being bordered by its own surface membrane. . . . " And regarding the significance of these fibrils he states further: ". . . it seems justified to assume that they represent a structure for conducting the state of excitation which is caused by the absorption of light energy in the outer segment, from the outer to the inner segment".

From the submicroscopic data presented in this paper it seems proper to conclude that this fibrous structure connecting the outer and the inner segment is of ciliary nature and for this reason it is proposed to designate it as "the connecting cilium." This conclusion is based mainly on the similarity of organization that the connecting cilium has with ordinary motile cilia which, as it is known, possess a structural submicroscopic pattern ubiquitously encountered, from protozoa to highest vertebrates (4) and probably similar to the one found in plant cilia. Our description of the cross-sections of the connecting cilium at different levels almost duplicates the description of Fawcett and Porter (4) of the cilia of mammals. Here too there is a typical basal body and a free port on. Each cilium possesses 9 pairs of peripheral filaments surrounded by an outer membrane. The main difference concerns the two internal single filaments of the cilium which are observed infrequently in this material. It is interesting to note that in usual cilia the central pair of filaments is not constantly present and tends to disappear near the basal body.

The upper portion of the connecting cilium is considerably altered after its connection with the outer segment. The 9 pairs of filaments become separated as they penetrate deeply into the outer segment. Their terminal limits cannot be ascertained with certainty from our electron micrographs but there are some indications from our study of morphogenesis of the outer rod segment (5) that these filaments may reach almost the distal end of the rod and that along the way they may be connected with the rod sacs or discs of the outer segment.

The interpretation of the connecting filaments as a cilium is further strengthened by the study of the submicroscopic morphogenesis of the rod

to be described elsewhere (5). This study permits one to conclude that the entire outer segment of the rod results from the differentiation of the distal portion of an original cilium, the proximal undifferentiated part of which remains in the adult as the *connecting cilium.*

This interpretation is not new, Fürst (14) in 1904 observed a diplosome in the inner segment of the rods and cones from which apparently a fine filament extended toward the outer segment and since then the ciliary nature of this filament has been described several times in the literature particularly with regard to the embryogenesis of the photoreceptors (for literature see references 15, 16, 5).

Homologizing the "connecting fibers" with ciliary filaments permits also an interpretation of the cross-striated fibrils described by Sjöstrand (3) as being in direct continuity with the "connecting fibers" in the inner rod segment of the guinea pig retina. Cross-striated fibers have been observed to constitute the ciliary rootlets particularly in invertebrate cilia (4) but they are poorly developed if not entirely absent in mammalia. In our material we have not observed such cross-striated fibrils and only a diffuse dense material is connected with the basal corpuscles of the cilia. Still another similarity with cilia is the fact that the cytoplasm beneath the basal corpuscles in ciliated epithelium is more richly supplied with mitochondria than the rest. This condition reaches its maximal expression in the inner segment of the rods in which mitochondria are exclusively concentrated in the distal part of the inner segment in the so called ellipsoid. This fact previously shown by Sjöstrand (3) with the electron microscope is also mentioned in the classical cytological literature (see reference 17).

Sjöstrand (3) stresses the fact that the inner and the outer segment are entirely separated except for the bundle of "connecting fibrils." This is true to a great extent but one should stress the fact that the surface membrane of the cilium is in direct continuity with the membranes of the outer and the inner segments (Text-fig. 1). This continuity of membranes should not be excluded in the explanation of the conduction of the excitatory state originated at the level of the double membrane sacs or discs of the outer segment by photochemical reactions. In fact the conduction of excitations is generally explained as a membrane phenomena, and in this connection it is to be noted that the structural units or sacs of the outer segment have an intimate structural relationship with the surface membrane (see Fig. 2). Our hypothesis regarding the functional significance of the connecting bundle of fibers considers it as a structure representing a remnant or vestige of a cilium whose upper portion becomes differentiated into the structural units or sacs of the outer segment. The surface membrane, which is common to all three portions

of the rod (outer and inner segment and cilium), and not the filaments of the cilium would probably be the site of conduction of the excitatory state down to the rod fiber and to the first synaptic junction.

Our observations on the structure of the inner segment reveal the presence of other components observed in all cell types. We will not discuss here the observation of material representing a Golgi zone or complex (12), the vacuoles and canaliculi similar to the endoplasmic reticulum of Porter (6) and its relationship with dense particles of about 80 A corresponding to those described by Palade (7). We want only to call attention to the finding of long protofibrils with denser smooth edges and of about 160 to 200 A in diameter which are observed in the proximal part of the internal segment and which collect into a definite bundle to constitute the rod fiber. This fibrillar component is essentially similar to the neuroprotofibrils observed in isolated axoplasm of nerves (13) and in sections of nerve cells particularly at the origin of the nerve axon. This finding is of particular interest for an interpretation of the nature of rod cells, because it would indicate the presence therein of a component that can be considered to be characteristic of nervous elements. These neuroprotofibrils are observed not only in the inner segment and in the outer rod fiber leading to the rod nucleus but also in the inner rod fiber starting at the rod nucleus and ending at the synaptic spherule. At this point the neuroprotofibrils are replaced by another component found in the synaptic junctions; the so called synpatic vesicles (18, 19, 11).

Thus the long rod cells, by the differentiation of a cilium at the distal end and its transformation into an apparatus for the reception of photochemical stimuli and by the nervous differentiation of the rest of the cytoplasm including the rod fibers and their terminal endings, seem to be specifically organized for the function of receiving the light stimuli, of conducting the excitatory state, and of transmitting it to the following neurone at the primary synaptic junction.

SUMMARY

The submicroscopic organization of the retinal rods of the rabbit has been studied with high resolution electron microscopy in thin longitudinal and cross-sections. The outer rod segment consists of a stack of flattened sacs or cisternae each of them limited by a thin homogeneous membrane of about 30 A. The membrane of the rod sacs is attached to the surface membrane and is also in continuity with short tubular stalks of about 100 to 150 A which apparently end in relation with the connecting cilium.

The bundle of filaments that constitute the connection between the outer and the inner segments is described under the name of *connecting cilium.*

This fibrous component has a structure that is very similar to that of the cilium. It shows 9 pairs of peripheral filaments of about 160 A in diameter, a matrix material, and a surface membrane. Very infrequently two central single filaments are observed. The connecting cilium has a typical basal body in the inner segment; its distal end penetrates the outer segment, where it establishes some structural relation to the rod sacs. The relationships and submicroscopic organization of the connecting cilium were studied in longitudinal and in cross-sections passing at different levels of the rod segments.

The inner rod segment shows two distinct regions: a distal and a proximal one. The distal region, corresponding to the ellipsoid of classical histology is mainly composed of longitudinally packed mitochondria. It also contains the basal body of the cilium, vacuoles of the endoplasmic reticulum, dense particles, and intervening matrix with very fine filaments.

In the proximal region of the inner segment the mitochondria are lacking and within the matrix it is possible to recognize elements of the Golgi complex, vacuoles of the endoplasmic reticulum, dense particles and numerous neuroprotofibrils of 160 to 200 A in diameter which collect and form a definite bundle at the exit of the rod fiber.

The interpretation of the connecting fibers as a portion of a cilium and of the outer segment as a differentiation of the distal part of a primitive cilium are discussed. The importance of the continuity of the surface membranes of the outer segment, connecting cilium, and inner segment is emphasized and its possible physiological role is discussed.

REFERENCES

1. Schmidt, W. J., *Zellforsch u. mikroskop. Anat.*, 1934, **22,** 485.
2. Sjöstrand, F. S., *J. Cell and Comp. Physiol.*, 1953, **42,** 15.
3. Sjöstrand, F. S., *J. Cell and Comp. Physiol.*, 1953, **42,** 45.
4. Fawcett, D. W., and Porter, K. R., *J. Morphol.*, 1954, **94,** 221.
5. De Robertis, E., data to be published.
6. Porter, K. R., *J. Exp. Med.*, 1953, **97,** 727.
7. Palade, G. E., *J. Biophysic. and Biochem. Cytol.*, 1955, **1,** 59.
8. Palade, G. E., *J. Exp. Med.*, 1952, **95,** 295.
9. Porter, K. R., and Blum, J., *Anat. Rec.*, 1953, **117,** 685.
10. Palade, G. E., *Anat. Rec.*, 1952, **114,** 427.
11. De Robertis, E., and Franchi, C. M., *J. Biophysic. and Biochem. Cytol.*, 1956, **2,** 307.
12. Dalton, A. J., and Felix, M. D., *Am. J. Anat.*, 1954, **94,** 171.
13. De Robertis, E., and Franchi, C. M., *J. Exp. Med.*, 1953, **98,** 269.
14. Fürst, C. M., *Lunds Univ. Arrskr.*, 1904, **40,** 1.

15. Kolmer, W., *in* Handbuch der Mikrospischen Anatomie des Menschen, (von Möllendorff, W., editor), Berlin, Springer, 1936, **3,** pt. 2, 295.
16. Detwiler, S., Vertebrate Photoreceptors, New York, The Macmillan Company, 1943.
17. Leplat, G., *Anat. Anz.*, 1914, **45,** 215.
18. De Robertis, E., and Bennett, H. S., *J. Biophysic. and Biochem. Cytol.*, 1955, **1,** 47.
19. De Robertis, E., *Act. Neurol. Latinoam.*, 1955, **1,** 3.

EXPLANATION OF PLATES

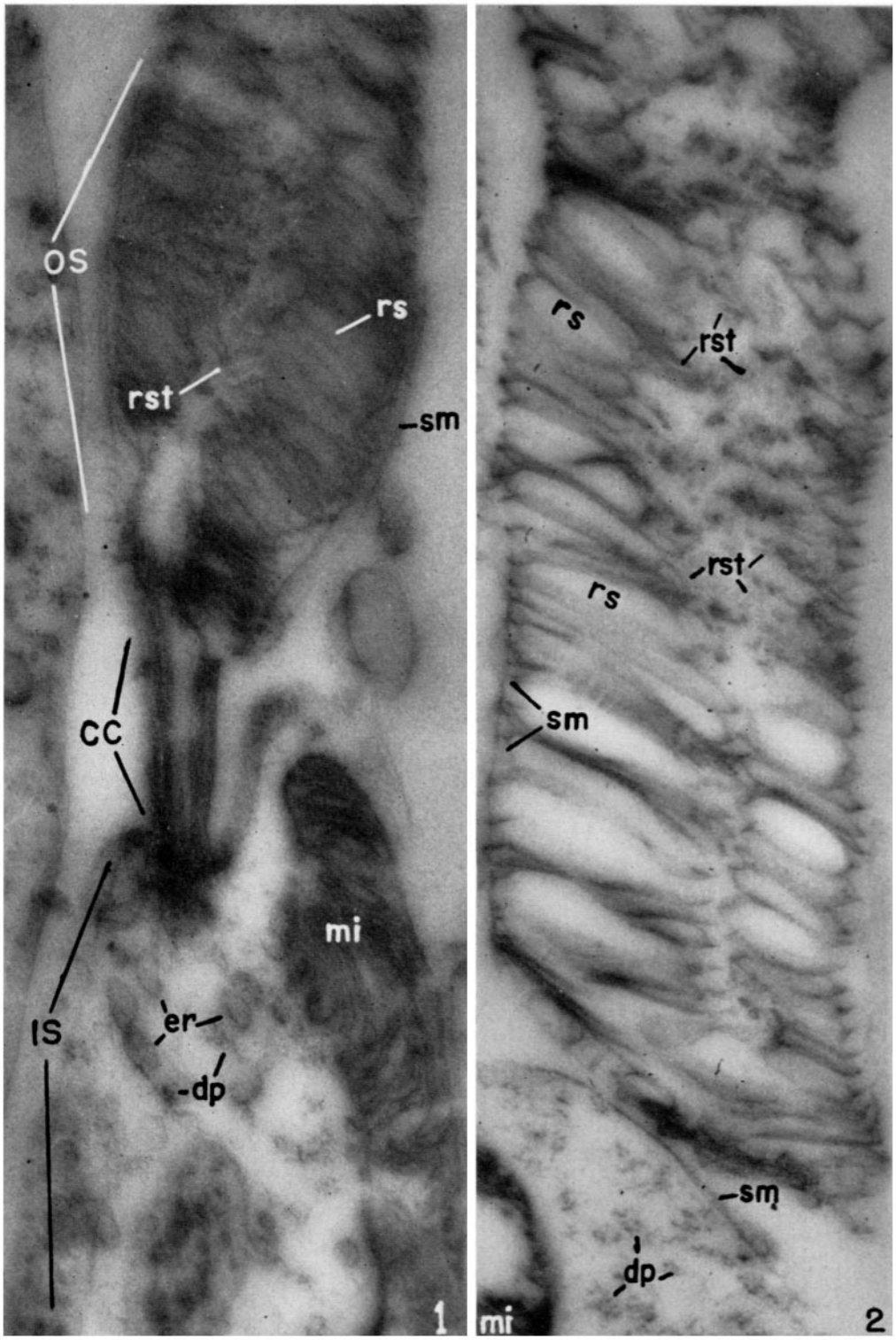
Description of Figures

bb, basal body.
CC, connecting cilium.
dp, dense particles.
er, endoplasmic reticulum.
GS, Golgi substance.
IS, Inner rod segment.
m, matrix of cytoplasm
mi, mitochondria.
mic, mitochondrial crista.
mv, microvillus.
nf, neuroprotofibrils
OS, outer segment.
rs, rod sacs.
rst, rod sacs tubules.
RF, rod fiber.
RN, rod nucleus.
sm, surface membrane.

PLATE 68

FIG. 1. Electron micrograph of a limited region of retinal rod cell (rabbit) which shows: a portion of the outer segment (*OS*) constituted by the rod sacs (*rs*) and limited by the surface membrane (*sm*); the connecting cilium (*CC*) showing several longitudinal filaments; and a small part of the distal region of the inner segment (*IS*) containing large mitochondria (*mi*), vacuoles of the endoplasmic reticulum (*er*), and dense particles (*dp*). In the outer segment note the short tubular stalks (*rst*) which connect the rod sacs with a region which is in continuity with the cilium (see further description in the text). × 49,000.

FIG. 2. Electron micrograph of the outer segment of the retinal rod showing that it is composed of a stack of rod sacs (*rs*). The cavity shown by the rod sacs is greatly exaggerated by the fixation but this helps to show their constitution and the intimate connection of the sacs with the surface membrane (*sm*). Note the short tubular stalks (*rst*) which connect with the rod sacs. (See description in the text). × 44,500.



(De Robertis: Submicroscopic organization of retinal rods)

PLATE 69

FIG. 3. Electron micrograph illustrating a longitudinal section of the connecting cilium with its basal body (*bb*), the ciliary filaments and the surface membrane (*sm*). On the cilium at the right the lines *a*, *b*, *c*, *d*, *e*, indicate the different levels of the cilium which are shown in the cross-sections of Figs. 4 to 10. × 49,000.

FIG. 4. Cross-section through the upper portion of the connecting cilium at (*a*) showing the ciliary filaments in intimate relationship with the rod sacs (*rs*) of the outer segment. × 34,500.

FIG. 5. Cross-section at the level of *c* showing the 9 peripheral filaments and the central less dense core with the faint cross-section image of two single filaments. The position occupied by the connecting cilium in relation to the recess in the inner segment is clearly shown. × 58,000.

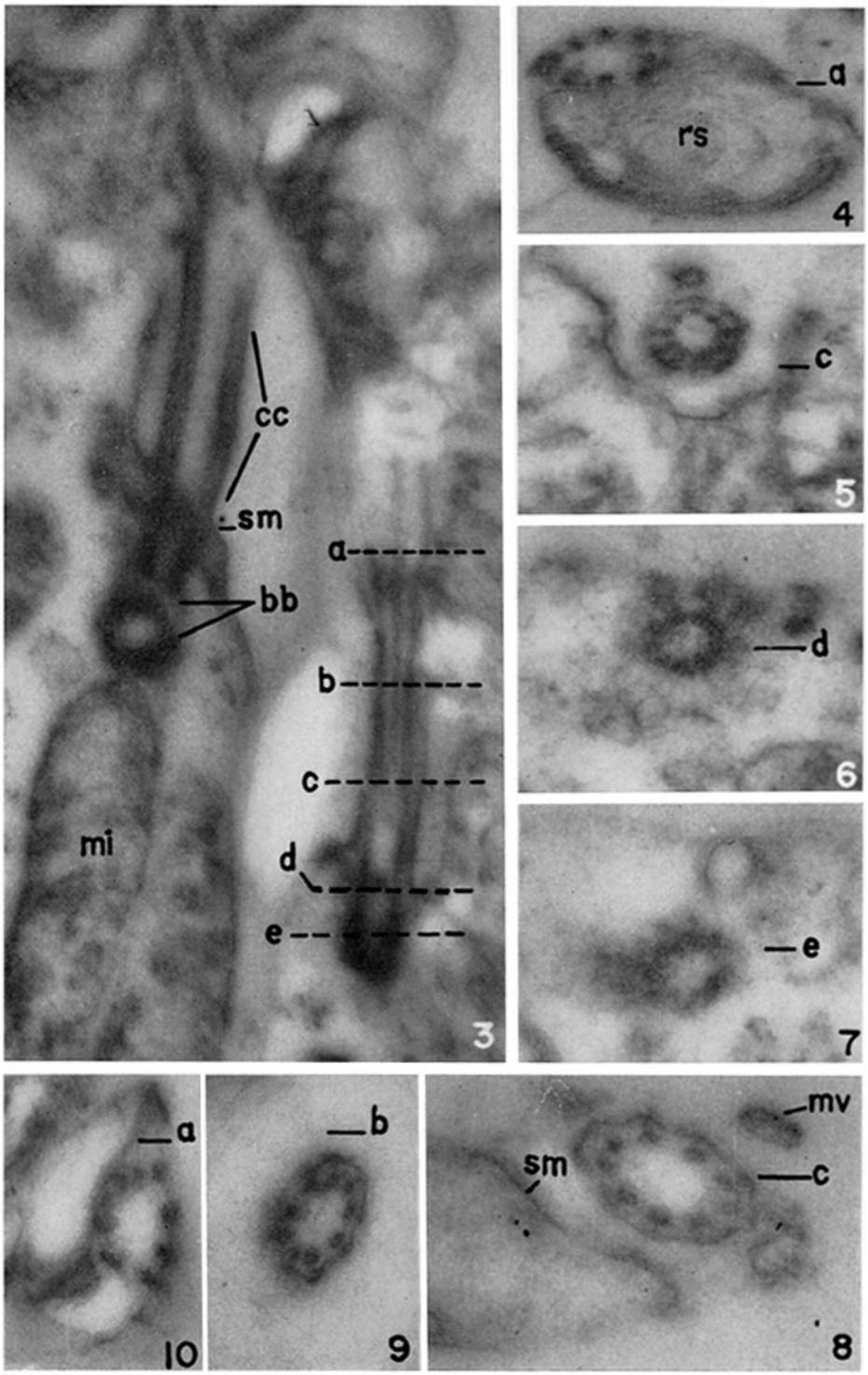
FIG. 6. Cross-section at the level of *d* near the basal body. (See description in the text). × 58,000.

FIG. 7. Cross-section at the level of the basal body (*e*) showing the asymmetrical distribution of dense material and the cross-section of tubular structures (see description in the text). × 66,000.

FIG. 8. Cross-section of the free portion of the connecting cilium (*c*) showing the 9 pairs of peripheral filaments with their annular appearance. Note the wavy disposition of the surface membrane (see further description in the text). × 81,000.

FIG. 9. Cross-section of the free portion of the cilium at the level of *b* (see description in the text). × 66,000.

FIG. 10. Cross-section at the level of *a* showing the relationship of the 9 pairs of ciliary filaments with the rod sacs of the outer segment. × 48,000.

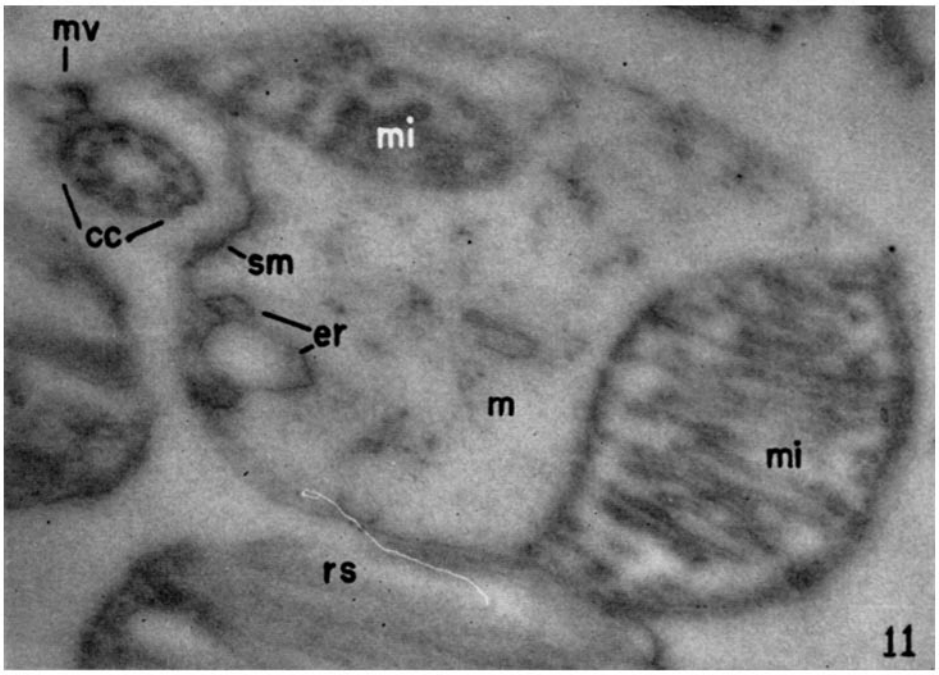


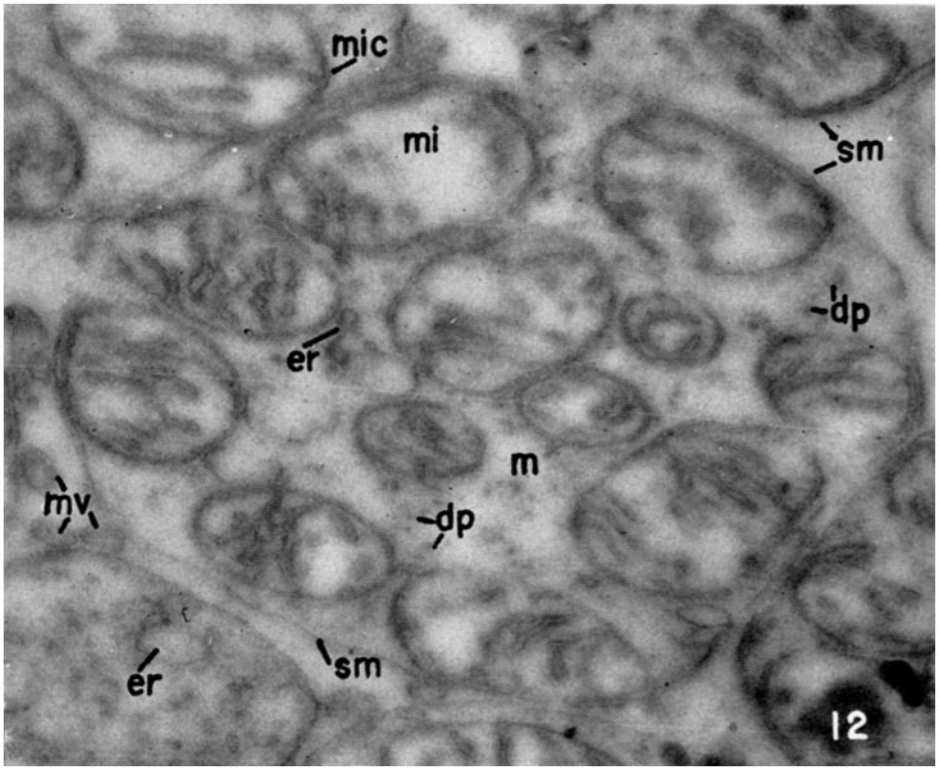
(De Robertis: Submicroscopic organization of retinal rods)

PLATE 70

FIG. 11. Cross-section of the distal portion of the inner segment of the rod at the level of the connecting cilium (*CC*) showing large mitochondria (*mi*), endoplasmic reticulum (*er*), and cytoplasmic matrix (*m*). × 54,000.

FIG. 12. Cross-section of the distal portion of the rod inner segment (ellipsoid) showing the profiles of 12 mitochondria (*mi*). The mitochondria have a definite double membrane and the mitochondrial cristae are clearly shown to be folds of the inner membrane (see at *mic*). In between the closely packed mitochondria a few elements of the endoplasmic reticulum and dense particles are seen. × 48,000.

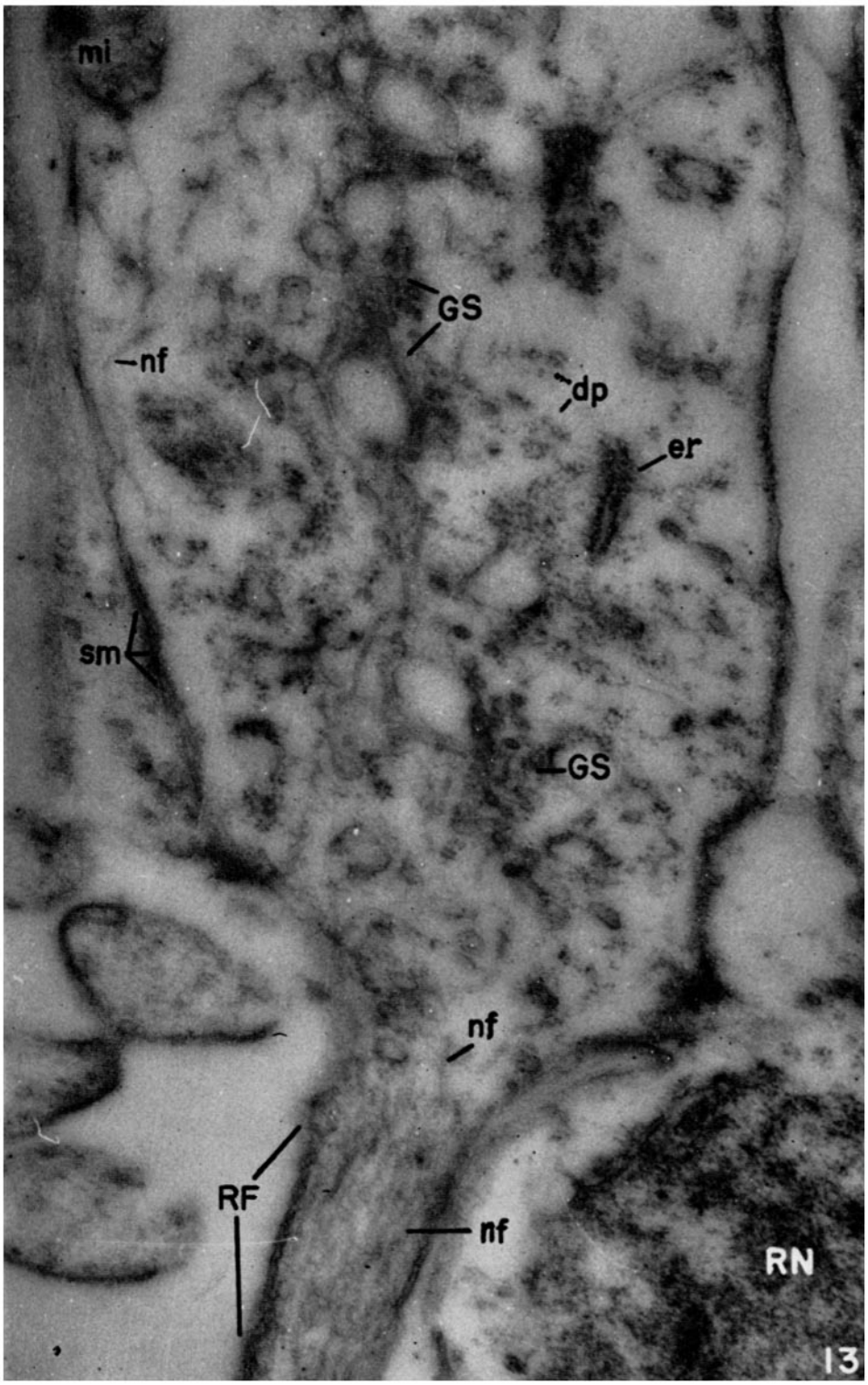




(De Robertis: Submicroscopic organization of retinal rods)

PLATE 71

FIG. 13. Electron micrograph illustrating the submicroscopic organization of the proximal region of the inner segment (see the description in the text). Note in the center the elements of the Golgi complex (*GS*) and in the rest of the segment the numerous neuroprotofibrils (*nf*) which collect at the exit of the rod fiber (*RF*). × 49,000.



(De Robertis: Submicroscopic organization of retinal rods)