SYNAPTIC ORGANIZATION OF CONE CELLS IN THE TURTLE RETINA

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[Plates I to VIII]

CONTENTS

The intercellular junctions of cone pedicles in the turtle retina were studied electronmicroscopically in tissue prepared by conventional techniques or impregnated by the method of Golgi. Dendritic branchlets of bipolar cells make specialized contacts with the basal surface of the pedicles. Processes ending laterally to wedge-shaped projections (synaptic ridges) of the pedicles probably belong always to horizontal cells, and make proximal and distal (to the synaptic ridges) junctions with the pedicles. Processes ending opposite the apex of the synaptic ridges are engaged also in two kinds of specialized contacts, termed apical and distal junctions. Basal processes of the cone pedicles make specialized contacts with adjacent pedicles, and with unidentified processes at the outer plexiform layer; their endings abut upon horizontal cell processes lodged within the pedicles of other cone cells.

Introduction

The synapses of the retinal visual cells have been probably more assiduously studied with the electron microscope than any other synapses in the central nervous system of vertebrates. Their main structural features were described by Sjöstrand (1953), DeRobertis & Franchi (1956), and Ladman (1958). Some of the sites of contact with second-order neurons were then identified

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by means of serial sectioning (Sjöstrand 1958; Missotten 1965), or electron microscopy of Golgi-stained retinas (Stell 1965, 1967). Furthermore, significant new detail has been added by extending the early observations to a variety of species (Cohen 1961, 1963, 1965; Dowling & Boycott 1966; Dowling 1968; Dowling & Werblin 1969). It is not without hesitation, therefore, that one undertakes a morphological study of visual cell synapses in yet another retina. Nevertheless, the turtle retina offered a special incentive in that the size of some of its neurons appeared to be suitable for intracellular recording with microelectrodes; thus, there could be hope that the morphological data would eventually find their electrophysiological counterparts.

Preliminary observations (Lasansky 1969) revealed interesting aspects of the structure of junctions between the basal surface of the cone pedicles and some unidentified cell processes. The observations to follow will show that some or all of the unknown processes belong to bipolar cells; they were identified in thin sections of turtle retinas stained by the method of Golgi (Stell 1965). The same approach helped to determine the destination of horizontal cell processes, and of basal processes of the cone pedicles. In addition, conventional methods of tissue preparation provided new data on the structure of cone cell synapses, and they will be reported also.

Methods

The posterior poles of eyes of the turtle *Pseudemys scripta elegans* were excised under ordinary conditions of illumination, and fixed overnight in cold 2 % glutaraldehyde (Sabatini, Bensch & Barrnett 1963) in 0.1 M phosphate buffer (pH 7.4). The retina and choroid were then detached from the sclera, washed in the phosphate buffer, and fixed for 1 h in cold 1 % OsO_4 in the same buffer.

Adding 4 % formaldehyde to the initial fixative did not improve significantly the general quality of the fixation, and resulted in a diminished difference in opacity between the cytoplasm of the visual cells and that of the second-order neurons. Since this difference was a very useful feature of glutaraldehyde fixation, few observations were made on glutaraldehyde-formaldehyde-fixed material, which is represented only by figures 5, plate I and 19, plate V.

Osmium tetroxide was also tried as a primary fixative. The retinas had then to be detached from the pigment epithelium to make up for the lack of penetrability of the fixative. Unfortunately, this manoeuvre caused the loss of many outer segments of the visual cells, which then

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Description of plate I

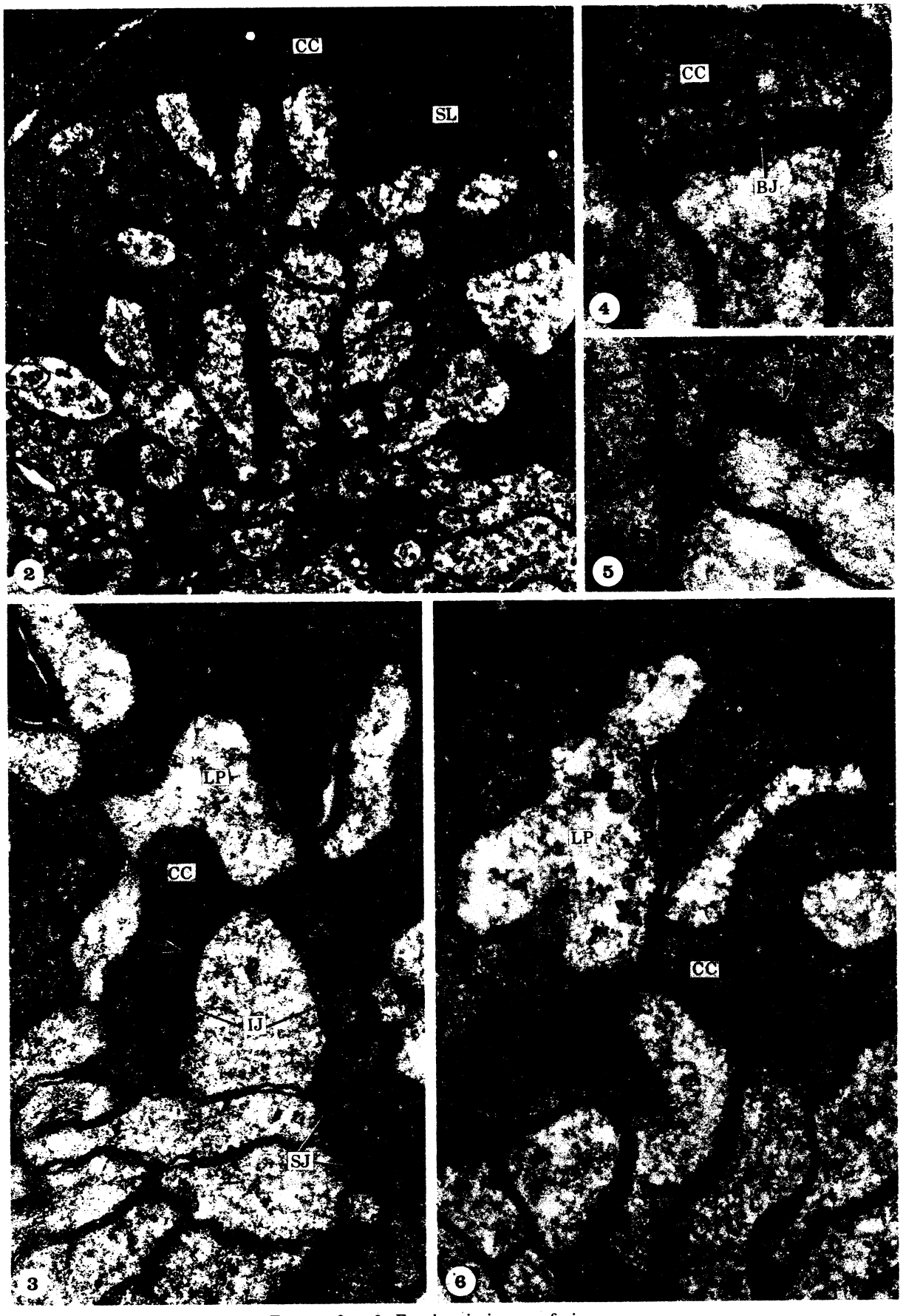
Figure 2. Electron micrograph of a cone pedicle (CC) in the turtle retina. Several basal junctions are indicated (arrows); they do not have any obvious spatial relationship to the synaptic lamellae (SL), and synaptic vesicles are few or absent within the immediately adjacent cone cell cytoplasm. (× 32000.)

Figure 3. Part of the basal surface of a cone pedicle (CC) showing one invaginated (IJ) and two possibly superficial (SJ) basal junctions. Focal accumulations of opaque cytoplasm (arrows) are seen on the cone cell membrane at the invaginated junction, which shows almost only narrow-gap segments. The tip of the invaginating process is close to a lateral process (LP) of a dyad. (× 65000.)

Figure 4. Opaque bars (longer period; see text) span the gap of a basal junction (BJ). CC, cone pedicle. (× 120000.)

Figure 5. Cross-striations (arrow) within the opaque cytoplasmic layer on the cone cell side of a basal junction. (× 108000.)

Figure 6. Face-on view of an invaginated basal junction. An orthogonal lattice pattern (arrow) is formed by two intersecting sets of equally spaced lines. The tip of the invaginating process is in contact with a lateral process (LP) of a cone dyad. CC, cone pedicle. (× 65000.)



FIGURES 2 to 6. For descriptions see facing page.

appeared swollen and almost devoid of cytoplasmic matrix. None of the present observations, therefore, was carried out in tissue fixed only in osmium tetroxide.

After fixation, some of the retinas were dehydrated in ethanol and embedded in Epon (Luft, 1961). This material invariably showed many discontinuities in the cell membranes, particularly at the boundaries between visual and horizontal cells; therefore, it was used only for some special purposes, and is illustrated in figures 4, plate I and 15, plate IV.

The cell membranes were better preserved when the blocks of tissue were soaked for 2 h, before dehydration, in a cold 2 % solution of uranyl acetate in maleate buffer (Farquhar & Palade 1965; Karnovsky 1967). All the micrographs included in this report—except those above noted otherwise and those of Golgi-stained material—illustrate tissue postfixed in uranyl acetate.

The sections from all blocks were stained with uranyl acetate (Watson 1958) and lead citrate (Reynolds 1963).

Preparation of Golgi-stained retinas for light and electron microscopy

The procedure followed has been described by Stell (1965). A minor departure consisted of prefixing the eyes overnight in cold glutaraldehyde-phosphate buffer as described above. The retina and choroid were then detached from the sclera, and soaked 2 h in cold 1 % OsO_4 in 3 % potassium dichromate, 1.5 to 2 days at room temperature in 0.25 % OsO_4 in 3 % potassium dichromate, and 2 days in 1 % silver nitrate. The treatment with the weaker OsO_4 solution and the silver nitrate was repeated once. An essential requirement for successful impregnation appeared to be the slicing of the retinas prior to OsO_4-dichromate fixation into strips about 2 mm wide.

The above procedure gave good impregnation of many retinal neurons. Those at the area centralis, however, were usually either unstained or so massively stained that it was not possible to obtain isolated cells for electron microscopic observation. The visual cells were also rarely stained. In order to trace their basal processes it was highly desirable to have many cone cells stained in a single block of tissue. This result was achieved only when the retinas were detached from the pigment epithelium prior to fixation, a procedure which, as already noted, caused extensive cytoplasmic extraction in many visual cells.

The impregnated blocks were dehydrated in ethanol, embedded in an Epon mixture without nadic methyl anhydride, and sectioned at 50 μm in a rotary microtome. The sections were mounted on glass slides with unpolymerized Epon and plastic coverslips, and examined in a light microscope after hardening overnight at 60 °C. Stained cells on a background uncontaminated by other stained elements were then selected and, after lifting the plastic coverslips, detached from the slides with the aid of a single-edge razor blade and remounted on Epon bases.

Thin sectioning of this material presented no special problems, except that most of the silver deposit was usually lost, leaving empty spaces in the tissue (Stell 1965). No improvement resulted from collecting the sections in saturated silver chromate solution (Blackstad 1965), and there was some suggestion that the deposits were fragmented or dragged by the knife, rather than dissolved in the water of the collecting boat. Since the identification of the stained processes in the electron microscope was in no way affected by the loss of the silver deposit, no further efforts were made to try to remedy this situation.

Observations

The visual cells of the turtle are single and double cones, and rods (Walls 1963). Because the latter are few—less than 10% of the visual cells in *Pseudemys*—turtle retinas have been sometimes regarded as pure cone retinas. Their duplex nature, however, first shown by Walls (1934), has been confirmed by the analysis of their spectral sensitivity with electroretinographic techniques (Deane *et al.* 1958).

Only the cone cell synapses will be considered in the following (except figures 21 and 27, plate VI, which show rod endings), since the information on rods is still insufficient. This is not only because rods are fewer, but also because the junctional surface of their endings is smaller, which further decreases the number of junctions appearing in any field of observation. The present observations had to be limited, furthermore, to the retina outside the area centralis, a need dictated by the lack of Golgi-stained material suitable for electron microscopical study of the cells in this area (see Methods).

Synaptic organization can be said to be the subject of this report in so far as it deals with structural aspects of the cone cell endings, but few of the intercellular contacts to be described can be safely assumed to be synapses. Therefore, they will be referred to as junctions, and this term will be used in its strict morphological sense, that is, to indicate any area of intercellular contact where the cell surfaces, or the intervening gap, or both, show any specialization which is clearly related to that area and contact.

Basal junctions of cone pedicles

The basal junctions link the basal surface of the pedicles to hundreds of fine cell processes (Lasansky 1969), and can be readily distinguished from other junctions of the pedicles because they are relatively superficial, and lack any associated intracellular organelles (figure 1; figures 2 and 3; plate I). When cross-sectioned in suitable planes, the basal junctions show opaque bars spanning the junctional gap (figure 4, plate I); in addition, a suggestion of

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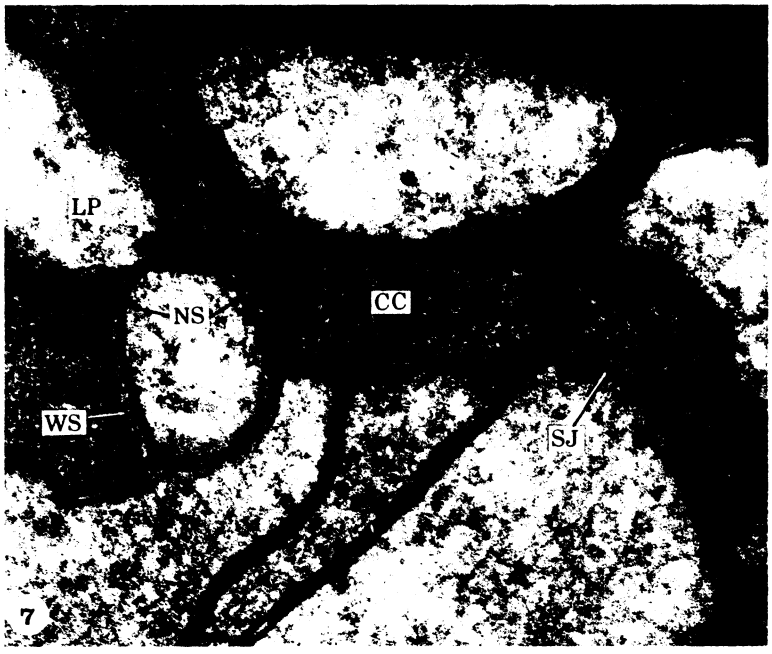
Description of plate II

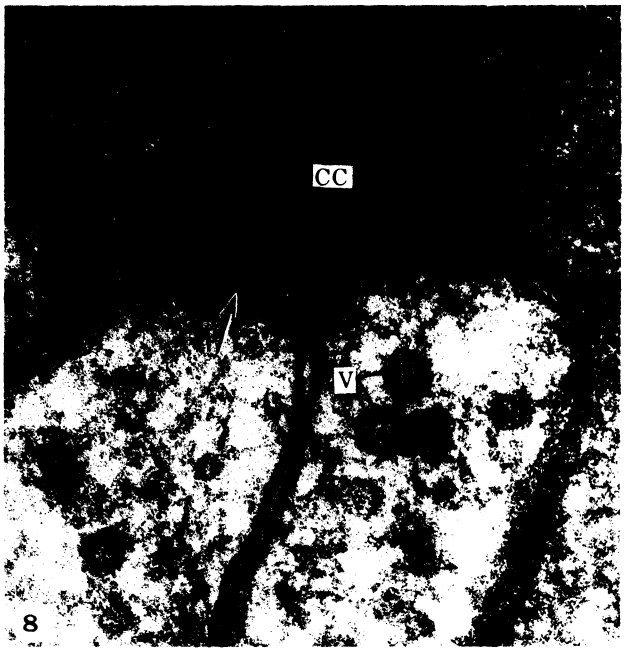
Figure 7. Wide-gap (WS) and narrow-gap (NS) segments at an invaginated basal junction. Focal accumulations, or a continuous layer of opaque cytoplasm, are seen only on the cone cell membrane at the narrow- and wide-gap segment, respectively. No surface specialization is found at the area of contact between the tip of the invaginating process and a lateral process (LP) of a nearby dyad. At another basal junction (SJ), possibly of the superficial type, the cell membranes are coated by symmetrical opaque layers. CC, cone pedicle. (× 86000.)

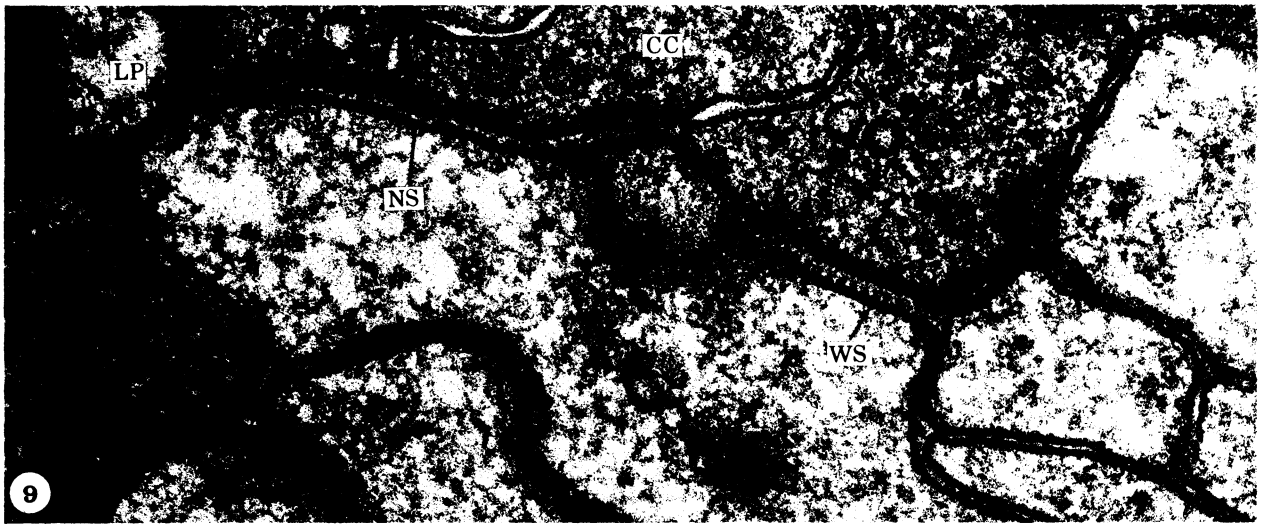
Figure 8. Two basal junctions, possibly of the superficial variety, showing only wide-gap segments (the narrow-gap area adjacent to the junction on the right shows no specialization of the gap or of the cell surfaces). A layer of opaque cytoplasm covers the inner surface of both junctional membranes, and the gap material at one of the junctions shows some cross-striation (arrow). The adjacent cone cell cytoplasm (CC) contains vesicles, but they are not particularly crowded. Vesicles (V) are also seen within the cell processes in contact with the pedicle. (× 126000.)

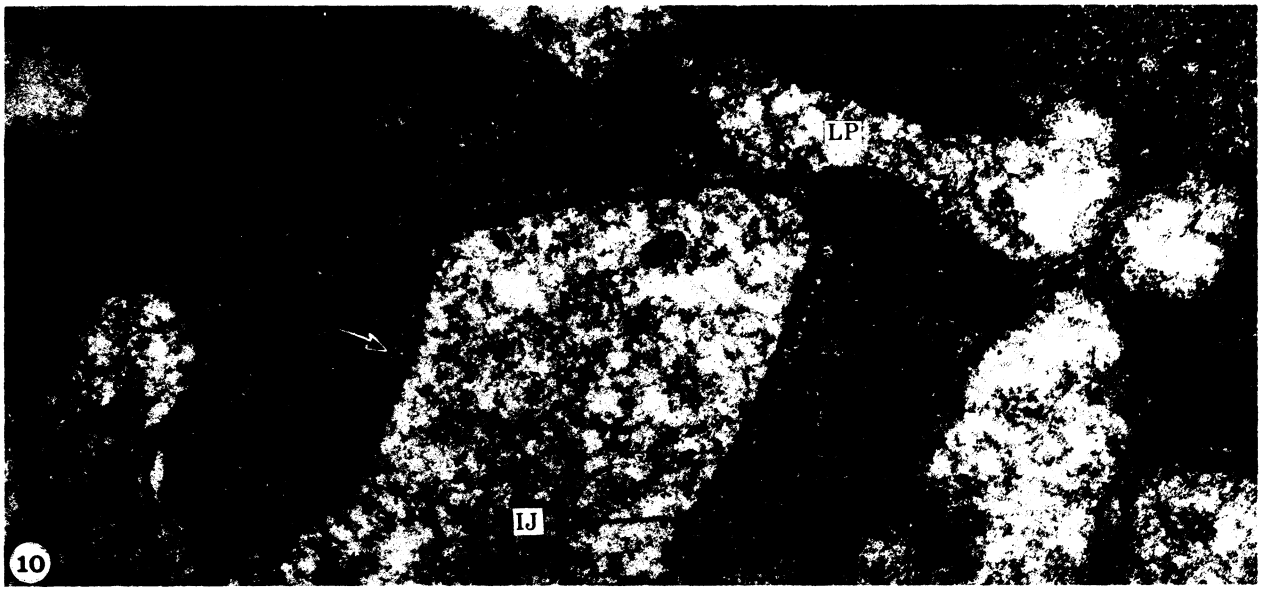
Figure 9. Invaginated basal junction. The junctional gap may be narrow and irregular (NS), or wide and uniform (WS). An opaque gap material is found everywhere; at the wide-gap segment it shows a periodicity of the shorter type. All the cone cell processes (CC) belong to the same pedicle. LP, lateral process. (× 108000.)

Figure 10. Invaginated basal junction (IJ); the wide-gap segments predominate. There is little cytoplasmic opacity on the cone cell membrane, and none on the opposite side. The junctional gap shows opaque cross-bars; at the left-hand side of the junction the period is shorter than at the other segments, and the cross-bars do not seem to reach the cone cell membrane (arrow). The tip of the invaginating process is in contact with a lateral process (LP) of a dyad. (× 100000.)









FIGURES 7 to 10. For descriptions see facing page.

cross-striation can be seen sometimes also within accumulations of opaque material lining the inner surface of the junctional membranes (figure 5, plate I). Face-on views of the junctional areas may reveal an orthogonal lattice pattern (figure 6, plate I), which presumably reflects the organization of some of the junctional components (Lasansky 1969).

Some basal junctions, which may be termed invaginated basal junctions, cover a relatively large surface in the form of a sleeve surrounding all but the very tip of the cell process in contact with the pedicle (figure 1; figure 3, plate I; figures 7, 9 and 10, plate II). The width of the junctional gap varies from about 7 to 18 nm. At some segments of these junctions the gap

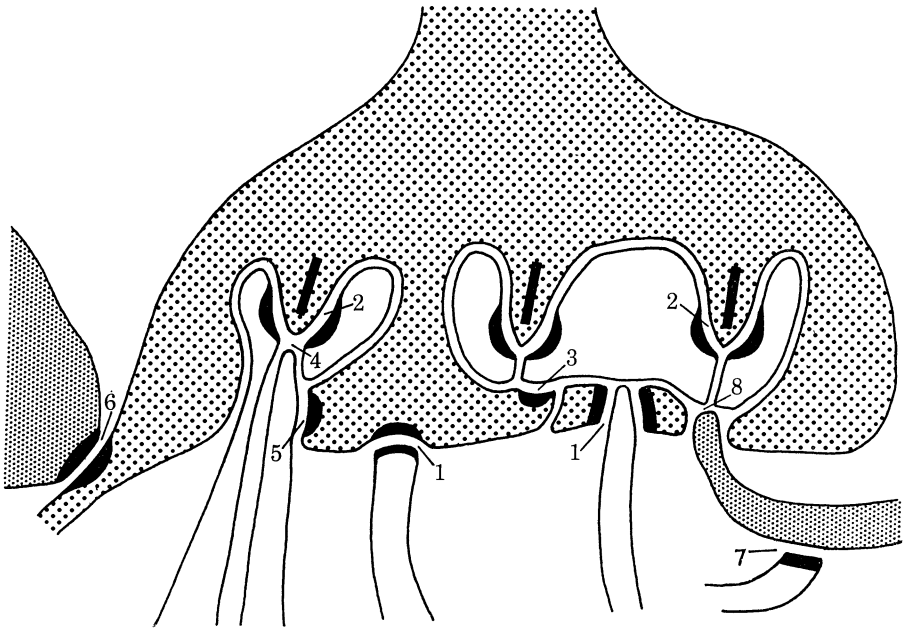


FIGURE 1. Diagram illustrating the location of the specialized contacts of a cone pedicle in the turtle retina. For greater clarity, only one or two junctions of each kind are either illustrated or indicated. 1, basal junctions (figures 3, 7, and 8, plates I and II); 2, proximal junctions of lateral processes (figures 12, 13, and 15, plate IV); 3, distal junction of a lateral process (figures 18 and 19, plate V); 4, apical junction of the central process of a triad (figures 12, plate IV and 20, plate VI); 5, distal junction of the central process of a triad (figures 20 and 21, plate VI); 6, junction with an adjacent cone pedicle (figure 38, plate VIII); 7, junction *en passant* of a basal process (figure 39, plate VIII); 8, end contact of a basal process arriving from another pedicle (figures 34 to 36, plate VIII).

is uniformly wide (16 to 18 nm) (figures 9 and 10, plate II), and the cell membranes are coated by discontinuous layers of opaque cytoplasm, which may or may not be seen, depending on the particular plane of section (figures 7 and 10). Other segments have a narrower and irregular gap-width (figure 3; figures 7 and 9), and sometimes show focal accumulations of opaque cytoplasm on the cone cell membrane (figure 3; figure 7). Since the structure of the invaginated junctions varies throughout their extent, their appearance also varies in different sections. Thus, the narrow-gap (figure 3) or wide-gap (figure 10) segments may predominate or be the only ones seen, or both types of segments may be seen at a single junction (figures 7 and 9). A gap substance which may show cross-striations is found at both kinds of segments of the invaginated basal junctions (figures 9 and 10).

Other basal junctions, referred to in the following as superficial basal junctions, differ from the previous type in that the tip of the cell processes making contact with the pedicles

is also involved in the junction and, therefore, it does not make an unspecialized contact with lateral processes (of dyads and triads), as seen at the invaginated junctions. The existence of the superficial basal junctions was established by examining serial sections of the pedicles, as it is otherwise not possible to predict from a single section whether an apparently superficial contact may or may not be seen to be invaginated at another plane of section. For this reason, the contacts labelled as superficial basal junctions in figures 3 and 7, and those shown in figure 8, should be regarded only as illustrating the most frequently observed appearance of these junctions, and not as evidence of their existence. In such typical instances, the superficial basal junctions are shallow cap-shaped contacts (figure 1); the width of the junctional gap again varies between 7 and 18 nm, but the wide-gap segments (16 to 18 nm) predominate, and usually are the only ones observed (figures 7 and 8, plate II).

When opaque cross-bars are seen within the intercellular gap at the basal junctions, they may seem to be complete bridges (figure 4), or there may be a suggestion that they end, without reaching the cone cell membrane, at about two-thirds of the distance from the membrane of the apposed cell process (figure 10). They may be evenly spaced at about 19 to 20 nm (figure 4), or at 13 to 16 nm (figures 9 and 10). The longer period may represent a lateral view of the lattice seen in tangential sections of the junctions (figure 6), with the line of vision parallel to either set of lines of the orthogonal pattern; adjacent lines in this pattern are also spaced at 19 to 20 nm. On the other hand, not even a tentative explanation can be given to the shorter periodicity. The opaque layers of cytoplasm lining the junctional membranes may contribute to the lattice pattern seen in tangential sections; they also seem to have a periodic structure (figure 5), but no measurements have as yet been made.

The synaptic vesicles of the cone cells not only fail to crowd near the junctional surfaces, but they are actually fewer than at other areas of the pedicles (figures 2 and 3, plate I; figure 11, plate III). Vesicular elements are also sometimes seen within the cell processes making basal junctions with the pedicles (figure 8, plate II; figure 21, plate VI).

Recessed junctions of the cone pedicles

The recessed junctions of the cone cells are specialized contacts with processes lodged within deep recesses of the pedicles, and clustered around the surface adjacent to the synaptic lamellae (figure 11, plate III) (DeRobertis & Franchi 1956; Ladman 1958). These appear in cross-section as pentalaminar ribbons (Lanzavecchia 1960) formed by three dark and two light layers (figures 12 to 14, plate IV). They bisect wedge-shaped projections of the pedicles —the synaptic ridges (figures 11 to 13) (Stell 1967)—and one of their edges is separated from

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Description of plate III

Figure 11. Triads (Tr) and dyads (Dy) in a cone pedicle (CC). The two triads seen are arranged in a fan-like manner, sharing a lateral process (LP_1) and the central process (CP). Another lateral process (LP_2) is shared with a dyad. A junction (J) adjacent to the triads is probably a distal junction of the central process, because of its deep location. One of the lateral processes (LP_3) of the dyad at the lower part of the figure, makes a distal junction (DJ) with a visual cell process (VP) at the distal end of the medial gap. At the same area of the other (upper) dyad no junctions are found, and the visual cell process abutting against the distal end of the medial gap belongs to the pedicle in the field of view, since it makes basal junctions (BJ) with other cell processes (see text). The area indicated by an arrow may suggest an enlarged extracellular space occupied by opaque material, but it almost certainly represents a tangential section of a visual cell process, as such spaces have not been found at this location in any other instance. SR, synaptic ridge. (× 65000.)

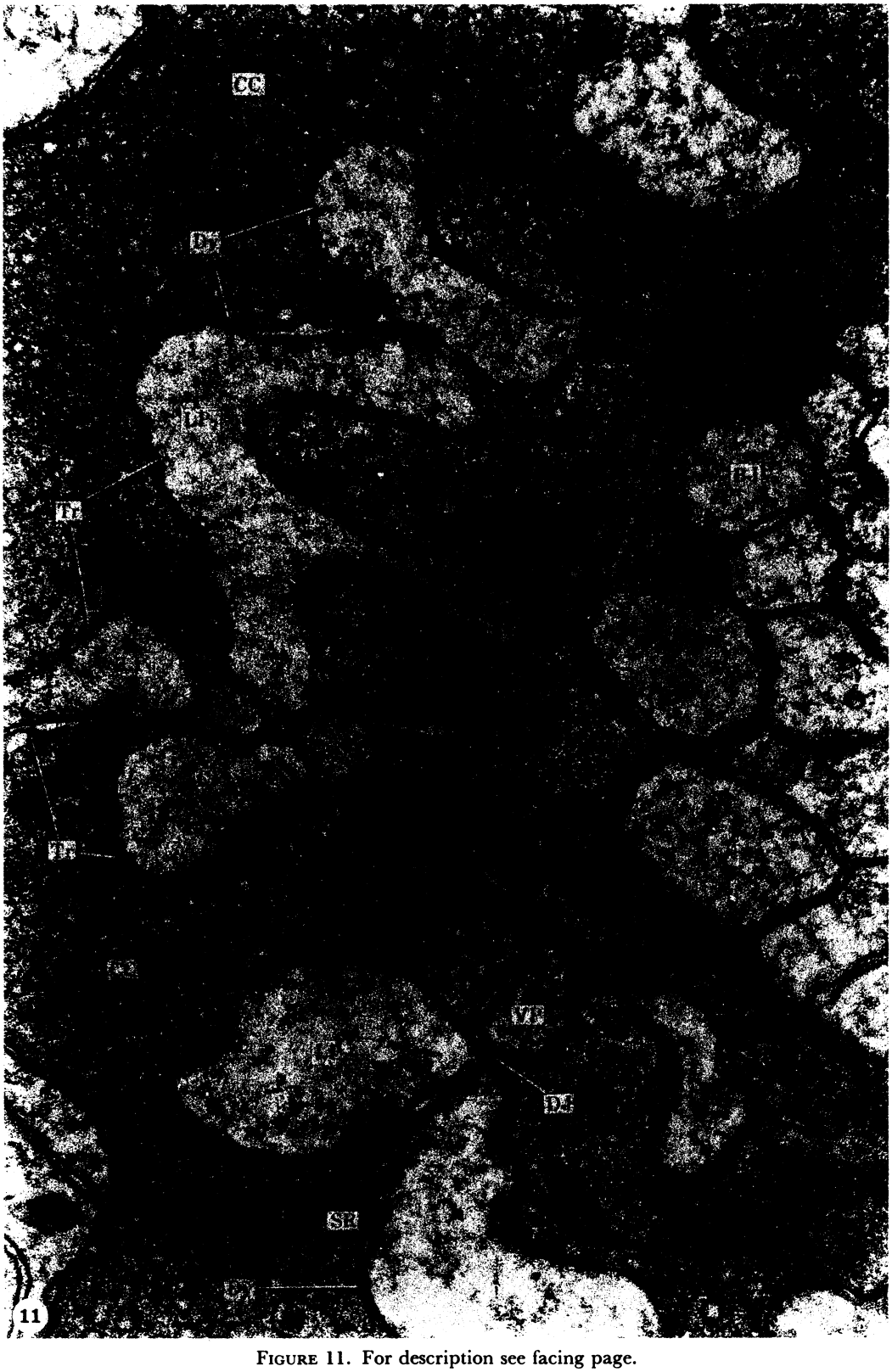


FIGURE 11. For description see facing page.

the cell membrane by an accumulation of opaque material known as the arciform density (Ladman 1958) (figures 12 and 13). In turtle cones the arciform density is seen sometimes as a closed loop attached to the edge of the lamella (figure 12).

Some of the cell processes within the recesses of the pedicles are positioned on each side of the synaptic ridges (figures 11 to 13; lateral processes), and may occasionally contain small vesicles (figure 14) (Ladman 1958). Other processes end opposite to the apex of the synaptic ridges (figures 11, 12 and 14; central processes), and are separated from it by a space containing a moderately opaque material (figure 12). A similar assembly of one central and two lateral processes has been described at cone pedicles in the primate retina and termed the 'triad' (Missotten 1965). In the turtle retina adjacent triads may share a lateral process and frequently also the central process (figure 11).

In other type of assembly the central process is missing, and the lateral processes are separated by a gap (medial gap) that can be as narrow as 5 to 6 nm (figure 11, plate III; figure 13, plate IV; figure 17, plate V). This assembly will be referred to as the dyad, in keeping with the existing terminology. Dyads also occur sometimes as fan-like pairs, or a dyad may share a lateral process with a triad (figure 11). In planes of section parallel to the retinal surface, dyads and triads have been seen to represent adjacent parts of a single type of junctional complex.

Each process of the triads and dyads makes two types of specialized contacts with the cone pedicles; they will be termed—in reference to their position relative to the synaptic ridge—proximal and distal junctions of the lateral processes, and apical and distal junctions of the central processes (figure 1).

Proximal junctions of the lateral processes

These junctions are found in both dyads and triads at the areas of contact between the lateral processes and the synaptic ridges. Their most conspicuous surface specialization is a layer of opaque cytoplasm underlying the plasmalemma of the lateral processes at the sides of the synaptic ridge. The thickness of the opaque material diminishes gradually beyond the apex (figures 12 and 13, plate IV; figures 17, plate V).

Other signs of surface specialization are ordinarily not obvious at the proximal junctions. On the visual cell side, the synaptic lamella and arciform density constitute very conspicuous junctional features, but the plasmalemma and its underlying cytoplasm do not show any specific thickening or increased density (figures 12 and 13). Any remaining doubts about the specialized nature of this area of contact are dissipated, however, by observations on retinas not postfixed in uranyl. In such material the plasmalemmas of the lateral processes and pedicles are poorly preserved, but the area of the proximal junction seems to be more stable and, therefore, it stands out more clearly (figure 15).

Near the proximal junctions, accumulations of a homogeneous opaque material are sometimes found within indentations of the cone cell membrane on the sides of the synaptic ridges (figure 16, plate IV; figure 37, plate VIII). At these areas, the membrane of the lateral processes is coated by a layer of opaque cytoplasm which is continuous with the opaque layer seen at the proximal junctions.

Distal junctions of the lateral processes

These occur only at dyads. At the distal end of the medial gap, one or more visual cell processes—which can be easily identified because of their relatively high electron opacity—abut upon the lateral processes (figure 13, plate IV). Sometimes, the gap between a visual cell process and one of the lateral processes, appears widened and filled by a moderately opaque material (figures 11, 16 to 19, and 37). This area of specialized contact will be referred to in the following as the distal junction of the lateral processes.

The structure of the distal junctions shows considerable variation. The opaque material within a widened gap may be the only specialization seen (figure 17, plate V), but on other occasions there is also some degree of parallelism between the junctional membranes (figure 11, plate III; figure 16, plate IV). The width of the junctional gap varies from 15 to 22 nm, and the profile of the junctions may be straight (figures 11, 16, and 37) or arched (figures 18 and 19, plate V). The cone cell membrane is sometimes coated by a layer of opaque cytoplasm (figures 18 and 19), which may also be found bilaterally (figure 37, plate VIII). Finally, the junctional gap may show some cross-striation (figure 19), and the distal junctions in those instances resemble the wide-gap segments of the basal junctions. This degree of structural variation is unusual for an intercellular junction, and would seem to suggest the existence of two types of distal junctions. At present, however, such division would be difficult to justify, because there is a continuous spectrum between extreme appearances (i.e. figures 17 and 19, plate V).

In some instances it is not possible to demonstrate continuity between the visual cell process involved in a distal junction and the main body of the pedicle (figure 11). In these cases the process may be the ending of a basal process originating in a distant visual cell (see below).

Description of plate IV

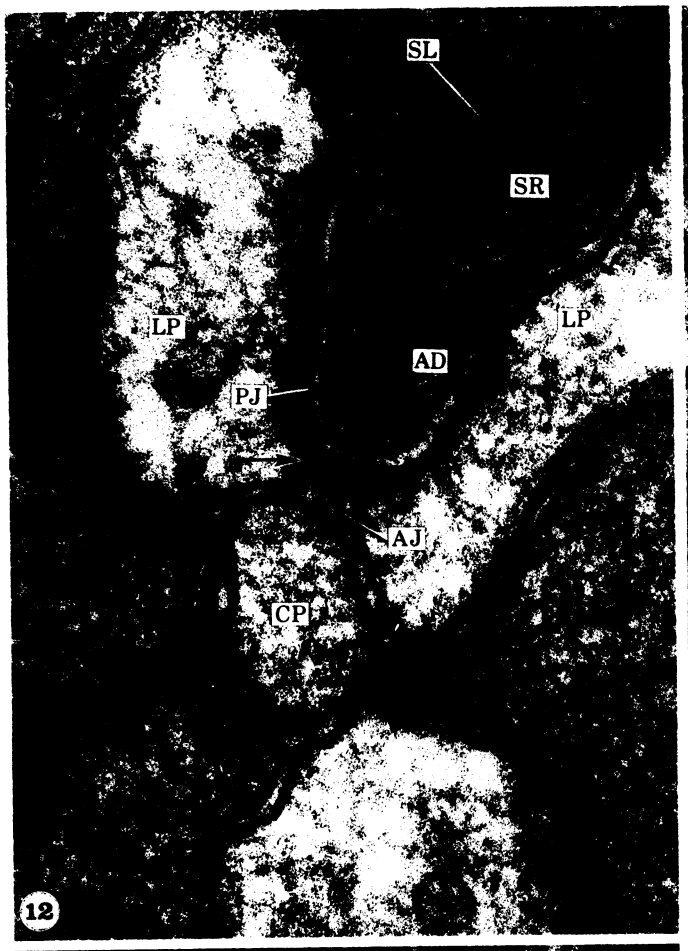
Figure 12. Triad in a cone pedicle. The synaptic ridge (SR) of the cone pedicle is bisected by a synaptic lamella (SL) showing a pentalaminar structure. The arciform density (AD) appears as a closed loop continuous with the outer edge of the lamella. At the proximal junction (PJ) the membrane of the lateral processes (LP) is coated by a thick layer of opaque cytoplasm ending (arrow) at about mid-way of the area exposed to the apical space (AJ). The apex of the central process (CP) shows no surface specialization, and the only structural feature specifically related to the apical junction is the opaque material within the apical space. Another apical space is seen on the right-hand side of the central process, but the opposite ridge does not show a lamella in this plane of section. (× 157 000.)

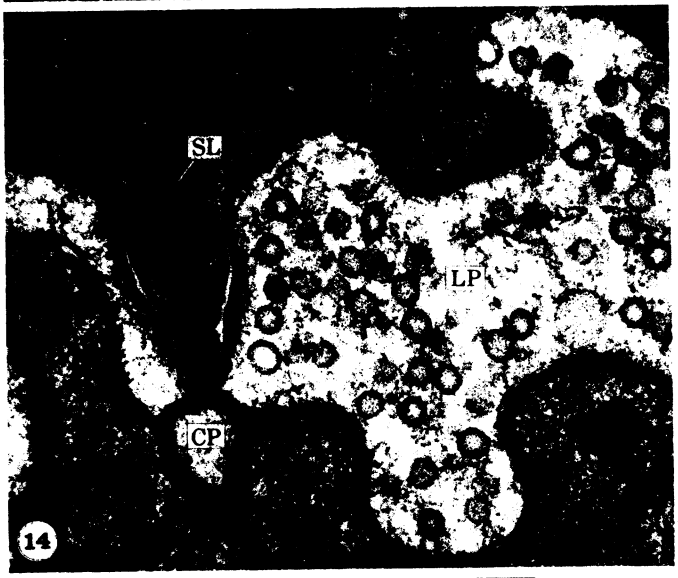
Figure 13. Dyad in a cone pedicle. Beyond the apex of a synaptic ridge (SR) of the pedicle, the lateral processes (LP) are separated from one another by a narrow medial gap (MG). At the proximal junction (PJ) with the cone pedicle, the membrane of the lateral processes shows a thick opaque coat. Visual cell processes (VP) are found at and near the distal end of the medial gap ('distal' makes reference to the distance from the apex of the synaptic ridge); no surface specializations can be seen at their contacts with the lateral processes of the dyad. SL, synaptic lamella; AD, arciform density. (× 157 000.)

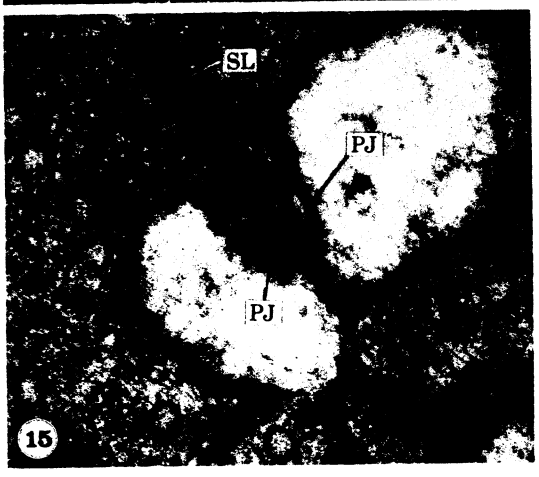
Figure 14. Triad in a cone pedicle. One of the lateral processes (LP) contains vesicles. CP, central process of the triad; SL, synaptic lamella bisecting the synaptic ridge of the pedicle. (× 63 000.)

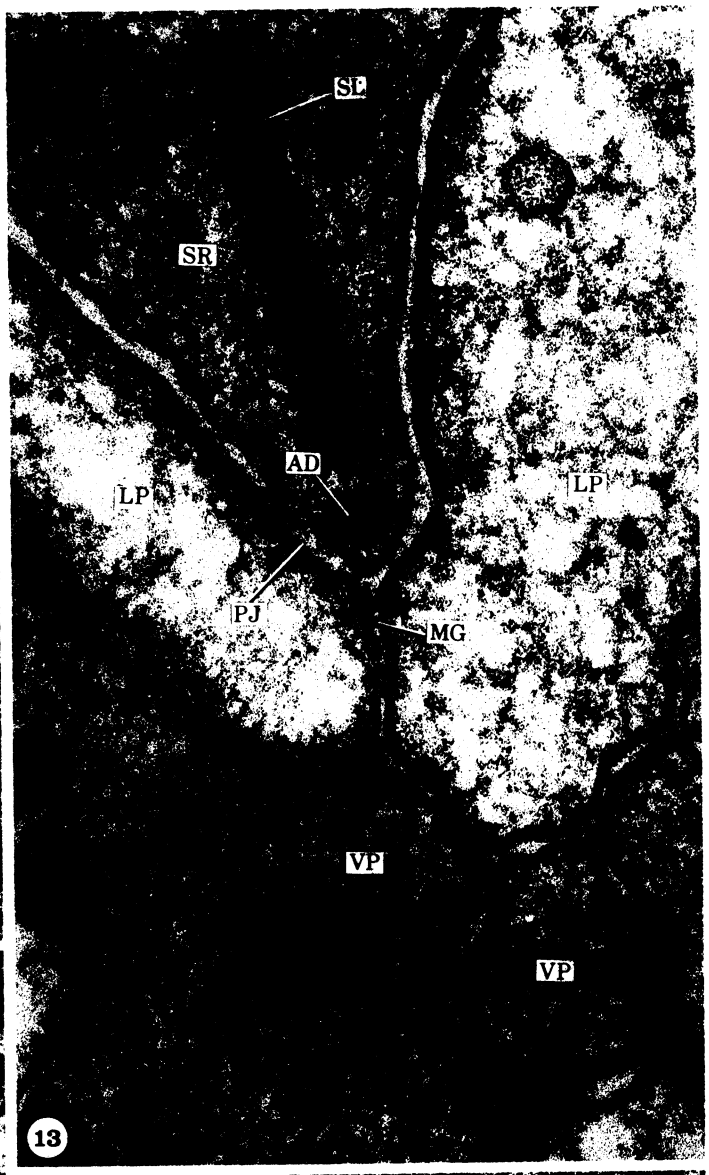
Figure 15. Proximal junctions (PJ) of the lateral processes of a dyad. The specialized nature of this area of contact is evidenced by the rigidity of the apposed cell membranes. SL, synaptic lamella within a synaptic ridge of the cone pedicle. (× 90 000.)

Figure 16. Distal junction (DJ) between a lateral process (LP) of a dyad and a visual cell process (VP). The junctional gap has a uniform width, and is occupied by an opaque material. On one side of the synaptic ridge the cone cell membrane is indented, and the resulting enlarged extracellular space (arrow) is filled by opaque material. PJ, proximal junction between the lateral process and the cone pedicle; CC, cone pedicle. (× 126 000.)









FIGURES 12 to 16. For descriptions see facing page.

On other occasions, however, the visual cell process contributing to a distal junction can be shown to belong to the same pedicle that encloses the lateral processes (figures 18 and 19). A cone pedicle, therefore, may make the two types of junctions, proximal and distal, with a single lateral process.

Apical junction of the central process of the triads

The apical junction is the area where the central process of a triad is opposite to the apex of the synaptic ridge (figure 12, plate IV; figure 20, plate VI). Within the intervening space (50 to 80 nm), which is flanked by the lateral processes, there is a moderately opaque material that has in most instances a homogeneous appearance (figure 12).

The structure of the cell surfaces bordering the apical space gives little indication as to which are in fact the junctional processes. The surface specializations at the synaptic ridge are the synaptic lamella and the arciform density, but they could be related only to the proximal junctions, as they are found also at the dyads. The membrane of the lateral processes is coated by a layer of opaque cytoplasm, which disappears gradually midway through the apical space (figures 12 and 20), and may represent just the remnants of the opaque coat present at the proximal junction. It may be assumed that the central process is involved in the apical junction, because the apical space, and its opaque content, are seen only at triads. Nevertheless, the surface of the central process shows no evidence of specialization (figure 12).

Distal junction of the central process of the triads

These junctions are structurally similar to basal junctions with respect to the presence of cytoplasmic opacities, and the width and opaque content of the intercellular gap (figure 11, plate III; figures 20 and 21, plate VI). No clear evidence has been seen, however, of a periodic organization of their gap material, but this lack of evidence could be due to an insufficient number of observations. The central processes appear rather infrequently in any field of view and, even then, the distal junction may not be included in the plane of section (figure 12, plate IV). Conversely, the basal junctions are present in almost every section of the pedicles, so that there are more chances of obtaining the critical orientation necessary to see clearly a cross-striation in the gap material. When this requirement is not met, the gap material at the basal junctions may look quite homogeneous, just as it may be the case at the distal junctions of the central processes (compare, for instance, the distal junction in figure 20, with the right-hand side basal junction in figure 8, plate II).

Cone cells *Light microscopy of retinas stained by the method of Golgi*

Two types of cone endings were identified in Golgi-stained turtle retinas; their relationship to the two kinds of cone cells is not known, because double cones were never impregnated as a pair, and perhaps not at all. One type of ending is a round pedicle, about 7 to 8 μm wide, joined to the perikarion by means of a thin fibre which may be straight (figure 22, plate VI) or bent to one side (figure 23, plate VI). These two subtypes correspond to the straight and oblique cones described by Ramón y Cajal (1933) in the retina of lizards. The basal rim of the pedicles gives origin to thin processes—henceforth referred to as basal processes—which are about 10 to 15 μm long and extend in all horizontal directions (figures 22 and 23, plate VI). They are initially oriented toward the inner layers of the retina, but then bend outward to end with a minute swelling at the level of the basal surface of other pedicles (figure 23).

The second type of cone pedicle instead has only one basal process, which is about 30 to 40 μm long (figures 24 to 26 plate VI) and may follow different directions in neighbouring cones (figure 26). It originates at the basal rim of the pedicles, and sometimes branches into finer processes which end with a swelling at the level of other pedicles (figure 24). On other occasions, the single basal process does not divide, but becomes progressively thinner, while sending vertically ascending branchlets to the pedicles of other visual cells (figure 25). The terminal branchlets also are frequently seen forming clusters at the origin of the single basal processes (figure 24).

All the pedicles described above belong to cones. Rod pedicles also give origin to long basal processes (figure 27, plate VI), but are easily identified because they are smoothly continuous with the perikaryon, without interposition of a fibre. Visual cells having these characteristic pedicles can be seen to lack an oil droplet when studied in toluidine-blue-stained sections (Richardson, Jarett & Finke, 1960) of Epon-embedded retinas. (The accessory members of the double cones also lack an oil droplet, but they do have a fibre.) Golgi-stained rod cells were not studied with the electron microscope.

Bipolar and horizontal cells

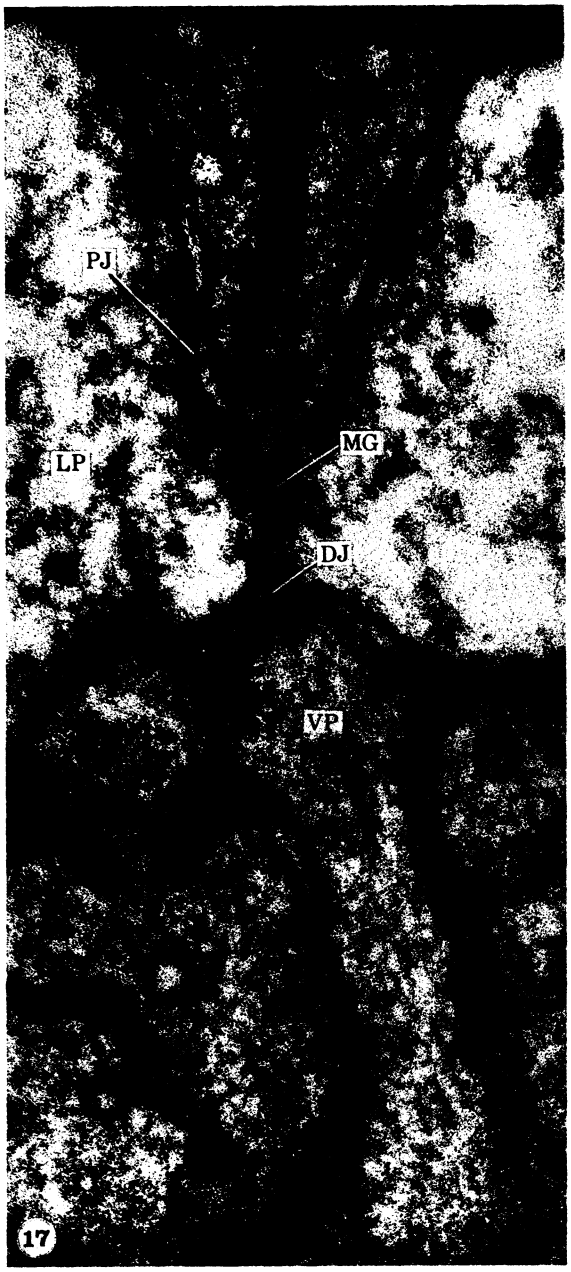
Most of the stained bipolar cells showed a Landolt club, and thus appeared to be analogous to the small bipolars of the lizard (Ramón y Cajal 1933). In the turtle, however, their dendrite and axon follow a more oblique course. The axon, for instance, may extend almost horizontally for more than 150 μm, and then bend rather abruptly to end at various levels within the inner synaptic layer. The electron microscopic observations (see below) suggest that another kind of bipolar cell, perhaps the counterpart of the large bipolars of the lizard (Ramón y Cajal 1933), failed consistently to be stained during the present study.

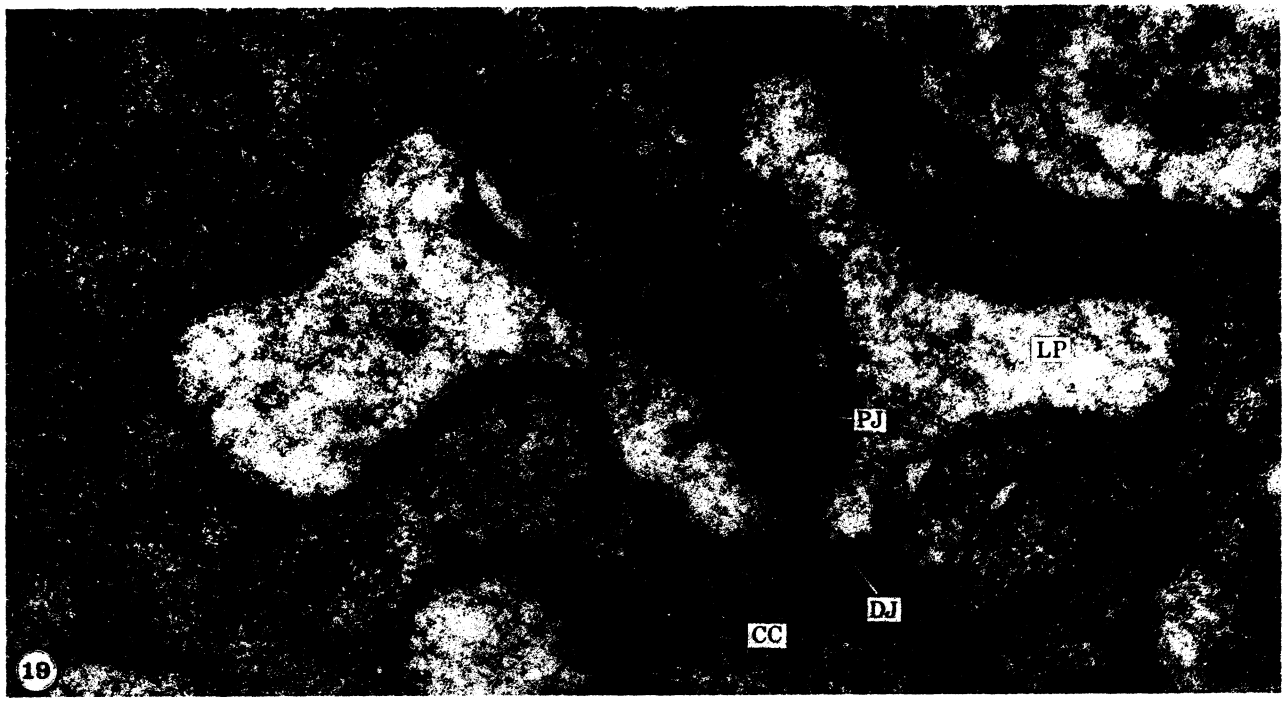
Two types of horizontal cells were observed. One resembles the 'brush' horizontal cells described by Ramón y Cajal (1933) in the lizard, and has a hemispheric body and short lateral branches. The other type is analogous to the 'stellate and flattened' horizontal cells of the lizard (Ramón y Cajal 1933), and has a spindle-shaped body and long processes that extend radially along a very tortuous course. Some horizontal cells gave origin to very fine processes which ended abruptly after a short distance, probably due to incomplete impregnation. Ramón y Cajal (1933) interpreted similar images in the retina of the lizard as the initial portion of horizontal cell axons, but he was also unable to follow them to their terminals. He thought those terminals to be certain arborizations at the end of isolated thin processes.

Description of plate V

Figure 17. Distal junction (DJ) between a lateral process (LP) and a visual cell process (VP) at the distal end of the medial gap (MG) of a dyad. The only junctional specialization consists of a widened intercellular gap filled by opaque material. The visual cell process engaged in the junction shows no connexion to the main body of the cone pedicle in the field of view, and cannot be identified, therefore, as to its pedicle of origin (see text). At the proximal junctions (PJ) the membrane of the lateral processes is lined by a thick layer of opaque cytoplasm. (× 157000.)

Figures 18 and 19. Distal junctions (DJ) between lateral processes (LP) of dyads and visual cell processes (CC) that can be traced to the main body of the cone pedicles enclosing the lateral processes. In addition to a uniformly wide gap filled by opaque material (note the cross-striation of the gap material in figure 19), the distal junctions show also an opaque cytoplasmic layer on the cone cell membrane. The cone pedicles also make proximal junctions (PJ) with the same lateral processes involved in the distal junctions. (Figure 18, × 118000; figure 19, × 108000.)





FIGURES 17 to 19. For descriptions see facing page.

Two of such arborizations were found during this study; both were examined with the electron microscope, and their branchlets found to make the same kind of end contacts as those originating from the body and thicker branches of the horizontal cells (see below).

Electron microscopy of cells stained by the method of Golgi

For these observations, well-impregnated cells were selected from thick sections of Epon-embedded tissue, and remounted for thin-sectioning and electron microscopy. All the processes found to contain opaque deposits, and empty spaces, were assumed to belong to the selected cell (Stell 1965, 1967). The assumption is justified only if it is certain that the remounted area does not contain processes from other stained cells. In general, it is not difficult to find stained cells surrounded by a completely clean background, and the danger of contamination can thus be minimized. Nevertheless, the reproducibility of an observation over a reasonably large number of specimens is the best safeguard against this kind of contamination.

Contacts of the cone pedicles with bipolar cells

All the Golgi-stained bipolar cells examined with the electron microscope were engaged in basal junctions—and only basal junctions—with the cone pedicles (figures 28 to 31, plate VII). A total of 22 bipolar cells (in individual blocks) were sectioned throughout, and all the grids examined.

In 16 of the cells examined, an average of two or three basal junctions per cell were identifiable on the basis of their intrinsic structural features (figures 28 to 31). At many other basal contacts the images were too obscure to permit an identification of the structure involved. Such contacts were regarded also as basal junctions, however, because none of the dendritic branchlets penetrated within the recessed areas of the pedicles, or related to the synaptic ridges in the manner characteristic of the lateral and central processes of triads and dyads. These criteria were the only ones available to identify as basal junctions the contacts of the remaining six bipolar cells. Some of the recognizable basal junctions were of the invaginated variety (figure 31); the appearance of others suggested that they were superficial junctions (figures 28 and 29), but no serial sectioning was attempted to test this presumption. Nevertheless, there is little reason to doubt that the superficial basal junctions are also bipolar cell contacts, as none of the stained horizontal cells and basal processes examined was found to make such junctions (see below).

Contacts of the cone pedicles with horizontal cells

The processes of all the Golgi-stained horizontal cells examined with the electron microscope (nine cells) ended as the lateral processes of triads and dyads (figures 32 and 33, plate VII); similar observations have already been reported in the goldfish and monkey retinas (Stell 1967; Kolb 1970). None of the horizontal cell processes made junctions with the basal surface of the cone pedicles.

Central processes of the triads

The central processes of the triads never appeared stained whenever any of the Golgi-stained cells was examined with the electron microscope. The most likely interpretation is that this process belongs to cells that failed to be stained during the present study.

End contacts of the basal processes

Each cone pedicle gives origin to about six to ten basal processes or, in the case of a single process, an equivalent number of endings. To increase the chances of finding those endings in thin sections of Golgi-impregnated material, it was advantageous to examine blocks containing many stained visual cells. Since the retinas impregnated after detaching from the pigment epithelium showed few stained elements other than visual cells, it was easy to select contamination-free blocks containing 10 to 15 stained cone cells. Eleven such blocks were examined, each containing both types of cone pedicles (figures 22 to 26, plate VI).

The endings of the basal processes of cone pedicles were found abutting against the lateral processes at the dyads of other cone pedicles (figure 1; figures 34 to 36, plate VIII). The assemblies could be recognized as dyads because of the narrow width of the medial gap; the stained endings were located at the distal end of this gap.

As shown above, two kinds of processes may be found at or near this location in conventionally prepared tissue. Some processes have a light cytoplasm and make invaginated basal junctions with the pedicles (figures 3 and 6, plate I). The Golgi-stained endings of the basal processes cannot be confused with them, since these endings do not make basal junctions either with the pedicles or with adjacent dendritic branchlets (figures 35 and 36, plate VIII). The other kind of processes at the distal end of the medial gap of dyads is represented by those having an opaque cytoplasm, heretofore identified as visual cell processes (figure 13, plate IV; figure 17, plate V). It was shown above that some of those opaque processes belong to the same pedicle that encloses the lateral processes of the dyads. It is now clear, however, that some others represent the endings of the basal processes arriving from distant pedicles.

The observations on Golgi-stained visual cells did not disclose the structure of the end contacts of the basal processes. Because of the region involved, they would be expected to be distal junctions with lateral processes. Nevertheless, the area of contact was always ill-defined due to insufficient staining of the membranes, masking by silver deposits, or just poor fixation (figures 34 to 36, plate VIII). This difficulty in identifying the hypothetical distal junctions may have been a consequence of their frequently subtle surface specialization (figure 16, plate

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Description of plate VI

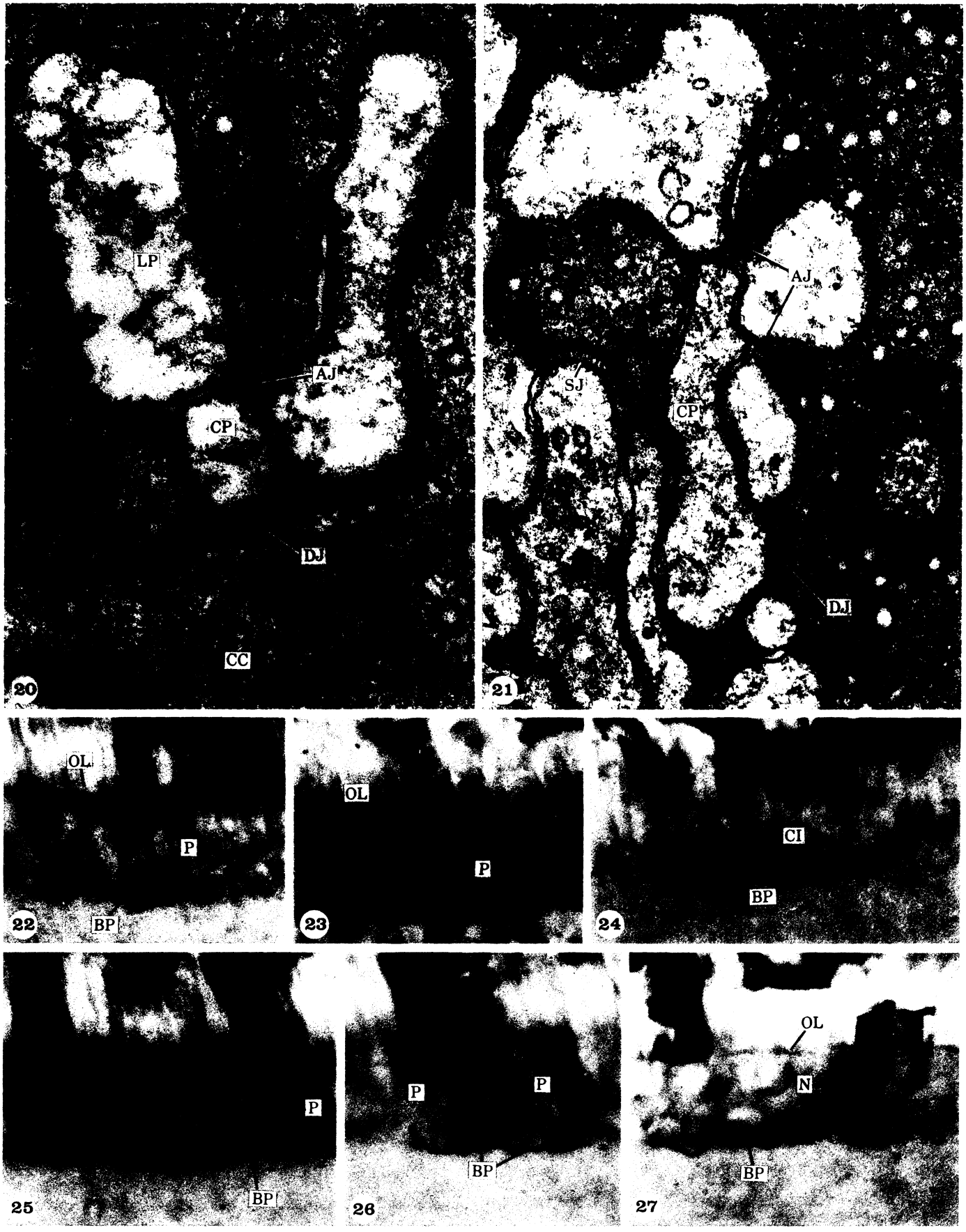
Figure 20. Apical junction (AJ) and distal junction (DJ) of a central process (CP) of a cone triad. At the apical junction the extracellular space is occupied by a homogeneous material, and the membrane of the lateral processes is partly covered (arrow) by opaque cytoplasm. CC, cone cell; LP, lateral process of the triad. (× 126 000.)

Figure 21. Rod pedicle in the turtle retina. A central process (CP) makes apical junctions (AJ) at two triads, and a distal junction (DJ) near the basal surface of the pedicle. A cell process engaged in a basal junction (SJ) contains some vesicular profiles. (× 86 000.)

Figures 22 and 23. Light micrographs of cone cells in the turtle retina stained by the method of Golgi. The pedicles (P) give origin to basal processes (BP) throughout the circumference of their basal rim. OL, outer limiting membrane. (× 800.)

Figures 24 to 26. The pedicles (P) of Golgi-stained cone cells give origin to a single basal process (BP), which may follow different directions in nearby cones (figure 26). The terminal branchlets of the basal processes end with a swelling (arrow) at the level of the basal surface of other pedicles. A cluster of terminal branchlets (Cl) may be seen at the origin of the basal processes in figure 24 (× 800.)

Figure 27. Rod cell in the turtle retina. Long basal processes (BP) originate from the pedicle, which is joined to the perikaryon (N) without interposition of a fibre. The outer segment was lost while detaching the retina from the pigment epithelium. OL, outer limiting membrane. (× 800.)



FIGURES 20 to 27. For descriptions see facing page.

IV; figure 17, plate V), as compared to the more easily identifiable basal junctions (figures 35 and 36, plate VIII). On the other hand, the end contacts may not be distal junctions at all, the only other alternative being that neither the basal processes, nor the lateral processes, show any surface specialization at the contacts.

In tissue prepared by conventional methods, visual cell processes making distal junctions with lateral processes can sometimes be followed for an appreciable length (figure 37, plate VIII). Such visual cell processes could conceivably be basal processes which originate from the pedicle in the field of observation and—after making a distal junction *en passant*—proceed to their final destination at another pedicle. This seems unlikely, however, because whenever it was possible to trace basal processes to their pedicle of origin, they were seen to be connected to the basal rim of the pedicle. Images such as figure 37, therefore, can at least be said to make tenable the view that the end contact of the basal processes is a distal junction with a lateral process.

Other contacts of the basal processes

Cell junctions between adjacent cone pedicles may be included in this category because usually the contact is brought about by means of a short projection of one of the pedicles (figure 38, plate VIII), which at least in some instances represents merely the initial portion of a basal process (figure 1). Similar junctions have been already described in other retinas (Cohen 1965; Dowling 1968). They consist of a segment with a wide and uniform gap occupied by opaque material, and a shorter segment with a narrower gap (figure 38). The junctional membranes are lined by symmetrical accumulations of opaque cytoplasm at the level of the wide-gap segment. Clusters of vesicles subjacent to the membranes are not present on either side of the junctions. No junctions of this type, or any other specialized contact between any two visual cell processes, have been found in the turtle retina at areas other than the peripheral rim of the pedicles.

The basal processes make additional specialized contacts within the outer plexiform layer. They can be identified at this level again because of their relatively high electron opacity, since none of the second-order neurons has an equally opaque cytoplasmic matrix. Their contacts within the outer plexiform layer are probably junctions *en passant* (figure 1), since none of the basal processes appears to end within this layer in well-impregnated visual cells. These junctions are reminiscent of basal junctions, except that they are highly asymmetrical because of the presence of a layer of opaque cytoplasm only on the side opposite the basal processes (figure 39; plate VIII); when asymmetries are observed at the wide-gap segment of basal junctions, they have an opposite direction (figure 7, plate II). Because of the asymmetry of the junctions *en passant*, it was not possible to identify in Golgi preparations the cell processes joining the basal processes, since when, and if, they were stained, the silver deposits masked the specialized nature of the contacts.

Discussion

Cone pedicles in the turtle retina engage in a remarkable variety of junctions. Some of these may represent merely adhesion plates, while others—or perhaps all of them—may also have a synaptic function. The structural observations do not give sufficient clues to make the distinction in each individual case, since none of the junctions is associated with crowding of vesicular elements near one of the junctional membranes—a feature generally regarded

as a distinctive mark of chemical synapses (Gray & Guillery 1966)—nor do they resemble the close membrane appositions thought to provide for electrical coupling between vertebrate neurons (Brightman & Reese 1969). Furthermore, even when the synaptic role of a junction can be presumed on purely architectural grounds, the same paucity of structural similarities with better known synapses precludes further speculation on the possible synaptic polarity, or on the significance of dissimilar junctional segments when present.

All these considerations apply in the case of the basal junctions, which can be assumed to be synapses because they are the only sites of contact between the cone pedicles and the processes of all the bipolar cells stained by the Golgi method during the present study. Junctions similar in location—although not necessarily in structure—to the basal junctions of turtle cones, have been reported at cone pedicles in retinas of primates (Cohen 1961; Missotten 1965; Dowling & Boycott 1966), reptiles (Kalberer & Pedler 1963), and amphibians (Dowling 1968); in the last two instances, cross-striations were observed within the junctional gap (Kalberer & Pedler 1963; Dowling 1968). In the primate retina the processes making these contacts have been identified, by means of serial sectioning (Missotten 1965) or electron microscopy of Golgi-stained retinas (Kolb 1970), as the dendrites of the diffuse cone bipolar cells. Therefore, it seems that all the turtle bipolars stained during the present study are the counterpart of the diffuse cone bipolars of primates.

It is likely that a second type of cone bipolar cell failed consistently to be impregnated in the turtle retina. This is suggested by the lack of impregnation of the central process of the triads, which in cone pedicles of the primate retina have been found to belong always to midget bipolar cells (Kolb 1970). If the cells originating the central process of the triads in the turtle retina are indeed bipolar cells, the distal junctions of the central processes may be functionally equivalent to the basal junctions of the other type of bipolar cells. On the other hand, it would be difficult to speculate on the possible significance of the apical junctions of the central processes.

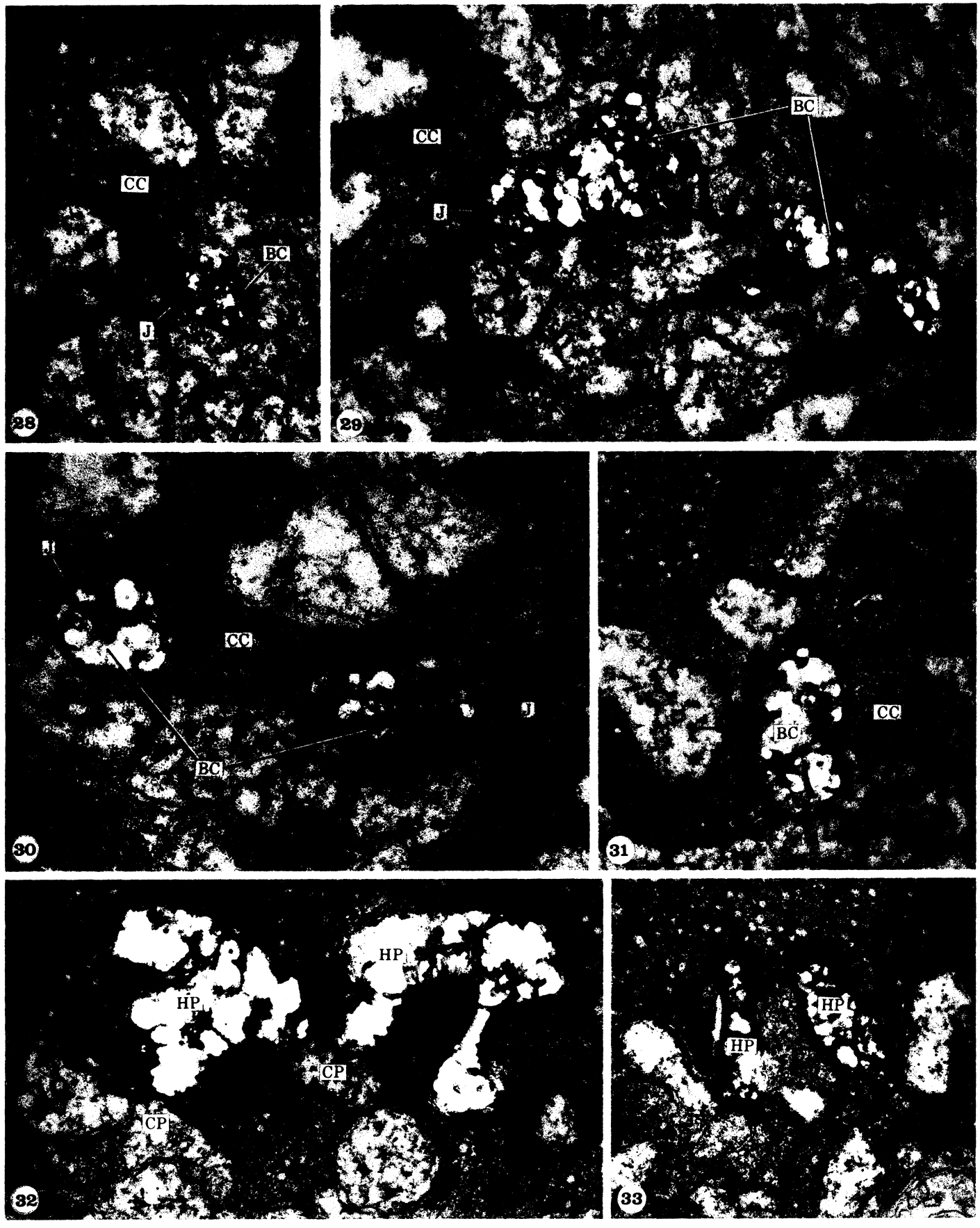
The processes of all the Golgi-stained horizontal cells were seen to end as the lateral processes at cone dyads and triads. Conversely, only horizontal cells were found to give origin to lateral processes. As mentioned above, at least one type of second-order neuron was never stained; therefore, it is not possible to be certain that all the lateral processes belong to horizontal cells. Nevertheless, this seems to be a reasonable assumption, since studies by the Golgi method in retinas of fishes and primates have also indicated that only horizontal cells give origin to lateral processes (Stell 1967; Kolb 1970).

Description of plate VII

Figures 28 to 30. Electron micrographs of Golgi-stained processes of bipolar cells (BC) making basal junctions (J) with the cone pedicles (CC). The junctional nature of the contacts is indicated by the widened and uniform intercellular gaps occupied by a cross-striated material. (Figures 28 and 29, × 48 000; figure 30, × 81 000.)

Figure 31. Golgi-stained process of a bipolar cell (BC) making an invaginated basal junction with a cone pedicle (CC). Focal accumulations of opaque cytoplasm (arrows) are seen on the cone cell membrane. (× 48 000.)

Figures 32 and 33. Electron micrographs of Golgi-stained horizontal cell processes (HC) ending as lateral processes at cone triads (figure 32) or dyads (figure 33). In micrographs of conventionally prepared retinas the same processes are labelled LP, because the observations on Golgi-impregnated material do not prove that the lateral processes belong always to horizontal cells, although this is likely to be the case (see text). One of the horizontal cell processes in figure 32 is shared by two triads. The stained horizontal cell in figure 33 contributes only one process to each of the dyads. CP, central process of the triads. (× 48 000.)



FIGURES 28 to 33. For descriptions see facing page.

The lateral processes in turtle cones engage in two types of specialized contacts: proximal junctions, found at both triads and dyads, and distal junctions, found only at dyads. The close association of the proximal junctions with the synaptic lamellae suggests that at these points the cone cells interact synaptically with the horizontal cells (Stell 1967); as it is well known, organelles similar to the synaptic lamellae are found at several synapses on the side known or presumed to be presynaptic (Smith & Sjöstrand 1961; Barets & Szabo 1962; Wersall, Flock & Lundquist 1965; Trujillo-Cenóz 1965; Derbin, Denizot & Szabo 1969). No equivalent clues are available, however, with regard to the function of the distal junctions. Recent electrophysiological work in the turtle retina indicates the existence of a reciprocal synaptic interaction between horizontal and cone cells (Baylor, Fuortes & O'Bryan 1971). It may be worthwhile, then, to consider the possibility that the proximal and distal junctions of the horizontal cell processes are synapses of opposite polarity, providing feed-back loops similar to those believed to occur at synapses between bipolar and amacrine cells in the retina and at dendrodendritic synapses in the olfactory bulb (Dowling & Boycott 1966; Rall, Shepherd, Reese & Brightman 1966).

The basal processes of the cone pedicles end at the dyads of other cone pedicles, which may be as far away as 40 μm from the cell of origin. Since it is logical to assume that the basal processes allow a visual cell to interact with surrounding elements, the end contacts of these processes can be regarded as synaptic with a good measure of confidence. The structure of the end contacts remains uncertain, however, and it cannot be decided whether the basal processes synapse with the lateral (horizontal cell) processes, or with the synaptic ridge at the opposite end of the long and narrow medial gap.

The purpose of the end contacts may be to bring about interaction between visual cells, either directly or through the mediation of the horizontal cells. In order to function as interneurons for this purpose, the horizontal cells would need to have an output on the cone cells; as already discussed, the present findings are compatible with this possibility. Lateral inhibition between ommatidial cells is a well-known property of the *Limulus* lateral eye (Hartline, Wagner & Ratliff 1956); its possible occurrence in the vertebrate retina has been already suggested, also because basal processes appeared to contact the basal surface of the visual cell endings (Sjöstrand 1958). Those contacts, however, were thought to be interreceptor junctions, probably similar to the junctions found in the turtle retina between adjacent cone pedicles.

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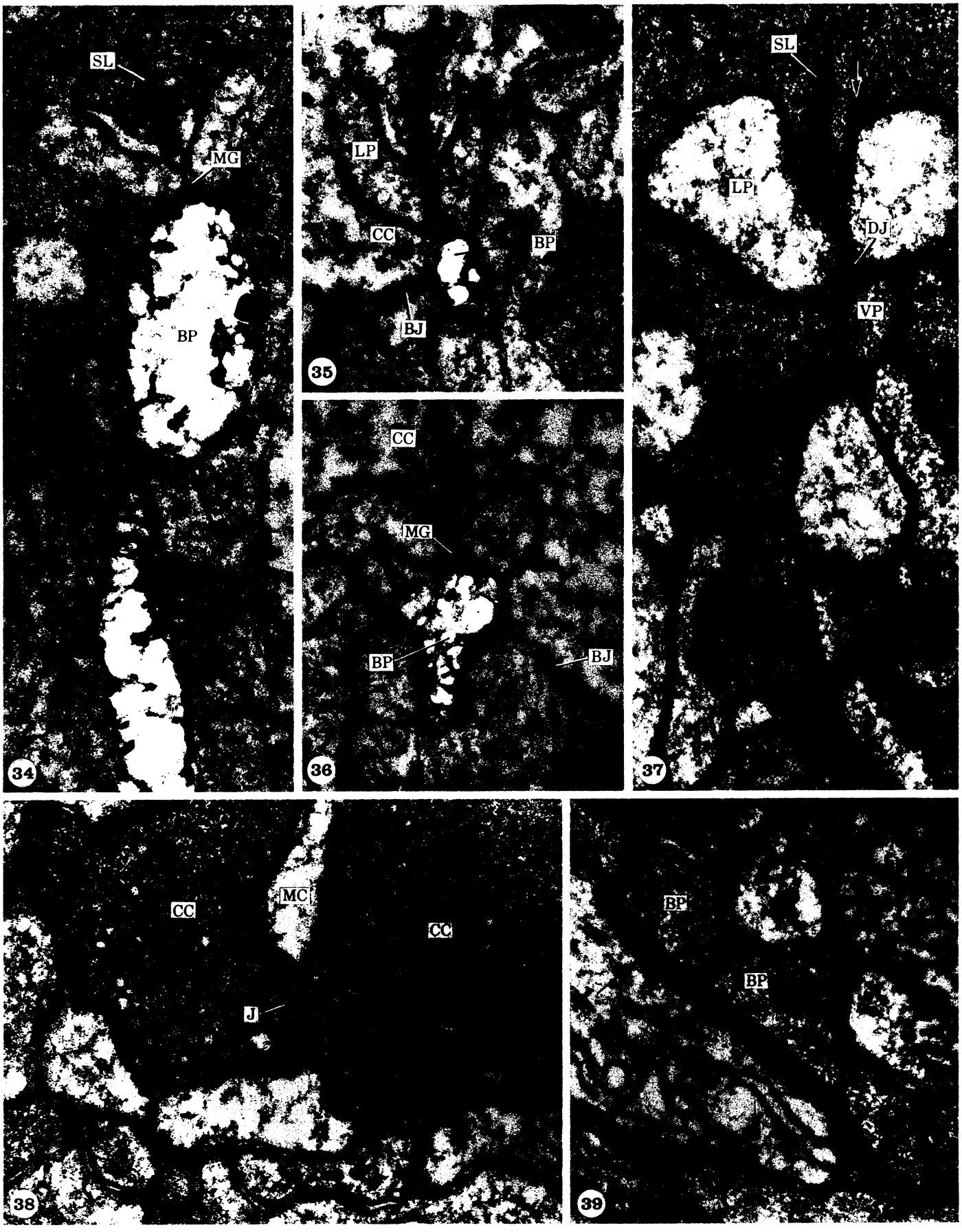
Description of plate VIII

Figures 34 to 36. Electron micrographs of the endings of basal processes (BP) belonging to cone cells stained by the method of Golgi. All the stained basal processes end in contact with lateral processes (LP) at cone dyads, which can be distinguished from triads because of the narrow width of the medial gap (MG). The cone pedicles (CC) enclosing the lateral processes in figures 35 and 36 appear almost devoid of cytoplasmic matrix; this is probably a consequence of the loss of their outer segments during fixation (see Methods). None of the stained basal processes is seen to make basal junctions with the cone pedicles, or with any other of the adjacent processes. None the less, basal junctions (BJ) between the cone pedicles and other cell processes can be recognized in this material (figures 35 and 36). SL, synaptic lamella. (× 48000.)

Figure 37. A lateral process (LP) of a cone dyad makes a distal junction (DJ) with a longitudinally sectioned visual cell process (VP), which could represent the terminal part of a basal process arriving from another pedicle (see text). At the distal junction both cell membranes are coated by opaque cytoplasm, and the gap contains a less opaque material. Opaque material is found also within an indentation (arrow) of the cone cell membrane at the base of the synaptic ridge; a pit of the cone cell membrane at this point appears to be a vesicle unloading or pinching-off from the membrane. Similar pits are frequently found also at other places along the boundary between cone pedicles and lateral processes. SL, synaptic lamella bisecting the synaptic ridge of the cone pedicle. (× 65000.)

Figure 38. Cell junction (J) between two adjacent cone pedicles (CC). MC, Müller cell. (× 81000.)

Figure 39. Junction between two basal processes (BP) and an unidentified cell process within the neuropil at the outer plexiform layer. Note that an opaque cytoplasmic layer is present only on the membrane of the unknown process (arrows). A few vesicles are seen within one of the basal processes. (× 78000.)



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FIGURES 34 to 39. For descriptions see facing page.

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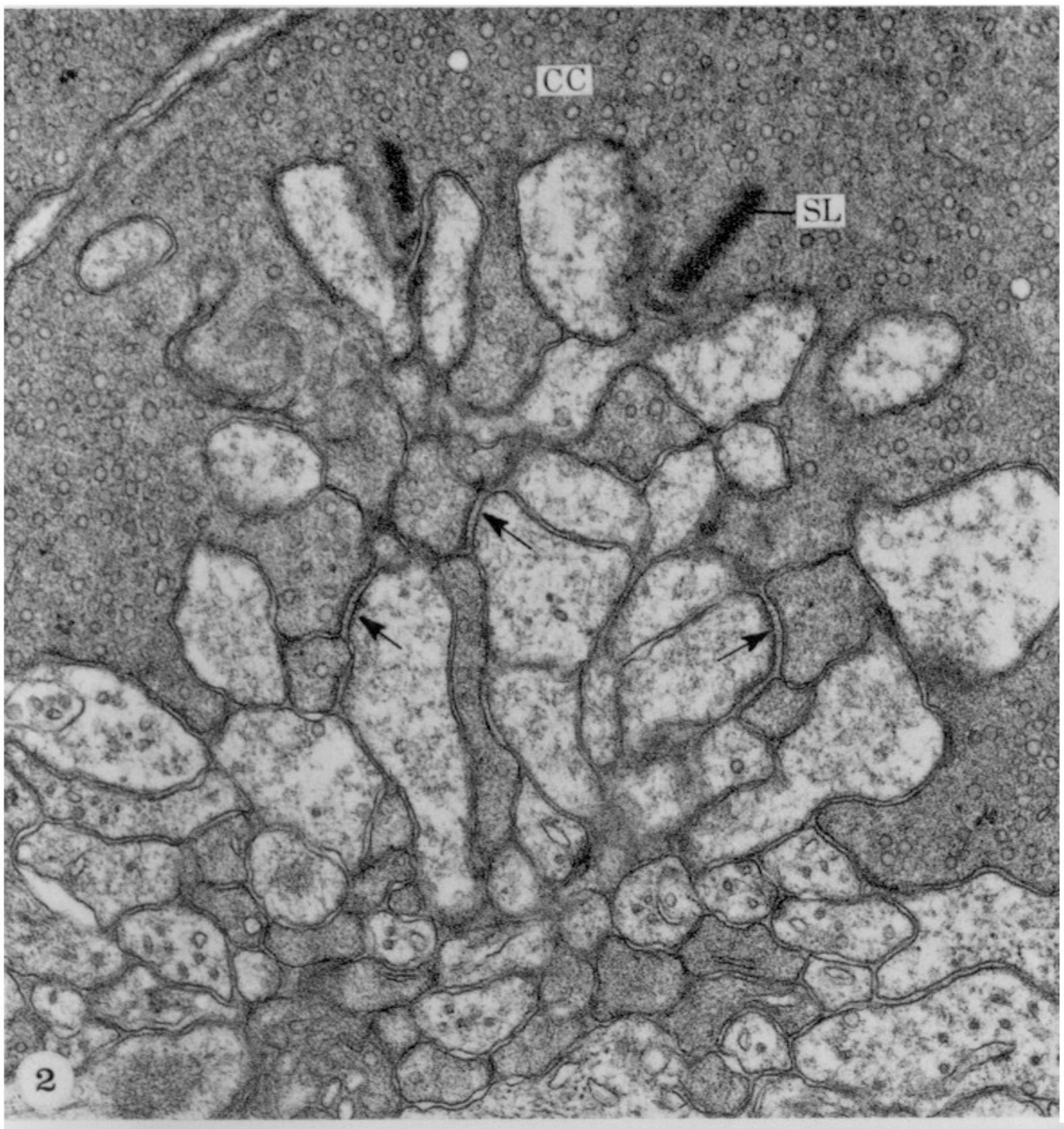
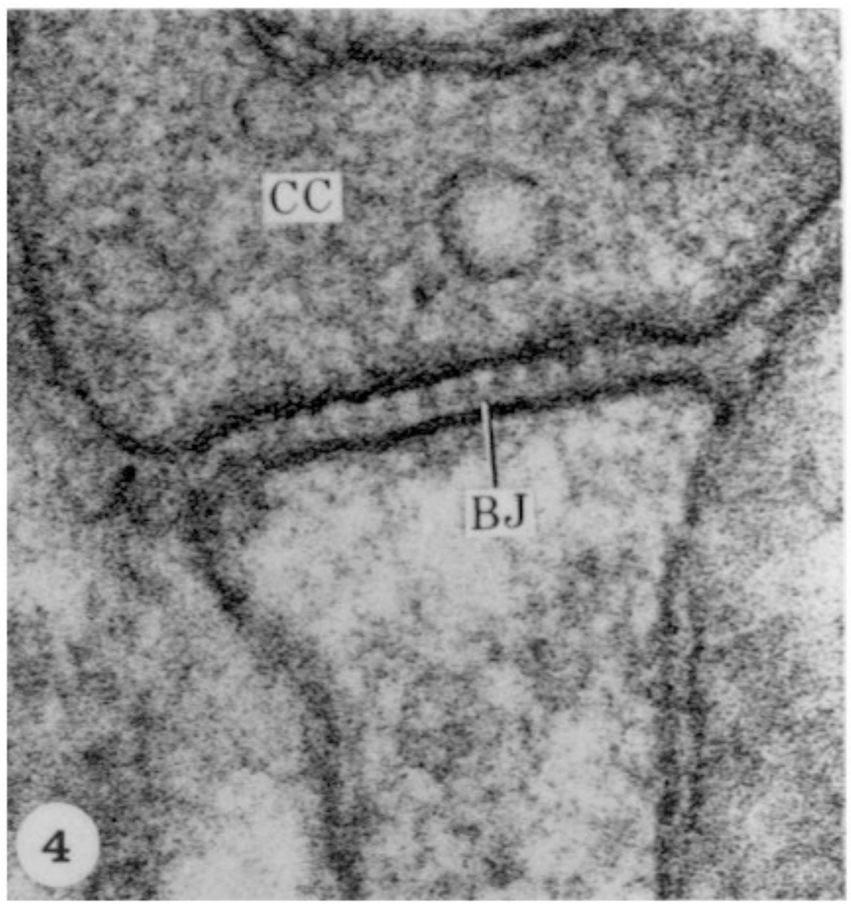
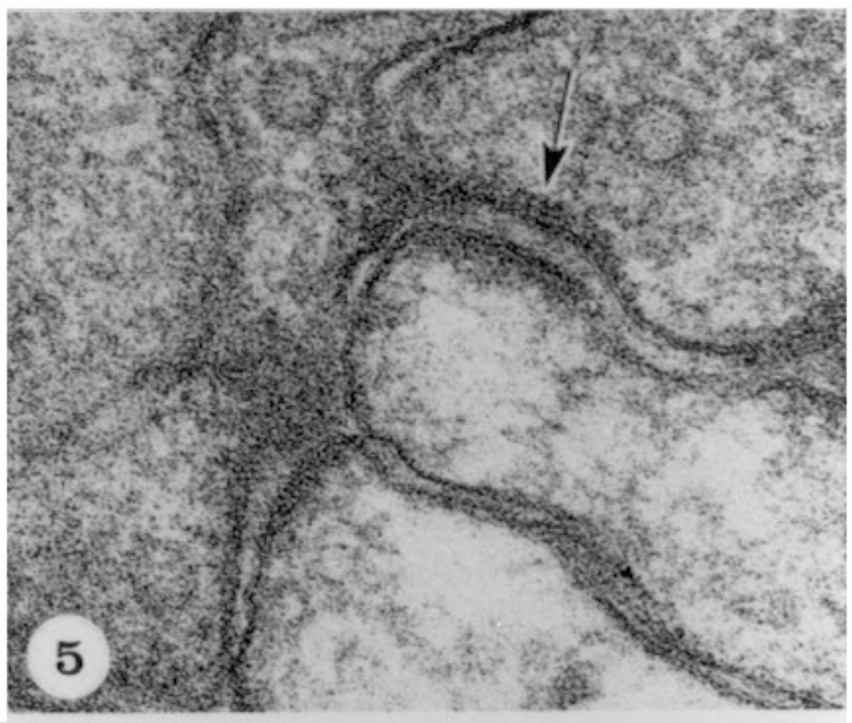
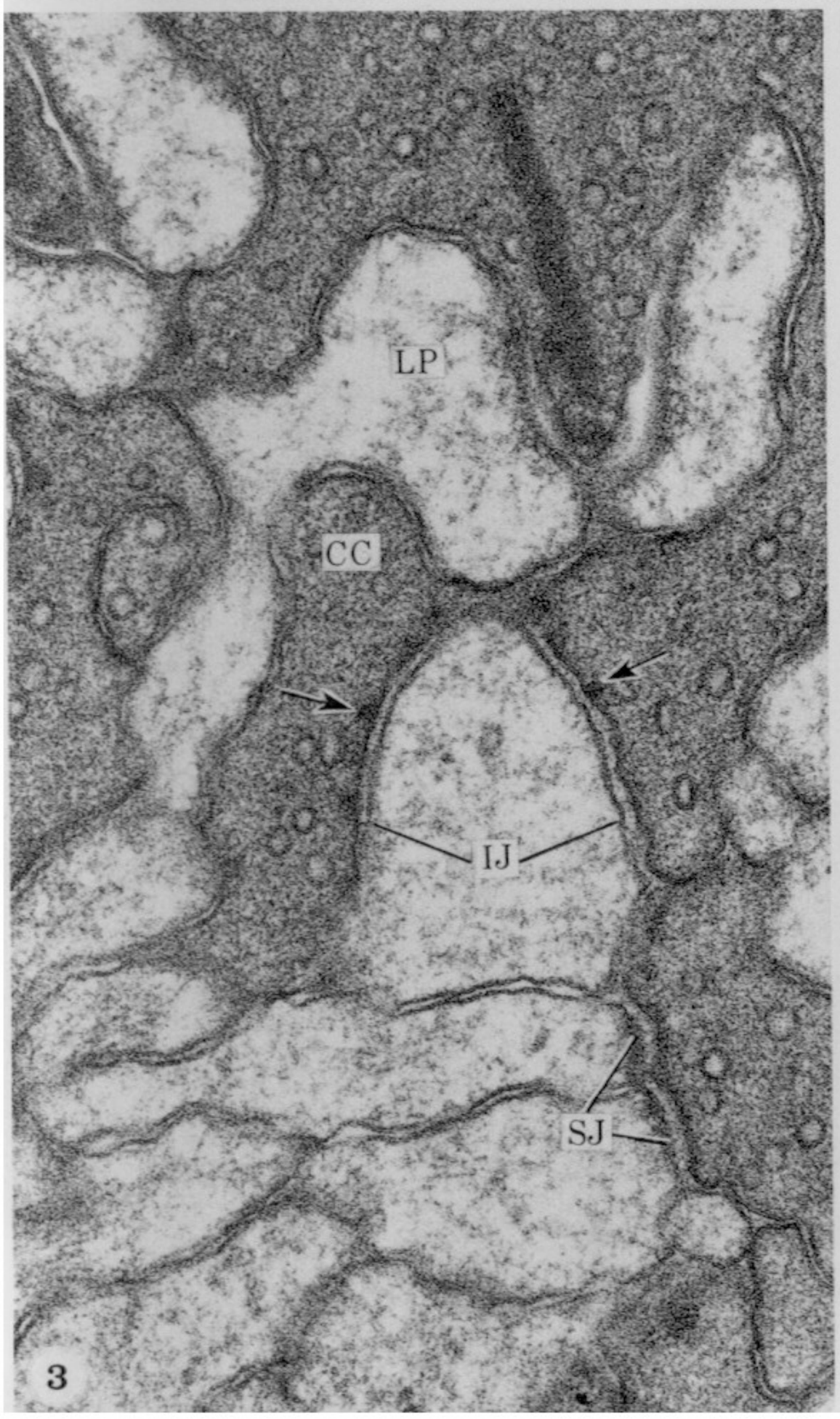
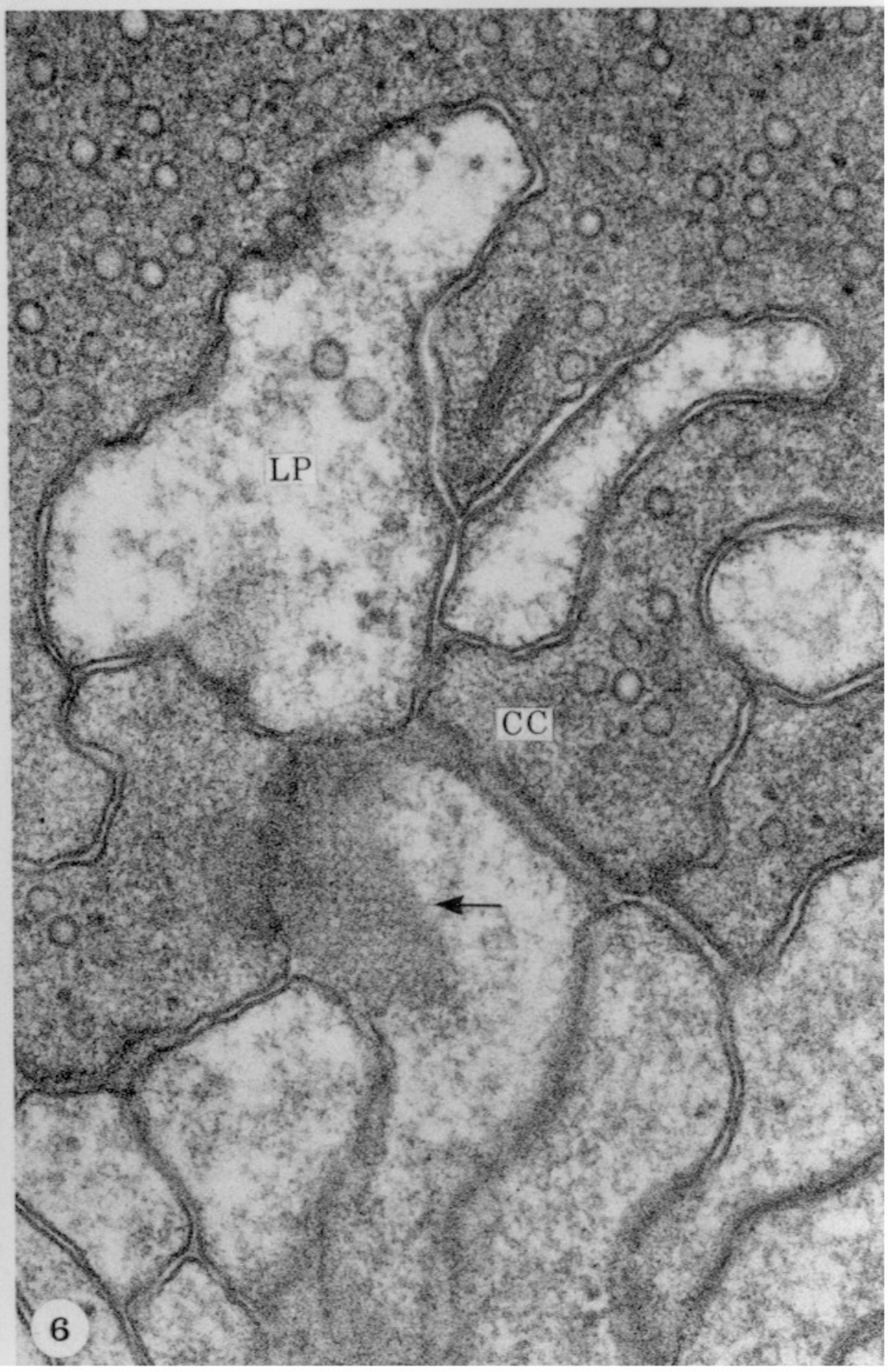
The plates were printed by J. Brunissen, Ateliers d'Impressions d'Art, Paris XIII.



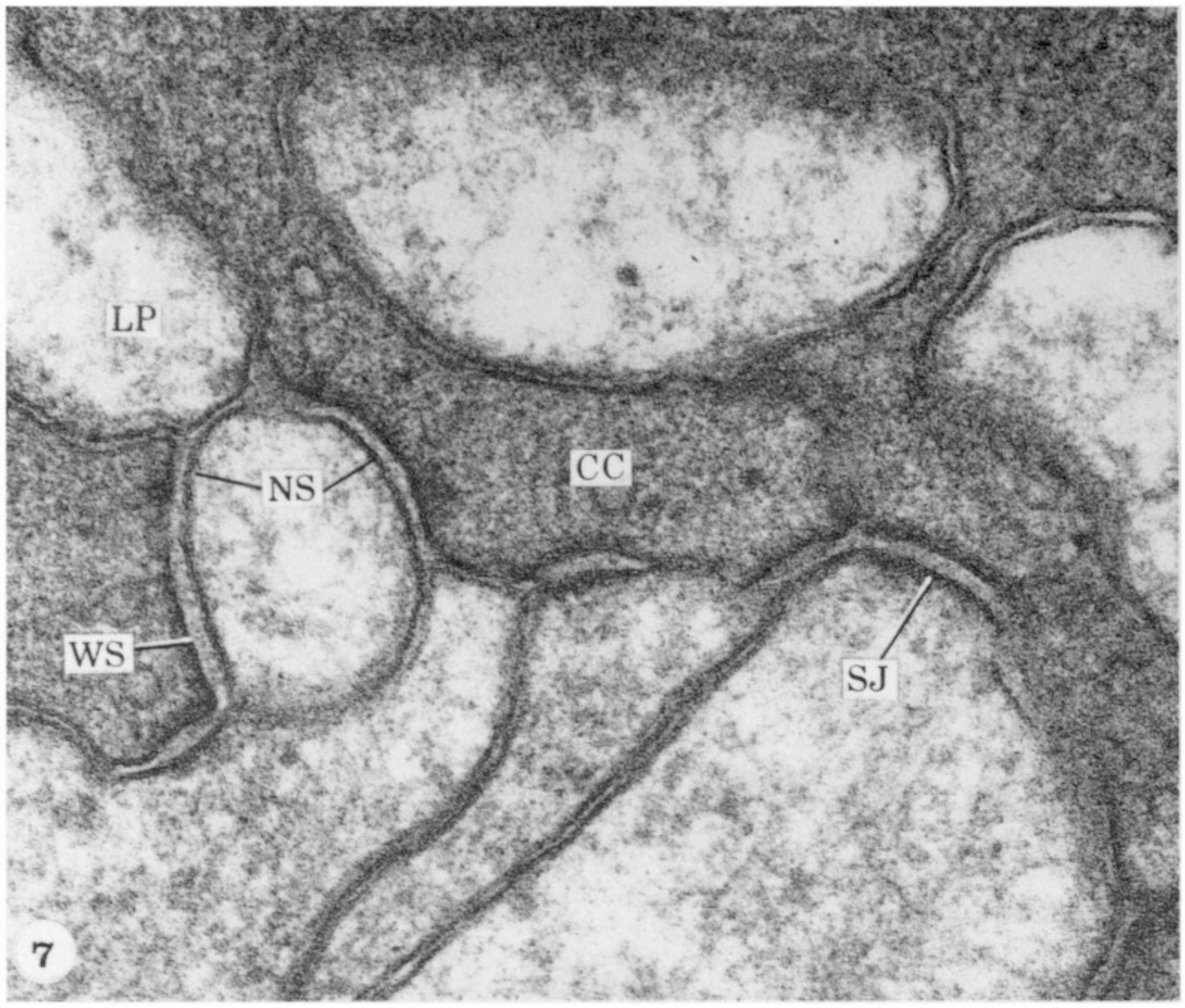


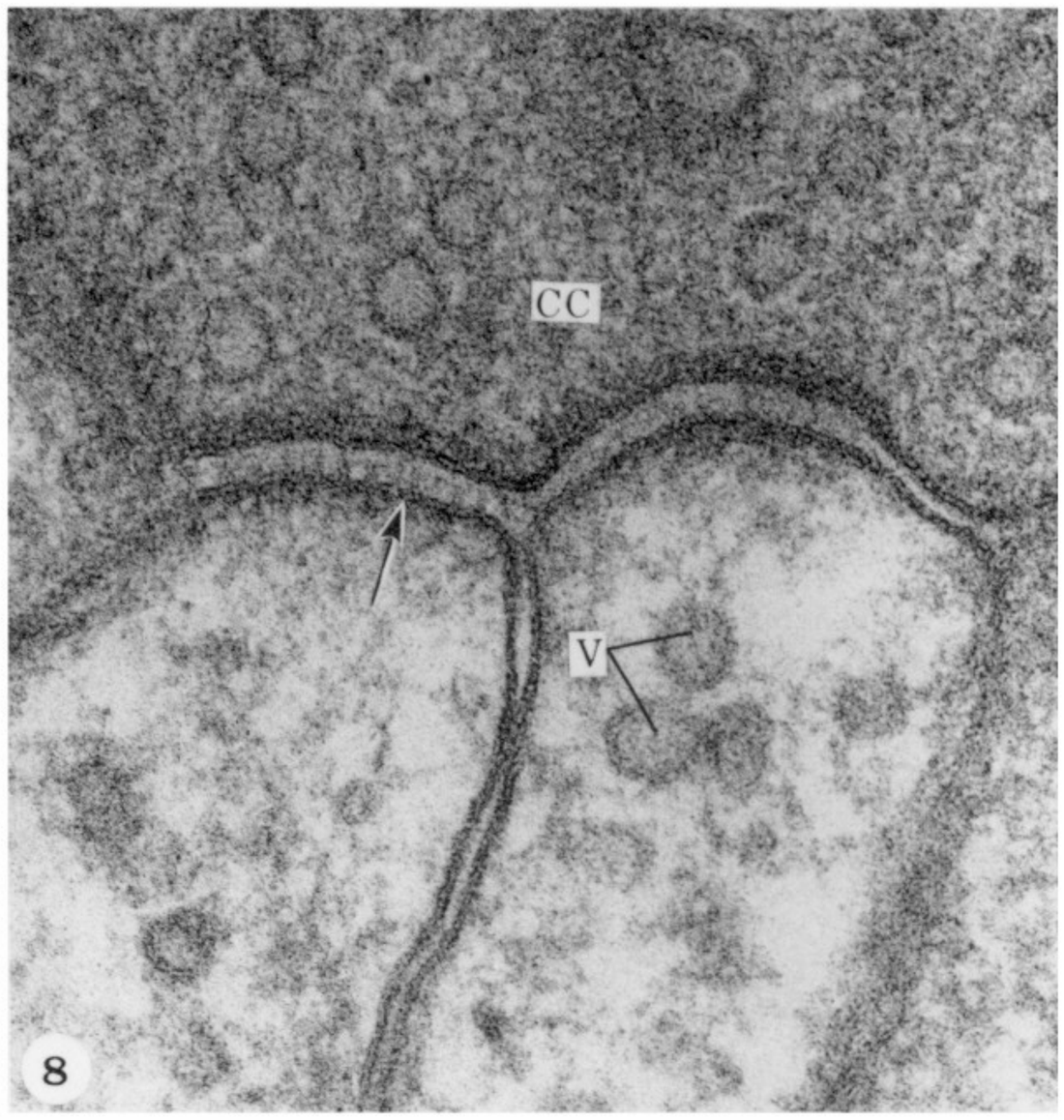


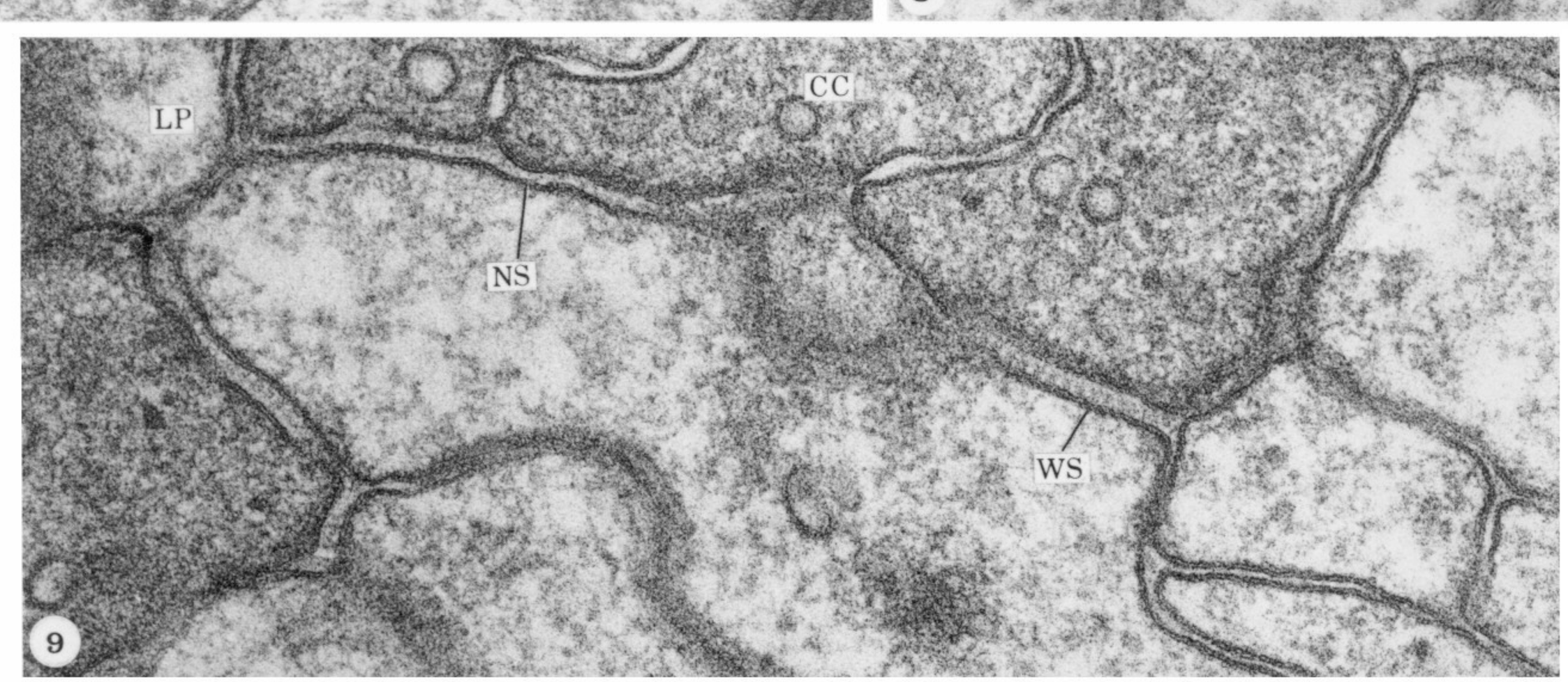


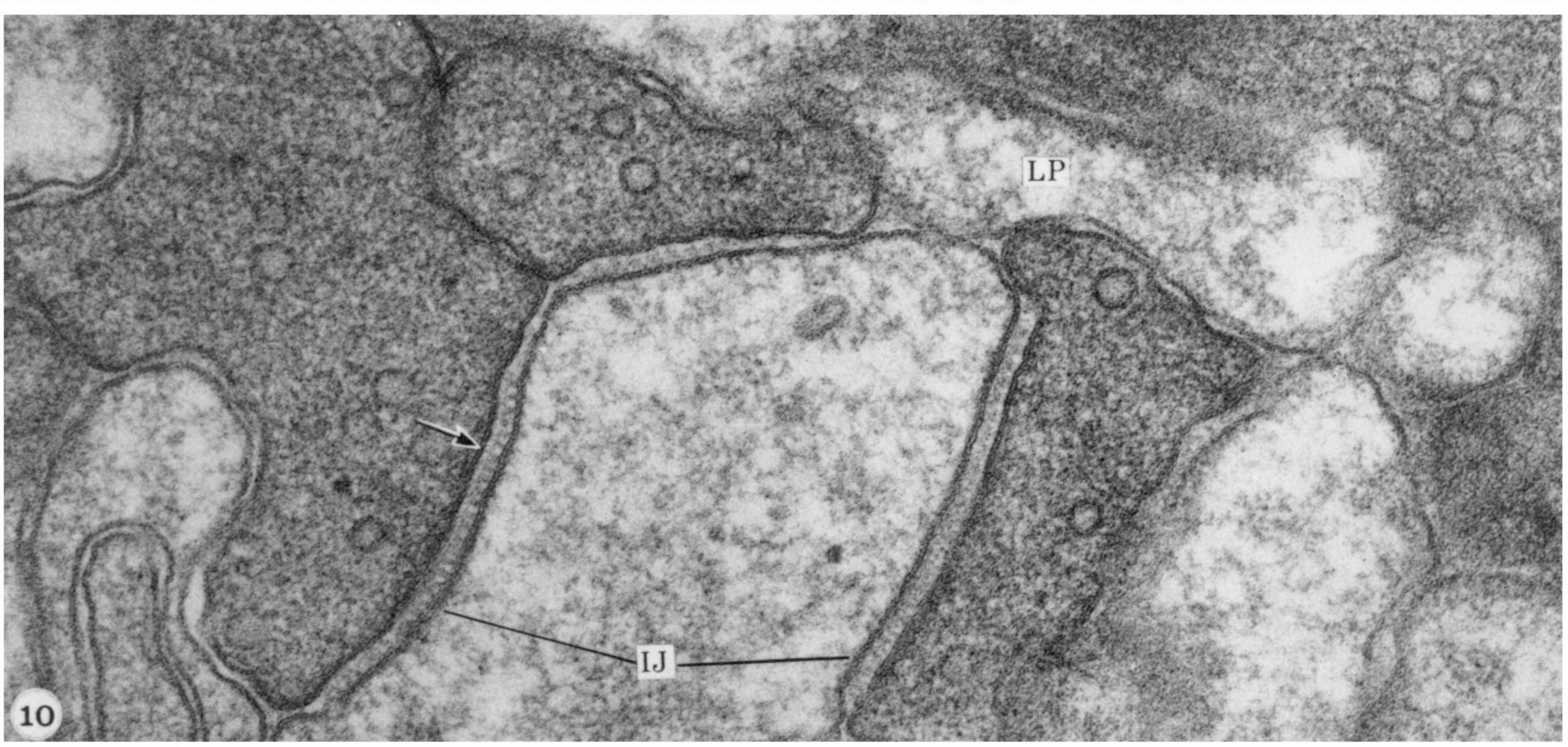


FIGURES 2 to 6. For descriptions see facing page.



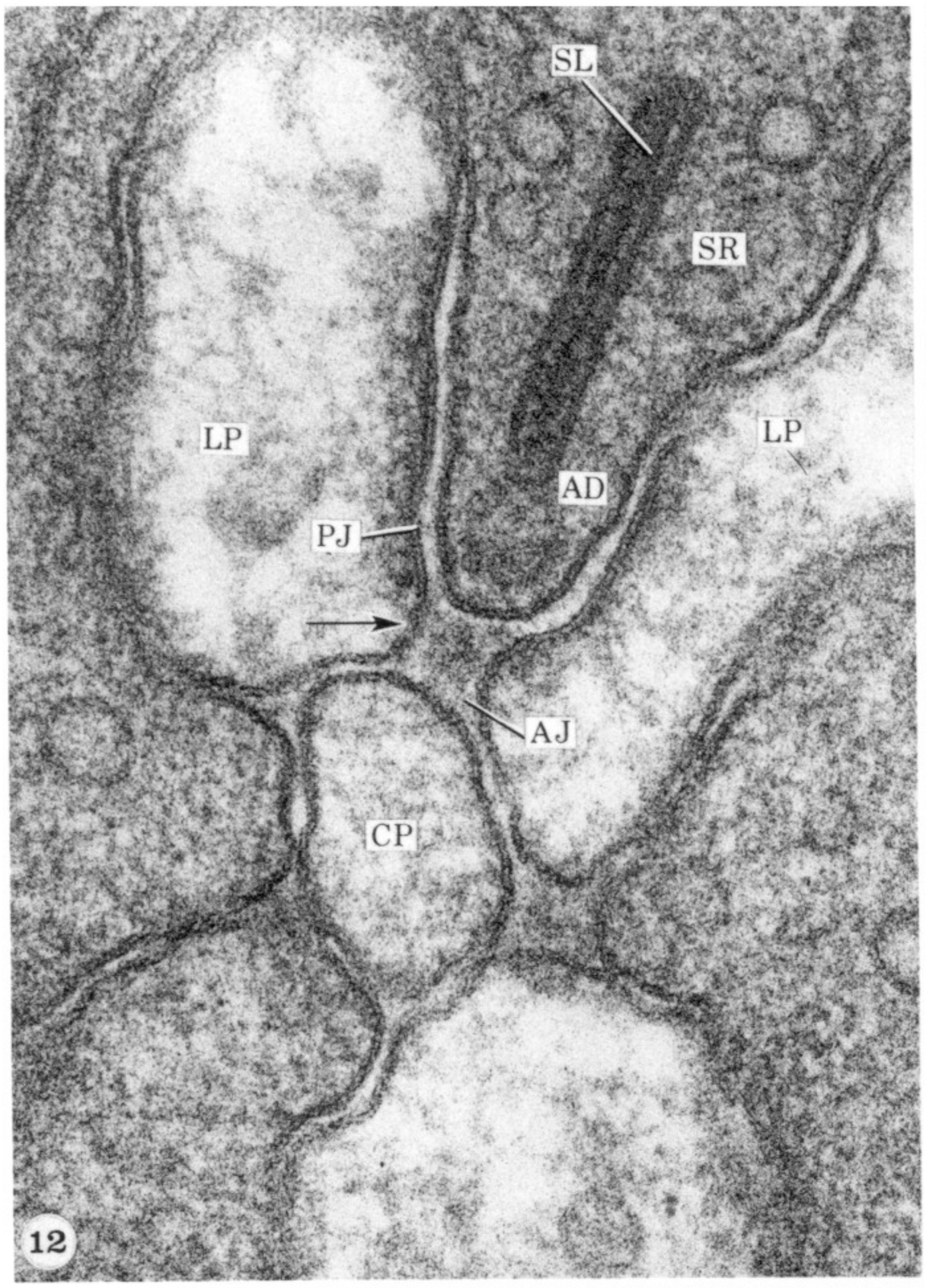


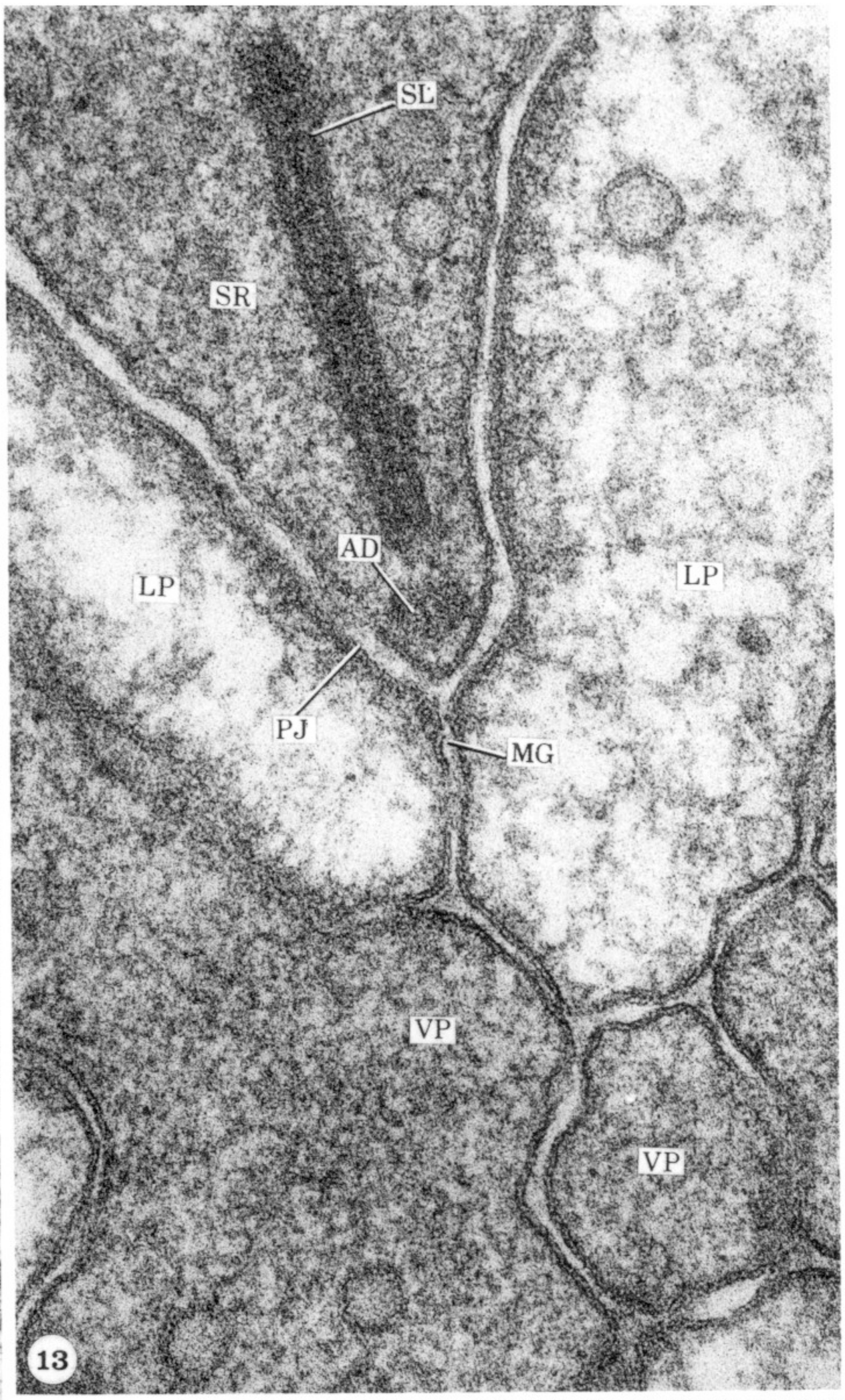


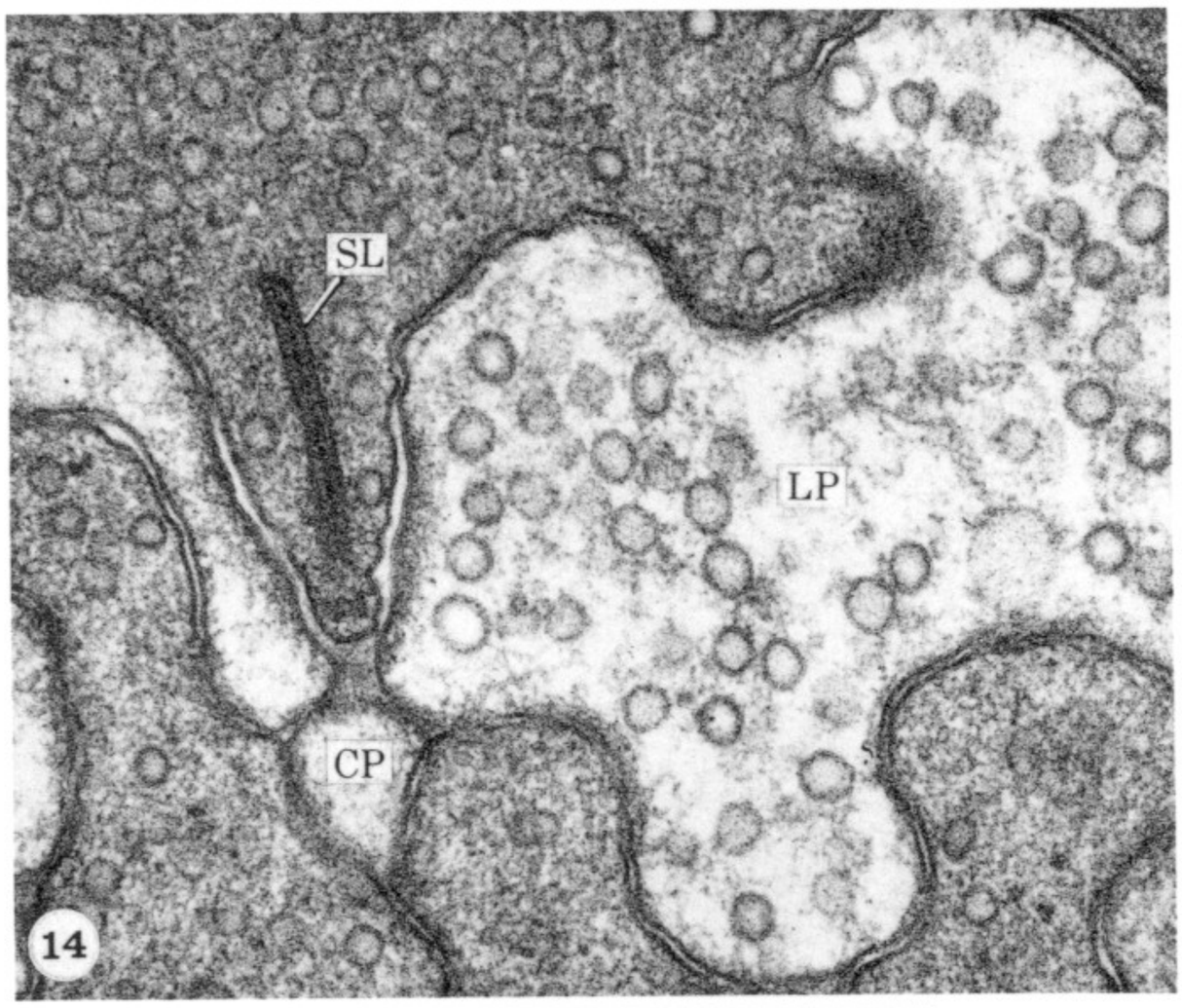


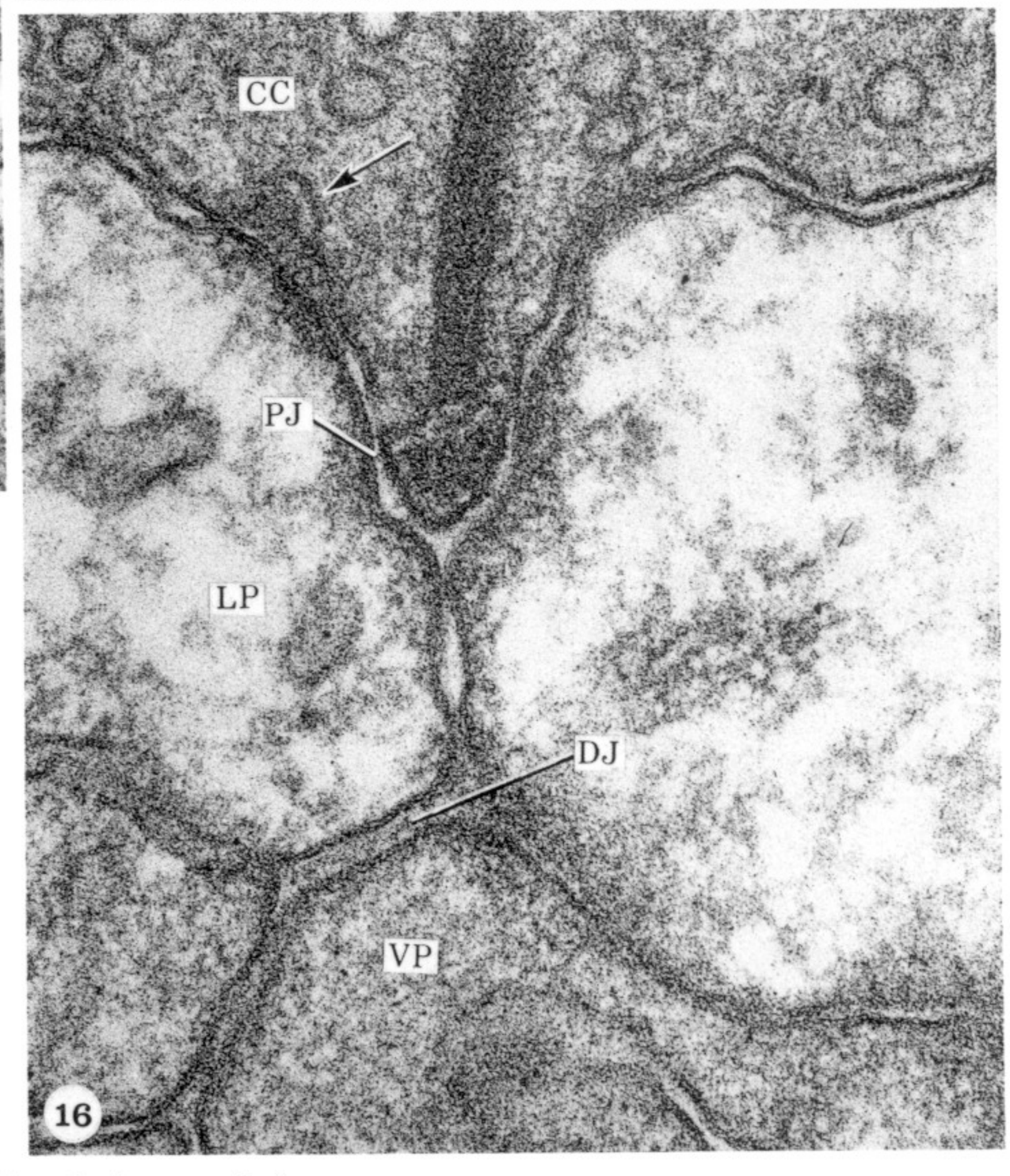
FIGURES 7 to 10. For descriptions see facing page.

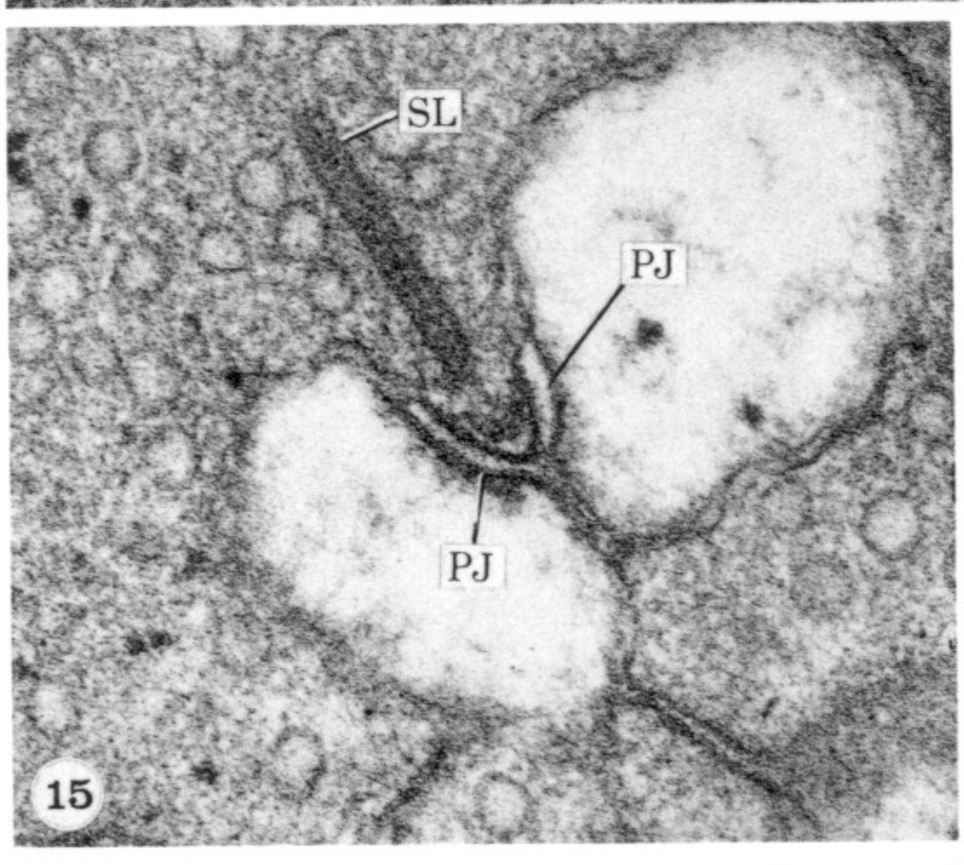
FIGURE 11. For description see facing page.



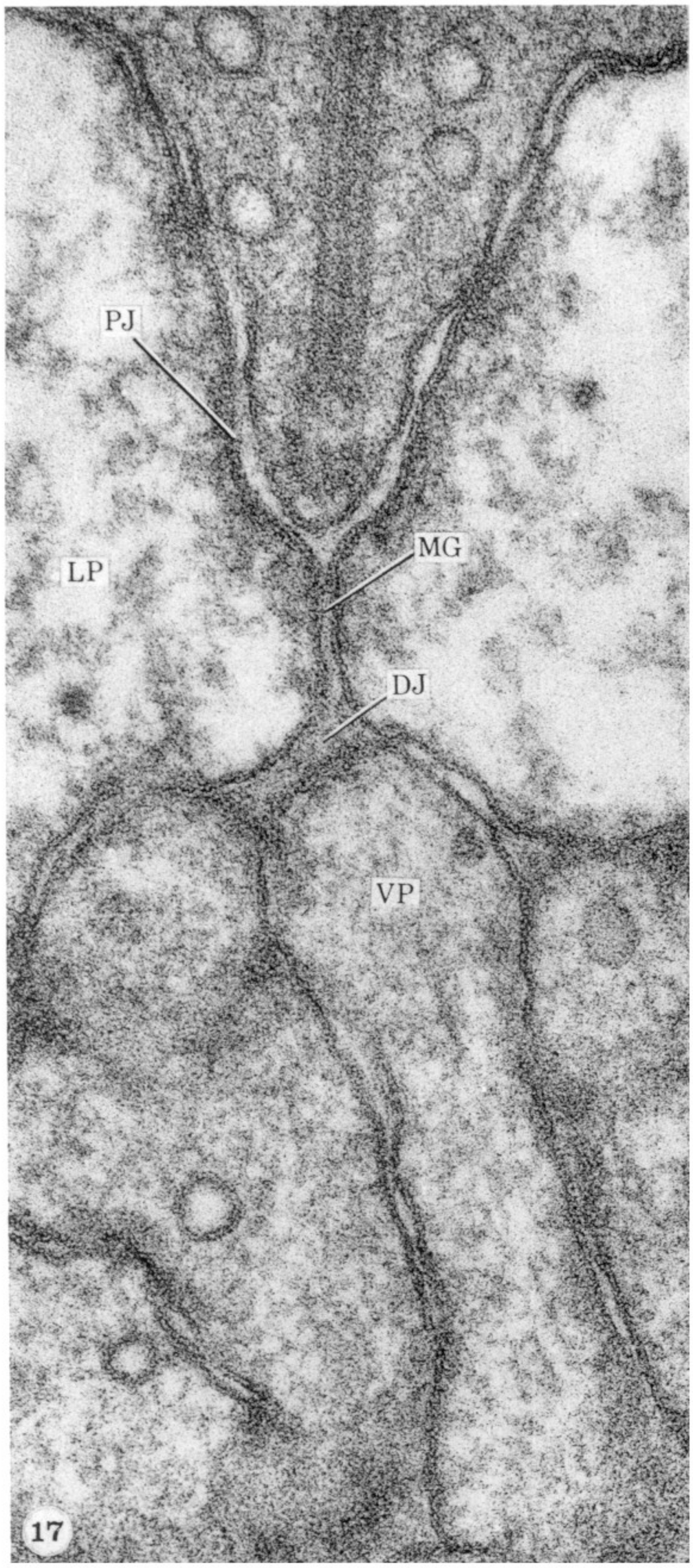


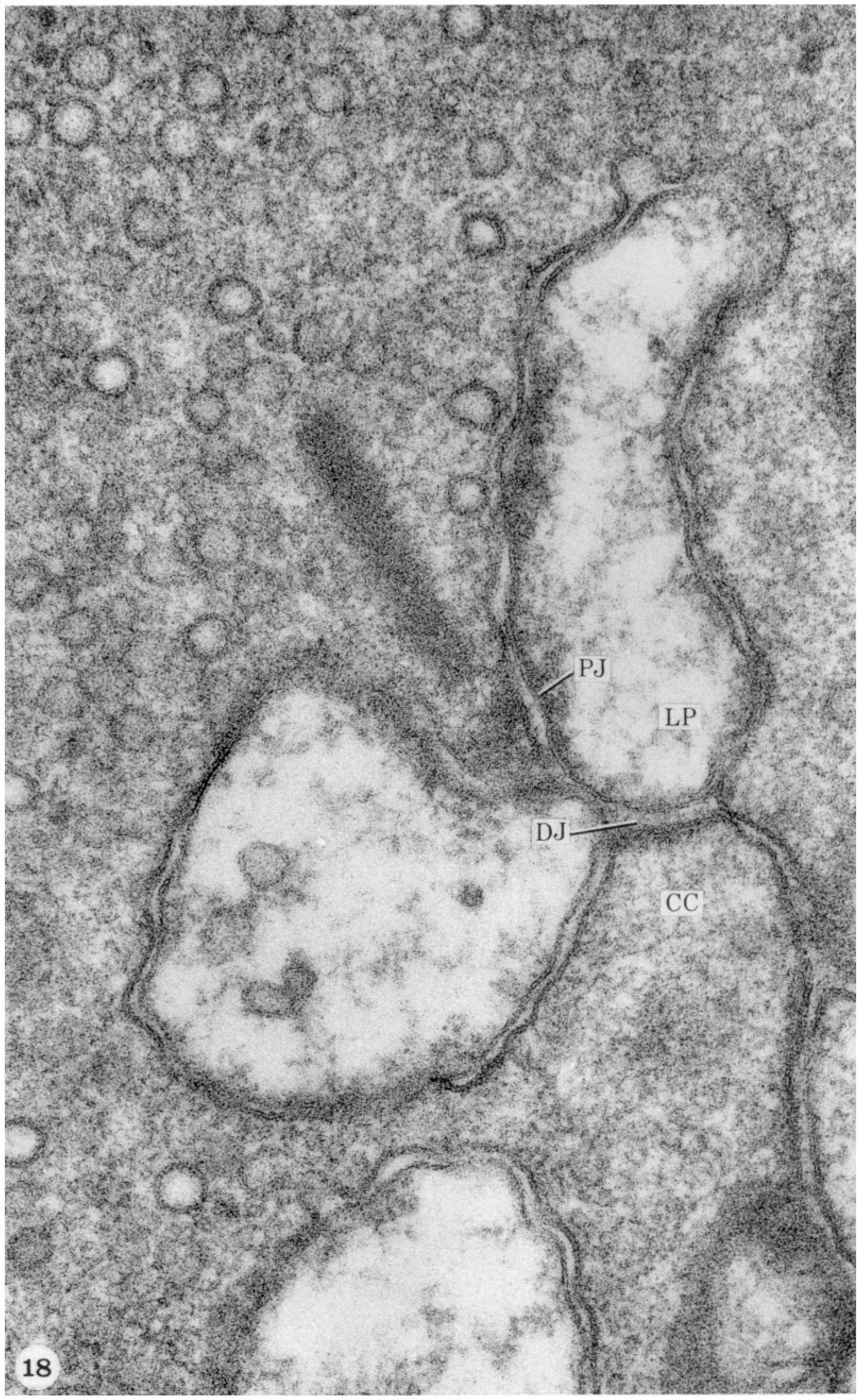


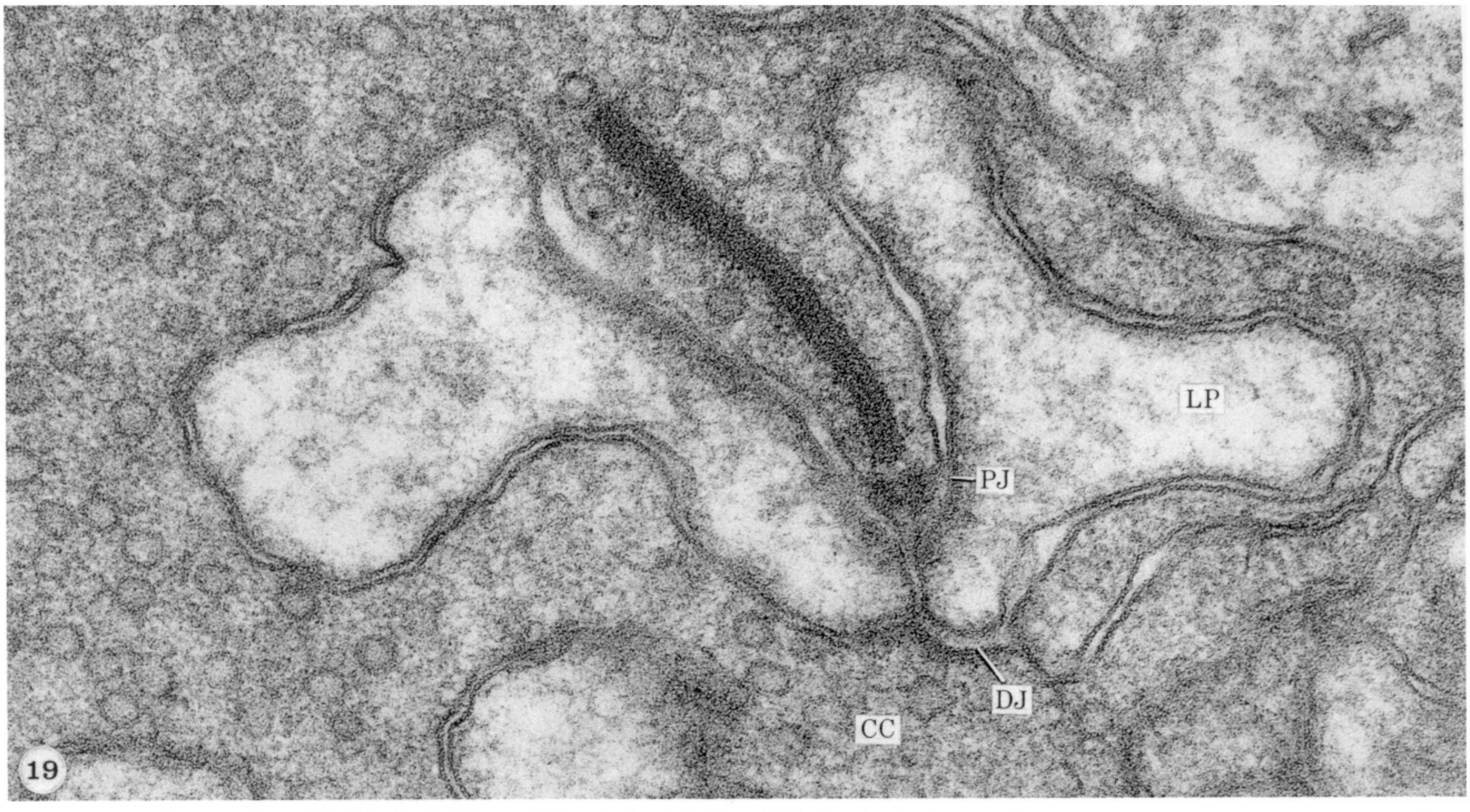




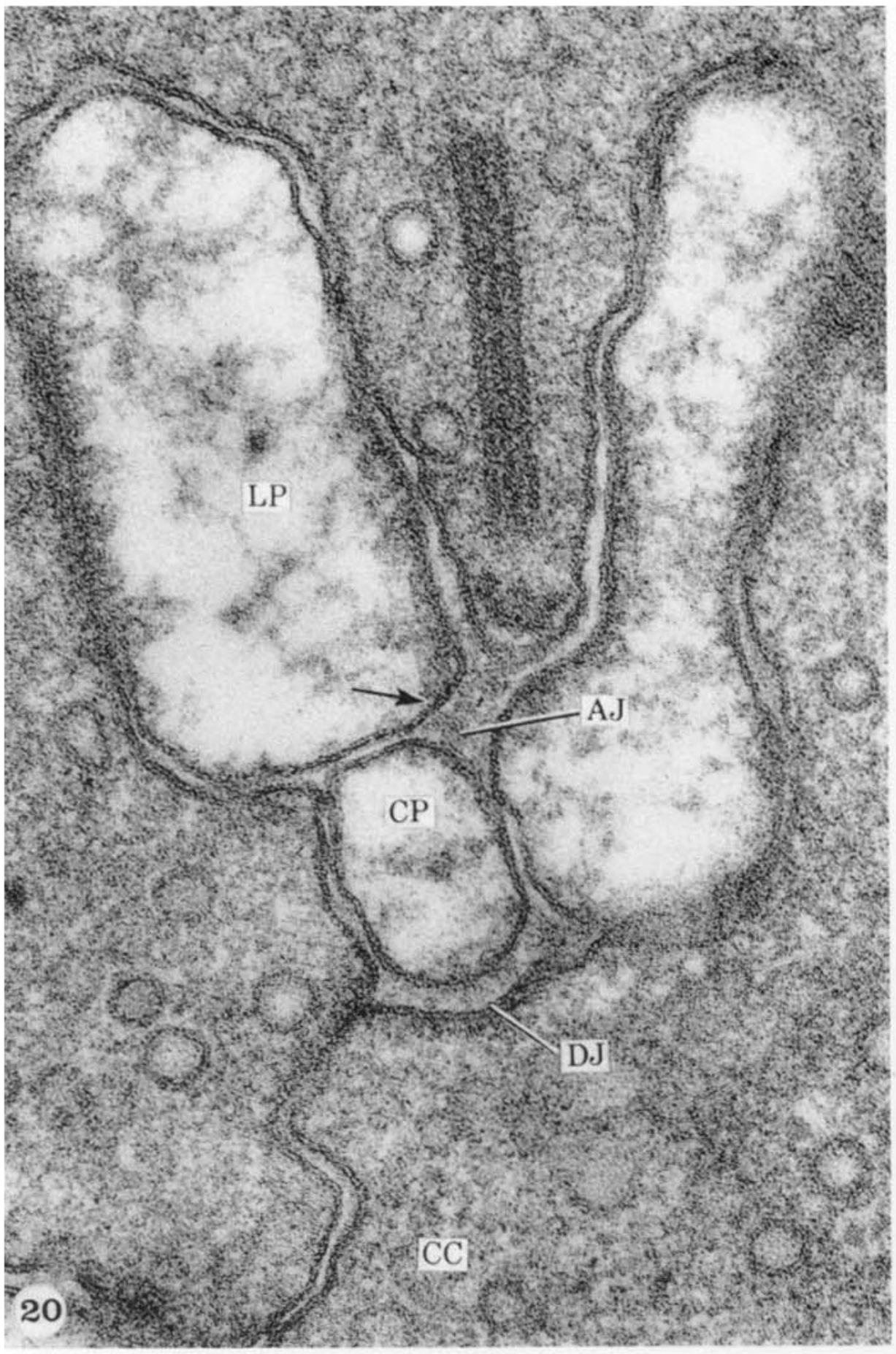
FIGURES 12 to 16. For descriptions see facing page.

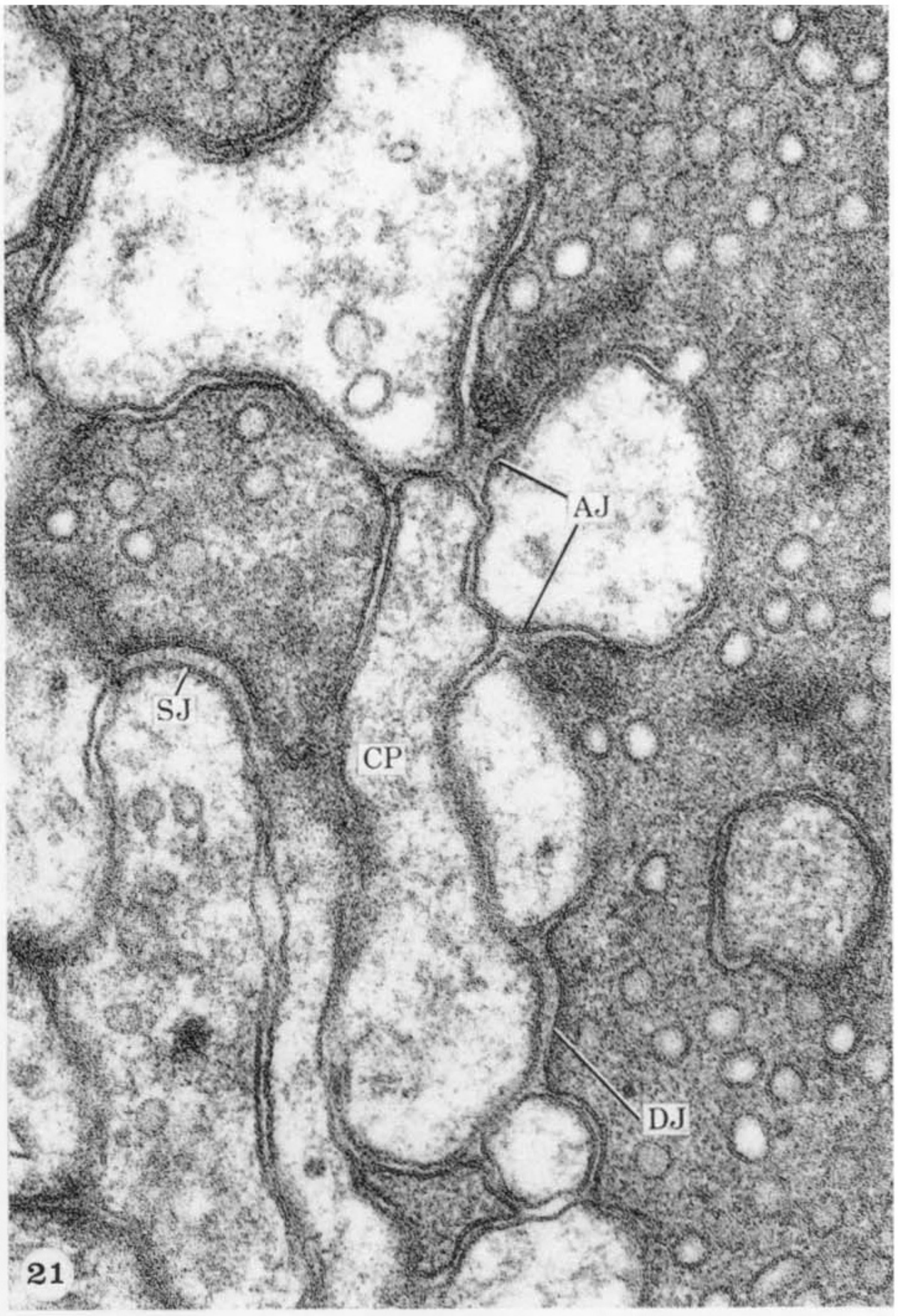


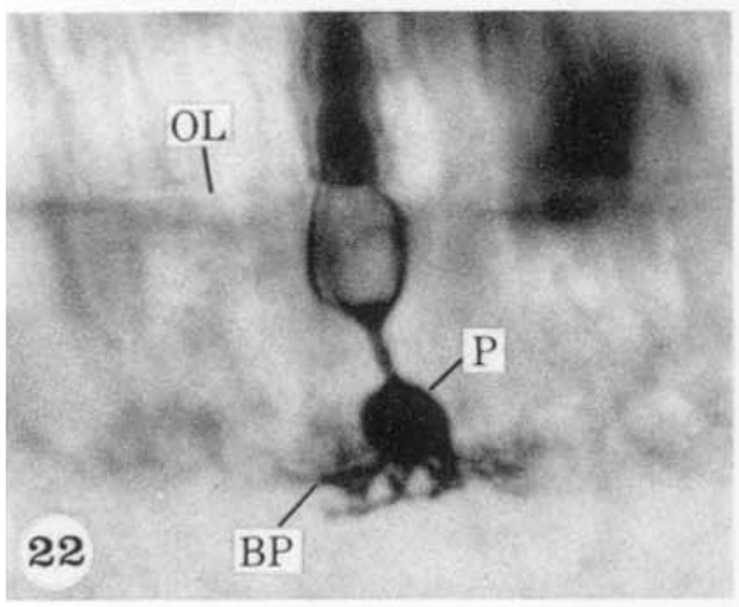


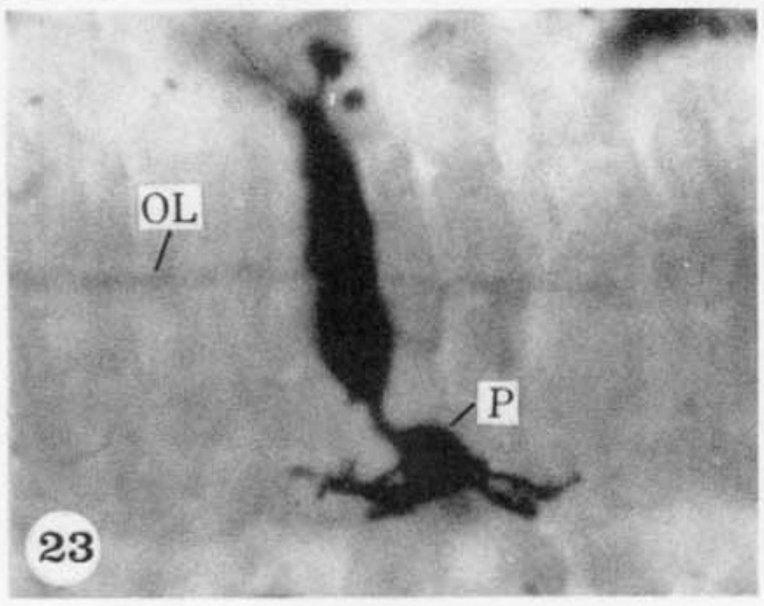


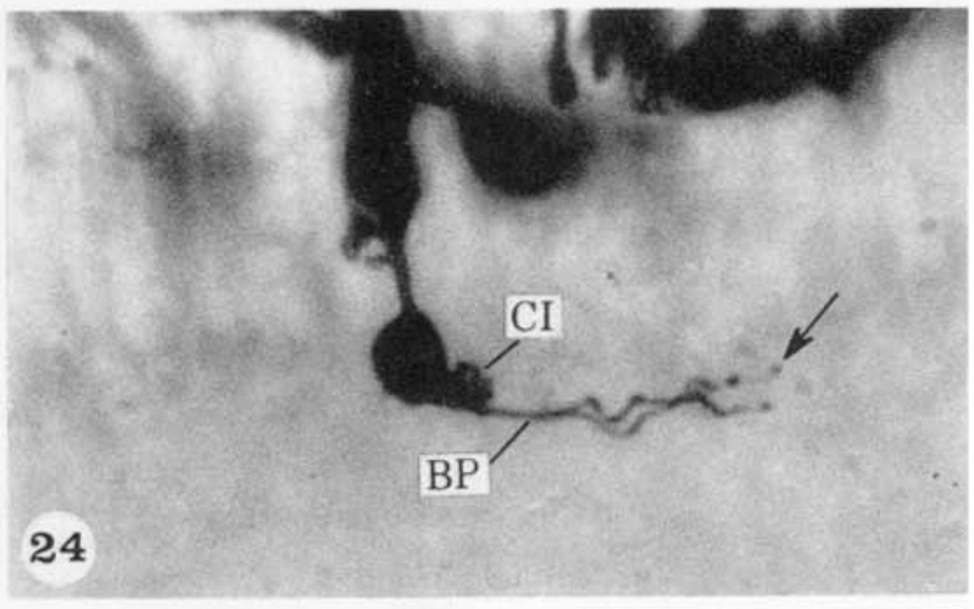
FIGURES 17 to 19. For descriptions see facing page.

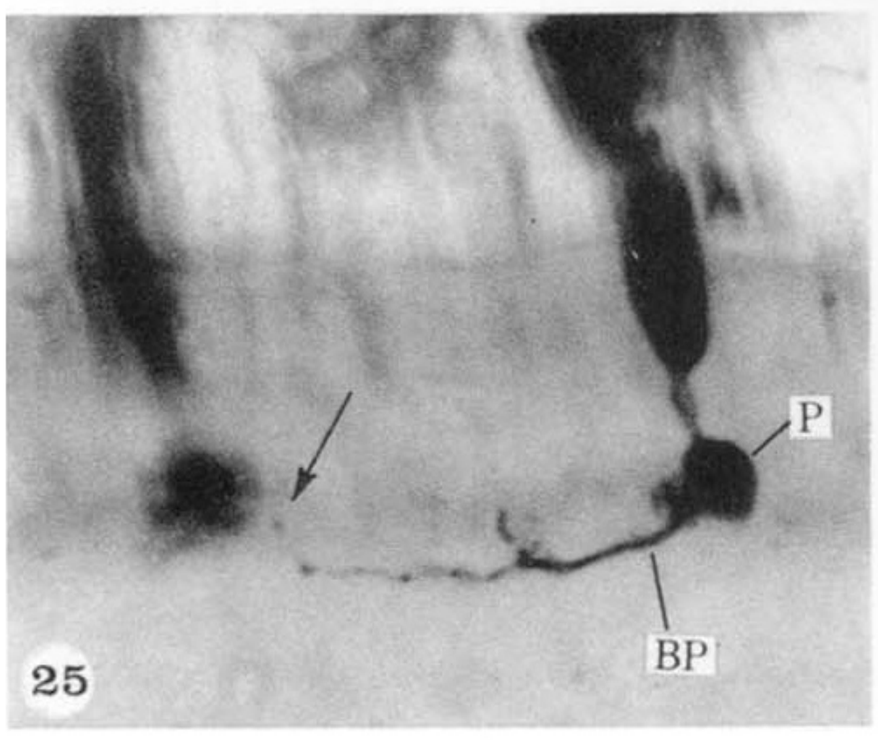


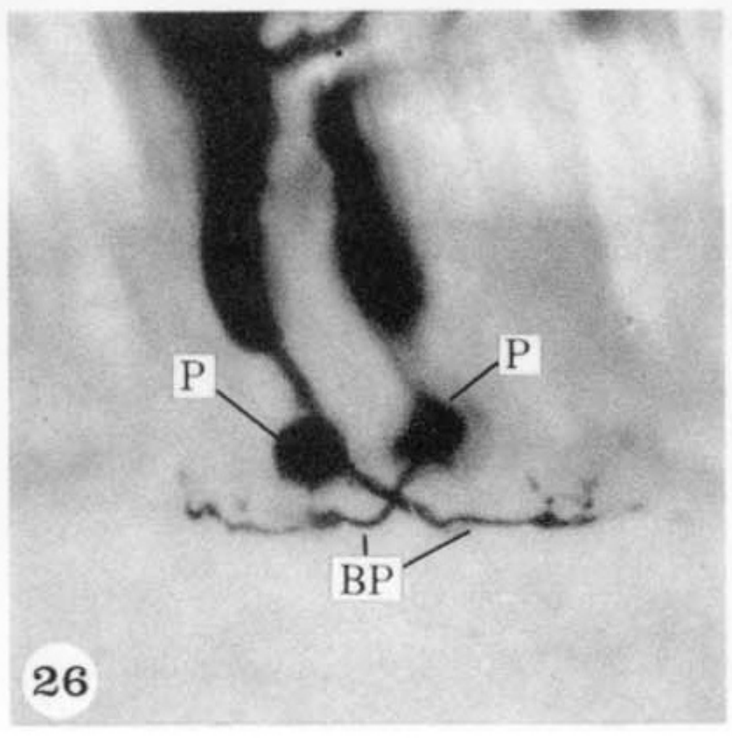


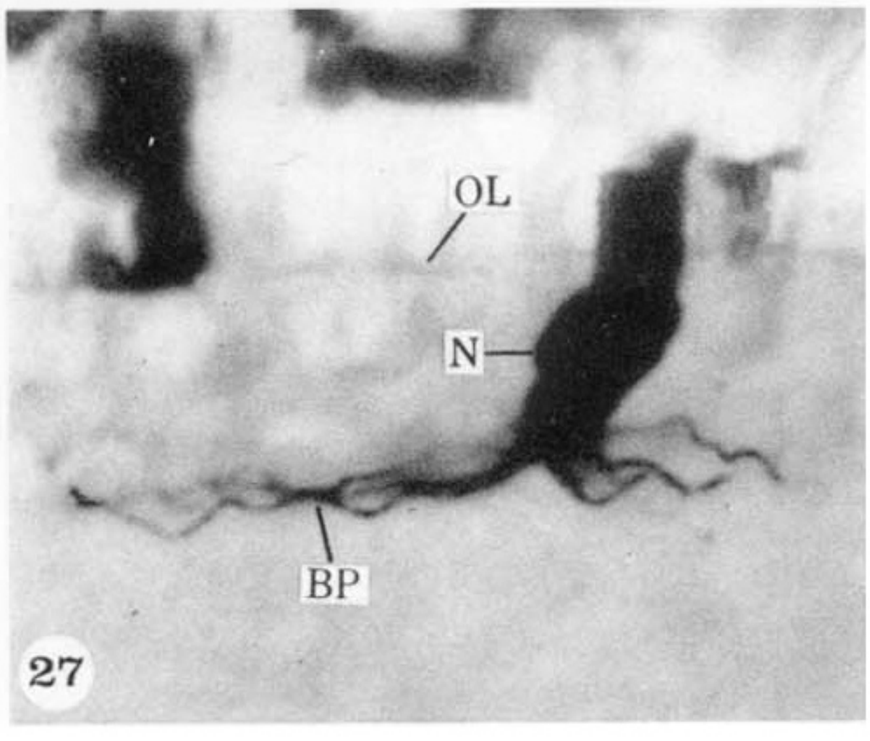




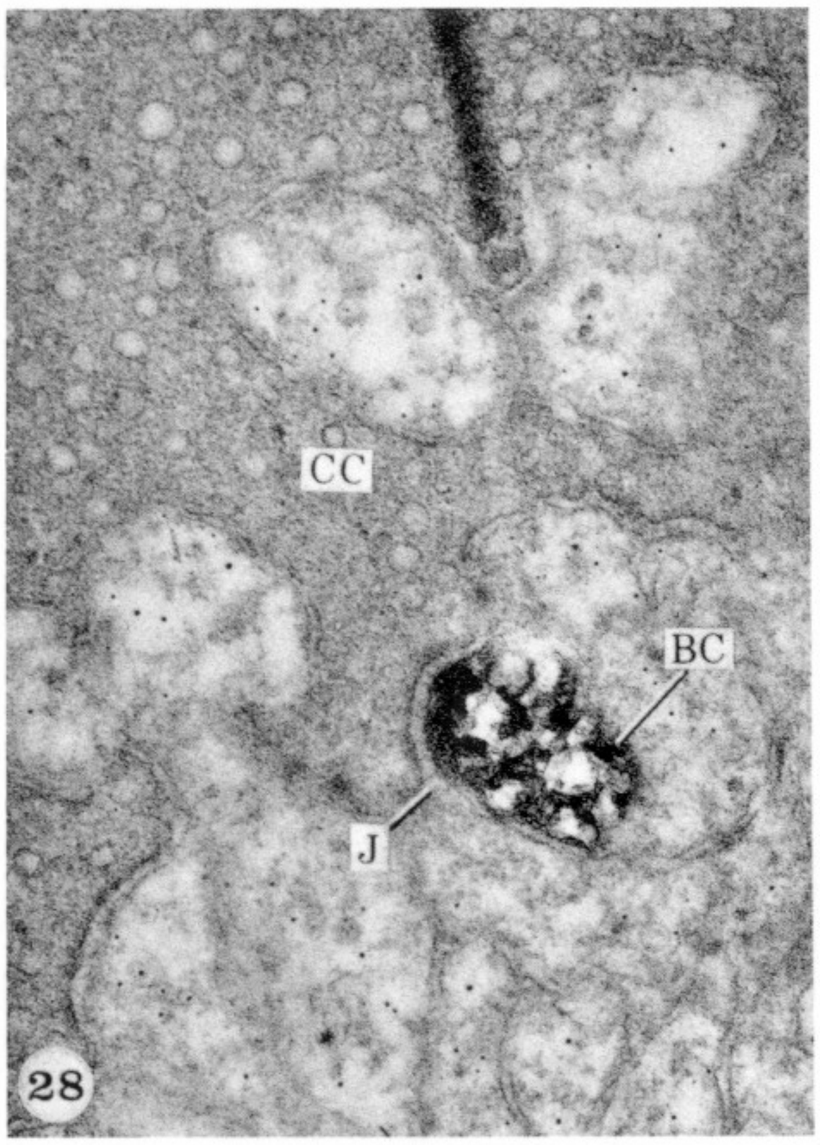


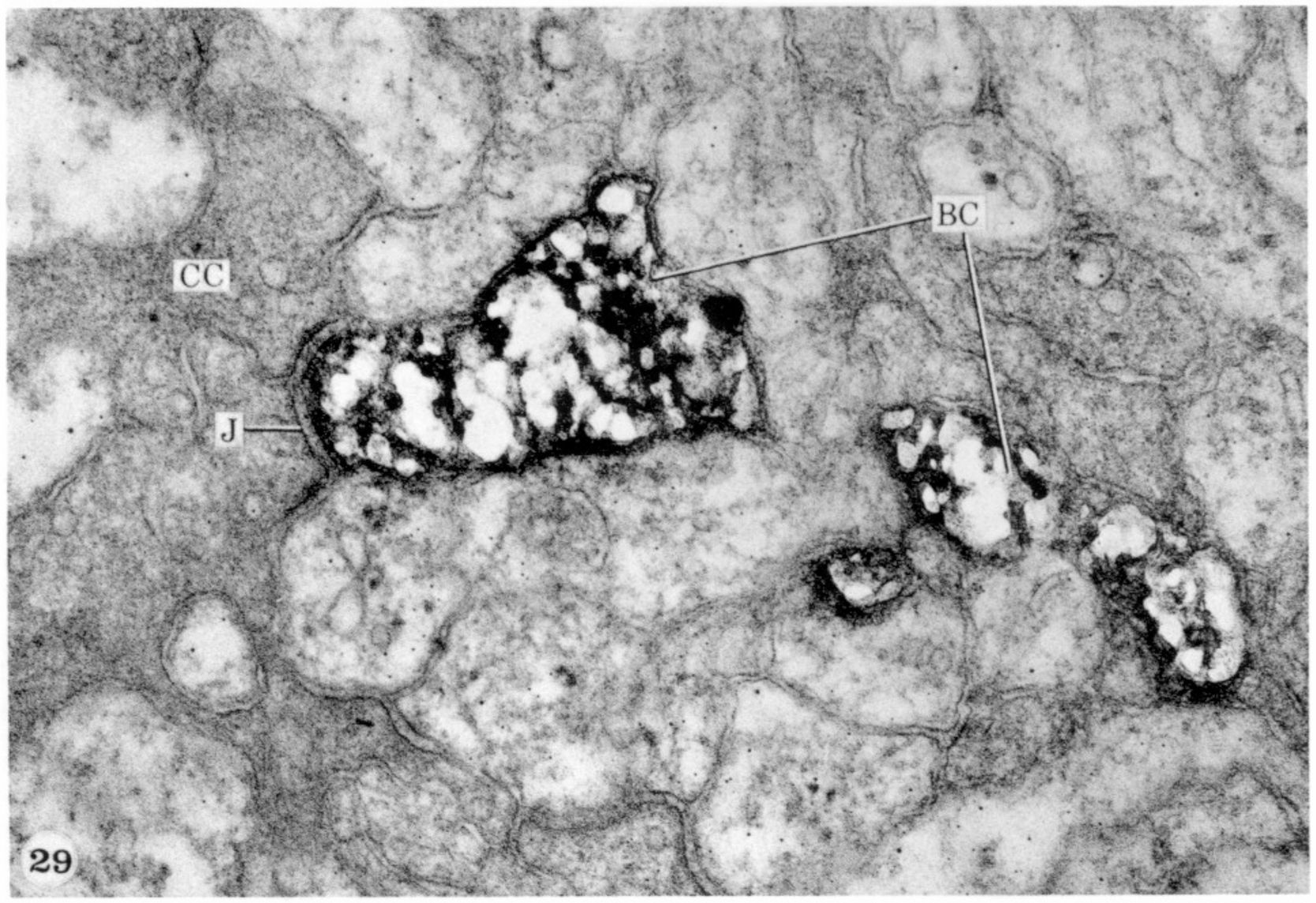


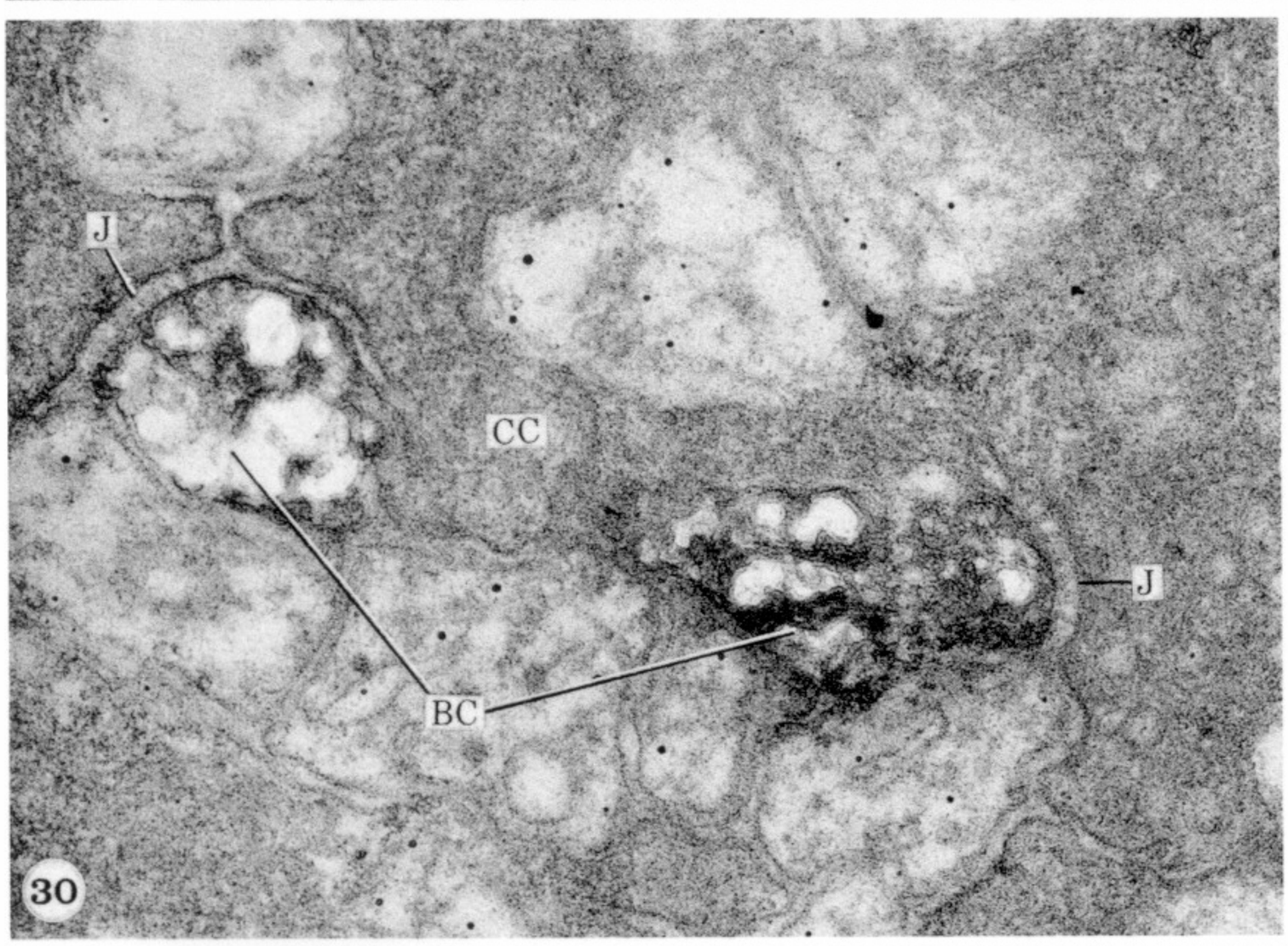


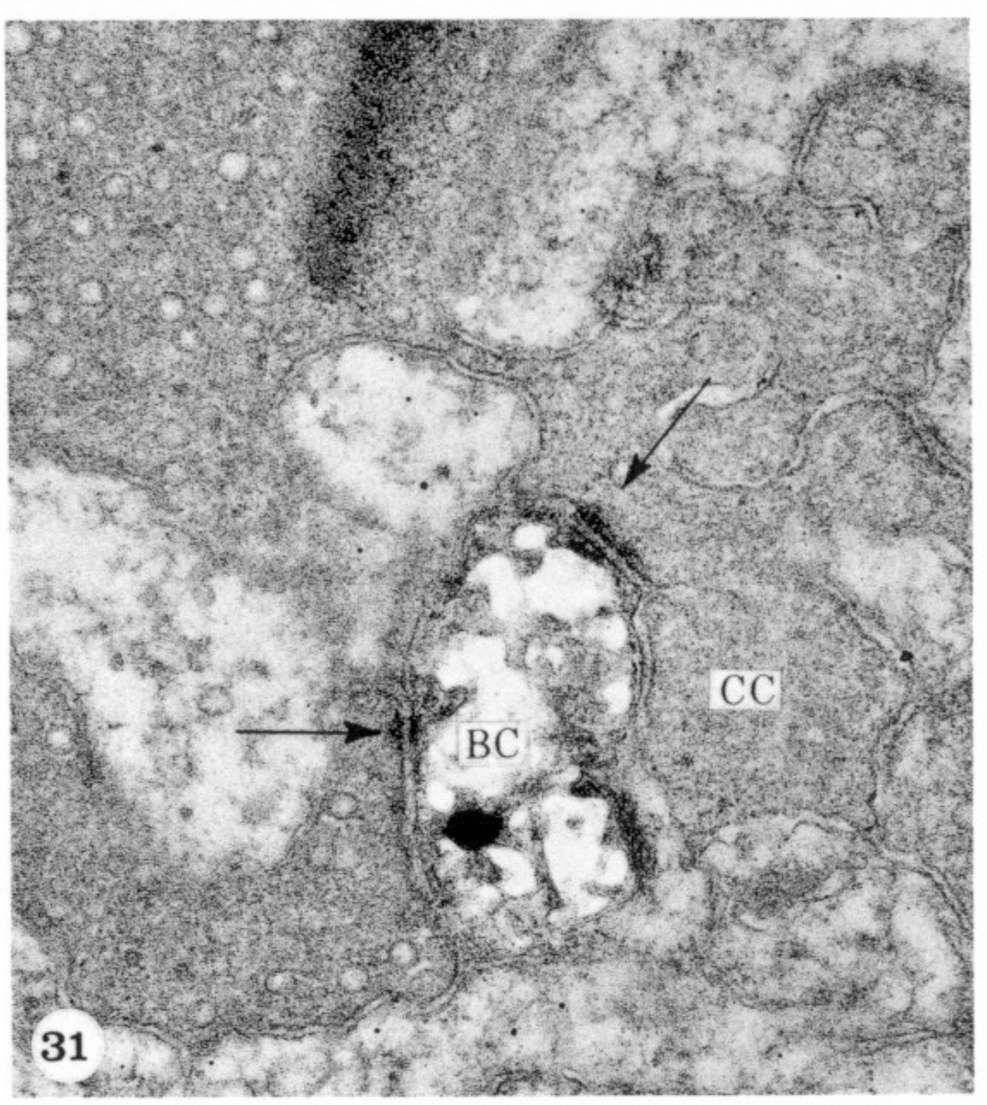


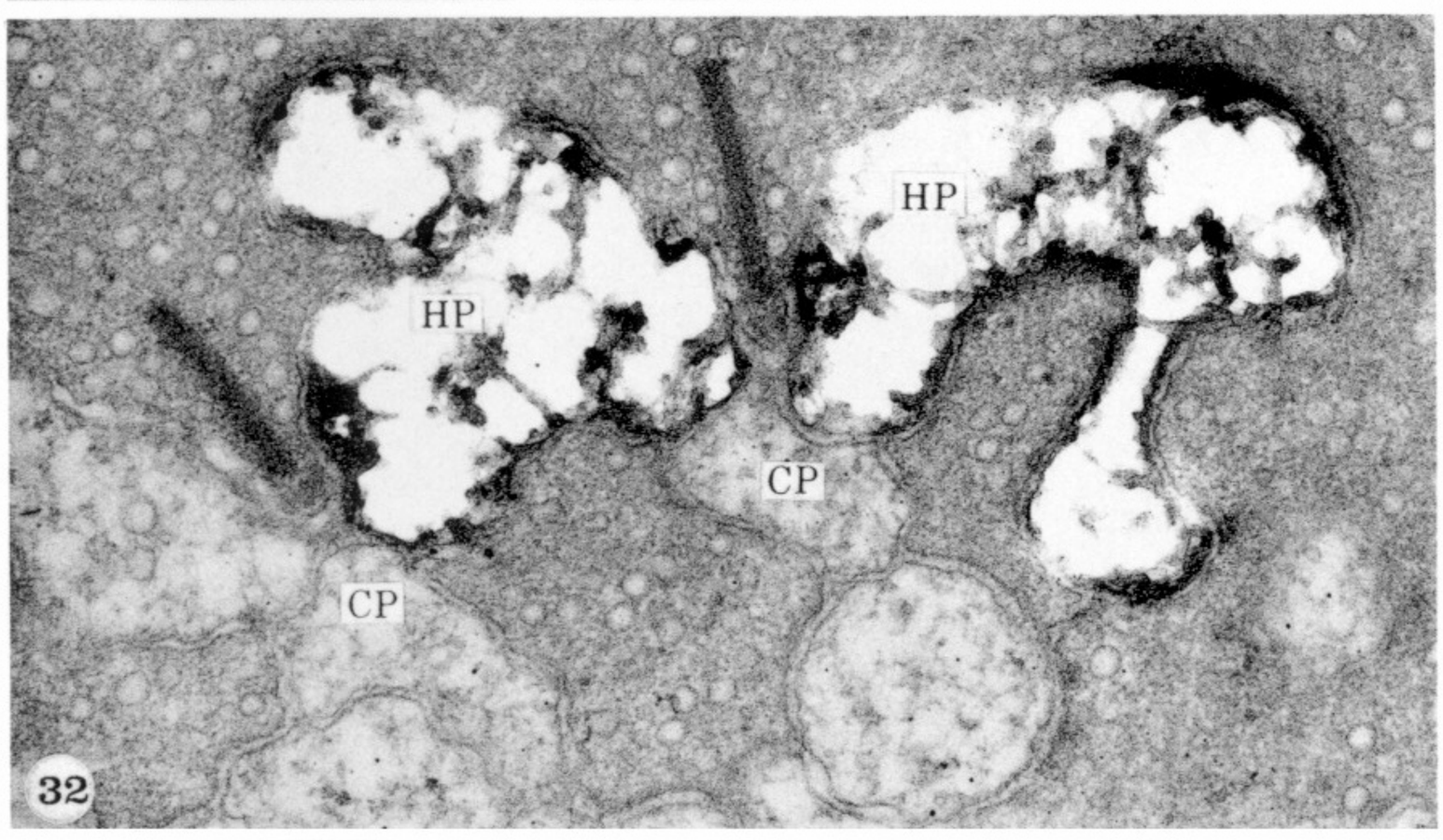
FIGURES 20 to 27. For descriptions see facing page.

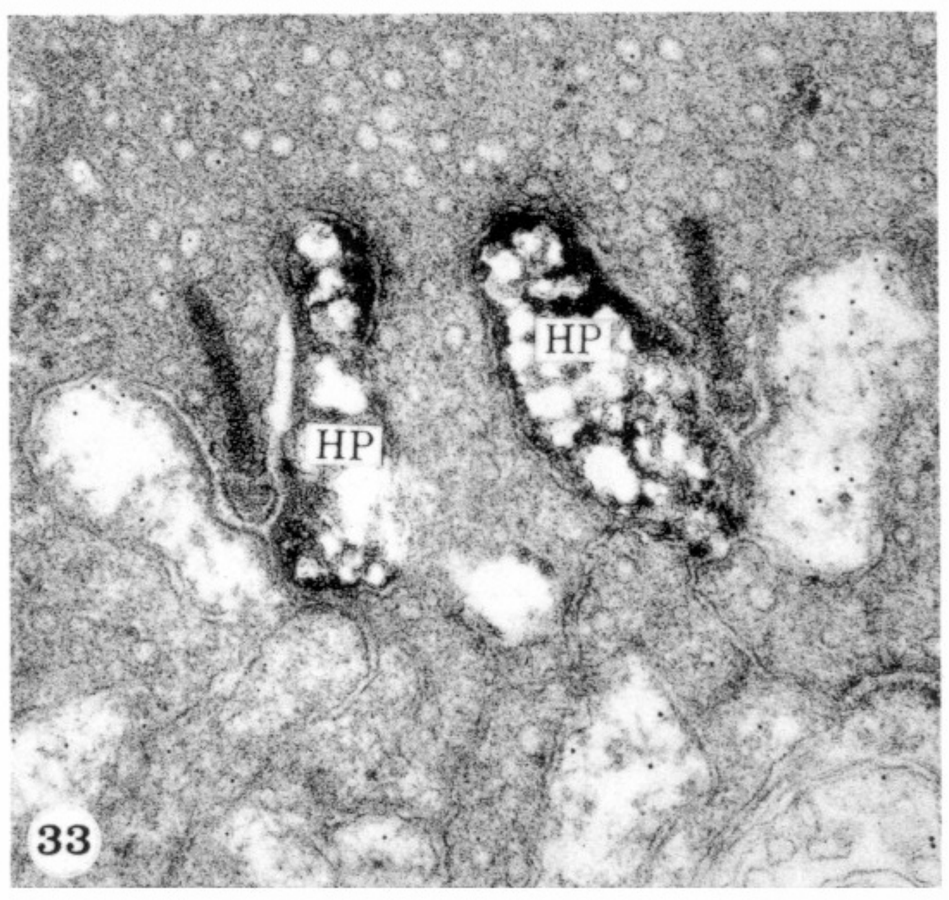




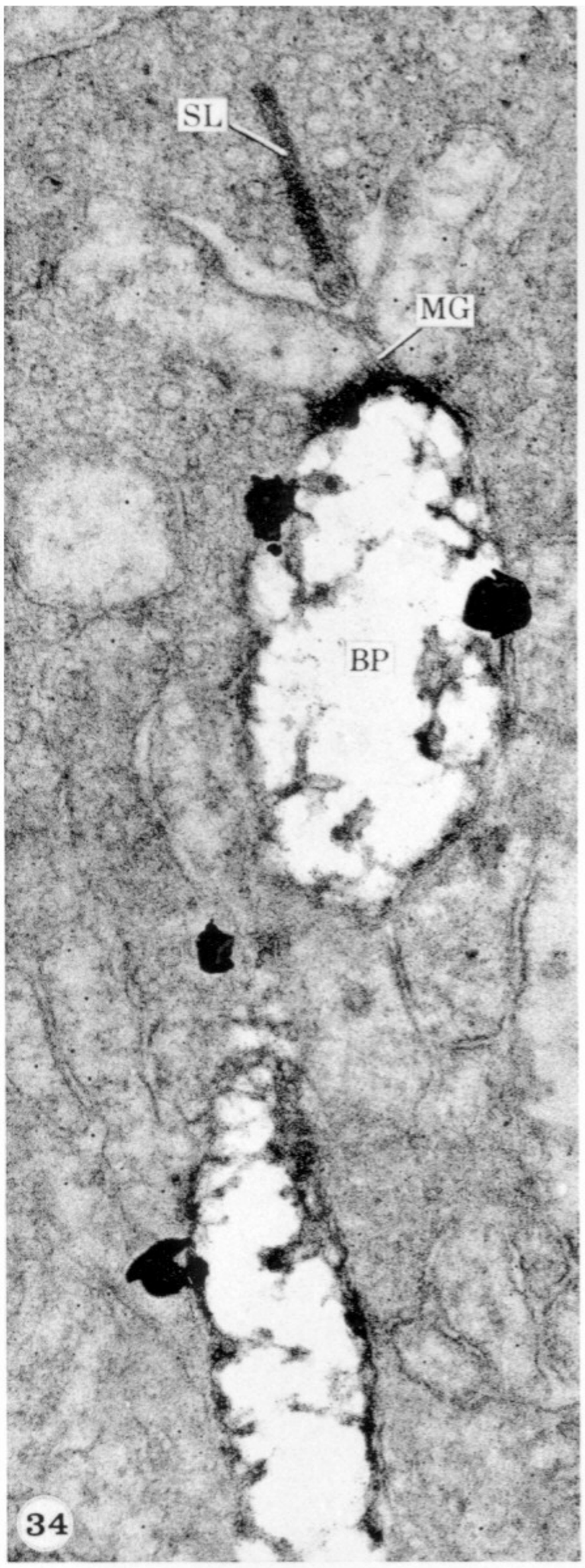


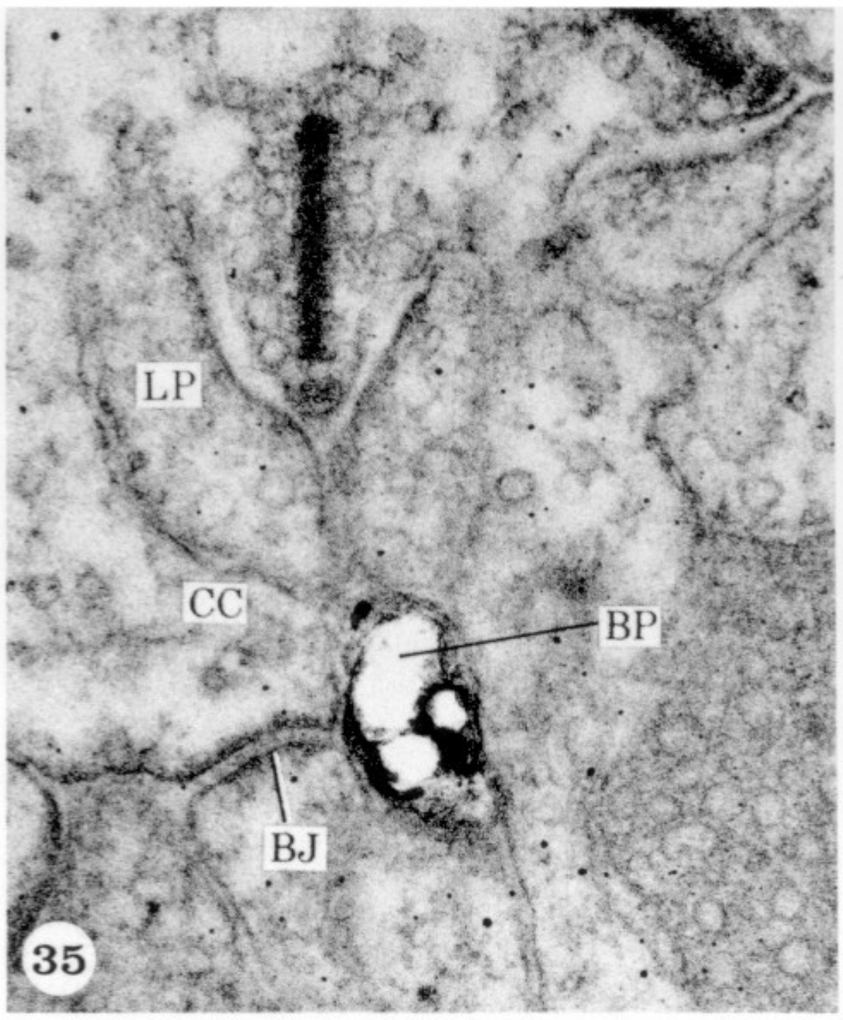


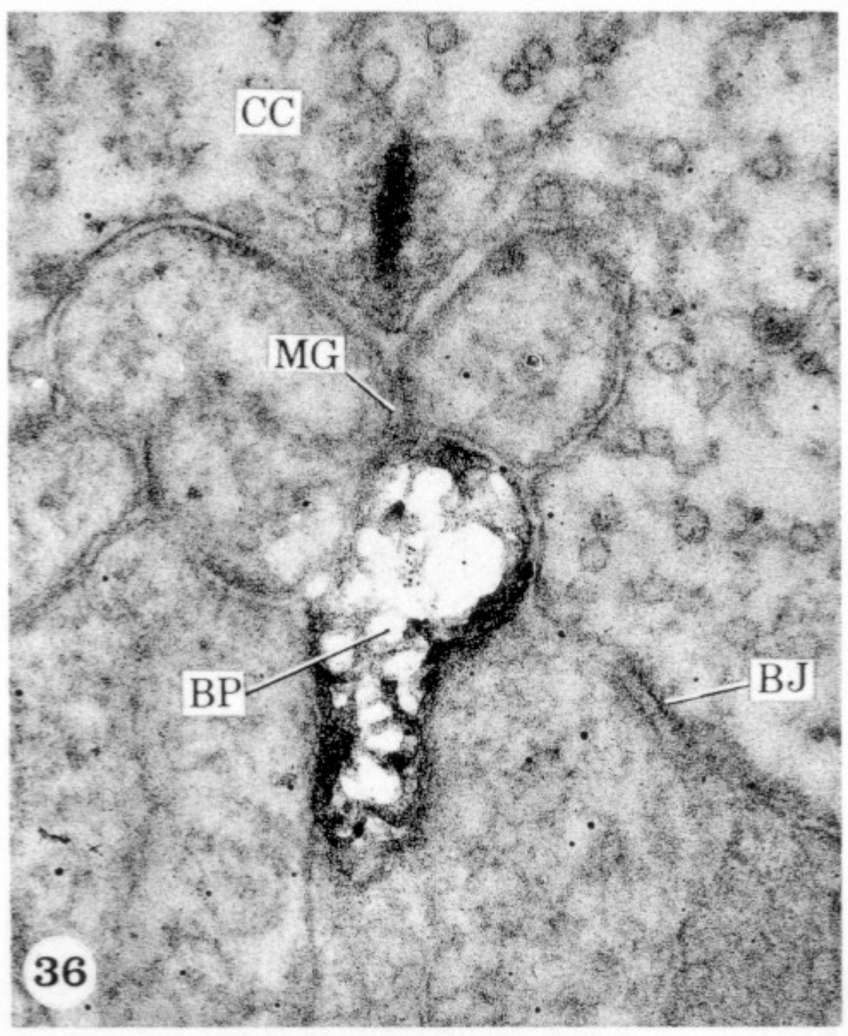


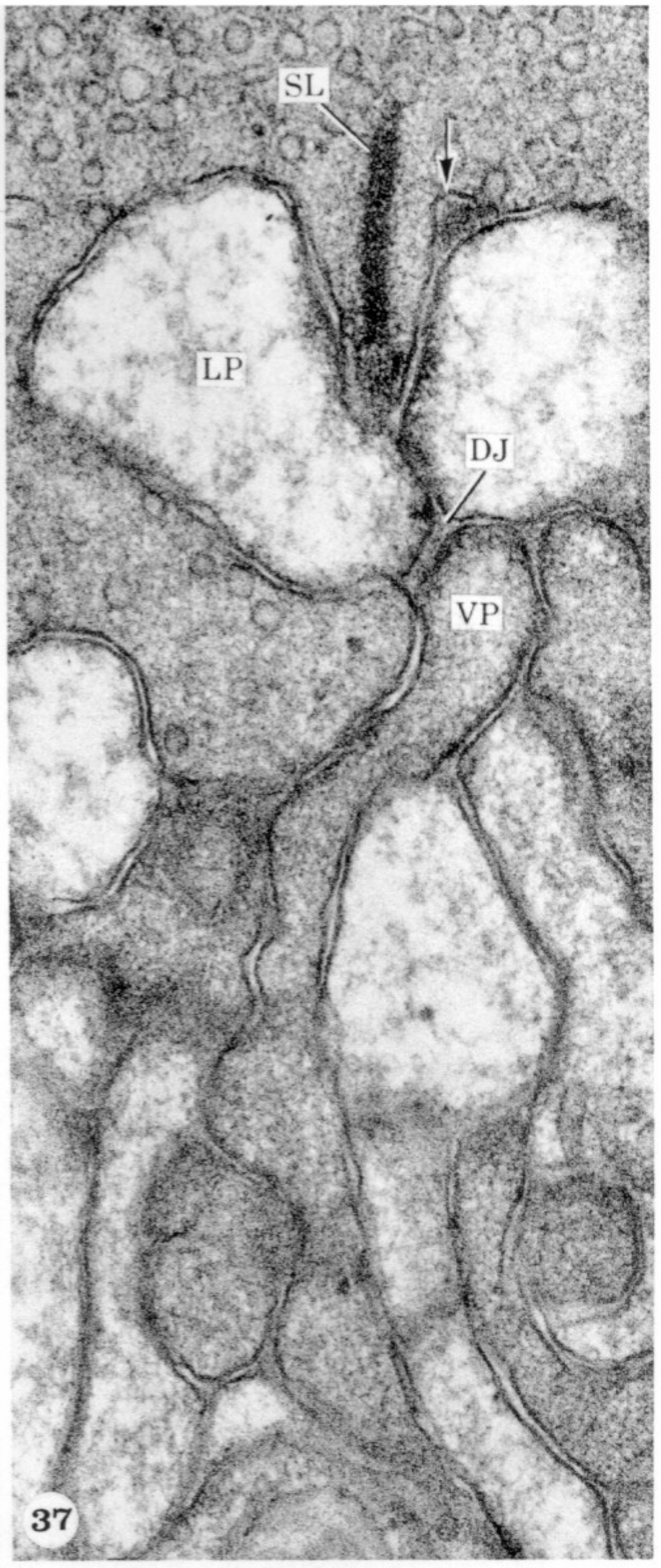


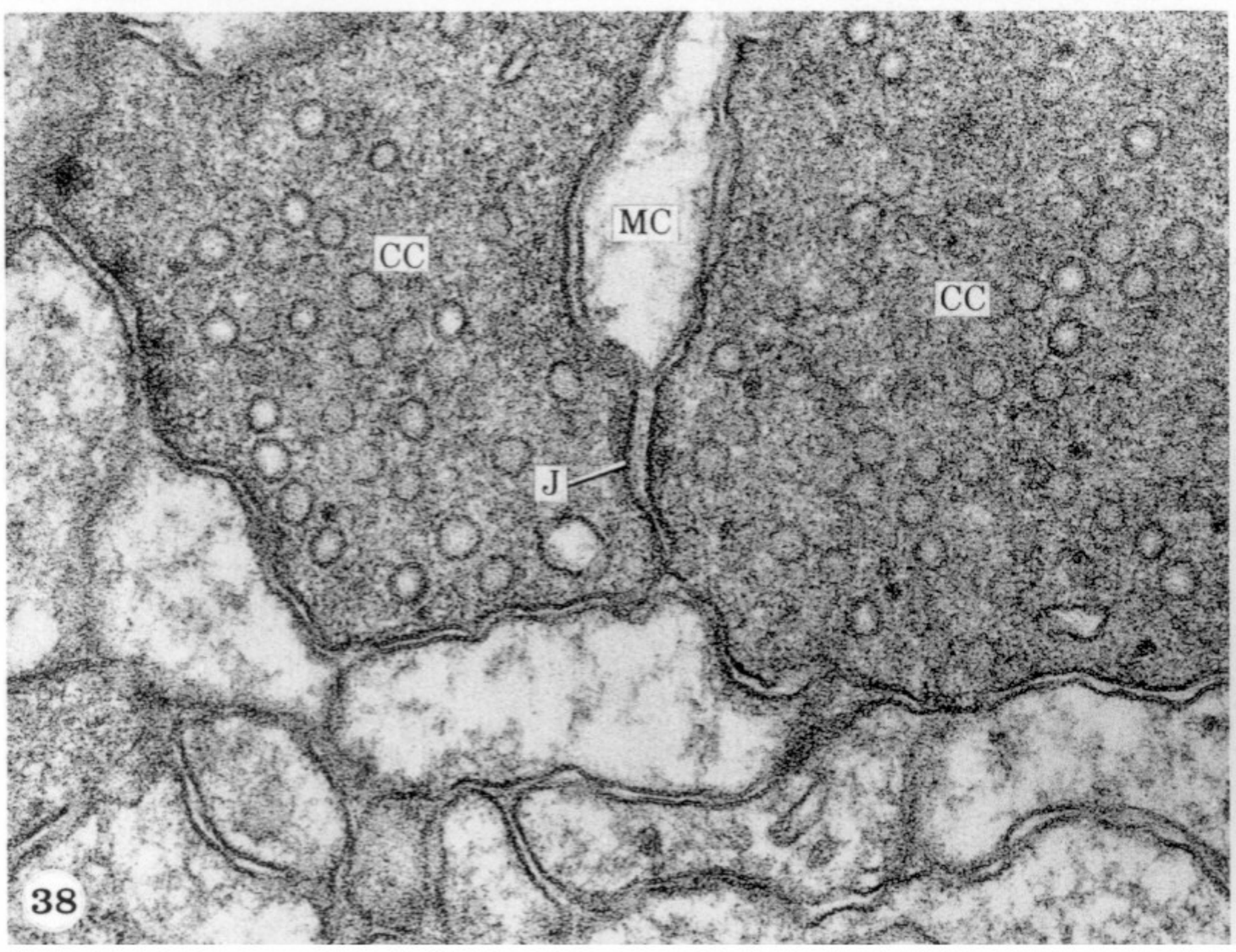
FIGURES 28 to 33. For descriptions see facing page.

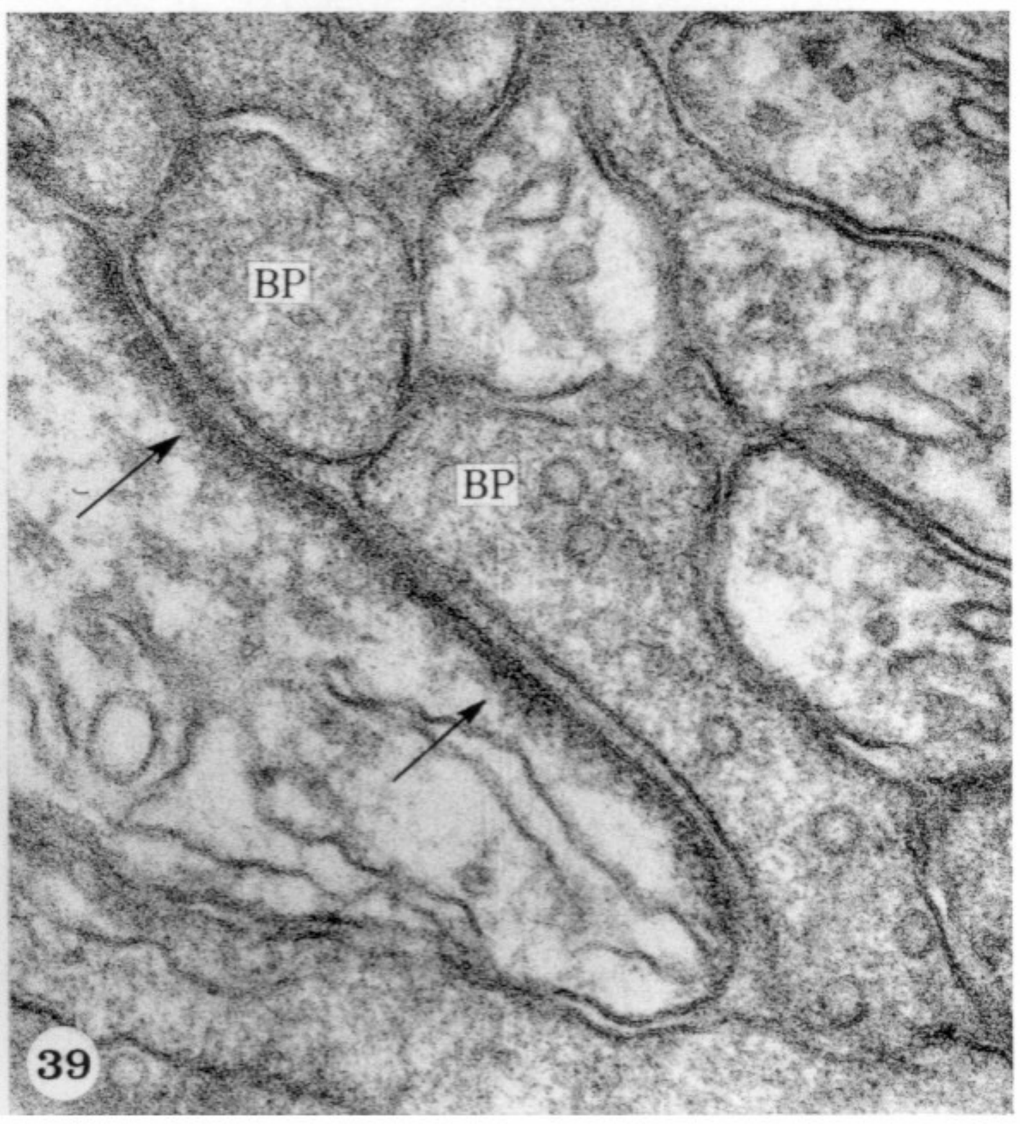












FIGURES 34 to 39. For descriptions see facing page.